Consejo Superior de Investigaciones Científicas

Real Jardín Botánico de Madrid

Universidad Autónoma de Madrid
Facultad de Ciencias

TESIS DOCTORAL

Taxonomía y sistemática del género *Trisetum* Pers. en el Paleártico y de la subtribu Aveninae (Poaceae: Pooideae: Poeae)

De acuerdo con la mención de Doctorado Internacional

PhD THESIS

Taxonomy and systematic of the genus *Trisetum* Pers. in the Paleartic and of the subtribe Aveninae (Poaceae: Pooideae: Poeae)

In agreement with the International Doctorate Mention

Patricia Barberá Sánchez
Madrid, 2018

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El Dr. Carlos Aedo Pérez, científico titular del departamento de Biodiversidad y Conservación del Real Jardín Botánico de Madrid, CSIC; y el Dr. Carlos Romero Zarco, profesor titular del departamento de Biología Vegetal y Ecología de la Universidad de Sevilla, certifican:

Que la presente memoria titulada "Taxonomía y sistemática del género *Trisetum* Pers. en el Paleártico y de la subtribu Aveninae (Poaceae: Pooideae: Poeae)" ha sido realizada bajo su dirección por Patricia Barberá Sánchez, y que cumple con los requisitos necesarios para aspirar al grado de doctor en Biología por la Universidad Autónoma de Madrid.

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Imagen de la portada: *Trisetum rigidum*, por A. Quintanar

A mis padres

AGRADECIMIENTOS

Quería agradecer a todas aquellas personas que me han ayudado de una manera u otra durante el desarrollo de esta tesis doctoral, que, sin duda, no hubiese sido posible sin el apoyo de todos ellos.

Agradezco a mis directores Carlos Aedo y Carlos Romero por haber confiado en mí para realizar este largo trabajo, por sus continuos consejos, haberme apoyado en todo momento, los conocimientos transmitidos y su interés en mi formación. Gracias al proyecto *Flora iberica* CGL2014–52787–C3–1–P y CGL2015–66161–P que ha financiado mi trabajo de todos estos años.
A mi tutora académica, Emma Ortúñez, por ayudarme siempre con todas las cuestiones burocráticas.

A los grupos de investigación que me recibieron en las diferentes estancias. A los compañeros del Instituto Komarov de San Petersburgo por su cálida acogida, dónde me llegué a sentir como en casa, entre ellos a Roman Ufimov, Elena Glazkova, Denis Melnikov, y al profesor Tzvelev, al que tuve la gran suerte de conocer. A todos aquellos amigos que vinisteis a verme y con los que compartí momentos inolvidables en Rusia y alrededores. Al personal del departamento de Botánica del Museo de Historia Natural de Washington, principalmente a Robert Soreng por preocuparse por mí en los momentos más difíciles y compartir conmigo sus conocimientos en gramíneas, y a Nancy Soreng por acogerme en su casa como a otra hija más. A Gabriel Johnson por enseñarme y aconsejarme en toda la parte de laboratorio durante mi estancia. Y por supuesto, por todo el cariño y ánimo recibido de la comunidad brasileña smithsoniana y demás compañeros que me aportaron muchísimo tanto personal como profesionalmente durante mi estancia. A mis amigos washingtonianos de fuera del museo, María, Christian y Brian por estar siempre ahí en todo momento, gracias de todo corazón.

Agradezco a Mauricio Velayos por haberme dado la oportunidad de empezar una carrera investigadora, así como por sus buenos consejos durante todos estos años que llevo en el jardín.

A Alejandro Quintanar, por haberme introducido en el mundo de las gramíneas y hacerme ver que son también plantas bonitas, y por apoyarme todo este tiempo profesional y moralmente.

A todos los que me han acompañado a las salidas de campo en busca de *Trisetum*: J.A. Alejandre, J.V. Ferrer, J.A. Devesa, Alejandro, Almu, Dani, Edu, Laura,… A los compañeros del proyecto *Flora iberica* y del Epifenómeno, con los cuales he tenido la suerte de salir al campo aprendiendo muchísimo y pasando momentos estupendos.

A todo el personal del Real Jardín Botánico (Herbario, Biblioteca, Administración, Seguridad, Limpieza, Informática,…) por facilitarme el trabajo diario de una u otra manera. A los amigos del herbario, a los que siguen y a los que ya no están, por haberme ayudado siempre con todos los préstamos, pliegos, etc.., y por los buenos momentos tanto antes como durante el período de la tesis. Gracias.

A todos los compañeros del laboratorio por enseñarme mucho y haber hecho todo más llevado y mucho más divertido. Ha sido todo un placer trabajar con vosotros. Gracias a mi hermano mayor Alberto y a Emilio por su extrema paciencia y siempre buen humor. A Inés Álvarez por su siempre generosidad en dejarme usar su espacio.

Muchas gracias a todos los conservadores de los herbarios y a aquellos investigadores que me han facilitado personalmente el material que he necesitado.

A Ramón Morales por sus constantes ánimos y las traducciones del alemán sin las que sin duda no hubiese podido hacer la tesis. A Anne Martin, María Morck, y Laura García por su ayuda con el inglés.

Un millón de gracias a Alicia, Alejandro y Toni por esos momentos de risas, charlas y café diarios, totalmente necesarios para afrontar el resto del día. Gracias a Alicia por compartir conmigo esos fines de semana jardineros que tanto unen. A mis compañeros de sitio, Adela y Toni, con los que he pasado tanto tiempo y han hecho más llevadero el día a día. Gracias Adela por ser como una madre y preocuparte siempre por nosotros. A ti Toni, por tu apoyo técnico y moral, y por esas buenas charlas filosóficas y reconfortantes.

A todos los compañeros del jardín, y muy especialmente a los que me han ayudado a resolver algún que otro problema y duda siempre con una sonrisa. Gracias Javi, Irene, Kina, Laura, Yure, Ana y Miguel Ángel García. Agradezco también al resto por los ratos agradables durante la comida o cualquier otro momento del día a día. También quiero agradecer a los amigos del jardín de etapas anteriores, especialmente a Gema, Maxi, Marta, Paco y Luz.

A mi familia de Melrose, con la que he convivido casi todos estos años, por sus ánimos continuos y por tantos buenos momentos compartidos. En general, mil gracias a todos mis amigos, a los que están lejos y a los que están cerca, que aún por los largos períodos de aislamiento, siempre me han mostrado toda la comprensión y el cariño.

Y por último, agradezco a mis padres y hermanos su plena confianza y fe incondicional en mí, y el saber que están ahí en todo momento. Gracias absolutamente por todo.

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Resumen

Trisetum Pers. es un género de gramíneas de la tribu Poeae R. Br. (Poaceae subfam. Pooideae Benth.), cuya taxonomía y sistemática, tanto subgenéricas como supragenéricas, son controvertidas. Las especies con distribución paleártica solo contaban con tratamientos taxonómicos para ámbitos geográficos más o menos reducidos, por lo que una revisión integradora de toda su diversidad que simplificase la compleja y extremadamente analítica clasificación previa era claramente necesaria. La serie de trabajos enmarcados en la presente tesis doctoral ofrecen una nueva revisión taxonómica para el género en la región paleártica (además de en otros territorios externos cuando eventualmente la distribución de algún taxon lo ha requerido), en donde se reconocen 21 especies organizadas en tres secciones: *T.* sect. *Trisetum, T.* sect. *Acrospelion* y *T.* sect. *Sibirica*. Para ello se han estudiado más de 2000 pliegos de unos 66 herbarios. En total se han realizado 42 lectotipificaciones y 2 neotipificaciones.

En cuanto a la taxonomía subgenérica, *Trisetum* sect. *Trisetum* se caracteriza por las panículas generalmente laxas, las espiguillas verdosas o con tintes purpúreos, a veces amarillentas, el callo con pelos cortos, la arista acodada o curvada, rara vez recta, y el ovario generalmente glabro a veces con pelos dispersos o densamente piloso en el ápice. *Trisetum flavescens*, especie tipo, es la más polimorfa y se extiende por Eurasia y el norte de África, por lo que tiene el área de distribución más amplia del género. En ella reconocemos dos subespecies, *T. flavescens* subsp. *flavescens*, cuya elevada variabilidad morfológica ha merecido reconocimiento como categorías específicas o infraespecíficas por parte de diversos autores, y *T. flavescens* subsp. *griseovirens*, endémica del Alto Atlas. A parte de esta, se reconocen otras siete especies de distribución localizada en diferentes sistemas montañosos euroasiáticos: *T. alpestre*, *T. altaicum*, *T. bertolonii*, *T. fuscum*, *T. glaciale*, *T. gracile* y *T. laconicum*.

Trisetum sect. *Acrospelion* es una sección endémica de Eurasia que cuenta con siete especies caracterizadas por la disposición dístico-pectinada de las hojas de los tallos jóvenes y por los pelos largos del callo y de la raquilla. Es más diversa en dos grandes conjuntos montañosos, el Cáucaso, con *T. rigidum* y *T. buschianum*, para los que se reconoce una subespecie adicional además de la típica (*T. rigidum* subsp. *teberdense* y T. *buschianum* subsp. *transcaucasicum*), y los Alpes, con *T. distichophyllum* y *T. argenteum*. Las otras tres especies de la sección son *T. macrotrichum* de los Cárpatos, *T. tamonanteae* de la isla de Fuerteventura en Canarias y *T. velutinum* del sudeste de España.

Por último, *Trisetum* sect. *Sibirica* está formada por seis especies, cuatro de ellas, *T. aeneum*, *T. bifidum*, *T. henryi* y *T. scitulum*, endémicas del este de Asia y Nueva Guinea. En la parte más occidental de su área de distribución se encuentran *T. turcicum*, que crece en Turquía y el Caúcaso, y *T. sibiricum*, este último con dos subespecies, *T. sibiricum* subsp. *sibiricum* y *T. sibiricum* subsp. *litorale*. *Trisetum sibiricum* es la especie más polimorfa y con el área de distribución más amplia de la sección, ya que se extiende desde el este de Europa hasta Alaska y el oeste del Canadá. A todas ellas caracterizan principalmente sus espiguillas doradas, el callo glabro o con pelos muy cortos y las aristas recurvadas, rara vez acodadas.

Resumen

El análisis filogenético con cuatro marcadores moleculares (ITS, *rpl32-trnL*, *rps16-trnK* y el intrón *rps16*) llevado a cabo con representantes del género *Trisetum* y afines, ofrece abundante información sistemática, tanto a nivel subgenérico como a nivel supragenérico. Además de un buen conjunto de secuencias publicadas ya en GenBank, aportamos 2044 nuevas secuencias que se corresponden con 275 especies pertenecientes a estos grupos. La subtribu Aveninae s.l., que incluye *Trisetum*, ha resultado monofilética e incluye tres subgrupos también monofiléticos: Aveninae s.s. (*Avena*, *Helictotrichon* y *Tricholemma*, más Sesleriinae según el marcador nuclear), Koeleriinae (*Trisetum*, *Koeleria* y géneros afines) y Lagurinae (*Lagurus*). Lagurinae es grupo hermano de Koeleriinae y esta se divide en dos grandes subclados, llamados "Koeleriinae clado I", donde aparecen todos los táxones paleárticos de *Trisetum*, y "Koeleriinae clado II". Los representantes de las especies de *T.* sect. *Acrospelion* se agrupan en un clado con escaso apoyo estadístico para las relaciones internas y que además incluye algunas especies eurasiáticas de *T.* sect. *Trisetum* y otras asiáticas de los géneros *Helictotrichon* y *Tzveleviochloa*, además de otro conjunto heterogéneo de taxones americanos de los géneros *Trisetum*, *Koeleria* y *Graphephorum* según el análisis del marcador nuclear. El clado que incluye *Koeleria* y su especie tipo también contiene *T.* sect. *Trisetaera*, con especies con panículas densas y compactas, que incluye las especies del complejo de *Trisetum spicatum*, su tipo, de distribución mundial y que ha sido excluido de las revisiones taxonómicas debido esta estrecha afinidad filogenética con *Koeleria* que justificaría su transferencia a este último género. Por último, los representantes de *T.* sect. *Sibirica* se agrupan en un clado con notable apoyo estadístico, independiente del resto de grandes subclados y grupo hermano de "Koeleriinae clado II", lo que podría justificar su tratamiento como género aparte.

En conclusión, la sistemática de la subtribu Koeleriinae es muy compleja, sobre todo porque la mayoría de los géneros de la subtribu no han resultado monofiléticos y la hibridación parece haber jugado un papel importante en el origen de varios de los géneros y las especies. Las incongruencias que revelan el papel de la hibridación aparecen tanto en "Koeleriinae clado I" como entre "Koeleriinae clado I" y "Koeleriinae clado II". Subrayamos la necesidad de desarrollar más estudios con genes nucleares de baja copia para esclarecer con más detalle la sistemática de estos grupos problemáticos y conseguir una clasificación natural para *Trisetum* y su subtribu en la que sea posible identificar con mayor certeza los distintos grupos naturales implicados.

Abstract

Trisetum Pers. is a genus of grasses of the tribe Poeae R. Br. (Poaceae subfam. Pooideae Benth.), whose taxonomy and subgeneric and suprageneric systematics are controversial. Up to now, the species with Palearctic distribution only had taxonomic treatments for more or less reduced geographical areas, so an integrative review of all their diversity which simplifies the complex and extremely analytical previous classification was clearly necessary. The series of works framed in the present PhD Degree offers a new taxonomic revision for the genus in the Palearctic region (as well as in other external territories when eventually the distribution of some taxon required it), which yields 21 recognized species organized in three sections: *T.* sect. *Trisetum*, *T.* sect. *Acrospelion*, and *T.* sect. *Sibirica*. More than 2,000 vouchers from about 66 herbaria have been studied. In sum, 42 names are lectotypified and two neotyfied.

With regard to the subgeneric taxonomy, *Trisetum* sect. *Trisetum* is characterized by generally lax panicles, spikelets greenish, callus with short hairs, angled or curved awn, rarely straight, and generally glabrous ovary sometimes with scattered hairs or densely hairy at the apex. *Trisetum flavescens*, the type species, is the most polymorphic species of the genus and is distributed throughout Eurasia and North Africa, also having the widest distribution area of the genus. Two infraspecific taxa of *T. flavescens* are recognized, *T. flavescens* subsp. *flavescens*, whose high morphological variability has been recognized at specific or infraspecific taxonomical ranks by various authors, and *T. flavescens* subsp. *griseovirens*, endemic to the High Atlas. Apart from this, seven other species of localized distribution in different Eurasian mountain systems are recognized: *T. alpestre, T. altaicum*, *T. bertolonii*, *T. fuscum*, *T. glaciale*, *T. gracile*, and *T. laconicum*.

Trisetum sect. *Acrospelion* is a section endemic to Eurasia that has seven species characterized by distichous leaves of the young stems, and callus and rachilla with long hairs. The highest diversity is located in two large mountainous areas, the Caucasus, with *T. rigidum* and *T. buschianum*, for which an additional subspecies is recognized besides of the type one (*T. rigidum* subsp. *teberdense* and *T. buschianum* subsp. *transcaucasicum*), and the Alps, with *T. distichophyllum* and *T. argenteum*. The other three species of the section are *T. macrotrichum*, endemic to the Carpathians, *T. tamonanteae* to Fuerteventura in the Canary Islands, and *T. velutinum* to the southeast of Spain.

Finally, *Trisetum* sect. *Sibirica* consists of six species; four of them, *T. aeneum*, *T. bifidum*, *T. henryi*, and *T. scitulum*, are endemic to eastern Asia and New Guinea. In the most western part of its distribution area are *T. turcicum*, which grows up in Turkey and the Caucasus, and *T. sibiricum*, the latter with two subspecies, *T. sibiricum* subsp. *sibiricum,* and *T. sibiricum* subsp. *litorale*. *Trisetum sibiricum* is the most polymorphic species of the section with the broadest distribution area, since it is distributed from Eastern Europe to Alaska and Western Canada. All of them are mainly characterized by their golden spikelets, glabrous callus or with very short hairs, and recurved awns rarely geniculate.

The phylogenetic analysis of four molecular markers (ITS, *rpl32*-*trnL*, *rps16*-*trnK* spacer, and *rps16* intron) carried out with representatives of the genus *Trisetum* and a wide range of related taxa, offers abundant systematic information at the subgeneric and suprageneric level. In addition to a good set of sequences already published in GenBank, we contributed with 2,044 new sequences corresponding to 275 species belonging to these groups. The subtribe Aveninae s.l., which includes *Trisetum*, has been resolved as monophyletic and encompasses three monophyletic subgroups: Aveninae s.s. (*Avena*, *Helictotrichon*, and *Tricholemma*, more Sesleriinae according to the nuclear marker), Koeleriinae (*Trisetum*, *Koeleria*, and related genera), and Lagurinae (*Lagurus*). Lagurinae is sister to Koeleriinae, which is divided in two large subclades, namely “Koeleriinae clade I”, where all the Palearctic taxa of *Trisetum* are placed, and “Koeleriinae clade II”. The representatives of *T.* sect. *Acrospelion* are grouped into a clade with weakly supported internal relationships and which also includes some Eurasian species of *T.* sect. *Trisetum*, as well as other Asian taxa of the genera *Helictotrichon* and *Tzveleviochloa*, in addition to another heterogeneous set of American taxa from the genera *Trisetum*, *Koeleria*, and *Graphephorum* according to the analysis of the nuclear marker. The clade that includes *Koeleria* and its type species also contains *T.* sect. *Trisetaera*, with species with dense and compact panicles, which groups the species of the *Trisetum spicatum* complex, its type, a species with worldwide distribution and here excluded from our taxonomic revision due to this closer phylogenetic affinity with *Koeleria* that would justify its transfer to this genus. Finally, the representatives of *T.* sect. *Sibirica* are grouped into a strongly support clade, which is independent from the rest and sister group of "Koeleriinae clade II"; this could justify its treatment as a separate genus.

In conclusion, the systematics of the subtribe Koeleriinae is very complex, especially since most of the genera of the subtribe have not been resolved as monophyletic taxa and the hybridization seems to have played an important role in the origin of several of these genera and species. The incongruences that reveal the existence of hybridization processes appear within "Koeleriinae clade I", as well as simultaneously between "Koeleriinae clade I" and "Koeleriinae clade II". We emphasize the necessity to develop new studies with nuclear low copy genes to clarify with more detail the systematics of these problematic groups and to obtain a more natural classification for *Trisetum* and its subtribe in which it is possible to identify with greater certainty the different involved natural groups.

INTRODUCCIÓN

Delimitación tradicional del género *Trisetum*

Trisetum Pers. es un género de gramíneas que pertenece a la tribu Poeae R. Br. (incl. Aveneae J. Presl., Poaceae subfam. Pooideae Benth.). Incluye alrededor de 70 especies de hierbas perennes que habitan principalmente pastizales o praderas en diversos ecosistemas de las zonas frías y templadas de ambos hemisferios, incluidas áreas alpinas o de tundra (Edgar, 1998; Hultén, 1959; Chrtek, 1965; Clayton & Renvoize, 1986; Randall & Hilu, 1986; Watson & Dallwitz, 1992; Finot et al., 2004, 2005a, b). Las gramíneas clasificadas en *Trisetum* son cespitosas, a veces con rizomas de longitud apreciable, y panículas claramente abiertas o más o menos contraídas. Las espiguillas tienen normalmente de 2 a 4 antecios, insertos en una raquilla glabra o pubescente que se prolonga normalmente por encima del antecio distal. Las glumas son heteromorfas, lanceoladas, de la misma longitud o desiguales –normalmente la inferior más corta y estrecha que la superior– y más o menos anchas. El lema tiene una arista dorsal inserta en un punto que puede estar situado desde la parte central del dorso hasta su tercio superior –raramente subapical–; su ápice puede ser bidentado –aunque algunas especies americanas pueden presentar 4 dientes– o bisetulado, con 2 arístulas que resultan de la proyección apical de dos de los nervios laterales del lema. Esta última configuración es la que da nombre al género (*Trisetum*, *-ii* n., “tres setas”; gr. *tri- (treîs, tría),* tres; lat. *sæta, -ae* f., cerda, crin, pelo áspero). El callo del antecio puede ser glabro o tener pelos –tricomas– de diversa longitud. La pálea es más corta que el lema, hialina y biaquillada. El androceo consta de tres estambres. El ovario es glabro o puede tener pelos cerca del ápice; su endosperma es fluido, más o menos líquido –sólido en algunas especies americanas–. Las lodículas son dos y membranáceas, a menudo apicalmente lobuladas. El hilo de la cariopsis es puntiforme. Su tipo, designado por Hitchcock (1920), es *T. flavescens* (L.) Beauv., una de las especies más polimorfas y ampliamente distribuidas del género. El elevado número de especies de *Trisetum* y la naturaleza de los problemas taxonómicos y sistemáticos que presenta, tanto a nivel subgenérico como a nivel supragenérico, hacen de este género un objeto idóneo para llevar a cabo nuevos estudios acerca de sus táxones y de las relaciones sistemáticas de los mismos entre sí y con otros géneros emparentados. Esbozaremos a continuación, a modo de introducción, estas complejidades que justifican nuestra elección y cuyo esclarecimiento constituirá nuestro principal objetivo.

Historia taxonómica y clasificación infragenérica

El género *Trisetum* fue descrito por Persoon (1805) a partir de una serie de especies que previamente se clasificaban en el género *Avena* L. En ocasiones ha incluido también al género de gramíneas anuales mediterráneas *Trisetaria* Forssk. [p. ej. Poiret (1808); Baumgarten (1817); Dumortier (1824); Ascherson & Graebner (1899); Boissier (1854); Paunero (1950)]. En nuestro estudio hemos mantenido la separación tradicional de ambos géneros, basándonos en su distinto ciclo de vida, al igual que se ha hecho últimamente en la mayoría de tratamientos taxonómicos o florísticos del género (Chrtek, 1965; Rechinger, 1970; Tzvelev, 1976; Pignatti, 1982; Mosulishvili, 1991; Finot et al., 2004, 2005a, b).

Introducción

La taxonomía subgenérica de *Trisetum* sigue actualmente presentando problemas, tanto en la delimitación de sus divisiones subgenéricas como en la de las especies y táxones infraespecíficos. En los tiempos más recientes se han llevado a cabo estudios taxonómicos detallados de las especies americanas y neozelandesas de *Trisetum* (Edgar, 1998; Finot et al., 2004, 2005a, b; Finot, 2010), mientras que las especies paleárticas del género no han recibido la misma atención y los tratamientos taxonómicos con que contamos son por lo general locales o regionales y por tanto necesitados de una revisión integradora de toda su diversidad geográfica.

En la tabla 1, basándonos en Quintanar et al. (2010), se compilan los tratamientos parciales de los diferentes autores sobre el género *Trisetum*, indicando las especies que cada autor incluye en cada grupo, con especial atención a las del Paleártico. Tradicionalmente, *Trisetum* se ha dividido en dos secciones, *Trisetum* sect. *Trisetum,* con panículas laxas y tallos glabros por debajo de la inflorescencia, y *Trisetum* sect. *Trisetaera* Asch. & Graebn., con panículas densas y tallos pelosos por debajo de la inflorescencia. Centrándose en las especies euroasiáticas y mediterráneas del género, el botánico checo Chrtek (1965, 1967, 1968) propuso nuevas divisiones infragenéricas para *Trisetum*. Chrtek (1965) separó las especies europeas del género en cuatro subgéneros –*T.* subg. *Trisetum*, *T.* subg. *Distichotrisetum* Chrtek, *T.* subg. *Glaciotrisetum* Chrtek y *T.* subg. *Graciliotrisetum* Chrtek–, basándose principalmente en el tipo de vernación (conduplicada o convoluta), en los caracteres anatómicos de las hojas y las raíces, además de en la disposición de las hojas de innovación, la longitud de las lígulas y de los pelos de la raquilla. El grupo más amplio de su tratamiento es *T.* subg. *Trisetum*, que incluye aquellas especies con vernación convoluta: *T. flavescens*, especie tipo del género, *T. agrostideum* (Laest.) Fr., *T. alpestre* (Host) P. Beauv., *T. baregense* Laffitte & Miégev., *T. burnoufii* Req. ex Parl., *T. fuscum* Schult., *T. hispidum* Lange, *T. macrotrichum* Hack., *T. rigidum* (M. Bieb.) Roem. & Schult., *T. sibiricum* Rupr., *T. spicatum* (L.) K. Richt. y *T. velutinum* Boiss. (Chrtek, 1965). Al mismo tiempo, Chrtek (1965) organizó *T.* subg. *Trisetum* en cinco secciones: *T.* sect. *Trisetum*, *T.* sect. *Carpatica* Chrtek, *T.* sect. *Hispanica* Chrtek, *T.* sect. *Rigida* Chrtek y *T.* sect. *Trisetaera*. *Trisetum* sect. *Carpatica* incluía únicamente la especie de los Cárpatos *T. fuscum*, caracterizada por sus largas lígulas y el lema, las quillas de la pálea y la arista pelosos. La extremadamente heterogénea *Trisetum* sect. *Hispanica* agrupaba dos especies endémicas de la Península Ibérica, *T. hispidum* y *T. velutinum*, y se caracterizó por sus células epidérmicas largas de la cara abaxial del limbo alargadas y rectangulares, con paredes laterales ligeramente sinuosas, por sus células buliformes poco visibles y sus hojas hirsutas. *Trisetum* sect. *Rigida* incluía las especies *T. macrotrichum* y *T. rigidum,* ambas con lígulas cortas, rachilla con pelos largos y hojas jóvenes en disposición dística. *Trisetum* sect. *Trisetaera* incluía al complejo formado por *T. spicatum* y especies afines, estudiado a fondo previamente por Hultén (1959) y caracterizado por Chrtek (1965) por sus panículas contraídas y sus hojas con el esclerénquima dispuesto en filamentos arqueados y bien desarrollados tanto en la cara abaxial como adaxial. En la sección típica, *T.* sect. *Trisetum,* incluyó las especies *T. flavescens, T. agrostideum*, *T. alpestre*, *T. baregense* y *T. sibiricum*, que se diferencian de

Trisetum Pers.

Trisetum subg. ***Trisetum***

Trisetum sect. ***Trisetum***

[incl. las especies americanas *T. cernuum* Trin., *T. curvisetum* Morden & Valdés-Reyna, *T. foliosum* Swallen, *T. irazuense* (Kuntze) Hitchc., *T. montanum* Vasey, *T. orthochaetum* Hitchc. (Finot et al., 2004, 2005a, 2005b); *T. henryi* Rendle, *T. scitulum* Bor ex Chrtek y *T. thospiticum* Chrtek, clasificados en *T.* ser. *Trisetum* (Chrtek, 1968b)]

Trisetum subsect. ***Trisetum***

[*T. flavescens* (Lam.) P. Beauv., *T. alpestre* (Host) P. Beauv. y *T. parvispiculatum* (Tzvelev) Prob. (Probatova, 1979)]

Trisetum subsect. ***Carpatica*** (Chrtek) Prob. (*T.* sect. *Carpatica* Chrtek)

[*T. fuscum* Schult. (= *T. ciliare* (Kit. ex Schult.) Domin (Probatova, 1979)]

Trisetum subsect. ***Sibirica*** (Chrtek) Prob. (*T.* ser. *Sibirica* Chrtek)

[*T. sibiricum* Rupr. y *T. turcicum* Chrtek (Probatova, 1979); más *T. aeneum* (Hook. f.) R.R. Stewart, *T. altaicum* Stephan ex Roshev., *T. micans* y *T. sikkimense* Chrtek (Chrtek, 1968b)]

Trisetum sect. ***Hispanica*** Chrtek

[*T. velutinum* Boiss. y *T. hispidum* Lange (Chrtek, 1965)]

Trisetum sect. ***Rigida*** Chrtek

[incl. *T. persicum* Chrtek (1968a); *T. macrotrichum* Hack., *T. rigidum* (M. Bieb.) Roem. & Schult., *T. buschianum* Seredin y *T. transcaucasicum* Seredin (Tzvelev, 1976)]

Trisetum ser. ***Laconica*** Chrtek

[*T. laconicum* Boiss. & Orph. y *T. rechingeri* Chrtek (Chrtek, 1967)]

Trisetum ser. ***Macrotricha*** Chrtek

[*T. macrotrichum* (Chrtek, 1967)]

Trisetum subsect. ***Monticola*** Mosulischvili (*T.* ser. *Rigida* Chrtek p.p.)

[*T. buschianum* y *T. transcaucasicum* (Mosulischvili, 1991)]

Trisetum subsect. ***Rigida*** (Chrtek) Mosulischvili (*T.* ser. *Rigida* Chrtek p.p.)

[*T. rigidum* (Mosulischvili, 1991); más *T. buschianum*, *T. daenense* (Boiss.) Balansa, *T. teberdense* (Litv.) Kharadze y *T. transcaucasicum* Seredin (Chrtek, 1968a)]

Trisetum sect. ***Trisetaera*** Asch. & Graebn.

[incl. *T. ambiguum* Rúgolo de Agrasar & Nicora, *T. barbinode* Trin., *T. caudulatum* Trin., *T. johnstonii* (Louis-Maire) Finot, *T. ligulatum* Finot & Zuloaga, *T. longiglume* Hack., *T. macbridei* Hitchc., *T. nancaguense* Finot, *T. oreophilum* Louis-Maire, *T. preslei* (Kunth) E. Desv., *T. projectum* Louis-Maire y *T. pyramidatum* Louis-Marie ex Finot (Finot et al., 2010)]

Trisetum subsect. ***Agrostidea*** Prob.

[*T. agrostideum* (Laest.) Fries (= *T. subalpestre* (Hartm.) Neuman) y *T. altaicum* (Probatova, 1979)]

Trisetum subsect. ***Koeleriformia*** Enustsch., nom. illeg., non Louis-Marie

[*T. spicatum* (L.) K. Richt., *T. alaskanum* Nash, *T. molle* (Michx.) Kunth, *T. mongolicum* (Hultén) Peschkova, *T. wrangelense* (V.V. Petrovsky) Prob. (Enushchenko, 2011)]

Trisetum subg. ***Deschampsioidea*** (Louis-Marie) Finot (*T.* subsect. *Deschampsioidea* Louis-Maire)

[*T. palmeri* Hitchc., *T. durangense* Finot & P.M. Peterson, *T. martha-gonzaleziae* P.M. Peterson & Finot, *T. pinetorum* Swallen, *T. spellenbergii* Soreng, *T. tonduzii* Hitchc., *T. viride* (Kunth) Kunth, *T. virletii* E. Fourn. (Finot et al., 2004)]

Trisetum subg. ***Distichotrisetum*** Chrtek (*T.* subg. *Argentaria* F. Herm.)

[*T. distichophyllum* (Vill.) P. Beauv. y *T. argenteum* (Willd.) Roem. & Schult. (Chrtek, 1965)]

Trisetum subg. ***Glaciotrisetum*** Chrtek

[*T. glaciale* (Bory) Boiss. (Chrtek, 1965)]

Trisetum subg. ***Graciliotrisetum*** Chrtek (*T.* sect. *Gracilia* Chrtek & Jirásek, p.p.)

[*T. gracile* (Moris) Boiss. (Chrtek, 1965)]

Incertae sedis: T. angustum Swallen, *T. bertolonii* Jonsell, *T. bifidum* (Thunb.) Ohwi, *T. filifolium* Scribn. ex Beal, *T. pringlei* (Scribn. ex Beal.) Hitchc. y *T. tamonanteae* Marrero Rodr. & S. Scholz.

Tabla 1. Síntesis actualizada de la clasificación de *Trisetum* basada en Quintanar et al. (2010), en la que se compilan los tratamientos parciales de los diferentes autores que han hecho propuestas sobre la clasificación del género. Se indican las especies incluidas por cada autor en cada grupo.

T. sect. *Trisetaera* por sus panículas laxas, lígulas cortas y esclerénquima claramente desarrollado de las hojas jóvenes.

Por último, el resto de subgéneros descritos por Chrtek (1965) tenían un menor número de especies de distribución menos amplia. *Trisetum* subg. *Distichotrisetum*, comprendía *T. distichophyllum* (Vill.) P. Beauv. y *T. argenteum* (Willd.) Roem. & Schult., principalmente distribuidas en los Alpes, con vernación conduplicada, esclerénquima de las hojas jóvenes poco desarrollado, éstas con disposición dística, y células endodérmicas de la raíz en forma de “C” y de “U”. La especie endémica de Sierra Nevada, *T. glaciale* (Bory) Boiss., fue clasificada en *T.* subg. *Glaciotrisetum*, con el mismo tipo de vernación y forma de las células de la raíz que el subgénero anterior, pero con diferente disposición del esclerénquima foliar. El último grupo, *T.* subg. *Graciliotrisetum,* incluía también únicamente una especie, *T. gracile*, con vernación conduplicada o convoluta, células endodérmicas de la raíz en forma de “O” y esclerénquima foliar bien desarrollado, tanto en la cara abaxial como en la adaxial.

Más tarde, Chrtek (1967) describió varias especies y dividió alguna de las secciones de *T.* subg. *Trisetum* en diversas series. Chrtek (1967) describió una nueva especie para Grecia, *T. rechingeri* Chrtek, y dividió *T.* sect. *Rigida* en tres series –*T.* ser. *Macrotricha* Chrtek, *T.* ser. *Laconica* Chrtek y *T.* ser. *Rigida* Chrtek–, que se distinguían por la longitud de los renuevos foliares y de los pelos del callo y la raquilla. *Trisetum* ser. *Macrotricha* incluía tan solo *T. macrotrichum*, una especie con los pelos del callo muy largos –que alcanzan la mitad de la longitud del lema– y renuevos foliares largos, mientras que *T.* ser. *Laconica* incluía los dos endemismos griegos *T. laconicum* Boiss. & Orph. y *T. rechingeri*, ambas con los pelos del callo y de la rachilla cortos y renuevos foliares también cortos. Las especies de *T.* ser. *Rigida*, *T. buschianum* Seredin, *T. daenense* (Boiss.) Balansa, *T. rigidum*, *T. teberdense* Seredin y *T. transcaucasicum* Seredin, tienen los pelos de la raquilla aún más largos –hasta de ¾ de la longitud del lema–, pelos del callo cortos y renuevos foliares cortos o largos.

En su revisión de táxones asiáticos, Chrtek (1968a) describió dos táxones endémicos de Irán, *T. persicum* Chrtek, incluyéndolo en la sect. *Rigida*, y la subespecie *T. rigidum* subsp. *demavandense* Chrtek. Ese mismo año, Chrtek (1968b) publicó dos nuevas especies, una endémica de Sikkim, *T. scitulum* Chrtek, y otra, *T. sikkimense* Chrtek, presente también en Nepal, sudeste del Tíbet y China. Además, añadió una nueva serie a la clasificación infragenérica del género, *T.* ser. *Sibirica* Chrtek, que incluía *T. sibiricum*, una especie del centro de Asia, *T. altaicum* Stephan ex Roshev. y, con dudas, dos especies himalaicas, *T. aeneum* (Hook. f.) R.R. Stewart y *T. micans* Chrtek (1968b); el resto de las especies tratadas permanecieron en *T.* ser. *Trisetum* (*T. flavescens*, *T. turcicum* Chrtek de Turquía y el Cáucaso, *T. thospiticum* Chrtek del lago Van en Turquía, y las asiáticas *T. henryi* Rendle y *T. scitulum* Bor ex Chrtek). Ambas series pueden ser distinguidas, según este autor, por la forma de las aristas, tan solo recurvadas en *T.* ser. *Sibirica*, y geniculadas y acodadas en *T.* ser. *Trisetum*.

Posteriormente, Tzvelev (1976) simplificó la clasificación de Chrtek en su tratamiento de las especies del género *Trisetum* de la Unión Soviética y aceptó únicamente tres secciones (*T.* sect. *Trisetum,* *T.* sect. *Rigida* y *T.* sect. *Trisetaria*), sin tener en cuenta el tratamiento de series desarrollado anteriormente por Chrtek. Tzvelev (1976) caracterizó las diferentes secciones según el tipo de crecimiento de los tallos subterráneos y vegetativos, la disposición de las hojas, la densidad de la panícula y la longitud de los pelos tanto del callo como de la raquilla, sin tener en cuenta los caracteres anatómicos a los que Chrtek (1965) dio tanta importancia. Probatova (1979), en su tratamiento de las especies caucásicas de *Trisetum*, separó *T.* sect. *Trisetum* en cuatro subsecciones, según el tipo de crecimiento de los tallos subterráneos y vegetativos, la forma del ápice del lema, la pilosidad del callo, de la arista y de las quillas de la pálea y la longitud de las anteras. Las subsecciones reconocidas por Probatova (1979) fueron la monospecífica *T.* subsect. *Carpatica* (Chrtek) Probat. –*T. fuscum*–, *T.* subsect. *Trisetum* –*T. flavescens, T. parvispiculatum* (Tzvelev) Prob. y *T. alpestre*–, *T.* subsect. *Sibirica* (Chrtek) Probat. –*T. sibiricum* y *T. turcicum*– y la *T.* subsect. *Agrostidea* Probat. –*T. altaicum* y *T. agrostideum*–. Por último, Enushchenko (2011), en su revisión del género *Trisetum* para el norte de Asia, trasladó la subsección *Agrostidea* propuesta por Probatova (1979) a *T.* sect. *Trisetaera,* separando a la vez las especies del complejo *T. spicatum* en la subsección *Koeleriformia* Enustsch. Enushchenko (2011) separó ambas subsecciones principalmente por el indumento de los tallos, siendo glabros en la subsect. *Agrostidea* y pelosos por debajo de la inflorescencia en la subsect. *Koeleriformia*.

A pesar del gran trabajo clasificatorio realizado por los autores aquí comentados, sus tratamientos solo abarcaron especies de *Trisetum* de regiones concretas, más o menos amplias, de Europa y de Asia. Por lo tanto, no proporcionan una visión global del género en la región paleártica, lo que pone de relieve la necesidad de un tratamiento integrador que actualice nuestro conocimiento del género en dicha área y que simplifiquen la compleja y extremadamente analítica clasificación a la que ha sido sometido.

Relaciones filogenéticas

En cuanto a sus relaciones sistemáticas a nivel supragenérico, *Trisetum* se ha clasificado últimamente en la subtribu Aveninae J. Presl. (Soreng et al., 2015, incl. subtribu Koeleriinae Asch. & Graebn.) de la tribu Poeae, la tribu más amplia y polimorfas de la subfamilia Pooideae, a su vez uno de los principales grupos de la familia Poaceae (R. Br.) Barnhart (Tzvelev, 1989; Soreng et al., 2007). La sistemática de los taxones clasificados en la tribu Poeae ha sido recientemente reestructurada gracias a los trabajos filogenéticos realizados con diversos marcadores moleculares. Soreng et al. (1990, 2000) fueron los primeros en identificar y reconocer los dos clados cloroplásticos principales en la tribu Poeae, los cuales han sido estudiados posteriormente en recientes trabajos moleculares (Grass Phylogeny Working Group II, 2012; Döring et al., 2007; Quintanar et al., 2007; Schneider et al., 2009; Saarela et al., 2015, 2017). Estos clados han recibido diferentes nombres, pero la forma más común es la utilizada por Soreng et al. (2015), nombrándolos como “Poeae chloroplast group 1” y “Poeae chloroplast group 2”. La subtribu Aveninae forma parte del clado “Poeae chloroplast group 1”, junto a otras seis subtribus, que son Agrostidinae Fr., Anthoxanthinae A. Gray, Brizinae Tzvelev, Calothecinae Soreng, Phalaridinae Fr. y Torreyochloinae Soreng & J.I. Davis (Soreng et al., 2015); la subtribu Sesleriinae es parte del clado “Poeae chloroplast group 2” con marcadores nucleares, mientras que se ubica en “Poeae chloroplast group 1” con los marcadores cloroplásticos (Quintanar et al., 2007; Gillespie et al., 2008; Saarela et al., 2010, 2017; Soreng et al., 2015), lo cual sugiere un posible origen híbrido y la existencia de procesos de reticulación profunda dentro de la tribu.

El género tipo de la subtribu Aveninae, donde Soreng et al. (2015) clasifican *Trisetum*, es *Avena* L., que incluye especies que representan varios de los cereales alimentarios más antiguos para la humanidad, en particular a *A. sativa* L., así como otras muchas hierbas de pastizal y forrajes de zonas templadas. Los miembros de esta subtribu se caracterizan por tener panículas simples con espiguillas comprimidas lateralmente que normalmente se desarticulan por encima de las glumas, las cuales pueden ser más cortas o más largas que los lemas adyacentes, con lemas múticos, bidentados o con arista dorsal, subapical o apical, además de cariopsis con gránulos compuestos de almidón (Tzvelev, 1989; Soreng et al., 2007). Esta clasificación de la subtribu Aveninae (Soreng et al., 2015), que naturalmente se ha fundamentado en los estudios más recientes sobre estos grupos (Grebenstein et al., 1998; Röser et al., 2001, 2009; Quintanar et al., 2007, 2010; Saarela et al., 2010), está así formada por 15 géneros y 302 especies, aunque el emplazamiento de varios de estos género siga siendo controvertido; así pues, se reconocieron: *Avena*, *Arrhenatherum* P. Beauv., *Avellinia* Parl., *Gaudinia* P. Beauv., *Graphephorum* Desv., *Helictotrichon* s.s. Besser, *Koeleria* Pers., *Lagurus* L., *Leptophyllochloa* C.E. Calderón, *Peyritschia* E. Fourn., *Rostraria* Trin., *Sphenopholis* Scribn., *Tricholemma* (Röser) Röser, *Trisetaria* Forssk. y *Trisetum*. A diferencia de Soreng et al. (2015), Kellogg (2015) redujo los rangos por debajo de las subfamilias, reconociendo dentro de la subtribu Aveninae 324 especies clasificadas en siete géneros, los cuales fueron *Arrhenatherum*, *Avena*, *Graphephorum*, *Helictotrichon*, *Lagurus*, *Sphenopholis* y *Trisetaria*. Kellogg (2015) trató a los géneros *Avellinia*, *Gaudinia*, *Koeleria*, *Leptophyllochloa*, *Peyritschia*, *Rostraria* y *Trisetum* como sinónimos de *Trisetaria*. Los últimos estudios han añadido dos nuevos géneros a la subtribu, *Trisetopsis* Röser & A. Wölk (Wölk & Röser, 2013, 2014) y *Tzveleviochloa* Röser & A. Wölk (Wölk & Röser, 2017), mientras que el género *Lagurus* ha sido separado como una nueva subtribu, Lagurinae Saarela (Saarela et al., 2017). Es necesario señalar que *Trisetum* también se ha clasificado en una subtribu Koeleriinae separada de Aveninae (Quintanar et al., 2007, 2010; Saarela et al., 2017), junto a los géneros que tradicionalmente se han considerado emparentados con *Trisetum* (*Trisetaria*, *Koeleria*, *Rostraria*, *Graphephorum* y *Sphenopholis*) y que, a grandes rasgos, coincide con el llamado "Grupo *Trisetum*" por Clayton y Renvoize (1986). Es precisamente con estos géneros con los que *Trisetum* mantiene mayores similitudes morfoanatómicas, como son los lemas aquillados y las páleas de gran tamaño. Varios autores (Clayton & Renvoize, 1986; Mosulishvili, 2000; Quintanar et al., 2007) han adjudicado un papel ancestral y basal a *Trisetum* en la evolución de este grupo justificándolo morfológicamente por la estructura menos reducida de sus lemas. De hecho, algunos de los estudios filogenéticos indicados anteriormente identifican dos clados principales dentro de la subtribu Aveninae (Quintanar et al., 2007; Saarela et al., 2017), uno que corresponde a una subtribu Aveninae s.s., restringida a los géneros *Avena*, *Arrhenatherum*, *Helictotrichon* y *Tricholemma* y otro que incluye a *Trisetum* y a los géneros agrupados en una subtribu Koeleriinae separada de la anterior (Quintanar et al., 2007; Schneider et al., 2009; Saarela et al., 2017). Este último clado incluye los dos grandes géneros de gramíneas perennes *Trisetum* y *Koeleria*, de distribución subcosmopolita, los americanos *Graphephorum*, *Leptophyllochloa*, *Peyritschia* y *Sphenopholis*, así como los anuales con distribución circumediterránea *Trisetaria*, *Rostraria*, *Avellinia* y *Gaudinia*. Además de todos ellos, este clado también incluye a todo un complejo de especies distribuidas por el centro y el sur de América y clasificadas hasta ahora en los géneros *Calamagrostis* Adans o *Deyeuxia* Clarion ex P. Beauv., y los recientemente descritos *Trisetopsis* y *Tzveleviochloa* (Wölk & Röser, 2013, 2014, 2017; Saarela et al., 2017). Gracias a todos estos trabajos filogenéticos, han ido saliendo a la luz algunos de los aspectos taxonómicos más problemáticos de la delimitación genérica de *Trisetum* con respecto a sus géneros más afines, entre los cuales destacamos su aparente carácter para o polifilético (Quintanar et al., 2007; Saarela et al., 2010, 2017). Es importante adelantar que a la luz de la información obtenida de nuestros recientes estudios moleculares, se han excluido del presente tratamiento taxonómico las especies del complejo formado por *T. spicatum* y especies afines (Apéndice 1), debido a que han resultado estar más relacionadas con *Koeleria* que con *Trisetum* s.s., una relación también fundamentada en la morfología y cuya discusión será objeto de futuras revisiones taxonómicas.

Por lo tanto, el establecimiento de los límites genéricos de *Trisetum,* así como la identificación de aquellas especies que formen grupos monofiléticos y la relación de estas con los géneros comentados anteriormente, justifican un mayor esfuerzo de muestreo de todos estos grupos que permita un análisis filogenético con marcadores moleculares más amplio que los que hasta ahora se han llevado a cabo y que arrojen luz adicional sobre estos problemas. En este trabajo presentamos una nueva filogenia expandiendo notablemente el número de muestras y de especies comparado con estudios anteriores. Se incluyen principalmente muestras de las especies de la subtribu Aveninae, poniendo especial énfasis en los representantes de *Trisetum* y *Koeleria*, así como un amplio muestreo de los demás miembros de la subtribu “Poeae chloroplast group 1”. Con ello, se pretende clarificar lo más posible los límites de los subgrupos de esta compleja subtribu, a la vez que contribuir a una nueva clasificación integrativa, apoyada tanto en los datos morfológicos como moleculares.

OBJETIVOS

Los **objetivos generales** de este trabajo son esencialmente dos. Por un lado se trata de obtener un tratamiento taxonómico moderno de las especies paleárticas de *Trisetum* en el que se integren todos los datos conocidos sobre su variabilidad y distribución. La restricción geográfica es imperativa para que el estudio sea viable en plazo de tiempo razonable y no afecta a la consistencia de este ya que tan solo una de las especies tratadas (*T. sibiricum*) sobrepasa el área de estudio a la que se restringe el trabajo. El otro objetivo principal tiene que ver con la sistemática de *Trisetum*, tanto en lo que se refiere a sus relaciones con otros géneros como a los subgrupos en los que se puede organizar. Las hipótesis de partida tanto en lo que se refiere a la delimitación de las especies como a sus relaciones filogenéticas se han desarrollado en detalle en la introducción.

Los **objetivos concretos** de estudio son:

1. Elaborar una clave artificial de identificación que incluya todas las especies reconocidas de Eurasia y el norte de África del género *Trisetum* (capítulo 1).

2. Preparar el tratamiento taxonómico del género *Trisetum* en Eurasia y el norte de África que tras un estudio preliminar se ha clasificado en las secciones *Trisetum*, *Acrospelion* y *Sibirica*. Los principales aspectos tratados en este estudio serán: claves de identificación, nomenclatura, descripciones, ilustraciones, mapas de distribución y descripción del hábitat. La base del mismo será el análisis del material de los principales herbarios del mundo y, en la medida de lo posible, de muestras colectadas en el transcurso del trabajo, a lo que se añadirá la integración de los resultados que se han ido obteniendo en los estudios filogenéticos con marcadores moleculares (capítulos 2, 3 y 4).

3. Comparación de los últimos esquemas clasificatorios que incluyen *Trisetum* y sus géneros más directamente emparentados de la tribu Poeae (Soreng et al., 2015; Kellogg, 2015); presentación de un nuevo árbol filogenético radial de la familia Poaceae que incluya los táxones estudiados y su clasificación actualizada, teniendo en cuenta los resultados que se han ido obteniendo de nuestro estudio filogenético con marcadores moleculares (capítulo 5).

4. Análisis filogenético de los táxones incluidos en el clado “Poeae chloroplast group 1”, que amplíe el número de muestras de los trabajos anteriores y esclarezca las relaciones supragenéricas e infragenéricas de las subtribus implicadas que incluyen, naturalmente *Trisetum* y su correspondiente subtribu. Más específicamente se pretende analizar las relaciones filogenéticas de los subgrupos detectados en *Trisetum*, su eventual polifilia o parafilia y sus relaciones con géneros afines. Para ello se utilizarán el marcador nuclear ITS y los marcadores cloroplásticos *rpl32-trnL*, el espaciador *rps16-trnK* y el intrón *rps16* (capítulo 6).

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CAPÍTULO I

General identification keys to the Paleartic sections and species of *Trisetum* s.s.

Here we present artificial keys to identify the Palearctic sections and species of the genus *Trisetum* Pers. *Trisetum* sect. *Trisetaera* Asch. & Graebn. [incl. *T. spicatum* (L.) K. Richt. and its subespecies, *T. spicatum* subsp. *alaskanum* (Nash) Hultén, *T. spicatum* subsp. *hultenii* Chrtek, *T. spicatum* subsp. *mongolicum* Hultén ex Veldkamp, *T. spicatum* subsp. *ovatipaniculatum* Hultén ex Jonsell, *T. spicatum* subsp. *virescens* (Regel) Tzvelev, *T. spicatum* subsp. *tibeticum* (P.C. Kuo & Z.L. Wu) Dickoré, and *T. spicatum* subsp. *wrangelense* V.V. Petrovsky], as well as some other more or less related species such as *T. clarkei* (Hook. fil.) R.R. Stewart, *T. geghamense* Gabrieljan, *T. hispidum* Lange, *T. kangdingense* (Z.L. Wu) S.M. Phillips & Z.L. Wu, *T. koidzumianum* Ohwi, *T. micans* (Hook. fil.) Bor, and *T. subalpestre* (Hartm.) Neuman, have been excluded from this treatment, and therefore from *Trisetum* s.s., due to the new available information about their systematic relationships. These taxa are characterized by its condensed panicles, upper part of the culm hairy and subequal glumes. The following keys have been built using the results obtained in the chapters 2, 3, and 4. Those chapters provide the taxonomic revisions of the sections *Trisetum*, *Acrospelion* (Besser) Pfeiff., and *Sibirica* (Chrtek) Barberá, all including a key of their respective taxa. Moreover, detailed descriptions, illustrations, and distribution maps are included in each revision to support the taxa identification.

Identification key to the Paleartic sections of *Trisetum* s.s.

1. Leaves of the young shoots distichous; callus usually with long hairs .... ***T.*** sect. ***Acrospelion***
1. Leaves of the young shoots indistinctly distichous; callus usually glabrous or with short hairs 2
    2. Spikelets goldish-brown; awns recurved or basally slightly twisted, rarely geniculate . ***T.*** sect. ***Sibirica***
    2. Spikelets greenish or purplish; awns distinctly geniculate at the middle or the base, rarely straight....... .... ***T.*** sect. ***Trisetum***

Identification key to the Paleartic species of *Trisetum* s.s.

1. Herbs (3–)8.9–14.1(–19.5) cm high; basal leaf-blades rigid, with the central nerve thickened; panicles (1.3–)2.2–3.8(–4.8) cm long, ovate in outline... 2
    2. Nodes enfolded by the sheaths; basal leaf-sheaths not inflated, densely pubescent; basal leaf-blades with the margins thickened, cartilaginous; callus hairs (0.2–)0.3–0.6(–0.9) mm long.............. ***T. glaciale***
    2. Nodes not enfolded by the sheaths, rarely enfolded; basal leaf-sheaths somewhat inflated, glabrous to sparsely pubescent; basal leaf-blades without thickened margins; callus hairs (0.7–)1–1.3 mm long......... .... ***T. gracile***
1. Herbs (6.9–)26–57(–164.5) cm high; basal leaf-blades rarely rigid, without thickened central nerve; panicles (2.8–)5.8–11.4(–28) cm long, elliptic to oblong or lanceolate in outline, rarely ovate................. 3
    3. Anthers (0.6–)1–1.2(–1.8) mm long.. 4
        4. Callus totally glabrous; awn (10.5–)13–14(–15) mm long.. ***T. scitulum***
        4. Callus with hairs (0.1–)0.3–0.5(–0.7); awn (2.8–)5.5–7.8(–12) mm long....................................... 5

5. Panicle lax; glumes unequal [ratio -- lower glume length/upper glume length = (0.11–)0.48–0.59(–0.67)]; awn (7–)8.2–10.6(–12) mm long.. ***T. bifidum***

5. Panicles somewhat dense to dense; glumes unequal to subequal [ratio -- lower glume length/upper glume length = (0.52–)0.72–0.84(–0.95)]; awn (2.8–)5.3–6.7(–8.7) mm long............. 6

6. Culm pubescent; basal leaf-blades scattered or distichous in juvenile culms; rachilla segments between first and second flower with hairs 0.1–0.3(–0.7) mm long........................ ***T. tamonanteae***

6. Culm glabrous; basal leaf-blades not distichous in juvenile culms; rachilla segments between first and second floret with hairs 0.7–1.4(–1.5) mm long... 7

7. Lemma brownish to yellowish, rarely greenish; callus hairs 0.1–0.3 mm long........ ***T. aeneum***

7. Lemma greenish, surrounded by purplish; callus hairs 0.3–0.5(–0.6) mm long...... ***T. altaicum***

3. Anthers (1–)2–2.5(–4) mm long... 8

8. Upper culm leaf-blade reaching to the panicle, with the central nerve conspicuously marked; panicles (16–)19–23(–28) × (4–)5–8.5 cm.. ***T. henryi***

8. Upper culm leaf-blade not reaching to the panicle, rarely reaching, with the central nerve similar to the lateral ones; panicles (2.8–)5.7–11(–23) × (0.7–)1.8–3(–10) cm......................... 9

9. Culm pubescent; awn (11–)11.5–16(–17) mm long .... ***T. bertolonii***

9. Culm glabrous, rarely pubescent; awn (3–)5.6–7.5(–13.4) mm long 10

10. Callus hairs (1.5–)2.2–3.8(–4.5) mm long 11

11. Herbs (33–)38.5–67(–77) cm tall; panicles (9–)9.2–12.2(–15) × (2–)2.5–5.5(–6) cm, oblong to elliptic in outline, rarely narrowly oblong to narrowly elliptic; upper culm leaf-blade (4.4–)5–7.2(–10) mm wide.. ***T. macrotrichum***

11. Herbs (14.8–)17.8–27.2(–41.5) cm tall; panicles (2.8–)4–6.3(–9.4) × (1.2–)1.6–2.5(–4.3) cm, ovate to broadly lanceolate in outline, sometimes oblong-elliptic; upper culm leaf-blade (0.4–)1.5–1.9(–2.5) mm wide .... ***T. distichophyllum***

10. Callus hairs (0.05–)0.2–0.8(–2.6) mm long 12

12. Herbs with basal leaf-blades markedly distichous.. 13

13. Ligules 0.3–0.5(–0.7) mm long... ***T. argenteum***

13. Ligules (0.5–)1.6–2.7(–4.2) mm long 14

14. Basal leaf-sheaths velutinous; rachilla segments between first and second floret with hairs (0.3–)0.7–1.6(–2.4) mm long.. ***T. velutinum***

14. Basal leaf-sheaths glabrous or hairy but not velutinous; rachilla segments between first and second floret with hairs (2.3–)3.5–4.5(–5.7) mm long............... 15

15. Ligules 3.5(–4.2) mm long; glumes unequal [ratio -- lower glume length/upper glume length = (0.45–)0.55–0.66(–0.83)], greenish on the central part, surrounded by yellowish or hyaline part....................................... ***T. rigidum***

15. Ligules (1.1–)1.5–2.1(–3) mm long; glumes unequal to subequal [ratio -- lower glume length/upper glume length = (0.69–)0.72–0.86(–0.94)], greenish to purplish .... ***T. buschianum***

12. Herbs with basal leaf-blades not markedly distichous 16

16. Ligules (3–)3.7–4.7(–4.8) mm long .... ***T. fuscum***

16. Ligules (0.5–)0.9–1.9(–4) mm long 17

17. Anthers (3–)3.3–4 mm long... ***T. turcicum***

17. Anthers (1–)1.9–2.4(–3.1) mm long 18

18. Callus hairs 0.6–0.9 mm long; palea 5.8–6 mm long........... ***T. laconicum***

18. Callus hairs (0.1–)0.2–0.4(–0.8) mm long; palea (2.2–)3.7–4.6(–6.7) mm long.. 19

19. Nodes mostly concentrated in lower part of the culm; ovary usually with an apical tuft of hairs 0.1–0.2(–0.3) mm long or with scattered hairs at the apex, rarely glabrous.. ***T. alpestre***

19. Nodes separated along the culm; ovary glabrous 20

20. Lemmas greenish to yellowish on the central part, sometimes with purplish; awn geniculate to slightly geniculate, more or less twisted at the base, rarely not twisted... ***T. flavescens***

20. Lemmas golden brownish or yellowish, rarely greenish, with narrow hyaline margins; awn slightly recurved and sometimes slightly twisted at the base... ***T. sibiricum***

CAPÍTULO II

Taxonomic revision of *Trisetum* section *Acrospelion* (Poaceae: Pooideae: Aveninae) from Eurasia

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Published in *Systematic Botany* 42(4): 754-781 (2017)

Abstract—A taxonomic revision of *Trisetum* sect. *Acrospelion* is presented. We include descriptions and synonyms of each taxon from a study of 670 vouchers from 45 herbaria. Detailed morphometric descriptions, illustrations, distribution maps, identification key, and habitat data are given for each taxon. Twelve names are lectotypified: *Aira halleri* Honck., *Avena argentea* Willd., *Avena brevifolia* Host, *Avena daenensis* Boiss., *Avena distichophylla* Vill., *Trisetum argenteum* var. *parviflorum* Parl., *Trisetum cavanillesianum* Borja & Font Quer, *Trisetum distichophyllum* subsp. *delphinense* Beauverd, *Trisetum macrotrichum* Hack., *Trisetum rigidum* var. *molle* Somm. & Levier, *Trisetum rigidum* var. *ovale* Somm. & Levier, and *Trisetum teberdense* var. *brevifolium* Kharadze. We recognize seven species of *Trisetum* into the section, which is endemic to Eurasia: *T. argenteum, T. buschianum* Seredin, *T. distichophyllum* (Vill.) P. Beauv., *T. macrotrichum*, *T. rigidum* (M. Bieb.) Roem. & Schult., *T. tamonanteae* Marrero Rodr. & S. Scholz, and *T. velutinum* Boiss.). Morphometric variation of the main characters is shown by box-plots. The highest diversity is located in the Caucasian Mountains and the Alps where two species were found in each area. Additionally, one species is endemic to the Canary Islands, a second to the south-eastern Spain, and a third to the Carpathian Mountains. In contrast with some regional treatments, *T. persicum* Chrtek is considered a synonym of *T. rigidum* (M. Bieb.) Roem. & Schult., and *T. cavanillesianum* Borja & Font Quer a synonym of *T. velutinum* Boiss. *Trisetum rigidum* subsp. *teberdense* (Litv.) Tzvelev and *T. buschianum* subsp. *transcaucasicum* (Seredin) Mosul. are recognized as subspecies. Vegetative propagation has been observed for the first time in specimens of *T. rigidum* and *T. velutinum*.

Resumen—Se presenta una revisión taxonómica de *Trisetum* sect. *Acrospelion*. Incluimos descripciones y sinónimos de cada taxon tras el estudio de 670 pliegos de 45 herbarios. Se proporcionan descripciones morfométricas detalladas, ilustraciones, mapas de distribución, clave de identificación y hábitat de cada taxon. Se han lectotipificado 12 nombres: *Aira halleri* Honck., *Avena argentea* Willd., *Avena brevifolia* Host, *Avena daenensis* Boiss., *Avena distichophylla* Vill., *Trisetum argenteum* var. *parviflorum* Parl., *Trisetum cavanillesianum* Borja & Font Quer, *Trisetum distichophyllum* subsp. *delphinense* Beauverd, *Trisetum macrotrichum* Hack., *Trisetum rigidum* var. *molle* Somm. & Levier, *Trisetum rigidum* var. *ovale* Somm. & Levier y *Trisetum teberdense* var. *brevifolium* Kharadze. Se reconocen siete especies de *Trisetum* en la sección, endémica de Eurasia: *T. argenteum, T. buschianum* Seredin, *T. distichophyllum* (Vill.) P. Beauv., *T. macrotrichum, T. rigidum* (M. Bieb.) Roem. & Schult., *T. tamonanteae* Marrero Rodr. & S. Scholz y *T. velutinum* Boiss. Se muestran las variaciones morfométricas de los principales caracteres en diagramas de caja. La mayor diversidad se localiza en las montañas del Cáucaso y de los Alpes, dónde dos especies se han encontrado en cada una de las áreas. Además, una especie es endémica de las Islas Canarias, una segunda del sudeste de España y una tercera de los Cárpatos. A diferencia de algunos tratamientos regionales, *T. persicum* Chrtek se considera sinónimo de *T. rigidum* (M. Bieb.) Roem. & Schult. y *T. cavanillesianum* Borja & Font Quer sinónimo de *T. velutinum* Boiss. Se reconocen *T. rigidum* subsp. *teberdense* (Litv.) Tzvelev y *T. buschianum* subsp. *transcaucasicum* (Seredin) Mosul. como subespecies. Se ha observado por primera vez propagación vegetativa en especímenes de *T. rigidum* y *T. velutinum*.

INTRODUCTION

Trisetum Pers. [Poaceae (R. Br.) Barnhart: subfamily Pooideae Benth.] is a perennial genus of grasses which belongs to the blue grass tribe Poeae R. Br. (including tribe Aveneae Dumort.; cf. Tzvelev, 1989; GPWG, 2001; Soreng et al., 2003, 2007; Quintanar et al., 2007), and to subtribe Aveninae J. Presl (Soreng et al., 2015).

Trisetum is comprised of approximately 70 species that inhabit temperate and cold regions, mainly in the Northern hemisphere, but are also found in South America, Australia, and New Zealand. Typically, they live in weedy places, meadows, mountain slopes, and alpine and tundra grasslands (Hultén, 1959; Chrtek, 1965; Clayton & Renvoize, 1986; Randall & Hilu, 1986; Watson & Dallwitz, 1992; Finot et al., 2004, 2005b). Detailed taxonomical revisions of American taxa, as well as taxa from New Zealand, have been made (Edgar, 1998; Finot et al., 2004, 2005a, 2005b); however, only partial revisions exist for Europe and Asia. All the species of *T.* sect. *Acrospelion* are endemic to this later area.

Prior to the publication of the genus *Trisetum* by Persoon (1805), the species included in the genus were considered to belong to the genus *Avena* L. The genus *Trisetaria* described by Forsskål (1775) (describing only one species, *Trisetaria linearis* Forssk.), was considerate synonym of *Trisetum* by some authors [e.g., Poiret (1808), Baumgarten (1817), Dumortier (1824), Ascherson & Graebner (1899), Boissier (1854)]. Others realized that *Trisetaria* had priority when the two genera are united [e.g., Maire (1942), Paunero (1950), Jonsell (1980)]. In this study, we continue the traditional separation of the two genera based on their perennial (*Trisetum*) versus annual (*Trisetaria*) life-cycles (e.g., Chrtek, 1965; Rechinger, 1970; Tzvelev, 1976; Pignatti, 1982; Mosulishvili, 1991; Finot et al., 2004, 2005a, 2005b); therefore, the proposal of Quintanar & Castroviejo (2010) to conserve *Trisetum* against *Trisetaria* is followed.

Trisetum has been traditionally divided into two sections: *T.* sect. *Trisetum*, with lax, open panicles and culms glabrous below the inflorescences, and *T.* sect. *Trisetaera* Asch. & Graebn., with dense, spiciform panicles, and culms pilose below the inflorescences. A review of the history of the genus can be found in Finot et al. (2005a).

Chrtek (1965) divided the Europaean species of *Trisetum* in four subgenera: *T.* subg. *Distichotrisetum*, *T.* subg. *Glaciotrisetum*, *T.* subg. *Graciliotrisetum*, and *T.* subg. *Trisetum*. To divide the aforementioned subgenera, Chrtek considered the most important characters to be the variation in vernation (conduplicate or convolute), sclerenchyma disposition in transverse sections of leaf-blades, and the endodermal cell disposition in transverse sections of roots. Other characters considered alongside the previous ones are the innovation leaves disposition, ligules length, and rachilla hairs length. The distribution of the species was also taken into account. The wide-ranging group, *T.* subg. *Trisetum*, was primarily characterized by the convolute vernation. *Trisetum flavescens* and related species, *T. fuscum*, *T. hispidum*, *T. macrotrichum*, *T. rigidum*, *T. spicatum*, and *T. velutinum* belong to this subgenus, along with *T. agrostideum* (Laest.) Fr., *T. alpestre* (Host) P. Beauv., *T. baregense* Laffitte & Miégev., *T. burnoufii* Req. ex Parl., and *T. sibiricum* Rupr. The other subgenera have fewer species and narrower distributions.

Trisetum subg. *Distichotrisetum*, comprising *T. distichophyllum* and *T. argenteum,* was characterized by having conduplicate vernation, leaves with sclerenchyma clearly developed on young leaves, endodermal cells of roots C and U shaped, and young leaves distichously disposed. Another species, *T. glaciale*, endemic to the Sierra Nevada in the south-eastern Spain, belongs to *T.* subg. *Glaciotrisetum*, showcasing the conduplicate vernation, endodermal cells of roots C and U-shaped, and leaf-blades with sclerenchyma only present on the abaxial side of the central vascular bundle, as a well-developed girder, and a cap of sclerenchyma at the margin. The last group, *T.* subg. *Graciliotrisetum* is made up of one species from Corsica and Sardinia, *T. gracile,* characterized by vernation conduplicate to convolute, endodermal cells of roots O-shaped, and leaf-blades with sclerenchyma adaxially and abaxially disposed in arched well-developed strand.

Chrtek (1965) divided also the subgenus *Trisetum* in five sections: *T.* sect. *Carpatica*, *T.* sect. *Hispanica*, *T.* sect. *Rigida*, *T.* sect. *Trisetaera,* and *T.* sect. *Trisetum*.

Chrtek (1965) proposed an extremely heterogeneous section endemic to the Iberian Peninsula, *T.* sect. *Hispanica* (comprising the type species *T. velutinum*, and *T. hispidum*), which shares elongated, rectangular long cells with slightly sinuous lateral walls, hirsute leaves, and inconspicuous bulliform cells. The monotypic *T.* sect. *Carpatica*, established for *T. fuscum* of the Carpathian Mountains, has slightly longer ligules than found in *T.* sect. *Hispanica,* and hairy palea keels. In *Trisetum* sect. *Rigida,* Chrtek (1965) included *T. macrotrichum* and *T. rigidum*, characterized by long rachilla hairs and distichous disposition of young leaves (sclerenchyma disposition and epidermal cells of abaxial side of innovation leaves as in *T.* sect. *Trisetum*). *Trisetum* sect. *Trisetaera* includes the *T. spicatum* complex with contracted panicles, and leaf-blades with sclerenchyma adaxially and abaxially disposed in arched, well-developed strand, as *T.* subg. *Glaciotrisetum*. *Trisetum* sect. *Trisetum* is separated from *T.* sect. *Trisetaera* by its lax panicles and leaves with the sclerenchyma clearly developed in young leaves. Chrtek (1965) noted that *T. agrostideum,* which belongs to *T.* sect. *Trisetum*, has a sclerenchyma disposition similar to *T.* sect. *Trisetaera*.

Chrtek (1967) described one new species from Greece, *Trisetum rechingeri* Chrtek, and divided sect. *Rigida* into three new series: *T.* ser. *Macrotricha*, *T.* ser. *Laconica* Chrtek, and *T.* ser. *Rigida*. *Trisetum* ser. *Macrotricha*, including only *T. macrotrichum*, was diagnosed by its long callus hairs (reaching to ½ of the lemma) and long innovation leaves, while *T.* ser. *Laconica* had shorter rachillas and callus hairs, and shorter innovation leaves. *Trisetum* ser. *Rigida*, including *T. buschianum*, *T. daenense*, *T. rigidum*, *T. teberdense*, and *T. transcaucasicum*, was characterized by its long rachilla hairs (reaching to ¾ of the lemma), short callus hairs, and short or long culm innovation leaves. Chrtek (1968) in his study of some Asian taxa described one species (*T. persicum* Chrtek) and one subspecies (*T. rigidum* subsp. *demavandense* Chrtek), both from Iran, in *T.* ser. *Rigida*.

Tzvelev (1976) simplified Chrtek´s classification recognizing three sections (*T.* sect. *Rigida*, *T.* sect. *Trisetaria*, and *T.* sect. *Trisetum*) in his treatment of *Trisetum* for the Soviet Union. He characterized the different sections by the type of growth of underground and vegetative shoots, the leaf disposition, the panicle density, and the rachilla and callus hairs length. He did not account for the anatomical characters used by Chrtek. Tzvelev included four species and two subspecies within *T.* sect. *Rigida*, and avoided discussion of the series of *T.* sect. *Rigida*. In the section, Tzvelev included plants with long creeping underground shoots, long vegetative shoots, with distant nodes and distinctly distichous leaves, panicles sparse or fairly dense, with somewhat scabrous (to almost smooth) branches, rachillas with hairs 2–4.2 mm long, callus hairs 0.6–3.5 mm long, and anthers 1.7–3 mm long.

Chrtek (1965, 1967) overlooked the name *Acrospelion*, coined by Roemer and Schultes (1827) for a group of *Trisetum*. This genus was later combined as section by Pfeiffer (1871) and typified on *Trisetum distichophyllum*. Therefore, because of its earlier date, the epithet *Acrospelion* has priority over the epithet *Rigida* in the sectional rank.

This work, together with that of Chrtek, provides the most comprehensive studies on this section to date. However, the complex and extremely analytical Chrtek subgeneric divisions proved unsatisfactory and impractical due to the overlap of some characters among his proposed groups. Consequently, we prefer to follow Tzvelev´s outline, and to recognize a broader and better characterized *T.* sect. *Acrospelion*, without resorting to anatomical characters. Therefore, *T.* sect. *Acrospelion* includes seven species, *T. argenteum*, *T. buschianum*, *T. distichophyllum*, *T. macrotrichum*, *T. rigidum*, *T. tamonanteae*, and *T. velutinum*. *Trisetum* sect. *Acrospelion* is here characterized by having young shoots with distichous disposition, more or less rigid, and also loosely tufted habit, panicles from lax to slightly dense, glumes unequal to subequal, and long hairs on the rachilla segments between first and second floret and callus.

We present a taxonomic revision of *Trisetum* sect. *Acrospelion* based on the careful review of herbarium material, as a first installment of a monograph of *Trisetum* in Eurasia. For technical reasons, and the large number of species in the genus, the work will be presented in various articles, of which this is the first.

MATERIALS AND METHODS

This revision is based on the study of 670 herbarium specimens from the following herbaria: A, ABH, ARAN, B, BC, BCN, BERG, BM, BP, C, F, FI, G, GB, GDA, GH, GOET, H, HBG, IBF, JE, K, L, LD, LE, LPA, M, MA, MO, MPU, MW, NY, O, P, PH, PR, S, SEV, TBI, UPS, US, VAL, W, WIS, and WU [acronyms according to Thiers (2017)].

One hundred and twenty specimens were included for the morphometric analysis, as operational taxonomic units (OTUs), selected to represent as far as possible, the geographical range and the morphological variability of the taxa. Fifty-nine quantitative characters, listed in Appendix 1, were recorded using a Mitutoyo CD-15DCX digital vernier caliper on 20 specimens of each species when available. Commonly used characters in *Trisetum* taxonomy were selected, as well as those observed to be variable and diagnostic in herbarium specimens. Spikelet measurements were taken on the distal spikelet from the longest branch of the second node of the panicle; floret measurements were taken from the proximal branches. Leaf-blade width was measured one cm above the ligule insertion. The segment between first and second flower is also referred to as rachilla. Each character was analyzed for its minimum, maximum, and lower and upper quartiles, using STATISTICA package (www.statsoft. com). Quantitative and qualitative characters were used to build up identification key and descriptions. Minimum and maximum values are noted in parentheses and the lower and upper quartile values are noted outside. A combination of morphological characters was employed to distinguish species. Transverse sections of top leaf-blades were prepared by hand, stained with Fasga (Tolivia & Tolivia, 1987), and photographed with a Nikon SMZ1000 optical microscope. For leaf anatomy, the terminology defined by Ellis (1976, 1979) was used.

Additional data on the habitat, distribution, and chromosome numbers was checked from literature and collection labels. Chromosome numbers were summarized from the literature, but the extant vouchers, if any, were not revised. The list of numbered collections, examined specimens, and coordinates used to produce distribution maps were generated by a Microsoft ACCESS database (Microsoft, Seattle, Washington) using ArcGis v.9.3 (ESRI, 2008). The material studied is listed below each species. The data for establishing coordinates was completed in almost all cases, using www.geonames.org database.

RESULTS

Morphology

HABIT—The species of *Trisetum* sect. *Acrospelion* are perennial grasses with short rhizomatous or stoloniferous rhizomes, with well-isolated shoots or loosely tufted habit (densely tufted in *T. tamonanteae*). They are also characterized by their young shoots with distinctly distichous leaf disposition, also noticeable in older leaves. Most of the species present intravaginal growth in the basal part, although occasionally extravaginal growth occurs in the upper nodes (with the exception of *T. rigidum* and sometimes *T. buschianum*, whose nodes are never enclosed by the sheaths).

VEGETATIVE BODY—The culms are straight, with (3)4–10 nodes, and usually shorter than 60 cm. The variation in size among the species of this section is smaller in those with more limited biogeographical ranges; *T. rigidum* is the most widespread species of the section, ranging from (18.5–)37 to 57(–76.3) cm in height. Culms are glabrous in most of the species, pubescent in *T. tamonanteae*, and slightly puberulous around the nodes in *T. rigidum*, or occasionally puberulous in the upper internode below the panicle in *T. macrotrichum* and *T. velutinum*.

LEAVES—The indumentum, shape, and size of ligules, leaf-sheaths, and leaf-blades are variable characters in the same plant, depending on their location on the plant, whether they are the basal or the top culm-leaf. There is also variation according to leaf length and age. Young leaf-blades are usually less hairy than mature ones. Therefore, notable heterophylly occurs between young and mature leaf-blades in *T.* sect. *Acrospelion*, as well as in the closely related genus *Koeleria* (Quintanar & Castroviejo, 2013).

LEAF-SHEATHS—Basal leaf-sheaths are puberulous to pubescent, and rarely glabrous (velutinous in *T. velutinum*). Top culm leaf-sheaths can be shorter or longer than their respective internodes, and are always glabrous (except in *T. tamonanteae*, which has pubescent to densely pubescent sheaths, sometimes puberulous in *T. velutinum*). Sheath margins are glabrous, except for those of *T. macrotrichum*, which are ciliate (rarely ciliate in *T. distichophyllum*).

LEAF-BLADES—The species of *Trisetum* sect. *Acrospelion* have flat to inrolled leaf-blades. Hermann (1956) classified both *T. distichophyllum* and *T. argenteum* as a different subgenus (*T.* subgen. *Argentaria* Hermann), because of the presence of young conduplicate leaf-blades. Chrtek (1965), using additional morphological and anatomical characters, divided those species with conduplicate or convoluted vernal leaf-blades into four separate subgenera (subgen. *Trisetum*, *Distichotrisetum*, *Glaciotrisetum*, and *Graciliotrisetum*). The indumentum of leaf-blades has traditionally been used as a distinctive character for taxon delimitation (Tzvelev, 1976; Jonsell, 1980; Pignatii, 1982). However, leaf-blade features (mainly indumentum and width) have been considered less important than those linked to spikelet morphology for the taxonomy of species with large distribution (i.e. *T. rigidum*) due to the high variability of leaf-blade traits, which are more important at the subspecific level (i.e. *T. rigidum* and *T. buschianum*). Most of the species are abaxially and adaxially puberulous to pubescent, with hairs also found on the margin, except for *T. rigidum*, which has been separated into two subspecies mainly because of the indumentum and size of leaf-blades: glabrous in *T. rigidum* subsp. *rigidum*, and with long hairs along the margin and wider leaf-blades in *T. rigidum* subsp. *teberdense* (Fig. 1A–B).

All of the species of *Trisetum* sect. *Acrospelion* are C_3 (XyMS+) and mesophytic or xerophytic grasses. While the abaxial surface of the leaf-blades often has a regular outline, the adaxial surface has ribs of varying depth, and the midrib is not readily distinguishable (Metcalfe, 1960; Watson & Dallwitz, 1992). The depth of the intercostal zones and associated ribs is more pronounced in xerophytic species. Chrtek (1965) conducted the first detailed study on the histology of European *Trisetum*. He used the distribution of sclerenchyma strands or girders along the young leaf-blades as a main taxonomical character in his subgeneric classification. Among the species of this section, all the vascular bundles are accompanied by more or less developed sclerenchyma girders and strands that attach to both the abaxial and adaxial sides of the leaf-blade. Those species from strongly xeric habitats have well-developed sclerenchyma strands, specifically on the abaxial side when the ribs are less developed. Thus, *T. velutinum*, *T. rigidum*, and *T. argenteum*, all from more xerophytic habitats, have wider strands of sclerenchyma, whereas *T. macrotrichum*, *T. distichophyllum* and *T. buschianum* have thinner strands. This layer is discontinuous and narrows at the adaxial surface, and it is often interrupted at the furrows.

LIGULES—The shape and size of ligules are variable, with those of basal leaves being shorter than those of top culm leaves. The ligule measurements used in this study were taken from the top culm leaf-blades. *Trisetum rigidum* has the longest ligules [3.4(–4.2) mm], while *T. argenteum* has the shortest [0.3–0.5(–0.7) mm] (Fig. 1C). The ligules are membranous, with a truncate, laciniate to slightly laciniate, sometimes denticulate apex, glabrous or almost glabrous, with some hairs in most of the species (mostly pubescent in *T. argenteum*, *T. distichophyllum,* and *T. velutinum*).

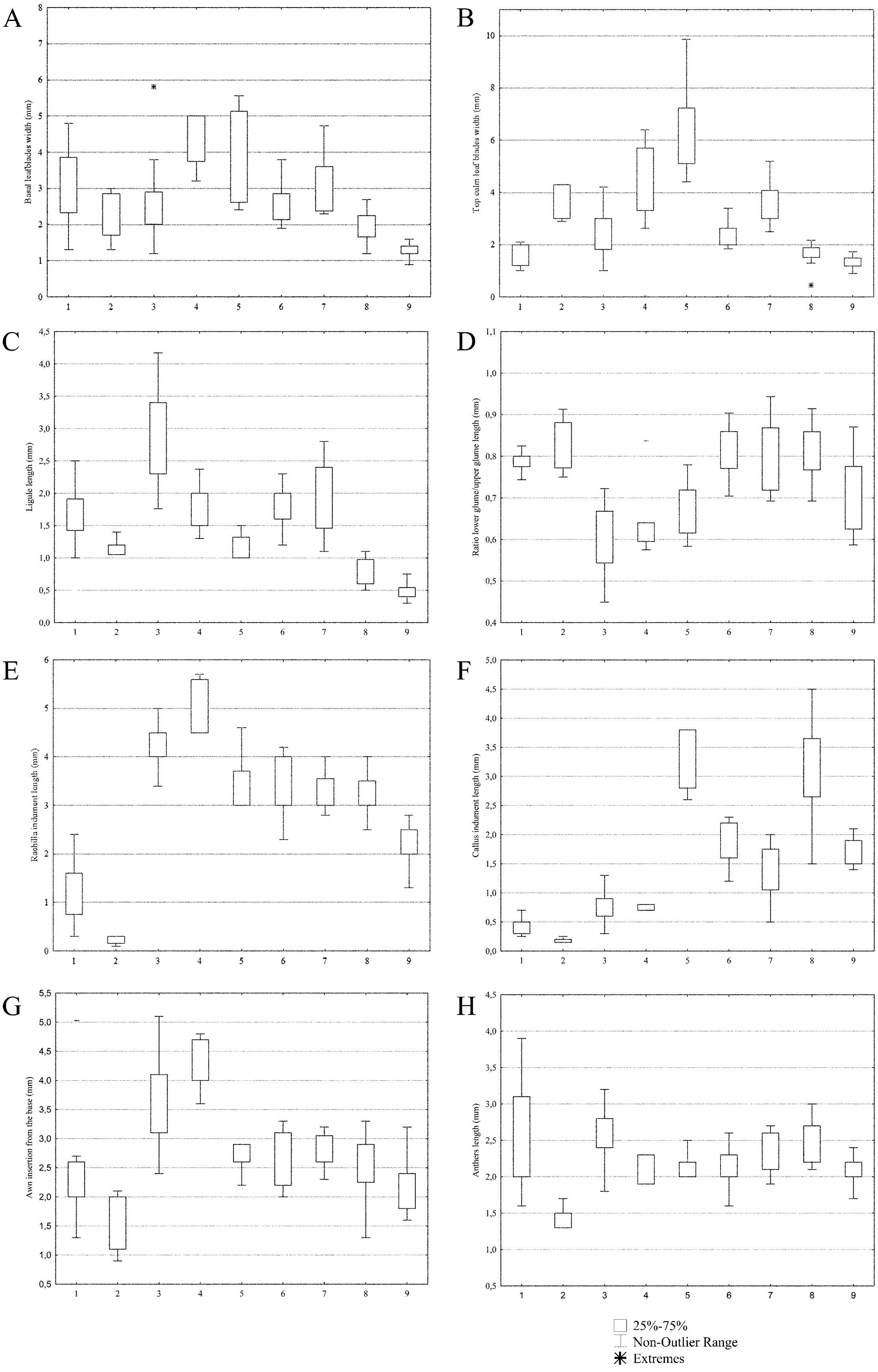

Figure 1. Box plots of a selection of studied variables. 1. *T. velutinum*; 2. *T. tamonanteae*; 3. *T. rigidum* subsp. *rigidum*; 4. *T. rigidum* subsp. *teberdense*; 5. *T. macrotrichum*; 6. *T. buschianum* subsp. *transcaucasicum*; 7. *T. buschianum* subsp. *buschianum*; 8. *T. distichophyllum*; 9. *T. argenteum*.

INFLORESCENCES—Inflorescences are paniculate, from lax to dense in *T. tamonanteae*, oblong to elliptic or lanceolate in outline, and sometimes ovate in *T. distichophyllum* and *T. buschianum* subsp. *transcaucasicum*. *Trisetum rigidum* and *T. macrotrichum* have the longest basal branches and panicles. *Trisetum* sect. *Acrospelion* has glabrous to slightly pubescent rachis, whereas *T. tamonanteae* has pubescent rachis with hairs up to 0.6 mm long.

Vegetative propagation has been observed in some specimens of *Trisetum rigidum* and *T. velutinum* for the first time; up until these observations, *T. tamonanteae* was the first species in the genus *Trisetum* in which this type of propagation was observed (Marrero & Scholz, 2013).

SPIKELETS—The size of the spikelets of *Trisetum* sect. *Acrospelion* varies according to the lemma length, being slightly longer, compared to the rest of species, in *T. rigidum*, and slightly shorter in *T. argenteum* and *T. tamonanteae*. For convenience, the awn is not included in the length of the spikelet. The variation in the number of florets, usually 2–3 per spikelet, is significant. *Trisetum macrotrichum* and *T. tamonanteae* have up to 4 and 5 florets per spikelet respectively.

Rachilla segments are always pubescent, with long white hairs between the first and second floret in most of the species, whereas they´re shorter in *T. tamonanteae*, *T. velutinum,* and *T. argenteum,* with hairs that are 0.1–0.3(–0.7) mm long, (0.3–)0.7–1.6(–2.4) mm long, and (1–)1.7–2.5(–3.4) mm long, respectively (Fig. 1E). The length of these hairs can be useful as a diagnostic character.

GLUMES—Glumes are always unequal in *Trisetum argenteum*, *T. macrotrichum*, and *T. rigidum*, and sometimes subequal in *T. buschianum*, *T. distichophyllum*, *T. tamonanteae*, and *T. velutinum*. Lower and upper glumes are acute to long acuminate, and glabrous, with some short hairs from the middle part to the top of the main nerve and along the margins. The lower glume is always shorter than the upper one, and usually has a main nerve reaching the tip, sometimes having one or two very short lateral nerves, extending at most to the middle part of the glume (Fig. 1D). The upper glume always has three nerves, the central one reaching the tip like in the lower glume, with the lateral ones more notable and only extending to the upper half.

LEMMA—The lemma of the species of *Trisetum* sect. *Acrospelion*, as well as that of the rest of the genus, is characterized by having a dorsal awn and a bifid apex with two apical teeth normally ending in two aristules separated by a more or less deep sinus. Aristules are the main lateral nerves protruding through each tooth apex (Nicora, 1978; Koch, 1979; Finot et al., 2006). Apical teeth and aristules are variable characters at the species level. The length of the lemma, without taking the awn into account, is a good diagnostic character, being shorter in *T. tamonanteae* and *T. argenteum* [(2.6–)3–4.3(–5.4) mm and (4–)4.4–5.2(–6.5) mm long, respectively] and longer in *T. rigidum* subsp. *rigidum* and *T. rigidum* subsp. *teberdense* [(5.3–)6.4–7.7(–9.3) and (6.7–)7–8.5 mm long, respectively]. The lemma is laterally compressed, from narrowly or broadly lanceolate to elliptic or oblong, with a glabrous to scabridulous or strigulous surface, having slightly longer hairs on the upper part.

CALLUS—The callus has an oblong to elliptic shape, sometimes rounded, always with hairs in the species of this section. The length of the callus indumentum is an important taxonomic character, with it being longer in *T. distichophyllum* and *T. macrotrichum* [(1.5–)2.2–3.7(–4.5) and (2.6–)2.8–3.8 mm long, respectively] and shorter in *T. tamonanteae* (0.1–0.3 mm long), *T. velutinum* [0.25–0.5(–0.7) mm long] and *T. rigidum* subsp. *rigidum* and *T. rigidum* subsp. *teberdense* [(0.3–)0.6–0.9(–1.4) and 0.7–0.8(–1) mm long, respectively] (Fig. 1F).

PALEA—The palea is enclosed by the margins of the lemma, opening only during the anthesis. The palea is a hyaline structure, with two keels extruding into two fine teeth, with very short hairs, also present along the outer edges. The length of both the palea and the lemma is unequal to subequal, being slightly less similar in *T. tamonanteae* and *T. rigidum* [ratio -- palea length/lemma length (0.56–)0.63–0.74 and (0.54–)0.66–0.81(–0.87), respectively].

LODICULES—The two lodicules flank the dorsal sides of the ovary or caryopsis, having a more or less oblanceolate shape. The apex is irregular to regularly lobulate (2–4-lobate) or denticulate, and glabrous, rarely with scattered hairs in *T. velutinum*.

AWN—The most important taxonomic character of the awn is length and the point of insertion on the lemma. The awn shape depends on the level of maturity of the specimens, but in general, it is more or less geniculate and twisted near the base, although almost straight in *T. tamonanteae*. This species has the shortest awn [(2.8–)3.4–5.1(–6.1) mm], but the length does not differ greatly in the rest of the species of the section. In *T. tamonanteae*, *T. velutinum*, and *T. argenteum*, the point of insertion is closer to the base of the lemma, compared to the rest of the species. *Trisetum rigidum* is the species with the most apical awn (Fig. 1G).

STAMENS—The length of the anthers is fairly constant within at the species level. *Trisetum tamonanteae* is the species with the smallest anthers [0.8–1.6(–1.8) mm long] (Fig. 1H).

OVARY AND CARYOPSIS—The ovary and caryopsis are very similar in all species, being glabrous, sometimes slightly puberulous on the apex in *T. rigidum*. The mature caryopsis is oblong in shape, narrowly elliptic in the transversal section, not sulcate, with puctiform hilum. The endosperm is liquid.

Taxonomic treatment

TRISETUM sect. ACROSPELION (Besser) Pfeiff., Nomencl. Bot. 1(1): 38. 1877. *Acrospelion* Besser, in Schult. & Schult. f., Mant. 3 (Add. 1): 526 [“326”]. 1827. *T.* [unranked] *Acrospelion* (Besser) Trin., Mém. Acad. Imp. Sci. St.-Petersbourg, sér. 6, Sci. Math. 1(1): 59. 1830.—LECTOTYPE: *T. distichophyllum* (Vill.) P. Beauv. [designated by Pfeiffer (1877: 38)].

T. sect. *Rigida* Chrtek, Bot. Not. 118(2): 222. 1965. *T.* ser. *Rigida* Chrtek, Acta Univ. Carol., Biol. 1966(2): 94. 1967. *T.* subsect. *Rigida* (Chrtek) Mosul., Zametki Sist. Geogr. Rast. 42: 33. 1991.—TYPE: *T. rigidum* (M. Bieb.) Roem. & Schult.

T. subg. *Argentaria* F. Herm., Fl. N.-Mitt.-Eur., 120, Stuttgart. 1956. *T.* subg. *Distichotrisetum* Chrtek, Bot. Not. 118(2): 223. 1965., nom. illeg.—TYPE: *T. distichophyllum* (Vill.) P. Beauv.

T. sect. *Hispanica* Chrtek, Bot. Not. 118(2): 222. 1965.—TYPE: *T. velutinum* Boiss.

T. ser. *Macrotricha* Chrtek, Acta Univ. Carol., Biol. 1966(2): 94. 1967.—TYPE: *T. macrotrichum* Hack.

T. subsect. *Monticolae* Mosul., Zametki Sist. Geogr. Rast. 42: 33. 1991.—TYPE: *T. buschianum* Seredin.

Herbs with or without loosely tufted habit (rarely densely tufted); young shoots with distichous disposition, ± rigid; panicles from lax to slightly dense (rarely dense); glumes unequal to subequal; rachilla segments between first and second flower and callus usually with long hairs.

Key to the taxa of Trisetum sect. Acrospelion

1. Top culm leaf-blades generally reaching or surpassing the panicles; rachilla segments between first and second flower with hairs 0.1–0.3(–0.7) mm long; paleas 2.3-3 mm long; anthers 0.8–1.6(–1.8) mm long.... .... ***T. tamonanteae***

1. Top culm leaf-blades not or rarely reaching the panicle; rachilla segments between first and second flower with hairs (0.3–)0.7-4.7(–5.7) mm long; paleas (2.4–)3.8–6(–6.6) mm long; anthers (1.5–)2–3.4(–4) mm long 2

  2. Sheaths velutinous; rachilla segments between first and second flower with hairs (0.3–)0.7–1.6(–2.4) mm long .... ***T. velutinum***

  2. Sheaths glabrous or hairy but not velutinous; rachilla segments between first and second flower with hairs (1–)3–4.2(–5.7) mm long 3

    3. Rachilla segments between first and second flower with hairs (3.2–)4–4.7(–5.7) mm long; callus hairs (0.3–)0.6–0.9(–1.4) mm long.. 4

      4. Plants (47–)50–67(–72) cm tall; basal leaf-blades (5–)7.5–8 (–8.6) cm long, not rigid, with hairs along the margins 0.4-1 mm long; top culm leaf-blades usually erect, sometimes reaching into the panicle.. ***T. rigidum*** subsp. ***teberdense***

      4. Plants (18.5–)34.3–56.5(–76.3) cm tall; basal leaf-blades (0.8–)2.8–5.2(–7) cm long, rigid, with hairs along the margins 0.05–0.6(–1) mm long; top culm leaf-blades divergent (rarely erect), not reaching into the panicle ....***T. rigidum*** subsp. ***rigidum***

    3. Rachilla segments between first and second flower with hairs (1–)2.5–3.5(–4.8) mm long; callus hairs (0.5–)1.5–2.9(–4.5) mm long.. 5

      5. Plants (33–)38.5–67(–77) cm tall; top culm leaf-blades (4.4–)5–7.2(–10) mm wide .... ***T. macrotrichum***

      5. Plants (10.6–)18.3–30.4(–41.5) cm tall; top culm leaf-blades (0.4–)1.4–2.5(–5.2) mm wide 6

        6. Habit slender; basal leaf-blades flat to inrolled, (0.9–)1.2–1.5(–1.7) mm wide...... ***T. argenteum***

        6. Habit more robust; basal leaf-blades flat, rarely inrolled, (1.2–)1.8–2.8(–4.7) mm wide 7

          7. Ligules 0.5-1 mm long, from densely to slightly pubescent on the surface and apex, sometimes glabrous; callus hairs (1.5–)2.2–3.7(–4.5) mm long ....***T. distichophyllum***

          7. Ligules (1.2–)1.5–2.1(–3) mm long, glabrous, rarely with few hairs on the apex; callus hairs (1.2–)1.6–2.2(–2.3) mm long 8

8. Plants (17–)23.7–30.7(–35) cm tall; nodes separated along the culm; top culm leaf-sheaths (6–)6.7–9(–10) cm long.. ***T. buschianum*** subsp. ***buschianum***

8. Plants (10.6–)13.6–18.6(–22.6) cm tall; nodes concentrated in the lower part of the culm; top culm leaf-sheaths (3–)3.6–6.2(–7.3) cm long.........***T. buschianum*** subsp. ***transcaucasicum***

1. TRISETUM DISTICHOPHYLLUM (Vill.) P. Beauv., Ess. Agrostogr.: 88. 1812. *Avena distichophylla* Vill., Prosp. Hist. Pl. Dauphiné: 16. 1779. *Avena disticha* Lam., Encycl. 1: 333. 1783., nom. superfl. *Trisetaria distichophylla* (Vill.) Paunero, Anales Jard. Bot. Madrid 9: 514. 1950.—TYPE: FRANCE. Dauphiné, 45º0'N, 5º15'E, *D. Villars s.n.* (lectotype, here designated, P-LA-564210!).

Aira halleri Honck., Verz. Gew. Teutschl.: 212. 1782.—TYPE: [unknown locality]. *V.A. Haller s.n.* [lectotype, here designated, P-Haller (image!); choice made by M. Kerguelen in sched.].

Avena brevifolia Host, Icon. Descr. Gram. Austriac. 3: 28, tab. 40. 1805. *Trisetum brevifolium* (Host) Roem. & Schult., Syst. Veg., 2: 665. 1817. *Trisetaria brevifolia* (Host) Baumg., Enum. Stirp. Transsilv., Mant.: 80. 1846. *Trisetum distichophyllum* subsp. *brevifolium* (Host) Pignatti, Giorn. Bot. Ital. 111(1-2): 59. 1977. *Trisetaria distichophylla* subsp. *brevifolia* (Host) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 382. 1996.—TYPE: AUSTRIA. Host herbarium, without locality or collector (lectotype, here designated, W-1885-0002402!).

Avena distichophylla var. *gracilis* Shuttlew., Mag. Zoo. Bot. 2: 17. 1838.—TYPE: SWITZERLAND. Valais, M. Gemmi, 46º23'N, 7º36'E, 30 Aug 1836, *R.J. Shuttleworth s.n.* (no original material found).

T. albanicum Jáv., Magyar Bot. Lapok 18: 1. 1920. *T. distichophyllum* subsp. *albanicum* (Jáv.) Hayek, Feddes Repert., Beih. 30(3): 313. 1932.—TYPE: ALBANIA. Hekurave Mountains, Djakova, Bunjaj, cacumine Stüla Gris, 42º23'N, 19º58'E, 24 Aug 1918, *S. Jávorka s.n.* (lectotype, designated by Kováts 2000: 35, BP!).

T. distichophyllum subsp. *delphinense* Beauverd, Bull. Soc. Bot. Genève, sér. 2, 26: 122, fig.1. 1934.—TYPE: FRANCE. Hautes-Alpes, Monétier, 44º59'N, 6º32'E, 25 Jul 1933, *G. Beauverd s.n.* [lectotype, here designated, G-386040 (image!); isolectotype, G-386041 (image!)].

Herbs (14.8–)17.8–27.2(–41.5) cm tall, loosely tufted, short rhizomatous, culms (0.3–)0.4–0.6(–0.7) mm diam., glabrous; nodes 4–5(7), concentrated in lower part of the culm, enclosed by the sheaths, sometimes the upper one exposed, glabrous. Basal leaf-sheaths pubescent, sometimes with longer hairs on the upper margins up to 0.1 mm long, decaying into fibers, brownish to yellowish, sometimes greenish; basal leaf-blades (1–)1.6–3.4(–7.7) cm long × (1.2–)1.6–2.2(–3.8) mm wide, markedly distichous, flat to slightly enrolled, sometimes conduplicate, from densely to slightly pubescent or scabridulous adaxially, slightly pubescent to glabrous abaxially, with hairs (0.05–)0.1–0.3(–1.3) mm long, greyish to greenish; top culm leaf-sheaths (3.3–)4.3–7(–10.8) cm long, shorter than the internodes, sometimes longer or almost equal, glabrous, without cilia on the margins, or rarely with cilia; top culm leaf-blades (0.5–)1.2–2.6(–6) cm long × (0.4–)1.5–1.9(–2.5) mm wide, conduplicate to inrolled, sometimes flat, adaxially pubescent to densely pubescent, abaxially pubescent to slightly pubescent, rarely almost glabrous, with hairs 0.05-0.1(–0.3) mm long along the margins, greenish to greyish; inner collar region glabrous to slightly pubescent, usually with scattered hairs on the margins 0.05–0.2(–1.5) mm long; ligules 0.5–1 mm long, laciniate to slightly laciniate, rarely slightly lobulated, from densely to slightly pubescent with hairs 0.05–0.2(–0.3) mm long on the abaxial surface and apex, sometimes glabrous. Basal node of the panicle glabrous. Panicles (2.8–)4–6.3(–9.4) cm long × (1.2–)1.6–2.5(–4.3) cm wide, ovate to broadly lanceolate in outline, sometimes oblong-elliptic, lax, rarely dense, with most rachis internodes plainly visible; rachis glabrous to slightly puberulous (mostly on the upper part), with hairs 0.05–0.15 mm long; longest basal branches (0.5–)0.6-1.8(–3.2) cm long. Spikelets (5.5–)7–8(–8.6) mm long × (2–)2.7–4.8(–7) mm wide, 2–3-flowered; pedicels (1.8–)2.7–4.2(–5) mm long, slightly pubescent with hairs 0.05–0.2 mm long, sometimes glabrous with scattered hairs distally. Glumes unequal to subequal [ratio -- lower glume length/upper glume length = (0.69–)0.77–0.86(–1)]; lower glume (3.6–)5–6.4(–7) mm long × (0.8–)1.1-1.6(–2) mm wide, narrowly to broadly lanceolate, sometimes elliptic or oblong [ratio -- lower glume width/lower glume length = (0.15–)0.22–0.26(–0.3)], acuminate to long acuminate, sometimes acute, (1–)2-3-nerved, glabrous, sometimes with short hairs up to 0.1 mm long from the center to the upper part of the main nerve, purplish to greenish, with margins hyaline; upper glume (5.2–)6.6–7.3(–8.1) mm long × (1.4–)1.8–2.2(–2.6) mm wide, elliptic to oblong, sometimes lanceolate, rarely slightly oblanceolate [ratio -- upper glume width/upper glume length = (0.23–)0.26–0.31(–0.4)], acuminate to long acuminate, rarely acute, 3-nerved, glabrous, usually with hairs up to 0.1 mm long, from the center to the upper part of the central nerve, purplish to greenish on the central part, margins mostly hyaline; rachilla segments between first and second floret (0.7–)1–1.3(–1.6) mm long, with hairs (2–)3–3.8(–4.8) mm long; rachilla segments to sterile floret (0.7–)1.3–2(–2.3) mm long, with hairs (1.4–)1.8–2.7(–3.5) mm long. Lemmas (4.5–)5.7–6.4(–7.5) mm long × (0.8–)1.1–1.6(–2) mm wide, elliptic to broadly lanceolate, rarely oblong [ratio -- lemma width/lemma length = (0.2–)0.26–0.32(–0.4)], scabridulous, with hairs 0.05-0.1(–0.8) mm long, the longest ones on the central part and on the awn insertion, greenish to yellowish on the central part, surrounded by purple; apical teeth absent or 0.2–0.4(1.2) mm long, with aristules (0.1–)0.2–0.4(–0.7) mm long; awn (4–)5.5–6.6(–8) mm long, inserted (1.3–)2.3–3(–3.3) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.2–)0.4–0.5], geniculate and twisted near the base, sometimes straight, with very short adpressed hairs up to 0.15 mm long; callus 0.2–0.4(–0.5) mm long, oblong to elliptic, with hairs (1.5–)2.2–3.7(–4.5) mm long. Paleas (3.8–)4.5–5.4(–6.6) mm long × (0.8–)1–1.3(–1.6) mm wide [ratio -- palea length/lemma length = (0.7–)0.78–0.87(–1)], elliptic to narrowly elliptic or oblong, with hairs from the center to the upper part of the outer edges; keels with short hairs mostly on the apex, ending in teeth 0.1–0.3(–0.4) mm long. Lodicules (0.6–)0.7–1(–1.2) mm long, with apex regularly or irregularly lobate, sometimes with a lateral linear lobe. Anthers 2.1-2.7(–3) mm long. Ovary (0.3–)0.6–1(–1.3) mm long, glabrous. Caryopsis 1.8–3 mm long × 0.4–0.8 mm wide. Figure 2.

Chromosome Number—2*n* = 28, 56 (Beuret, 1974; Lippert, 2006).

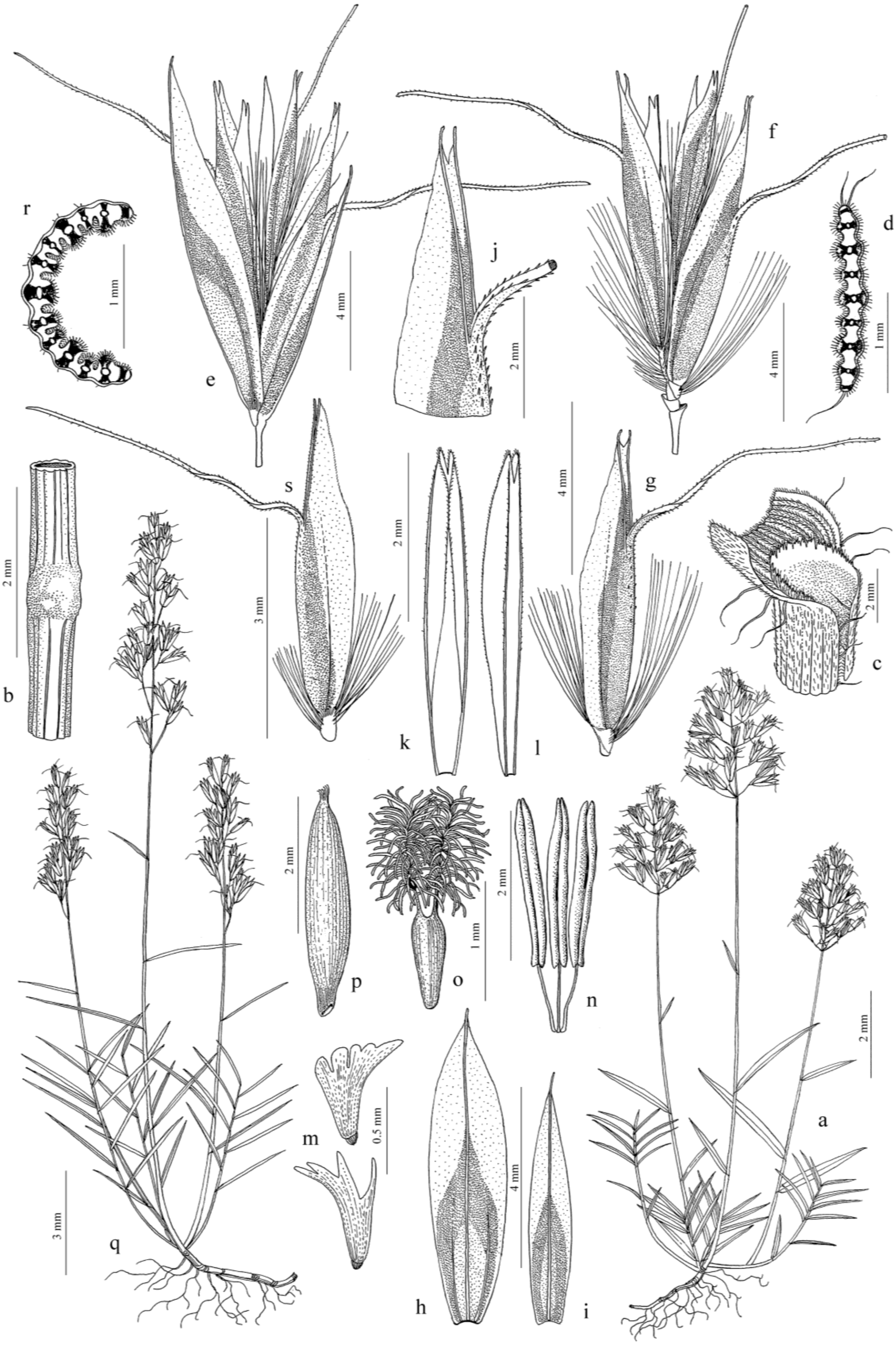

Figure 2. *Trisetum distichophyllum*. A. Habit. B. Portions of the culm and node. C. Sheath, ligule, and portion of the blade. D. Transverse section of leaf-blade. E. Spikelet. F. Florets. G. Floret. H. First glume, dorsal view. I. Second glume, dorsal view. J. Lemma, upper part, lateral view. K. Palea, ventral view. L. Palea, dorsal view. M. Lodicules.n. Stamens. O. Pistil. P. Caryopsis. *Trisetum argenteum*. Q. Habit. R. Transverse section of leaf-blade. S. Floret. (Reinecke s.n., JE, A; Huter s.n., PR-807305, B-O; Hellweger et Huter s.n., PR-807301, P; Bornmüller s.n., B-100526133, Q-S).

Phenology—Flowering from June to September.

Distribution and Habitat—Trisetum distichophyllum occurs in the Alps, from west to east, reaching to the Albanian Alps between Montenegro and Albania; at 950–2700 m elevation; around rocks and pebbles, mostly in calcareous soils, also in granites. Figure 3.

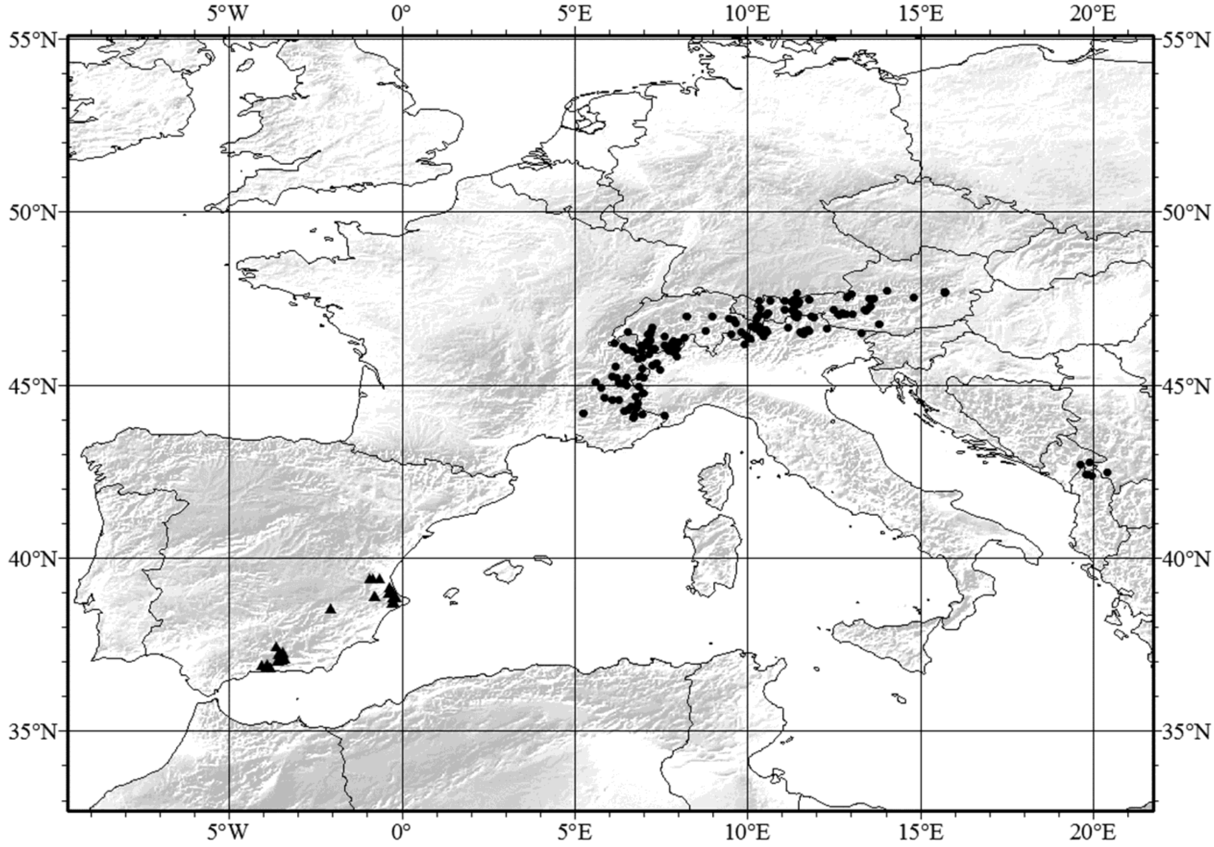

Figure 3. Distribution of *Trisetum velutinum* (triangles) and *T. distichophyllum* (dots).

Specimens Examined—**ALBANIA. Kukës County:** Tropojë district, on the northern slope of mt. Maja e Ershelit, above village Peraj, 42º29'N, 19º85'E, 15 Jul 2014, *Barina s.n. & al.* (BP); Qafa Valbons, inter vallem Valbona et Theti, 42º24'N, 19º48'E, 4 Jul 1955, *Jávorka s.n.* & *Ujhelyi* (BP); Beriscus, sub rupe Maja Drosks versus cacumin Maja Hecuravet, 42º23'N, 19º58'E, 1 Jul 1955, *Ujhelyi s.n.* (BP). **AUSTRIA. Carinthia:** Heiligenblut, Heiligenblüter Cavern, 47º2'N, 12º50'E, 28 Jul 1906, *Jeanpert s.n.* (F); Val Pasterze, au-dessus d´Heiligenblut, 47º4'N, 12º46'E, 26 Jul 1869, *Leresche s.n.* (L); Alpes d´Heiligenblut, Col de Kals, versant nord, 47º2'N, 12º50'E, 31 Jul 1869, *Leresche s.n.* (G, L); Heidelberger Hütte, 46º56'N, 10º16'E, Aug 1952, *Raabe s.n.* (HBG). **Lower Austria:** Raxalpe, Preiner Schütt, 47º42'N, 15º43'E, Jul 1883, *Beck s.n.* (W); Mt. Raxalpe, 47º42'N, 15º43'E, Aug 1879, *Halácsy s.n.* (B, F, JE, PR, WU); Raxalpe, auf der Schütt der Griesleiten, 47º40'N, 15º44'E, Aug 1871, *Halácsy s.n.* (PR, W, WU). Salburg: Radstädter Tauern, Lantschfeldgraben im Taurachwinkel, 47º15'N, 13º33'E, Aug 1916, *Vierhapper s.n.* (W); Hauptkamm, Höcknerin im Lantschfeldgraben des Taurachwinkels, 47º15'N, 13º33'E, Sep 1916, *Vierhapper s.n.* (W); Dachteingebiet, nächst der Kolpinghütte, 47º29'N, 13º32'E, 17 Aug 1916, *Vetter s.n.* (UPS). **Styria:** Dachstein-Südwand, 47º27'N, 13º36'E, Aug 1957, *Baschant s.n.* (MA). **Tyrol:** Aufstieg vom Hallerangerhaus zum Sunsiger, 47º21'N, 11º28'E, 28 Aug 1950, *Bot. Exk. 740* (HBG); Dorferalpe in Praegrasen, 47º3'N, 12º37'E, 7 Aug 1865, *Gander s.n.* (JE, MO); Pettneu, in den Alpen, Weg zur Feuerspitze, 47º12'N, 10º22'E, 17 Jul 1928, *Gross s.n.* (US); vallis Gleirsch, 47º10'N, 11º5'E, *Hellweger s.n.* & *Huter* (B, C, F, GH, HBG, K, L, NY, O, PR, W, WU); Tyrol sept. ad pedem mt. Tribulaun in Obernberg, 46º59'N, 11º22'E, Aug 1885, *Huter s.n.* (PR); Höttingergraben bei Innsbruck, 47º18'N, 11º22'E, 1868, *Kernu s.n.* (WU); Karwendel, 47º25’N, 11º28’E, Jun 1930, *Michaelis s.n.* (JE); Halltal, 47º19’N, 11º29’E, 5 Jul 1936, *Milne-Redhead 2316* (K); Häufig am Innsbruck, 47º15’N, 11º23’E, Jul 1881, *Murr s.n.* (B); Alpes de Stubai, Vallée de Gschnitz, près du sentier de Gschnitz au Innsbrucker Hütte, au sud de Kalkwand, 47º3’N, 11º22’E, 19 Aug 1985, *Podlech 42147* (B, C, H, L, MA); Stubaier Alpen, Fulpmes, Aufstieg Froneben bis Schlicker Alm, 47º9’N, 11º18’E, 26 Aug 1990, *Polatschek s.n.* (B, C); West Tirol, im Gmeiertal zwischen Pfunds (Oberinntal) und Paznaun, 47º0’N, 10º20’E, 18 Aug 1906, *Handel-Mazzetti s.n.* (WU); zwischen dem Groder und der Brücke über den Ködnitz Bach, 47º0’N, 12º40’E, 19 Jul 1905, *Handel-Mazzetti s.n.* (WU); Nord-Tirol, am Gipfel der Marchreisenspitze in Stubai im Gerölle, 47º10’N, 11º18’E, 25 Sep 1902, *Handel-Mazzetti s.n.* (W); Nörd-Tirol, Sonnwendgebirge bei Jenbach, Spieljoch gegen Osten, 47º28’N, 11º47’E, 18 Aug 1904, *Handel-Mazzetti s.n.* (W); Hohe Tauern, im Kleiner Iseltale bei Trägraten, 47º10’N, 12º30’E, 7 Aug 1923, *Vetter s.n.* (UPS); Nordtirol, Sonnwendgebirge, 47º28’N, 11º47’E, Jul 1905, *Vierhapper s.n.* (W); Nordtirol, Stubaier Alpen, Peilspitze nordwestl, Trins im Gschnitztal, 47º6’N, 11º23’E, 23 Aug 1971, *Wagenitz 1738* (GOET). **Upper Austria:** Totes Gebirge, Prielgruppe, Klinserscharte, 47º43’N, 14º3’E, 8 Aug 1989, *Hörandl 1739* (W); ad pedem meridionalem montis Dachstein, 47º28’N, 13º36’E, Sep 1905, *Hayek s.n.* (L, LE, W).

FRANCE. Auvergne-Rhône-Alpes: Isère, Col de l´Arc, près Grenoble, 45º4’N, 5º37’E, 15 Jun 1884, *Beaudouin s.n.* (JE); Isère, Mont Chamoux, 45º32’N, 6º12’E, Jul 1897, *Bernard s.n.* (HBG); Haute-Savoie, Mt. Vargy, 46º1’N, 6º30’E, 26 Jul 1880, *Bernét s.n.* (NY); Les Fiz, 45º59’N, 6º41’E, 7 Sep 1909, *Bouchard s.n.* (GB, JE, L, MA, MO, US); Savoie, Maurienne, Saint-Sorlin-d´Arves, 45º13’N, 6º14’E, 31 Jul 1852, *Didier s.n.* (BM, HBG, JE, L, LE, MPU); Savoie, near Col du Mont Cenis, just S of barrage in the Lake, 45º14’N, 6º55’E, 16 Jul 1954, *Jacobs 3893* (L); Haute-Savoie, Col d´Isoard, 44º14’N, 6º26’E, 11 Aug 1912, *Jeanpert s.n.* (F); Isère, Mont Sineipy, près de la Mure, 44º54’N, 5º47’E, 6 Jul 1890, *Moutin 475* & *Bernard* (FI, MPU); Haute-Savoie, entre le Col de Gers et Col de Platé, 45º57’N, 6º43’E, 8 Aug 1908, *Palibine s.n.* (LE); Savoy, Vallée de Larocheur, en Maurienne, 45º13’N, 6º30’E, 27 Aug 1856, *Perrier de la Bathie s.n.* (GH); Savoie, Dauphiné, Le Briançonnais, Serre Chevalier, Rocher Blanc, 45º14’N, 6º6’E, 25 Jul 1959, *Segelberg s.n.* (S). **Provence-Alpes-Côte d'Azur:** Hautes-Alpes, Lautaret, 45º2’N, 6º24’E, 16 Aug 1923, *Chandler s.n.* (BM); Hautes-Alpes, Ceillac, prés du torrent de Vallon, 44º40’N, 6º46’E, 8 Aug 1984, *Charpin 19140* (G); Alpes-Maritimes, Saint Martin d´Entraunes, 44º8’N, 6º45’E, 11 Aug 1982, *Charpin AC17607* & *Salanar* (G, LE); Basses-Alpes, Barcelonnette, col de Valgelage, 44º23’N, 6º39’E, 2 Aug 1897, *Coste s.n.* (MPU); Hautes-Alpes, Montagne des Trois-Évêchés, au-dessus du village de Goleffe, comm. du Villard-d´Arène, cant. de La Grave, arr. de Briançon, 44º17’N, 6º32’E, 15 Sep 1856, *De Valon s.n.* (B, G, GB, GH, L, LE, PR); Hautes-Alpes, Savoie, crete du Galibier, 45º3’N, 6º24’E, 23 Jul 1955, *Dettmann s.n.* (B); Hautes-Alpes, Monétier-les-Bains, 44º58’N, 6º30’E, 22 Aug 1908, *Faure s.n.* (L); Alpes-Maritimes, Mont Mounier bei Beuil, 44º8’N, 6º58’E, 4 Aug 1931, *Fiedler s.n.* (B); Vaucluse, Mont Ventoux, 44º10’N, 5º16’E, 1852, *Godron s.n.* (UPS); Hautes-Alpes, Villar d´Arêne, 45º2’N, 6º20’E, 1851, *Grenier s.n.* (UPS); Hautes-Alpes, Briançon, La Combe au Col d´Isoard, 44º14’N, 6º26’E, 1 Jul 1867, *Guillon s.n.* (UPS); Hautes-Alpes, La Monta près Abriès, Vallon de la Caillante, lac Eugourgeau, 44º46’N, 6º59’E, 19 Aug 1913, *Jeanpert s.n.* (F); Hautes-Alpes, La Monta près Abriès, Torrent de Bouchou, 44º46’N, 6º59’E, 18 Aug 1913, *Jeanpert s.n.* (F); Col d´Isoard, 44º14’N, 6º26’E, 15 Aug 1912, *Jeanpert s.n.* (F); Hautes-Alpes, Col du Lautaret, western slopes of Pyramide de Laurichard, 45º2’N, 6º24’E, 22 Jul 1959, *Klimmek s.n.* (HBG); Hautes-Alpes, La Grave, 45º2’N, 6º18’E, 10 Jul 1861, *Mathonnet s.n.* (JE, LE, MPU, NY, PH); Hautes-Alpes, Gap, Mont Aurouse, 44º38’N, 5º53’E, 30 Aug 1871, *Reverchon s.n.* (GH); Alpes-Maritimes, Montagne de Rio Freddo, 44º7’N, 7º36’E, 15 Jul 1886, *Reverchon s.n.* (US); Vaucluse, sommet du Ventoux, 44º10’N, 5º16’E, 12 Jul 1877, *Reverchon s.n.* (JE, MPU); Basses-Alpes, Aurent, près Annot, 44º2’N, 6º42’E, 7 Jul 1887, *Reverchon 255* & *Derbez* (MA); Alpes-Maritimes, Mont Mounier bei Beuil, Val Demant, 44º8’N, 6º58’E, 4 Jul 1931, *Ronniger s.n.* (NY); Alpes-Maritimes, Haute-Tinée, Hänge ober Bousiéyas an der Pass-Straße zum Col de Restefond, ca. 9 km NW St. Etienne-de-Tinée, 44º20’N, 6º48’E, 10 Jul 1998, *Schneeweiss s.n. & al.* (WU); Hautes-Alpes, am Weg vom Col du Lautaret im oberste Romanche-Tal, 45º2’N, 6º24’E, 14 Aug 1961, *Spanowsky s.n.* (JE). **GERMANY. Bavaria:** Wimbach Thal, prope Berchtesgaden, 47º37’N, 13º0’E, 29 Jul 1858, *Ball s.n.* (US); Mt. Schneeberg, 47º29’N, 13º39’E, Aug 1884, *Beck s.n.* (W); Aug 1881, *Beck s.n.* (WU); Tölz, Benediktenwand, 47º39’N, 11º27’E, 15 Aug 1894, *Bornmüller s.n.* (B, JE); Wimbachtal, W. sup. Watzmann, 47º33’N, 12º55’E, 20 Jul 1915, *Bornmüller s.n.* (B); Wetterstein gebirge Schachenplan, 47º25’N, 11º6’E, 14 Aug 1950, *Bot. Exk. 447* (HBG); Berchtesgadener Alpen, Wimbachtal, bei der Kirche, 47º32’N, 12º53’E, 9 Aug 1963, *Lippert s.n.* (MA); Wettersteingebirge, westl. Thörlspitze, 47º25’N, 11º5’E, 14 Aug 1947, *Mäckel s.n.* (HBG); Oberstdorf, am Nebelhorn, 47º25’N, 10º20’E, Jul 1890, *Schmidt s.n.* (HBG); Bayerische Alpen, Karwendel, Brunnensteinspitze, 47º24’N, 11º17’E, 24 Jul 1957, *Scholz s.n.* (B). **ITALY. Aosta Valley:** Cogne, Val de Grauson, 45º38’N, 7º23’E, Aug 1878, *Buchenau s.n.* (GH); Courmayeur, salendo al Col de Checrouit, 45º47’N, 6º56’E, 20 Aug 1916, *Fiori s.n.* (FI); prope Lac de Combal, 45º46’N, 6º51’E, 11 Aug 1849, *Parlatore s.n.* (FI); Gran Paradiso, Gran Lauson nara Cogne, 45º34’N, 7º16’E, 30 Jun 1965, *Strid s.n.* (S). **Friuli-Venecia Julia:** Udine province, Kanantal, Pontebba-Chinsaforte, 46º30’N, 13º18’E, 18 Jul 1913, *Ronniger s.n.* (BM). **Lombardy:** Sondrio, Valfurva, pr. St. Catarina, 46º24’N, 10º29’E, 10 Aug 1870, *Ball s.n.* (GH, US); Monte Braulio, 46º31’N, 10º23’E, 10 Aug 1904, *Camperio s.n.* (LE); Sondrio, partie inferieure du valle Zebrù, 46º28’N, 10º27’E, 29 Jul 1887, *Cornaz s.n.* (MA). **Piedmont:** Val de Cogne, 45º36’N, 7º21’E, 13 Aug 1866, *Ball s.n.* (US); environs de l´hospice de Valdobbia, 45º49’N, 7º57’E, 26 Aug 1858, *Billot s.n.* (LE, MPU); Monte Rosa, 45º56’N, 7º52’E, 23 Jul 1847, *Dufft s.n.* (JE); Grasjon, 28 Jul 1862, *Haussknecht s.n.* (JE); M. Chavanisse, 27 Jul 1862, *Haussknecht s.n.* (JE); Turin, Colle Sestrière, 44º57’N, 6º52’E, Jul 1864, *Rostan s.n.* (US); Parque Nacional del Gran Paradisso, Valle del Orco, del Gran Piano de Moasca a la Bocheta del Ges, 45º25’N, 7º28’E, 9 Aug 1952, *Sappa s.n.* & *Galiano* (MA); Valle di Jura, Moncenisio, rupi Petro l´Ospizio, 45º12’N, 6º59’E, 6 Aug 1914, *Vignolo-Lutati s.n.* (GH). **Trentino-Alto Adige/Südtirol:** Bolzano, Selva di Val Gardena, Dantercepies, hauteur de Wolkenstein, 46º33’N, 11º45’E, 17 Aug 1986, *Buggenhout s.n.* (B, C, H, MA, MPU); Val Gardena, Coronella, Gruppo del Catinaccio, 46º27’N, 11º37’E, 18 Aug 1932, *Chiarugi s.n.* (FI); monte du Stelvio, 46º35’N, 10º32’E, 31 Jul 1890, *Cornaz s.n.* (JE, LE); valle Sulden, 46º31’N, 10º35’E, 1884, *Hackel s.n.* (US); Brenner, Schelleberg, 46º57’N, 11º26’E, Aug 1887, *Huter s.n.* (JE); Sulden, 46º31’N, 10º35’E, 9 Jul 1938, *Ronniger s.n.* (BM); Schlern, 46º30’N, 11º34’E, Jul 1890, *Schmidt s.n.* (HBG); Wolferkogl bei Luttach, 46º56’N, 11º55’E, 22 Aug 1894, *Treffer s.n.* (JE); Riedberg bei Gossensass [Colle Isarco], 46º56’N, 11º26’E, 22 Aug 1904, *Handel-Mazzetti s.n.* (W); Val Gardena, im Langental in Gröden, 46º34’N, 11º40’E, 3 Aug 1903, *Vetter s.n.* (UPS); Ahrntal, im Grus gegen den Gipfel des Schönberg bei Luttach, 46º58’N, 11º52’E, 29 Aug 1927, *Vierhapper s.n.* (W). **Veneto:** Belluno, Drei Zinnen (Tre Cime di Lavaredo), 46º37’N, 12º18’E, 16 Aug 1964, *Raabe s.n.* (HBG). **MONTENEGRO. Vasojevići:** Kom Vasojevićki, 42º41’N, 19º39’E, Aug 1906, *Rohlena s.n.* (HBG, PR); montium Ljubonicka planina "dict. Loco Jankova pluga" nominato, 42º45’N, 19º55’E, Aug 1914, *Vandas s.n.* (PR). **SWITZERLAND. Bern:** Rauflihore spitze [Bluttlighore], 46º31’N, 7º728’E, 12 Sep 1903, *Tranzschel s.n.* (LE). Fribourg: versant N des Morteys, 46º34’N, 7º14’E, 3 Aug 1883, *Castella s.n.* (US). **Geneva:** Genève, 46º12’N, 6º9’E, 1839, *Grenier s.n.* (UPS). Glarus: Glernisch, 46º59’N, 8º59’E, 18 Aug 1846, *Dufft s.n.* (JE). **Grisons:** Arosa, beim Arlenwald, 46º47’N, 9º40’E, 8 Aug 1913, *Beger s.n.* (B); Puschlav auf dem Sassalbo, 46º20’N, 10º5’E, 20 Aug 1964, *Eckardt 615* (B); Samedan, Piz Padella, 46º31’N, 9º50’E, 6 Aug 1935, *Heimans s.n.* & *Jansen* (L); Engadin, an der Ofenpass-Strasse unter Ova Spin hinter Zernez, 46º41’N, 10º8’E, 23 Jul 1936, *Koch s.n.* (NY); Averstal, Val Bergalga, nördl. Teil südl., Avers-Juppa, 46º27’N, 9º32’E, 26 Jul 1990, *Lewejohann s.n.* (GOET); Silvretta, Heildelberg Hütte am Piz Davo Sassé, 46º54’N, 10º16’E, 12 Aug 1954, *Raabe s.n.* (HBG); Calanda über Chur (Coira), 46º54’N, 9º28’E, Sep 1917, *Schröter s.n.* & *Braun-Blanquet* (C, GH, O, PR, W); Alp Sesvenna und Scarl, 46º42’N, 10º20’E, 10 Aug 1949, *Simon s.n.* (GB); Passhöhe des Ofenpasses, 46º38’N, 10º17’E, 29 Jul 1966, *Simon s.n.* (C, H); Chur, Gromserkopf [Gromser Chopf], près de la Fürstenalp, près de Coire, 46º52’N, 9º36’E, 15 Aug 1888, *Stebler 114* & *Schröter* (C, LE, NY); Graubunden, Zerner, M. Buffalora, 46º37’N, 10º15’E, 27 Jul 1923, *Thaysén s.n.* (H); Lango de Spoor bij Bernina-häuser, 46º24’N, 10º0’E, Jul 1929, *Soest s.n.* (L); Val Plavna, 46º42’N, 10º13’E, Jul 1932, *Jansen s.n.* (L). **Lucerne:** Mt. Pilato, 46º58’N, 8º15’E, *Baching s.n.* (HBG); Obwalden, Pilatus vid Ringfluhe, 46º58’N, 8º15’E, 20 Sep 1812, *Wahlenberg s.n.* (UPS). **Ticino:** Lukmanierpass, Campo Solario, 46º33’N, 8º48’E, 20 Jul 1912, *Beger s.n.* (B). Tyrol: in alpibus Leontinis, 8 Aug 1954, *Duty s.n.* (JE). **Valais:** convalle alpina Nicolai Thal prope Zermatt, 46º11’N, 7º48’E, Aug 1845, *Ball s.n.* (GH); Gemmi, 46º23’N, 7º36’E, 1851, *Bamberger s.n.* (B, JE, L, MO, PR); Massif du Mont Rose, moraines du glacier de Gorner, 45º58’N, 7º48’E, 31 Aug 1916, *Beauverd s.n.* (NY); supra Zinal, 46º8’N, 7º37’E, 13 Aug 1887, *Bernoulli s.n.* (MA, MPU); Saastal, Wege nach Plattjen, 46º6’N, 7º55’E, 15 Jul 1945, *Bührer s.n.* (UPS); L´Erié, Grand Chavalard, chemin du Lac de Fully, 46º10’N, 7º6’E, 13 Jul 1990, *Castroviejo 11213 SC & al.* (MA); Zermatt, Schwarzsee, 46º39’N, 7º16’E, 11 Aug 1894, *Clarke 48718* (K); Zermatt, moraene van de Findelenglesscher, 46º6’N, 7º51’E, 29 Jul 1922, *Danser 5050* (L); Val des Dix, Pas du Chat, extrémité sud du Lac des Dix, 46º27’N, 7º12’E, 1 Aug 1971, *Dutoit s.n.* (HBG, UPS); Verbier, 46º5’N, 7º12’E, 10 Aug 1968, *Eckardt 1056* (B); Mattmark, 46º2’N, 7º57’E, 1901, *Goethart s.n.* & *Jongmans* (L); Gornergletscherns ändmorän, 46º0’N, 7º44’E, 27 Jul 1883, *Huld s.n.* (H); Zermatt, moraine van de Findelenglesscher, 46º6’N, 7º51’E, Aug 1937, *Jansen s.n.* (L); in valle Binn, 46º21’N, 8º11’E, *Lagger s.n.* (UPS); Westseite des Trifthorn östl. Saas-Fee, 46º6’N, 7º55’E, 13 Jul 1981, *Lewejohann* *s.n.* (GOET); Gornergletscher, 45º58'N, 7º49'E, Aug 1894, *Linder s.n.* (MA); Saasthal, 46º8'N, 7º56'E, 15 Aug 1872, *Morthier s.n.* (JE); Saas-Fee und der Gletscheralpen, 46º6'N, 7º55'E, 28 Jul 1910, *Poeverlein s.n.* (LE); Simplon, an der Strasse nördlich der Passhöhe, 46º15'N, 8º1'E, 28 Jul 1906, *Handel-Mazzetti s.n.* (WU); Portail de Fully, 46º9'N, 7º5'E, 21 Jul 1874, *Vigener s.n.* (B); Zermatt, über dem Riffelberg, 45º59'N, 7º45'E, Aug 1901, *Wolf s.n.* (B, C, GH, JE, L, LE, MA, O, PR, S, US, W). **Vaud:** Anzeindaz, Alpes de Bex, eboulis de Diablerets, 46º18'N, 7º11'E, 10 Aug 1880, *Chenevard s.n.* (JE); Alpes de Châteaux-d´Oex, à la Hausseresse et sous le rocher des Tours, 46º28'N, 7º7'E, *Leresche s.n.* (F, K, JE).

Notes—Jonsell (1980), who probably followed Paunero (1950), cited *Trisetum distichophyllum* from the eastern Pyrenees. Unfortunately, this record corresponds to material collected by Rivas Mateos which labelling is questioned by many authors (i.e. Rothmaler, 1935, Benedí & Sáez, 1996, Bolòs & Vigo 2001). After the study of the herbarium material of this species, we found that the most western populations of *T. distichophyllum* are found in the French Alps.

Jávorka (1919) described a new species from the mountains of northern Albania, *T. albanicum* Jávorka, separating it from *T. distichophyllum* because of its flat, less rigid, and green leaves with less marked nerves, less puberulous surfaces and margins always with hairy to ciliate, more contracted panicles, and shorter callus hairs. Later, Hayek (1932) combined it as a subspecies of *T. distichophyllum* and Rohlena (1942) published a new record of the subspecies from eastern Montenegro. We consider this subspecies a synonym of *T. distichophyllum*, not finding significant differences from the rest of the material to justify separation. The specimens studied from the Balkans have greyish to greenish leaves, flat to conduplicate basal and top leaf-blades, and variable indumentum. Comparing the shape of the panicles, we have observed that it is quite variable in the specimens from Albania and the Alps, while the length of the callus indumentum in the Alps specimens is similar to that in the Albanian ones [(1.5–)2.2–3.7(–4.5) mm, and 2.5–3 mm length, respectively].

Beauverd (1934) described a new subspecies from the French Alps, *T. distichophyllum* subsp. *delphinense* Beauverd, characterized by its apically and irregularly torn-toothed ligules with ciliate margins, lower glumes with one or two lateral rudimentary nerves, and upper glumes with an acuminate or muticous apex. We consider this subspecies a synonym of *T. distichophyllum*. The material of the species we studied is highly variable, having ligules 0.5–1 mm long, with a laciniate to slightly laciniate apex, rarely slightly lobulated, lower glumes with a variable number of nerves, and upper glumes with an acuminate to long acuminate apex, sometimes acute. Beauverd also differentiated this subspecies by the inrolled or conduplicate leaves, contrasting it with *T. argenteum*, but these characters are also present in *T. distichophyllum*.

2. TRISETUM ARGENTEUM (Willd.) Roem. & Schult., Syst. Veg. 2: 665. 1817. *Avena argentea* Willd., Enum. Pl.: 125. 1809. *Trisetum distichophyllum* var. *argenteum* (Willd.) Ducommun, Taschenb. Schweiz. Bot.: 858. 1869. *Trisetaria argentea* (Willd.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 382. 1996.—TYPE: [unknown locality and collector] [lectotype, here designated, B-W-02187-020 (image!)].

T. argenteum var. *parviflorum* Parl., Fl. Ital. 1: 264. 1850.—TYPE: ITALY. Bergamo, Monte Resegone, 45º51’N, 9º28’E, 1844, *L. Rota s.n.* [lectotype, here designated, FI!; isolectotype, BERG-31548 (image!)].

Herbs (14.7–)23.3–35.4(–36.6) cm tall, short rhizomatous, loosely tufted, culms (0.2–)0.3–0.5 mm diam., glabrous; nodes (3–)4–5(–6), concentrated in lower part of the culm, glabrous. Basal leaf-sheaths puberulous, with hairs up to 0.2 mm long, decaying into fibers, brownish to yellowish, sometimes greenish; basal leaf-blades (1.2–)2.4–3.8(–6.7) cm long × (0.9–)1.2–1.5(–1.7) mm wide, flat to enrolled, pubescent to slightly puberulous adaxially and abaxially, sometimes glabrous, with hairs (0.05–)0.1(–0.8) mm long, greyish to greenish, sometimes yellowish to brownish; top culm leaf-sheaths (4–)6–8.7(–9) cm long, shorter than the internodes, sometimes longer or almost equal, glabrous, without cilia, or sometimes with; top culm leaf-blades (1.7–)2.2–3.5(–6) cm long × 0.9–1.5(–1.8) mm wide, flat to conduplicate, rarely parallel to the culm, glabrous to pubescent adaxially, puberulous to slightly puberulous abaxially, sometimes with short hairs on the margins up to 0.1 mm long, greenish to greyish; inner collar region glabrous, with scattered hairs or slightly puberulous on the margins, with hairs (0.05–)0.2–0.8(–1) mm long; ligules 0.3–0.5(–0.7) mm long, pubescent, rarely glabrous or with some scattered hairs on the surface, apex laciniate with hairs up to 0.15 mm long. Basal node of the panicle glabrous. Panicles (3.7–)5.4–7(–7.6) cm long × (0.9–)1.2–2.3(–3.2) cm wide, oblong to elliptic in outline, sometimes narrowly elliptic to lanceolate, lax; rachis glabrous, rarely slightly puberulous or pubescent, with hairs up to 0.08 mm long; longest basal branches (0.4–)0.8–1.3(–2.2) cm. Spikelets (4.8–)5.6–6.5(–8) mm long × (1.4–)2–4(–5.7) mm wide, (1–)2–3-flowered; pedicels (2.2–)3.2–4.2(–5.4) mm, glabrous to slightly pubescent, with hairs up to 0.1 mm long. Glumes unequal [ratio -- lower glume length/upper glume length = (0.59–)0.65–0.78(–0.87)]; lower glume (2.7–)3.5–4.3(–5.7) mm long × 0.5–0.8(–1.4) mm wide, narrowly to broadly lanceolate, sometimes narrowly elliptic or linear (ratio -- lower glume width/lower glume length = (0.14–)0.16–0.21(–0.25), acuminate, sometimes acute, 1-nerved, glabrous, sometimes with short hairs up to 0.1 mm long from the center to the upper part of the nerve, greenish to yellowish, sometimes surrounded by purple on the laterals and upper part; upper glume (4.6–)5–6(–7.3) mm long × (1.2–)1.4–1.6(–2) mm wide, narrowly elliptic or elliptic to narrowly lanceolate or oblong, rarely oblanceolate (ratio -- upper glume width/upper glume length = (0.22–)0.24–0.3), acuminate to long acuminate, rarely acute, 3-nerved, glabrous, with short hairs up to 0.08 mm long from the middle to the upper part of the central nerve, greenish to yellowish on the central part, usually surrounded by purple; rachilla segment between first and second floret (0.6–)1.1–1.3(–1.4) mm long, with hairs (1–)1.7–2.5(–3.4) mm long; rachilla segments to sterile floret 1.3–1.7(–2) mm long, with hairs (0.8–)1.2–1.6(–2) mm long. Lemmas (4–)4.4–5.2(–6.5) mm long × 0.5–0.8(–1.4) mm wide, broadly lanceolate to oblong or elliptic, rarely narrowly lanceolate [ratio -- lemma width/lemma length = (0.19–)0.25–0.33], glabrous to scabridulous, with hairs up to 0.1 mm long on the central and upper part, greenish on the central part, sometimes yellowish, usually surrounded by purple; apical teeth without or 0.1–0.3(–0.4) mm long, with aristules (0.1–)0.3–

0.5(–0.7) mm long; awn (3.7–)5.2–6.4(–7.2) mm long, inserted (1.6–)1.8–2.4(–3.2) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.35–)0.42-0.46(–0.5)], geniculate and slightly twisted near the base, with very short adpressed hairs up to 0.1 mm long; callus (0.2–)0.3 mm long, oblong to elliptic, with hairs (0.7–)1.4–1.8(–2.6) mm long. Palea (3.5–)3.8–4.2(–5.8) mm long × (0.9–)1–1.3(–1.4) mm wide [ratio -- palea length/lemma length = (0.73–)0.79–0.89(–0.98)], narrowly elliptic to elliptic, glabrous or with hairs from the middle till the upper part of the outer edges; keels with short antrorse hairs mostly on the upper part, rarely glabrous, ending in teeth 0.1–0.3(–0.4) mm long. Lodicules (0.4–)0.5–0.8(–0.9) mm long, with apex shortly and irregularly lobate. Anthers (1.5–)1.9–2.3(–2.4) mm long. Ovary (0.4–)0.6–0.8(–2.3) mm long, glabrous. Caryopsis 2–2.7 mm long × 0.4–0.7 mm wide. Figure 2.

Chromosome Number—2*n* = 28 (Beuret, 1974; Lippert, 2006).

Phenology—Flowering from June to September.

Distribution and Habitat—*Trisetum argenteum* occurs in eastern Alps, from Austria and Italy, reaching to Slovenia; at 200–2330 m elevation; around rocks and pebbles, in calcareous soils. Figure 4.

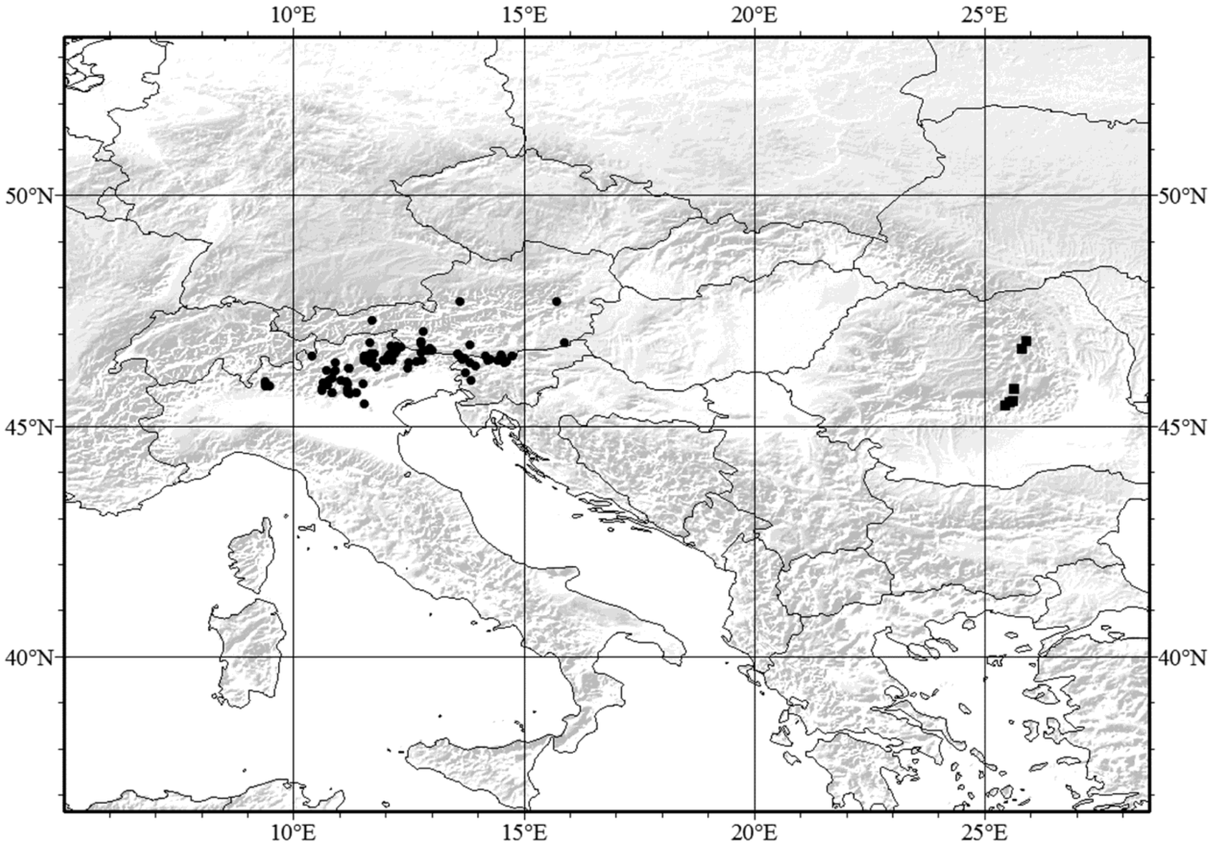

Figure 4. Distribution of *Trisetum argenteum* (dots) and *T. macrotrichum* (squares).

Specimens Examined—**AUSTRIA. Carinthia:** Loiblpass, Tschanko-Fall, 46º26’N, 14º16’E, 12 Jul 1954, *Lohmar s.n.* (HBG); in valle Bartolograben, prope Saifnitz, 46º34’N, 13º34’E, 24 Jul 1914, *Aust s.n.* (GB); Volaia, 46º37’N, 12º53’E, 21 Sep 1857, *Ball s.n.* (K, US); Polinik Gipfel, 46º37’N, 12º58’E, 12 Aug 1952, *Doppelbaur s.n.* (M); in glareosis vallis Loibel

[Loibl], 46º26’N, 14º16’E, Aug 1883, *Jabornegg s.n.* (B, BM, C, F, FI, MO, NY, PR, W, WU); Ostkarawanken, Petzen, am Hauptweg zw. Berg- u. Talstation der Gondelbahn, 46º30’N, 14º44’E, 13 Aug 1996, *Kalheber 96-1385* (M); Karawanken, Hochobir-Süd, Auffahrt zur Eisenkappler Hütte, Seitentälchen unterh, Berghaus Fladung, 46º29’N, 14º31’E, 20 Aug 1991, *Leute s.n.* & *Kosch* (WU); Carinthia, 46º45’N, 13º49’E, Aug 1878, *Marchesetti s.n.* (W); Karawanken, Zell-Pfarre, am Hochobir, 46º34’N, 13º34’E, 11 Aug 1949, *Merxmüller 5533* & *Wiedmann* (M); Sanntaler Alpen, Sulzbach, 47º41’N, 13º37’E, 2 Sep 1904, *Hayek s.n.* (GB); Karnische Alpen, Sittmoosergraben bei Mauthen, 46º41’N, 12º57’E, 30 Aug 1926, *Vierhapper s.n.* (W); Petzen-Alp, ober Ritschberg, 46º30’N, 14º44’E, *Welden s.n.* & *Freyer* (B, JE, UPS, WU); Karawanken, bei Feistritz im Rosental nahe der Kirche, 46º31’N, 14º10’E, 16 Jul 1956, *Wagenitz 1738* (GOET). **Lower Austria:** Raxer Alpen, 47º42’N, 15º43’E, *Hausmann s.n.* (B). **Styria:** Sulzbach, 46º48’N, 15º53’E, *Unger s.n.* (M); prope refugium alpinum "Okreselhütte" in alpibus Lithopolitanis (Steiner-sive Sanntaler Alpen), 46º22’N, 14º34’E, Aug 1904, *Hayek s.n.* (BM, GB, H, L, O, W). **Tyrol:** juxta Lienz, 46º49’N, 12º46’E, 9 Sep 1854, *Ball s.n.* (F, US); pr. Lienz, Kerschbaumeralpe, 46º49’N, 12º46’E, 19 Aug 1872, *Gander s.n.* (JE); Sep 1855, *Molendo sn.* (M); ober Tres im Nonsberg an steinigen Stellen, 47º17’N, 11º42’E, 26 Aug 1902, *Handel-Mazzetti s.n.* (W); Kerschbaumer bei Lienz, 46º46’N, 12º46’E, 30 Jul 1883, *Witting s.n.* (B). **ITALY: Friuli-Venecia Julia:** Provincia di Udine, prope Forno Avoltri, 46º35’N, 12º46’E, Sep 1857, *Ball s.n.* (MO); Udine province, vallée de la Cimoliana [Cimolais], Rifugio Pordenone, 46º22’N, 12º29’E, 7 Aug 1979, *Charpin 15786* (GOET, MA); Prov. Udine, Alpi Carniche, ander Strasse Misurina-Tolmezzo, im Tal des Tagliamento bei Forno di Sotto, 46º23’N, 12º40’E, 16 Jul 1992, *Lippert 26158* (M); Prov. Pordenone, Prealpi Carniche, Spalti di Toro range N Cimolais, 46º15’N, 12º28’E, 11 Sep 2012, *Müller 10983* (JE); Raibl-Mangart, 46º26’N, 13º39’E, *Vierhapper s.n.* (W). Lombardy: monte Campione prope Lecco, 45º51’N, 9º23’E, 8 Sep 1857, *Ball s.n.* (US); Lecco province, montis Grigna, versus Lacum Larium [Como Lake], 45º57’N, 9º23’E, 15 Sep 1855, *Ball s.n.* (US); Como province, Grigna meridionale, Canale Porta, 45º55’N, 9º23’E, 17 Jul 1950, *Berger s.n.* (M); Alpes de Lecco, montant de Ballabio à la Grigna, 45º53’N, 9º25’E, 16 Aug 1859, *Leresche s.n.* (JE, L); Mt. Braulio, 46º31’N, 10º23’E, 3 Aug 1902, *Longe s.n.* (MPU); Como, Grigna Meridionale, "Piana delle Groppe", 45º56’N, 9º23’E, 27 Jul 1965, *Simon s.n.* (HBG, S). **Trentino-Alto Adige/Südtirol:** Grigna Meridionale, Cresta Segantini, 46º12’N, 10º42’E, 12 Aug 1952, *Reznik s.n.* (M); Pusteria, Landro, 46º37’N, 12º13’E, *Auperdorfer s.n.* (PR). Montis Schlehren supra Ratzes, 46º30’N, 11º34’E, 23 Aug 1869, *Ball s.n.* (US); Val di Fassa, 46º26’N, 11º42’E, 27 Aug 1860, *Ball s.n.* (US); supra Val Rendena, montis Brenta, 46º10’N, 10º53’E, 4 Sep 1858, *Ball s.n.* (GH); supra Val Selva, prope jugum Crostè [Cima Groste], 46º11’N, 10º54’E, Aug 1875, *Ball s.n.* (US); Trento prov., in sinu Val Selva prope Malè, 46º21’N, 10º54’E, 18 Aug 1860, *Ball s.n.* (US); Seiseralp, 46º31’N, 11º32’E, 24 Aug 1860, *Ball s.n.* (F, US); Trento province, in monte Scanuppia, 45º57’N, 11º9’E, 11 Aug 1860, *Ball s.n.* (MO, US); Giudicaria, Monte Tombea, 45º48’N, 10º37’E, Jul 1952, *Baschant s.n.* (B, JE, MA); Val dei Concei (W. van het Gardameer), 45º54’N, 10º43’E, 9 Aug 1959, *Boom s.n.* (L); Monte Cristallo, 46º34’N, 12º11’E, 23 Aug 1896, *Bornmüller s.n.* (B, JE); in rupestribus vallis Prags, 46º43’N, 12º7’E, 20 Aug 1896, *Bornmüller s.n.* (B, BM, C, F, FI, K, L, MO, NY, PR, S, W, WU); Bolzano, Pustaria, Geierwände bei Schenderbach-Landro, 46º37’N, 12º13’E, 20 Aug 1896, *Bornmüller s.n.* (JE); Monte Cristallo, Val Fonda, 46º34’N, 12º11’E, 23 Aug 1896, *Bornmüller s.n.* (B); Monte Bondone, 45º59’N, 11º1’E, *De Sardagna s.n.* (W); Bocca di Brenta, 9 Aug 1884, *De Sardagna s.n.* (W); Bolzano province, Tiers östlich Bozen, Südseite des Tschafon, 46º28’N, 11º31’E, 21 Jul 1984, *Dersch 4488* (GOET); Bozen, Daumkofel (Prags), 0.6 km SSE Daumkofel, 12º8’N, 46º41’E, 26 Jul 2003, *Hilpold s.n.* & *Kiebacher* (W); Pusteria, Landro, 46º37’N, 12º13’E, 27 Jul 1869, *Huter 1171* (B, MPU); Bolzano, Schlern, 46º30’N, 11º34’E, 15 Jul 1967, *Huter s.n.* (B); Pusteria, valle Virchlein, Sexten, 46º42’N, 12º20’E, 23 Aug 1878, *Huter s.n.* (GB); Bad Ratzes, 46º30’N, 11º34’E, 3 Aug 1893, *Jaap s.n.* (HBG); Val d'Adige [Etschtal], Salurn, 46º14’N, 11º12’E, 2 Jun 1952, *Merxmüller 5534* & *Wiedmann* (M); Fassatal valley, Moena, 46º22’N, 11º39’E, Jul 1912, *Paul s.n.* (L); vallis di Bono, 46º1’N, 10º50’E, Jul 1889, *Porta s.n.* (JE); Ledro, 45º53’N, 10º44’E, 2 Aug 1883, *Porta s.n.* (B, G, MA, WU); Val di Ledro, 45º53’N, 10º44’E, 20 Jul 1881, *Porta s.n.* (JE); vallis di Bono, 46º1’N, 10º50’E, Jul 1892, *Porta s.n.* (M); circa pagum Cologna, 45º55’N, 10º38’E, Jul 1896, *Porta s.n.* (MPU); San Martino di Castrozza, 46º16’N, 11º48’E, 5 Aug 1895, *Saint-Lager s.n.* (G, L, NY); pr. Salurn, 46º14’N, 11º12’E, *Sauter s.n.* (W); Ratzes, 46º30’N, 11º34’E, 13 Jul 1903, *Schultz s.n.* (B); Bade Ratzes, 46º30’N, 11º34’E, 6 Jul 1896, *Schultz s.n.* & *Schultz* (B); Prov.de Trento, Calliano-Folgaria, 45º54’N, 11º10’E, 19 Aug 1960, *Segelberg s.n.* (S); Trento province, Ost for Cima Valdritta pa Monte Baldo, 45º43’N, 10º50’E, 6 Aug 1968, *Thornberg s.n.* (C); Bolzano, Wolkenstein (Selva di Val Gardena), Grödnertal (Val Gardena), à gauche du Rio Gardena, 46º33’N, 11º45’E, 7 Aug 1985, *Buggenhout s.n.* (B, C, H, L, M, MA);

Bolzano (Bozen), am Wege von St. Constantin nach Hanenstein, im Gerölle, 46º 32’N, 11º31’E, 12 Jul 1905, *Handel-Mazzetti s.n.* (GB, WU); monte Schlern, 46º30’N, 11º34’E, 4 Aug 1884, *Vatke s.n.* (JE); Val Gardena, im Langental in Gröden bei Wolkenstein, 46º34’N, 11º40’E, 12 Aug 1907, *Vetter s.n.* (UPS); Saint Ulrich in Gröden [Ortisei], 46º34’N, 11º40’E, 20 Aug 1913, *Zinsmeister s.n.* (M); Seiser Alp, 46º31’N, 11º32’E, Jul 1828, *Zuccarini s.n.* (M). **Veneto:** Monte Pasubio, 45º47’N, 11º10’E, *Ball s.n.* (NY); Val de Signori, prope Schio, 45º42’N, 11º21’E, 27 Aug 1858, *Ball s.n.* (US); in verticibus Pasubio et Covelalto, 45º47’N, 11º10’E, 27 Aug 1858, *Ball s.n.* (US); Vicenza province, near Recoaro, 45º41’N, 11º13’E, Jun 1863, *Ball s.n.* (GH, NY); Cortina d´Ampezzo, in Monte Tofana, 46º32’N, 12º3’E, 30 Aug 1870, *Ball s.n.* (US); Val di Portole, Sette Comuni, 45º54’N, 11º30’E, Sep 1860, *Ball s.n.* (US); Lago di Alleghe, 46º24’N, 12º0’E, 4 Aug 1865, *Ball s.n.* (US); Judikarien, Gavardina-Pass, 45º58’N, 10º45’E, Aug 1925, *Beger s.n.* (B); Belluno province, Canazei, langs de Avisio, 46º27’N, 12º0’E, 25 Jul 1959, *Boom s.n.* (L); Verona province, E Monte Baldo, in glareosis Giari di Valbrutta vocatis, 45º43’N, 10º49’E, 29 Jun 1880, *Goiran s.n.* (F, L, M, WU); Monte Baldo, vallis del Trovai, 45º43’N, 10º49’E, 6 Jul 1908, *Rigo 1411* (FI, GH, K, LE, W); Rocca Pietore, le long du chemin qui va à Sottoguda, 46º25’N, 11º56’E, 29 Jul 1895, *Saint-Lager s.n.* (G, H, MA, NY, US); bei Ampezzo, 46º25’N, 12º47’E, Aug 1863, *Sonklar s.n.* (W); Prov. Verona, Monte Baldo Wetseite, Abstieg, nach Malcesine, 45º43’N, 10º49’E, 17 Jul 1910, *Frimmel s.n.* (W). **SLOVENIA. Gorenjska:** Julijske Alpe, Ponca, Na Vrtcu, 46º27’N, 13º42’E, 14 Aug 2008, *Frajman s.n.* & *Schönswetter* (WU); Julische Alpen, Wochein [Bohinj], 46º18’N, 13º56’E, *Freyer s.n.* (M); Karawanken, S Loiblpass, Westteil der Kosuta (Koschuta), WNW unter der Kote 1602 bzw. 0,3 km S Pri Jurji, 46º25’N, 14º25’E, 18 Jul 1995, *Greimler s.n.* (WU); Julische Alpen, Massiv des Triglav, am Dom na Komni westlich des Wocheiner Sees, 46º22’N, 13º50’E, 30 Jul 1972, *Holtz s.n.* (GOET). **Goriska:** Alpi Giulie, Santa Lucia, 46º8’N, 13º44’E, Aug 1897, *Marchesetti s.n.* (FI); Selva di Tarnova, M. Golaki, 45º58’N, 13º51’E, 28 Aug 1966, *Sauli s.n.* (H). **Savinjska:** Styriae montibus Sulzbacher Alpen, in sinu Logarthal, 46º23’N, 14º36’E, 24 Aug 1867, *Ball s.n.* (NY, US); Sannthaler Alpen, Rinkafall, Logarthal, 46º23’N, 14º37’E, 22 Aug 1879, *Dingler s.n.* (GOET).

Notes—Trisetum argenteum is separated from *T. distichophyllum* because of its more slender habit, narrower and more slender leaves [basal leaf-blades (0.9–)1.2-1.5(–1.7) mm wide], larger panicles, always 1-veined lower glume, and shorter callus hairs [(0.7–)1.4-1.8(–2.6) mm long]. In the studied material, some intermediate specimens were found, mostly in the Central and Eastern Alps. The panicle shape and the number of nerves in the lower glume are highly variable, with *T. distichophyllum* having 1-3 nerves, a character that could be related to the size of the glume. In his work on the cytology and distribution of *T. distichophyllum* and *T. argenteum*, Beuret (1974) separated tetraploid (mostly in the Western Alps), octoploid (Eastern Alps), and hexaploid (dispersed in both the Western and Eastern Alps) races of *T. distichophyllum*. *Trisetum argenteum* was always tetraploid. Comparing this cytological information with the morphology of the plants, Beuret concluded that these three races are very closely related. According to his hypothesis, the tetraploid populations were separated because of the glaciations, and are real vicariants. However, our morphological data do not support the taxonomical separation of these entities.

3. TRISETUM MACROTRICHUM Hack., Magyar Bot. Lapok 2: 110. 1903. *Trisetaria macrotricha* (Hack.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 383. 1996.—TYPE: ROMANIA. Timis river, 45º48’N, 25º39’E, 17 Aug 1881, *J. Barth s.n.* (lectotype, here designated, LD-1213569!)

T. tarnowskii Zapal., Rozpr. Wydz.Mat.-Przyr. Akad. Umiejetn., Dzial B, Nauki Biol., III, 4: 167. 1904.—SYNTYPES: ROMANIA. in montanis Bucovinae, monte Dadul, prope Kirlibaba, 47º34’N, 25º7’E, *F. Herbich s.n.*; monte Pietrile Domnei (Piatra Domnei) prope Rareu, 45º23’N, 23º46’E, *A. Rehmann s.n.* (no original material found).

Herbs (33–)38.5–67(–77) cm tall, not tufted, stoloniferous rhizomes, culms 0.6–1.1 mm diam., glabrous, sometimes slightly puberulous at the top, with hairs up to 0.1 mm long; nodes 4–6(7), separated along the culm, enclosed by the sheaths, sometimes the upper ones not enclosed, glabrous or puberulous. Basal leaf-sheaths densely pubescent, with hairs 0.9–1.6 mm long, decaying into fibers, brownish, sometimes yellowish; basal leaf-blades (3–)3.8–5.7(–6.5) cm long × (2.4–)2.6–5.4(–5.6) mm wide, flat, sometimes enrolled, pubescent to slightly pubescent or with scattered hairs abaxially, densely pubescent adaxially, margins with hairs (0.1–)0.5–1.1(–1.4) mm long, brownish to greenish; top culm leaf-sheaths (9.3–)9.7–17.5(–18) cm long, slightly longer than the internodes, sometimes shorter, glabrous, rarely scabridulous, with cilia along the margins; top culm leaf-blades (5.3–)5.4–7.8(–11.3) cm long × (4.4–)5–7.2(–10) mm wide, flat, rarely conduplicate, glabrous to slightly pubescent abaxially and adaxially, with hairs on the margins (0.1–)1–1.6(1.8) mm long, greenish; inner collar region with the same indumentum as the leafblade or sheath, with hairs 0.05–1.2(–1.7) mm long; ligules 1–1.3(–1.5) mm long, slightly laciniate, rarely slightly dentate, glabrous to pubescent, with hairs 0.1–0.3 mm long. Basal node of the panicle glabrous, rarely scabridulous, with hairs 0.2 mm long. Panicles (9)9.2–12.2(–15) cm long × (2–)2.5–5.5(–6) cm wide, oblong to elliptic in outline, rarely narrowly oblong to narrowly elliptic; rachis scabridulous to pubescent, with hairs up to 0.15 mm long; longest basal branches (1.3–)1.6–3(–3.5) cm. Spikelets (5.6–)6–8(–8.2) mm long × (2.5–)3.7–4.85(–5.2) mm wide, (2–)3-4-flowered; pedicels 2.8–3.5 mm long, pubescent, with hairs 0.1(–0.2) mm long. Glumes unequal [ratio -- lower glume length/upper glume length = (0.58–)0.62–0.72(–0.78)]; lower glume 3.2–4.6(–6) mm long × (0.6–)0.7–1(–1.2) mm wide, narrowly lanceolate, rarely narrowly elliptic [ratio -- lower glume width/lower glume length = (0.19–)0.2–0.22(–0.25)], acuminate to long acuminate, 1(–2)-nerved, glabrous, with very short hairs on the midrib up to 0.1 mm long, sometimes on the upper part of the margins, greenish to yellowish on the central part, rest hyaline; upper glume (4.8–)5.2–6.7(–7.7) mm long × 1.9–2.2(–2.4) mm wide, elliptic to oblong, sometimes oblanceolate or narrowly lanceolate [ratio -- upper glume width/upper glume length = (0.29–)0.31–0.38(–0.42)], acuminate to long acuminate, 3-nerved, glabrous, with very short hairs up to 0.07 mm long, from the middle to the upper part of the central nerve, sometimes also on the upper part of the margins, greenish to yellowish on the central basal part, rest hyaline; rachilla segment between first and second floret (0.6–)0.7–1.1 mm long, with hairs 3–3.7(–4.6) mm long; rachilla segments to sterile floret 1-1.5 mm long, with hairs (1.2–)1.7–2(–2.3) mm long. Lemmas (5–)5.5–6.1(–6.7) mm long × (0.6–)0.7–1(–1.2) mm wide, elliptic to broadly lanceolate [ratio -- lemma width/lemma length = (0.23–)0.26–0.3(–0.34)], scabridulous, sometimes with hairs up to 0.1 mm long from the central to the upper part of the midrib, greenish to yellowish; apical teeth (0.2–)0.3–0.4(–0.6) mm long, with aristules 0.3–0.4 mm long; awn (4.5–)5.3–6.7 mm long, inserted (2.2–)2.6–3(–3.7) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.42–)0.44–0.5(–0.61)], geniculate and slightly twisted near the base, with very short adpressed hairs 0.05–0.1 mm long; callus 0.2–0.4 mm long, oblong to elliptic, rarely rounded, with hairs (2.6–)2.8–3.8 mm long. Paleas 4-5 mm long × 1–1.3(–1.5) mm wide [ratio -- palea length/lemma length = (0.71–)0.73–0.8], narrowly elliptic or elliptic to oblong, with short hairs along the outer edges; keels with short hairs on the apex, ending in teeth 0.1–0.2 mm long. Lodicules (0.7–)0.8(–1.1) mm long, with apex regularly toothed, sometimes with a lateral lobe. Anthers (1.6–)2–2.2(–2.5) mm long. Ovary (0.7–)0.9–1(–1.2) mm long, glabrous. Caryopsis c. 1.5 mm long × 0.5 mm wide. Figure 5.

Chromosome Number—2*n* = 56 (Frey, 1991).

Phenology—Flowering from June to September.

Distribution and Habitat—This species is endemic to the Romanian Carpathians, in the region of Transylvania; at 800–1600 m elevation; around limestone rocks and pebbles. Figure 4.

Specimens Examined—**ROMANIA. Transylvania:** Comit. Csik, in valle Békás-szoros prope pagum Gyergyóbékás, 46º51’N, 25º55’E, 25 Jul 1943, *Baschant s.n.* (B, GB, HBG, M, S); Comit. Brassó, prope Felsö-Tömös, 45º31’N, 25º34’E, 10 Jun 1904, *Degen s.n.* (C); Tömös, 45º48’N, 25º39’E, Jun 1904, *Wagner s.n.* (GB, PR); Comitat Brassó, am Fusse des Berges Piatra, 45º33’N, 25º38’E, 20 Jul 1904, *Degen s.n.* (B, C, G, GB, H, IBF, K, L, LE, MA, MO, O, P, PR, S, US, W); Comit. Brassó, prope Felsö-Tömös, 45º31’N, 25º34’E, 15 Jun 1905, *Degen s.n.* (B, FI, MA, P); Comit. Brassó, ad pedem montis Piatra mare supra Felsö-Tömös, 45º33’N, 25º38’E, 13 Aug 1903, *Degen s.n.* (B, BM, G, GB, GH, JE, K, LE, O, S, W); Tömös, 45º48’N, 25º39’E, Mar 1904, *Wagner s.n.* (PR); Brasov [Kronstadt], Tömös, 45º48’N, 25º39’E, 25 Jun 1909, *Hermann s.n.* (B); Carpatti Orientali, Muntii Hasmasul Mare, Umgebung der Schutzhütte Cabana Piatra Singuratica und Bergrücken gegen den Gipfel des Berges Hasmasul Mare (Nagy Hagymás), 46º40’N, 25º50’E, 23 Aug 1989, *Ehrendorfer s.n.* (WU); Bucegi, 45º26’N, 25º27’E, Oct 1955, *Schwarz s.n.* (JE); Öcsém, 46º40’N, 25º50’E, 13 Aug 1885, *Barth s.n.* (M, P). [unknown locality], Jul 1909, *Hermann s.n.* (JE).

Notes—Chrtek (1965) already included *Trisetum macrotrichum* in sect. *Rigida*, together with *T. rigidum*. Apart from the anatomical characters, these species share ± short ligules, longer rachilla hairs, and young culms with distichous leaves. *Trisetum macrotrichum* is easily differentiated because of the notable width of basal leaf-blades [(2.4–)2.6–5.4(–5.6) mm wide] and flat top culm leaf-blades [(4.4–)5.1–7.2(–10) mm wide] with ciliate margins, with the internodes evenly distributed along the culm, and callus indumentum length [(2.6–)2.8–3.8 mm long].

Trisetum macrotrichum has been misidentified as *Avena carpatica* auct., non Host (1809) and *T. distichophyllum* auct., non (Vill.) P. Beauv. (1812). Sãvulescu (1972) noticed that *T. distichophyllum* has been cited from Romanian Carpathians in floristic literature and stated that both *T. macrotrichum* and *T. distichophyllum* are vicariant taxa and easily confused. Apart from the different size of the plants, both species are easy to differentiate using the aforementioned characters.

4. TRISETUM RIGIDUM (M. Bieb.) Roem. & Schult., Syst. Veg. 2: 662. 1817. *Avena rigida* M. Bieb., Fl. Taur.-Caucas. 1: 77. 1808. *Avena brevifolia* Schrad. ex Spreng., Syst. Veg. (ed. 16) 1: 334. 1824, nom illeg. *Trisetaria rigida* (M. Bieb.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 385. 1996.—TYPE: AZERBAIJAN. Baku: Kuba district, Schirvaniensi altiore ca. Kurt-Bulak [Gora Kara-Bulag] lecta, 41º04’N, 48º20’E, *F.A. Marschall von Bieberstein s.n.* [lectotype, designated by Tzvelev (1976: 261), LE-1009635!].

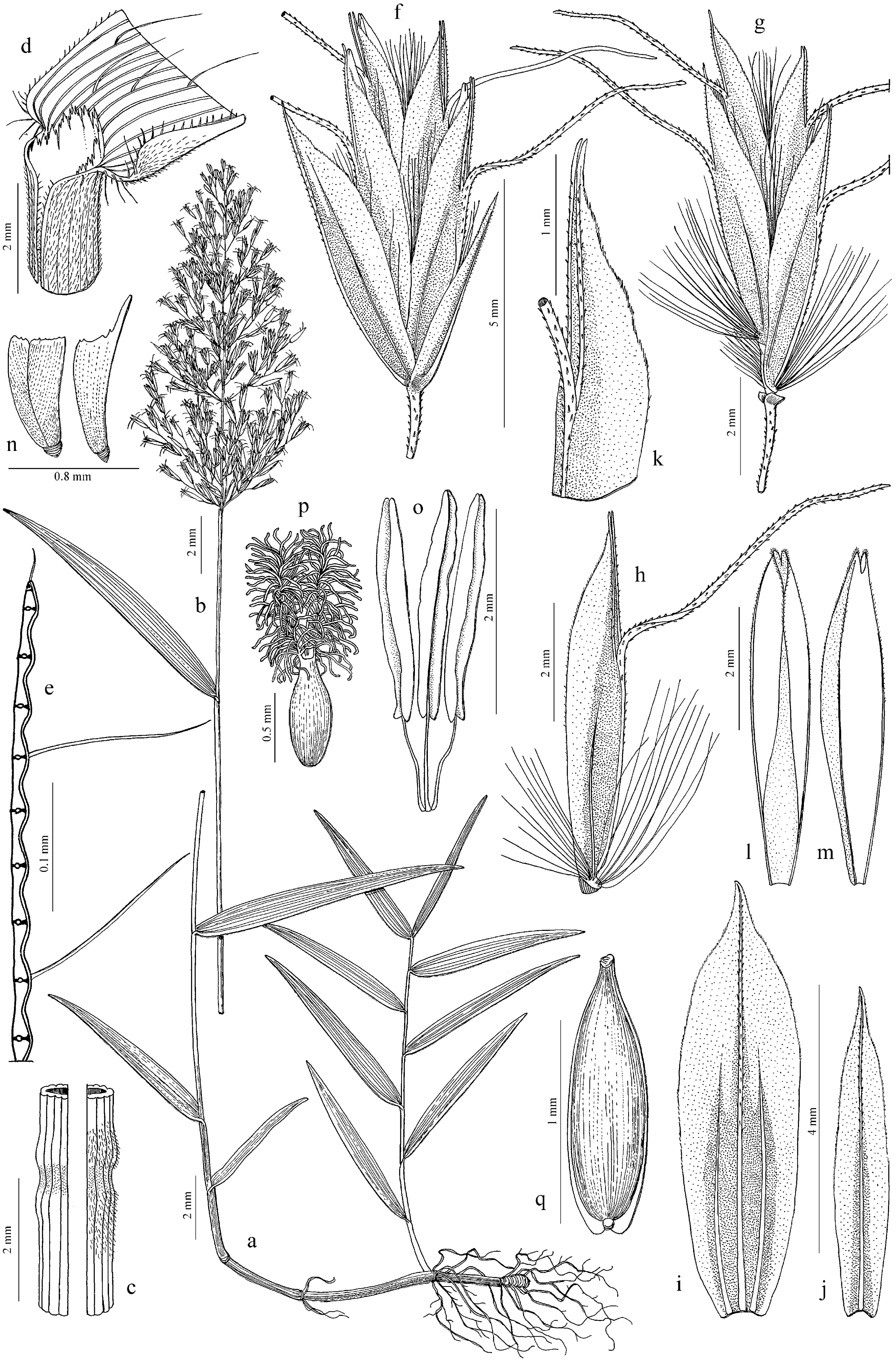

Figure 5. *Trisetum macrotrichum*. A. Habit. B. Inflorescence. C. Portions of the culm and node. D. Sheath, ligule, and portion of the blade. E. Transverse section of half of the leaf-blade. F. Spikelet. G. Florets. H. Floret. I. First glume, dorsal view. J. Second glume, dorsal view. K. Lemma, upper part, lateral view. L. Palea, ventral view. M. Palea, lateral view. N. Lodicules. O. Stamens. P. Pistil. Q. Caryopsis. (*Degen 160*, JE, O-V2126613, A-P; *Hermann s.n.*, B-100526317, N, Q).

Herbs (18.5–)37–57(–76.3) cm tall, not to loosely tufted, short rhizomatous or with stoloniferous rhizomes, culms 0.4–0.9(–1.2) mm diam., glabrous; nodes (4)5–7(12), internodes, sometimes concentrated in lower part, not enclosed by the sheaths, puberulous with hairs 0.3-0.6 mm long, or sometimes glabrous. Basal leaf-sheaths densely pubescent, rarely glabrous, with hairs (0.1–)0.3–0.7(–1.5) mm long, becoming fibrous in age, brownish to yellowish; basal leaf-blades (0.8–)2.8–5.5(–8.6) cm long × (–1.2)2–3.5(–7.6) mm wide, rigid or not, flat, sometimes slightly enrolled, from glabrous to pubescent abaxially and adaxially, with hairs (0.05–)0.2–0.6(–1) mm long along the margins, greenish to greyish; top culm leaf-sheaths (5.3–)10–13.4(–17) cm long, shorter than the internodes, rarely longer, glabrous, without cilia on the margins; top culm leaf-blades (1–)2.5–5(–10.7) cm long × (1–)1.8–3.3(–6.4) mm wide, flat, usually parallel to the culm, glabrous or with scattered hairs abaxially and adaxially, margins without or with hairs (0.05–)0.1–1(–1.5) mm long, greenish to greyish; inner collar region glabrous, sometimes with scattered hairs along the margins (0.1–)0.3–1(–1.3) mm long; ligules (1.3–)2–3.1(–4.2) mm long, laciniate, glabrous, usually with few hairs (0.05–)0.1–0.4 mm long on the apex. Basal node of the panicle glabrous. Panicle (5.8–)7.5–13(–16) cm long × (1.3–)2.2–3.2(–5.5) cm wide, oblong to elliptic in outline, rarely lanceolate, lax to slightly dense; rachis glabrous, sometimes slightly pubescent, with hairs up to 0.1 mm long; longest basal branches (0.4–)1–2.3(–5) cm. Spikelets (5.3–)7.5–9.1(–11.5) mm long × (1.6–)3.2–5(–6.2) mm wide, 2–3(–4)-flowered; pedicels (1.6–)3.3-4.3(–5) mm long, glabrous to pubescent, with hairs up to 0.1 mm long. Glumes unequal ratio -- lower glume length/upper glume length = (0.45–)0.55–0.66(–0.83)]; lower glume (2.4–)3.7–5.2(–6.2) mm long × (0.4–)0.7–0.9(–1.2) mm wide, lanceolate to narrowly elliptic [ratio -- lower glume width/lower glume length = (0.11–)0.15–0.22(–0.26)], acuminate, rarely acute, 1-nerved, glabrous, with scattered hairs up to 0.08 mm on the nerve and upper part, greenish on the central part, surrounded by yellowish or hyaline part; upper glume (5.3–)6.6–8(–10.2) mm long × (1.4–)1.7–2(–2.4) mm wide, oblong to elliptic, rarely lanceolate or oblanceolate [ratio -- upper glume width/upper glume length = (0.19–)0.23–0.28(–0.32)], acuminate or long acuminate, rarely acute, 3-nerved, glabrous, with very short hairs up to 0.08 mm from the middle to the upper part of the central nerve, sometimes also on the upper part of the margins, greenish on the central part, surrounded by yellowish or hyaline part; rachilla segment between first and second floret 1–1.5(–2.2) mm long, with hairs (3.2–)4–4.7(–5.7) mm long; rachilla segments to sterile floret (0.8–)1.5–2(–2.5) mm long, with hairs (1.6–)2.5–3.3(–4.2) mm long. Lemmas (5.3–)6.4–8.2(–9.3) mm long × (0.4–)0.7–0.9(–1.1) mm wide, narrowly elliptic to narrowly lanceolate, rarely oblong [ratio -- lemma width/lemma length = 0.18–0.24(–0.28)], strigulose, sometimes with hairs up to 0.1 mm long on the aristules and midrib, greenish to yellowish, rarely purple; apical teeth (0.1–)0.2–0.5(–1.2) mm long, with aristules (0.3–)0.4–1(–1.7) mm long; awn (4.3–)5.7–7.3(–8.6) mm long, inserted (2.4–)3.2–4.2(–5.1) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.4–)0.45–0.55(–0.62)], recurved near base to straight, not twisted to slightly twisted, with very short adpressed hairs 0.05 mm long; callus 0.2–0.4(–0.5) mm long, elliptic to oblong, with hairs (0.3–)0.6–0.9(–1.4) mm long. Paleas (4–)4.9–5.8(–6.6) mm long × 1–1.3(–1.8) mm wide [ratio -- palea length/lemma length = (0.54–)0.66–0.81(–0.87)], narrowly elliptic to oblong, rarely slightly oblanceolate, with short hairs along the outer edges; keels with short hairs on the apex, ending in teeth (0.1–)0.2–0.3(–0.5) mm long. Lodicules (0.4–)0.6–0.7(–0.9) mm long. Anthers (1.8–)2.3–2.8(–3.4) mm long. Ovary (0.4–)0.6–0.9(–2.1) mm long, glabrous, rarely with few hairs 0.1–0.3(–0.6) mm long or slightly puberulous on the apex. Caryopsis 1.4–3 mm long × 0.3–0.4 mm wide.

a. subsp. RIGIDUM

Arundo wilhelmsii Ledeb., Mem. Acad. Sci. Petersb. 6: 593, tab. 19. 1818. *Avena wilhelmsii* (Ledeb.) Spreng., Syst. Veg. 1: 333. 1824. *Trisetum wilhelmsii* Ledeb. ex Schult. in J.J. Roemer & J.A. Schultes, Mant. 2: 367.1824.—TYPE: GEORGIA. Ex Iberia, *C. Wilhelms s.n.* [lectotype, designated by Tzvelev (1976: 261), LE!; isolectotypes: P-2255872!].

Avena daenensis Boiss., Diagn. Pl. Orient. 7: 123. 1846. *Trisetum daenense* (Boiss.) Bal., Bull. Soc. Bot. France 21: 14. 1874.—TYPE: IRAN. Kuh-e Dana Mountain, Dscheschme-Pias Bsource, 30°44'N, 51°36'E, 29 Jul 1842, *K.G.T. Kotschy 754a* (lectotype, here designated, P-2255864!; isolectotypes, BM-959384! G-176318!, P-2255902!).

T. teberdense var. *brevifolium* Kharadze, Zametki Sist. Georg. Rast. (Tbilisi), 1: 16. 1938.—TYPE: GEORGIA. Samegrelo-Zemo Svaneti: Fontaine Chalde-čalai, 42º42’N, 42º12’E, 9 Aug 1931, *A.L. Kharadze s.n.* [lectotype, here designated, TBI (image!)].

T. rigidum subsp. *demavandense* Chrtek, Acta Univ. Carol., Biol. 1967: 96. 1968.—TYPE: IRAN. Teheran, in the country near the city, 35º42’N, 51º25’E, *K.G.T. Kotschy 390* (holotype, BM-1134941!; isotypes, LE!).

T. persicum Chrtek, Acta Univ. Carol., Biol. 1967: 98. 1968.—TYPE: IRAN. Kellal mountain, 33º58’N,48º25’E, 3050 m, 6 Sept 1868, *H.C. Haussknecht s.n.* (holotype, BM-959383!; isotypes, K-808701!, LE!).

Herbs (18.5–)34.3–56.5(–76.3) cm tall. Basal leaf-sheaths densely pubescent, rarely glabrous, with hairs (0.1–)0.3–0.7(–1) mm long; basal leaf-blades (0.8–)2.8–5.2(–7) cm long × (1.2–)2–3(–5.8) mm wide, rigid, glabrous abaxially and adaxially, sometimes slightly pubescent, margins with hairs 0.05–0.6(–1) mm long; top culm leaf-sheaths (5.3–)9–13(–17) cm long, shorter than the internodes, sometimes slightly longer; top culm leaf-blades (1–)2.5–4.6(–10.7) cm long × (1–)1.8–3(–5.6) mm wide, divergent, rarely erect, not reaching into the panicle, glabrous abaxially and adaxially, usually with hairs up to 0.4 mm long on the margins; inner collar region glabrous, rarely with few hairs on the margins 0.1–0.8 mm long; ligules (1.8–)2.3–3.4(–4.2) mm long. Panicles (5.8–)8.1–13.9(–16) cm long × (1.3–)2.3–3.2(–5.5) cm wide, oblong to oblong-elliptic in outline, sometimes lanceolate; longest basal branches (0.4–)1–2.3(–5) cm. Spikelets (5.3–)7.4–9(–11.5) mm long × (1.6–)3.2–5(–6.2) mm wide; pedicels (1.6–)3.4–4.2(–5) mm long, glabrous to slightly pubescent. Glumes unequal [ratio -- lower glume length/upper glume length = (0.45–)0.54–0.63(–0.72)]; lower glume (2.4–)3.5–5.2(–6.2) mm long × (0.4–)0.6–1.2 mm wide [ratio -- lower glume width/lower glume length = (0.11–)0.14–0.22(–0.26)], greenish on the central part, sometimes purple, laterals and upper part hyaline; upper glume (5.3–)6.4–8(–10.2) mm long × 1.6–2.2(–2.4) mm wide [ratio -- upper glume width/upper glume length = (0.2–)0.25–0.29(–0.32)], greenish on the central basal part, usually also the nerves, laterals hyaline or yellowish, sometimes purple; rachilla segment between first and second floret with hairs (3.2–)4.2–4.6(–5) mm long. Lemmas (5.3–)6.4–7.7(–9.3) mm long × (–0.4)0.6–1.1 mm wide, narrowly elliptic to narrowly lanceolate, sometimes elliptic, rarely oblong [ratio -- lemma width/lemma length = 0.18–0.24(–0.28)]; awn (4.3–)5.5–7(–8.6) mm long, inserted (2.4–)3–4.2(–5.1) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.4–)0.46–0.53(–0.62)]; callus with hairs (0.3–)0.6–0.9(–1.4) mm long. Lodicules with apex slightly lobulate to denticulate, rarely with long lobules or teeths. Anthers (1.8–)2.5–2.8(–3.4) mm long. Figure 6.

Chromosome Number—2*n* = 28 (Tzvelev, 1976).

Phenology—Flowering and fruiting from June to August.

Distribution and Habitat—It is distributed from East Anatolia in Turkey to Caucasus and north-northeast Iran; at 600–3000 m elevation; on rocky or pebbles slopes, from open to shrubby places, often in riversides. Figure 7.

Specimens Examined—**ARMENIA. Ararat:** Ararat district, montes "Gegamski khrebet", loco Aruni Dzor, 40º12’N, 44º56’E, 11 Jul 1975, *Vasak s.n.* (B, K, M, MA). **Gegharkunik:** pr. Pambak, 40º23’N, 45º32’E, 20 Jun 2005, *Aedo 11798* & *al.* (MA); Nor-Bajazet district, in monte Inak-dagh, 40º14’N, 45º52’E, 28 Jul 1928, *Zedelmejer s.n.* & *Gejdeman* (LE). **Kotayk:** Gekhard, 40º9’N, 44º47’E, 5 Jul 1928, *Araratian s.n.* (LE). **Shirak:** Akhuryan district, the Shikarskiy Range, northwest of Dzhadzhur Pass, 40º51’N, 43º59’E, 23 Jun 1960, *Tzvelev 160* & *Cherepanov* (LE). **Syunik:** Megri district, to the valley of a right tributary of the Megriget River near Vardanadzor, 38º58’N, 46º12’E, 29 Jun 1965, *Egorova 1477* & *al.* (LE); montes "Karabakhskoie nagorje", ad orientem versus ab oppido Goris, 39º30’N, 46º20’E, 25 Jul 1975, *Vasak s.n.* (K). **Vayots Dzor:** cordillera Vardenis, cerca de 8 km antes del paso de Selim, 39º56’N, 45º14’E, 23 Jun 1900, *Herrero 2718* (B, O). **AZERBAIJAN.** Nachrespublica, in mte Ljakatach, 10 Aug 1933, *Gadzhiev s.n.* & *al.* (LE). **Absheron:** Kuba district, ad fl. Kussar-czai supra p. Dshagar, 41º34’N, 48º43’E, 2 Jul 1899, *Alexeenko 1101* (LE); Kuba district, prope St. Kussary, 41º25’N, 48º25’E, 20 Jun 1899, *Alexeenko 392* (LE); Kuba district, in valle fl. Ata-czai, 23 Jul 1900, *Alexeenko 5623* (LE); Schemacha district, montis Dibrar, 40º53’N, 48º53’E, 25 Jul 1900, *Alexeenko 6104* (LE); Schemacha district, in decliviis m. Nijal supra p. Zarnova, 40º48’N, 48º20’E, 31 Jul 1900, *Alexeenko 7396* (LE); Baku, Kuba Uyezd, Gilskie polya, 1900, *Grigor’ev s.n.* (LE); Baku, Bibi-Eibat, 40º18’N, 49º48’E, 24 May 1912, *Holmberg 974* (K, S); Shemacha district, iter pass pasc. Neregele et Kaladzhich, 30 Jul 1928, *Sachokjia s.n.* (LE). **Aran:** Araesch district, Montes Arczan-dagh, Oghrudsha, 41º16’N, 48º0’E, May 1908, *Schelkownikow s.n.* & *Woronow* (G, H, LE, MW, W). **Daglig-Shirvan:** road Agsu-Shamakhi, 40º38’N, 48º28’E, 12 Jun 1949, *Eideman s.n.* (LE). **Ganja-Qazakh:** 20-40 km ENE Tabriz usque 1 km ultra pontem trans fluvium Talkheh Rud (Atschi Tschai), 38º4’N, 46º17’E, 31 May 1971, *Rechinger 40731* (G, M, MO, S). **Lankaran:** Lerik district, in the vicinity of the urban-type settlement of Lerik, 38º46’N, 48º24’E, 18 Aug 1963, *Bobrov 574 & Tzvelev* (LE). **Nakhchivan:** Ordubad Dist., a gorge 1,5 km east of Ordubad, 38º54’N, 46º1’E, 9 Jun 1956, *Egorova 433 & al.* (LE); in jugo Zangezur, inter p. Aravsa et monte Dashurry-Dagh, 39º17’N, 45º47’E, 5 Jul 1928, *Gavrilov s.n.* (LE); slopes of the Zangezur Range, a slope to the Kyuki-chay River, 39º12’N, 45º24’E, 4 Jul 1952, *Smol’yaninova s.n.* (LE). **Shaki-Zaqatala:** Zaqatala district, Dzhary, a mount 300 m west of the mansion of the Zagatala State Reserve, south macroslope, 41º39’N, 46º40’E, 12 Jun 1946, *Il’inskaya s.n. & Kirpichnikov* (LE). **Yukhari-Karabakh:** Shusha, 39º45’N, 46º45’E, 14 Jun 1893, *Lipskiy s.n.* (LE). **GEORGIA. Abkhazia:** Gudauta district, in vicinitate lacus Rica, 43º28’N, 40º32’E, 21 Jun 1977, *Vasak s.n.* (M). **Imereti:** The Meskhiyskiy Range, [Guminda Ioriy] summit, 42º11’N, 43º36’E, 4 Aug 1930, *Dzens-Litovskaya 99* (LE); Oprtsheti pr. Fl. Rion, 42º21’N, 42º42’E, Jun 1877, *Brotherus s.n.* & *Brotherus* (H). **Kakheti:** Greater Caucasus, Tusheti, Pirikiti Khersureti, 42º21’N, 45º39’E, 20 Aug 1997, *Gagnidze 2524* & *al.* (MO); Terek River valley, the Darlyalskoe Gorge, pebbles by “Tamara Castle” (downstream of the mouth

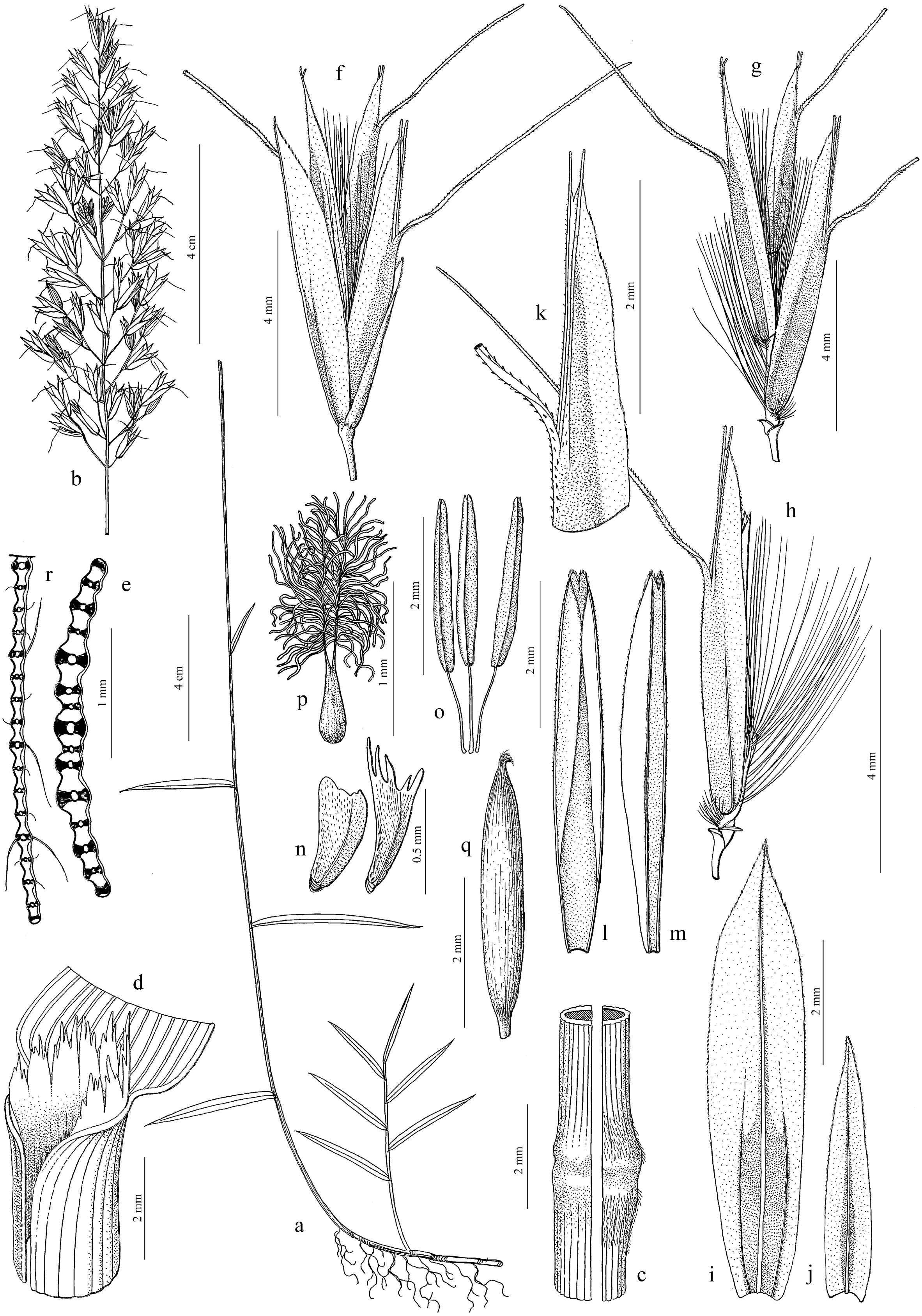

Figure 6. *Trisetum rigidum* subsp. *rigidum*. A. Habit. B. Inflorescence. C. Portions of the culm and node. D. Sheath, ligule, and portion of the blade. E. Transverse section of leaf-blade. F. Spikelet. G. Florets. H. Floret. I. First glume, dorsal view. J. Second glume, dorsal view. K. Lemma, upper part, lateral view. L. Palea, ventral view. M. Palea, dorsal view. N. Lodicules. O. Stamens. P. Pistil. Q. Caryopsis. *T. rigidum* subsp. *teberdense*. R. Transverse section of half of the leaf-blade. (*Amirhanov 34*, MW, A-B; *Gauba 1243*, B-100526552, C-P; *Alexeenko 9071*, LE, N; *Vasak s.n.*, K, Q; *Soreng 8009*, US-3600681, R).

of Kistinka river), 42º44'N, 44º37'E, 24 Aug 1949, *Novopokrovskiy 681* (LE); Telav, 41º55'N, 45º28'E, 22 Jul 1918, *Pastuchov s.n.* (LE, NY). **Mtskheta-Mtianeti:** Kazbegi region, vill. Targmani area, about 200m N of vill. Targmani, about 80 m left of country road, about 50 m SW of gas pipeline, 42º39'N, 44º39'E, 7 Jul 2004, *Abdaladze 332* & *al.* (NY); Kazbegi region, vill. Tsdo area, about 2 km SE of vill. Tsdo, 42º41'N, 44º37'E, 7 Aug 2004, *Abdaladze 409* & *al.* (NY); Georgian Military Road, south slope by the way to the Krestoviy Pass, 42º30'N, 44º27'E, 8 Aug 1950, *Beydeman s.n.* (LE); inter Tiflis et Wendikaukas, supra stationem Mleti, 42º25'N, 44º29'E, 10 Aug 1902, *Bornmüller 33* (B); upper reaches of the Ksanka River, the left side of a gorge near the selo of Gorga, 42º8'N, 44º24'E, 5 Aug 1933, *Bush s.n.* & *Bush* (LE); between Mlety and Passanauri, 42º21'N, 44º41'E, 28 Jun 1897, *Fedtchenko s.n.* & *Fedtchenko* (LE); Greater Caucasus, Khevi, Kazbegi, Karkucha, 42º34'N, 44º40'E, 25 Aug 1997, *Gagnidze 2941* & *al.* (W); prope pagum Kasbek, 42º38'N, 44º38'E, 9 Aug 1844, *Kolenati 2204* (MO); Khevi, Kazbegi, riv. Tergi Gorge, about 500 m south of vill. Gergeti, about 200 m left of riv. Tergi, 42º39'N, 44º38'E, 18 Aug 2001, *Nakhutsrishvili 103* & *Abdaladze* (NY). Racha-Lechkhumi and **Kvemo Svaneti:** Kassarskoe Gorge upwards of the village of Tli, left side of the Ardon River, 42º29'N, 43º51'E, 10 Aug 1939, *Shiffers s.n.* & *Moreva* (LE). **Samegrelo-Zemo Svaneti:** Gul glacier, 43º4'N, 42º40'E, 21 Jul 1911, *Schelkownikow s.n.* (TBI, photo!). **Samtskhe-Javakheti:** past Abastuman, on the road to the Zekarskiy Pass, 41º45'N, 42º49'E, 24 Jun 1903, *Borodin 197* (LE); Achalzich district, inter Zarzma et Kanly, 41º40'N, 42º39'E, 14 Jul 1914, *Litwinow 2809* (C, G, GH, K, M, MW, S, US). **South Ossetia:** Java district, Ermani area, the south slope of Mt. Fidar-khokh, 42º28'N, 44º14'E, 11 Sep 1947, *Abramov s.n.* (LE); the Chaparukhskoe Gorge, pebbles along the Chaparukh-don River, 23 Jul 1930, *Bush s.n.* & *Bush* (LE); The Sbiyskoe Gorge, the left side of the gorge, slightly downwards of the selo of Nizhnyaya Sba, 42º33'N, 44º10'E, 30 Jul 1929, *Bush s.n.* & *Bush* (LE); upper course of the Ksanka River, the Sagoy Gorge, near the selo of Bagin, 3 Aug 1930, *Bush s.n.* & *Bush* (LE); Ermani, pebbles on the left side of the Mid. Ermanskaya, 42º31'N, 44º11'E, 20 Aug 1937, *Semenova s.n.* (LE). **Tbilisi:** Hänge am Cerepasce-See, 31 May 1968, *Fritsch s.n.* (JE); Trockene Hügel bei Gladni, 41º49'N, 44º49'E, 14 Jun 1968, *Fritsch s.n.* (JE); Tiflis, 41º41'N, 44º50'E, 10 Jun 1919, *Grossheim 76* (G, LE, MW, PR, S); Tblisi surroundings, environs of Kodjori, Mt. Udzo, ca. 1,5 km N of Kodjori, ca. 50 m W of the church,

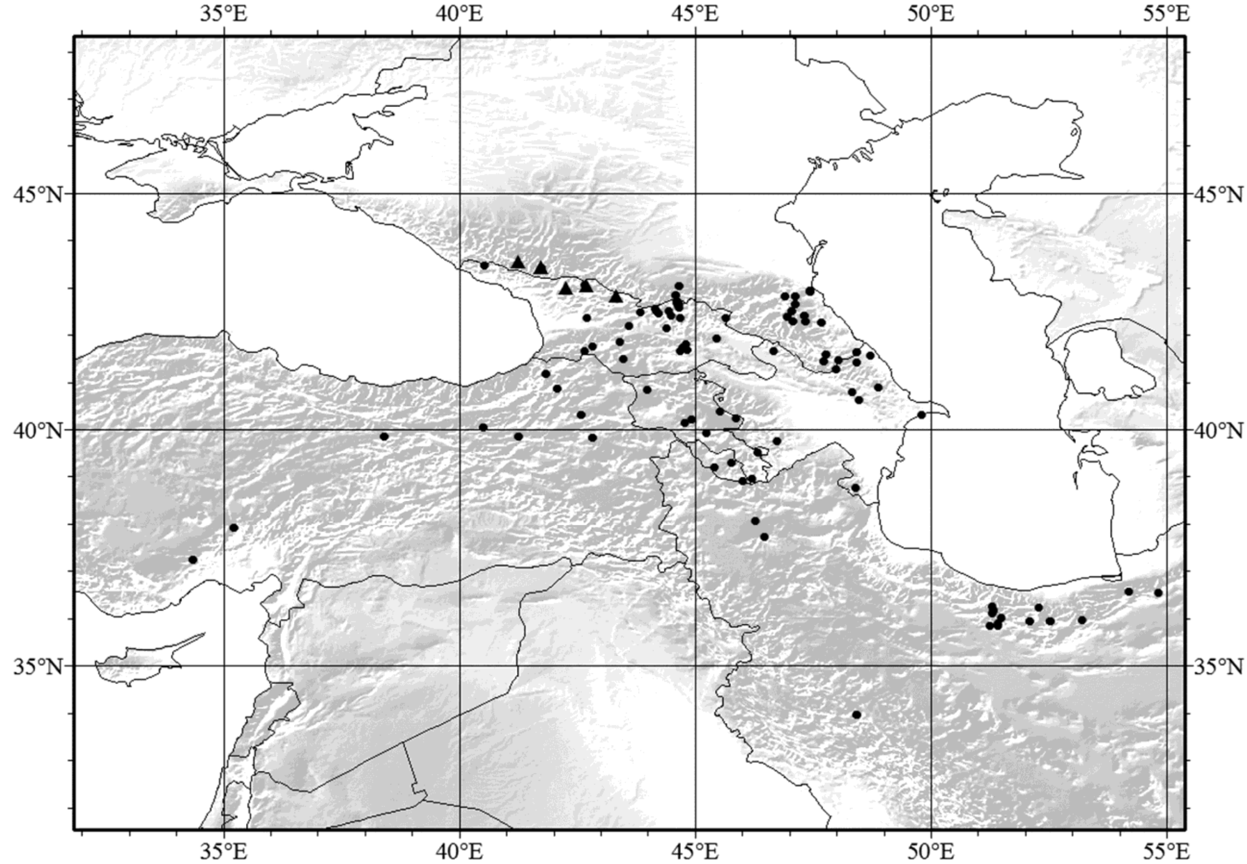

Figure 7. Distribution of *Trisetum rigidum* subsp. *rigidum* (dots) and *T. rigidum* subsp. *teberdense* (triangles).

41º40’N, 44º41’E, 18 Jun 2006, *Lachashvili 189* (NY); Lisi-See, westl. D. Stadt, 41º44’N, 44º44’E, 30 Jun 1969, *Lepper s.n.* & *al.* (JE); Akhaltsikhe uyezd, the Zekarskiy Gorge, 20 Jun 1892, *Lipskiy s.n.* (LE); Tiflis, prope urbem, 41º41’N, 44º50’E, 6 Jul 1890, *Sommier 1359* & *Levier* (FI, LE). **IRAN. Alborz:** Mont. Elburs, valle Lur, ad pagum Getschesär, 36º6’N, 51º18’E, 23 Jun 1902, *Bornmüller 8383* & *Bornmüller* (B). **Est Azerbaijan:** Isperechan m. Sahand, 37º43’N, 46º29’E, 4 Aug 1884, *Knapp s.n.* (W). **Golestan:** M. Shahvar prope Hajjilang, 36º34’N, 54º12’E, Jul 1948, *Rechinger 6091* (B, M). **Khorāsān-e Shomālī:** Akher-Dagh mountain, 37º34’ N, 57º12’E, Jul 1907, *Haradjian* 1619 (S). **Mazanderan:** Mont. Elburs, Junesar, dictionis m. Demavend, 35º57’N, 52º32’E, 2 Jul 1902, *Bornmüller 8384* & *Bornmüller* (B); road of Haraz, 18 Jul 1972, *Dini-Arazm 12132* (K); Elburs, Pole Zangule, 36º11’N, 51º20’E, 14 Jun 1937, *Gauba 1243* (B); Montes Elburs centr., jugi Kandava [Kandovan], 36º9’N, 51º19’E, 14 Jun 1937, *Gauba s.n.* (US); ad radices m. Demawend, 35º57’N, 52º6’E, 24 Jun 1843, *Kotschy 391* (G, LE, P); *Kotschy 393* (L, LE, P); in faucibus vallis Chalus supra Valiabad, 36º15’N, 51º18’E, 21 Jun 1974, *Rechinger 48369* (G, M); Nur district, inter Kamarband et jugum Naftab, 36º13’N, 52º17’E, 8 Aug 1948, *Rechinger 6447* & *Rechinger* (US); Kudjur district, in monte Ulodj, 9 Aug 1948, *Rechinger 6509 & Rechinger* (M, US). **Qazvin:** Montes Elburs centr., Hesarband mountain, 35º50’N, 51º15’E, 24 Jul 1935, *Gauba s.n.* (M, US). **Semnan:** Shahrud-Bustam district, montium Shahvar supra Nekarman (Nigarman), 36º32’N, 54º50’E, Jul 1948, *Rechinger 5891* (K, M, US); Elburz mts., Nezva Kuh area, above Taru, 35º58’N, 53º12’E, 7 Jul 1959, *Wendelbo 1218* (LE). **Tehran:** Zentral-Elburs, am Südabhang des Totschal im Tal von Pasghaleh nördlich von Teheran, 35º50’N, 51º25’E, 8 Jul 1948, *Aellen 1898* (F, MO, S); Zentral-Elburs, am Südabhang des Totschal im Tal Häfthous nordwestlich von Teheran, 35º53’N, 51º25’E, 4 Jul 1948, *Aellen 1982* (H); Mont. Elburs, ad basin septentr. Alpium Totschal, prope Scheheristanek, 35º57’N, 52º32’E, 15 Jun 1902, *Bornmüller 8381* & *Bornmüller* (B, PR); *Bornmüller 8382* & *Bornmüller* (BM, JE, MPU, W); Mont. Elburs, alpe Totschal, prope Scheheristanek, 35º57’N, 52º32’E, 8 Jul 1902, *Bornmüller 8385* & *Bornmüller* (B, HBG, JE, LE, PR, W); 10 Jun 1902, *Bornmüller 8385b* & *Bornmüller* (B, G); Elburz 24' NNE of Teheran, 35º57’N, 52º32’E, 11 Jul 1962, *Furse 3141* (LE); Montes Elburz, Shemshak, 36º0’N, 51º29’E, 25 Apr 1977, *Rechinger 57178* (M). **RUSSIA. Dagestan:** Samur district, prope pagum Gedym, 41º38’N, 48º25’E, 17 Aug 1900, *Alexeenko 9071* (LE); Kürinskii district, prope pagum Kgirchan (Gelchan), 23 Jul 1898, *Alexeenko s.n.* (LE); Dargi district, prope Murguk, 42º16’N, 47º41’E, 7 Jul 1898, *Alexeenko s.n.* (LE); Dargi district, prope silvam Gumra-duz inter Akuscha et Muhi (Meha), 42º17’N, 47º21’W, 14 Jul 1898, *Alexeenko s.n.* (LE); prope Lewaschi, 42º25’N, 47º19’E, 2 Jul 1898, *Alexeenko s.n.* (LE); Dargi district, in declivitate meridionali jugi Shamchal-dag, 5 Jul 1898, *Alexeenko s.n.* (LE); Dargi district, prope pagum Chodshal-makhi, 12 Aug 1898, *Alexeenko s.n.* (LE); Tenir-Chan-Schura district, inter pag. Ischkarty et Temir-Chan-Schura, 42º49’N, 47º7’E, 30 Jun 1897, *Alexeenko s.n.* (LE); Achty, 41º27’N, 47º43’E, 17 Jun 1880, *Becker s.n.* (JE, LE); Makhach-kala district, SE slope of Mt. Tarku-Tau, 42º56’N, 47º27’E, 8 Jun 1925, *Bogdanovskaya-Gienef s.n.* (LE); Gunib district, the selo of Chokh, Mt. Turchidag, 42º18’N, 47º4’E, 10 Aug 1940, *Elenevskiy s.n.* (LE); Magaramkentskiy district, the selo of Garakh, slopes of a mount by the Samur River, 41º28’N, 48º2’E, 15 Aug 2006, *Kotseruba 30* (LE); valley of the Kurakh River, 12 km downwards of the selo of Kurakh, 41º35’N, 47º46’E, 13 Jul 1956, *Medvedeva s.n.* & *al.* (LE); Lakskiy district, along the Kazikukhumskoe Koysu River, Kazi-Kukhum, 42º30’N, 47º3’E, 2 Sep 1927, *Poretskiy 543* & *Shults* (LE); Makhachkala district, the Narat-tyube Range, west of Agach-aul, 42º55’N, 47º27’E, 1 Jul 1955, *Prokhanov 339* (LE); Buynaksk district, the Gimrinskiy Range, ca. 1 km away from a pass (near the aul of Verkhniy Karanay), 42º49’N, 46º54’E, 23 Aug 1953, *Prokhanov 163* & *Cheldyshev* (LE). **Kuban:** Teberda, 43º26’N, 41º44’E, 5 Jul 1905, *Litwinow 257* (LE). **North Ossetia-Alania:** SE slopes of Mt. Kandyl above Dzhekharovskoe (Georgian Military Road), 42º50’N, 44º36’E, 20 Jul 1940, *Schiffers 5* & *Moreva* (LE); valley of the Terek River, 37 km south of Dzaudzhikau (former Vladikavkaz), 43º2’N, 44º40’E, 24 Aug 1949, *Vasilchenko 668* & *al.* (LE). **TURKEY:** partie supérieure du Bousdouan-dagh [Bozdoğan], au dessus de Khabakhor (Lazistán), 40º52’N, 42º5’E, 30 Aug 1866, *Balansa s.n.* (L); région alpine du Taurus, au-dessus de Boulgarmaden, 37º14’N, 21º51’E, IX, *Balansa s.n.* (L); Erzurum, Palandöken dagi unmittelbar S der Stadt Erzurum, 0.2 km oberhalb der Schilift-Talstation, 39º51’N, 41º16’E, 26 Jul 1978, *Ehrendorfer s.n.* & *al.* (WU); Erzincan/Sivas, Kızıldağ Geçidi, 42 Str.-km W Refahiye, 30 Str. Km E Imranli, 39º51’N, 38º24’E, 3 Aug 1978, *Ehrendorfer s.n.* & *al.* (WU); Erzurum, zwischen Askale und Bayburt auf dem Kopdagi geçidi steiniger, 40º3’N, 40º30’E, 2 Aug 1973, *Holtz 978* & *al.* (GOET); Aladağlar, Emli Bogazi, ca. 1-1.5 km SE des Karasay Tepe, 37º55’N, 35º13’E, 12 Aug 1992, *Parolly s.n.* (B); Kars, Sarikamis, am Pass 10 km westlich der Stadt and der Strasse nach Horasan, 40º19’N, 42º35’E, 23 Jul 1981, *Raus 4431* (B); between Erzurum and Agri, 25 km west of Toprakkale village, Keeitepe mountain, 39º50’N, 42º49’E, 18 Jul 1976, *Tatli 4865*

(GOET); Batumi, Artvin district, between the villages of Dabatsvril and Skhloban, 41º10’N, 41º50’E, 16 Jul 1911, *Woronow 6256* (LE).

b. subsp. TEBERDENSE (Litv.) Tzvelev, Novosti Sist. Vyssh. Rast. 7: 62. 1971. *Trisetum rigidum* var. *teberdense* Litv., Spisok Rast. Gerb. Fl. S.S.S.R. Bot. Inst. Vsesojuzn. Akad. Nauk 9: 11. 1932. *Trisetum teberdense* (Litv.) Kharadze, Zam. Sist. Georg. Rast. (Tbilisi) 1: 14. 1938.—TYPE: RUSSIA. Kuban Region, Teberda river, 43º26’N, 41º44’E, 10 Jul 1905, *D.I. Litwinow 2810* [lectotype, designated by Tzvelev (1976: 260), LE!; isolectotypes, A!, C!, G-305395!, M-210841!, MW!, S-13-32730!, US-2119656!, WISv-262239].

T. rigidum var. *ciliatifolium* Roshev. in Kom. (ed.), Fl. URSS 2: 256. 1934.—TYPE: [unknown locality and collector] (no original material found).

Herbs (47–)50–67(–72) cm tall. Basal leaf-sheaths densely pubescent, with hairs up to 1.5 mm long; basal leaf-blades (5–)7.5–8 (–8.6) cm long × (3.2–)3.7–5(–7.6) mm wide, not rigid, from glabrous to pubescent abaxially and adaxially, margins with hairs 0.4-1 mm long; top culm leaf-sheaths 11-15 cm long, shorter than the internodes; top culm leaf-blades (3.7–)6.3–6.7 cm long × (2.6–)3.3–5.7(–6.4) mm wide, usually erect, sometimes reaching into the panicle, with scattered hairs abaxially and adaxially, margins with hairs 0.05–0.4(–1.5) mm long; inner collar region glabrous, with scattered hairs on the margins (0.4–)0.6–1.3 mm long; ligules 1.3–2.4 mm long. Panicles 11–15.5 cm long × (2–)2.8–4 cm wide, narrowly elliptic to oblong; longest basal branches 2-4.7 cm long. Spikelets (7.5–)8–9 mm long × (2.8–)3.4–4.6 mm wide; pedicels 3.5–5 mm long, pubescent to slightly pubescent. Glumes unequal [ratio -- lower glume length/upper glume length = 0.57–0.64(–0.83)]; lower glume 4–5.5 mm long × 0.5–0.8(–1) mm wide (ratio -- lower glume width/lower glume length = 0.13–0.18), greenish on the central part surrounded by yellowish; upper glume 6.6–8.4 × 1.4–1.8 mm long (ratio -- upper glume width/upper glume length = 0.19–0.26), greenish or sometimes purplish on the central part, surrounded by part hyaline or yellowish; rachilla segment between first and second floret with hairs 4.5–5.7 mm long. Lemmas (6.7–)7–8.5 mm long × 0.5–0.8(–1) mm wide, narrowly elliptic to narrowly lanceolate (ratio -- lemma width/lemma length = 0.14–0.24); awn 7–8.6 mm long, inserted 3.6-4.8 mm from the base (ratio -- awn insertion from the base length/lemma length = 0.5–0.6); callus with hairs 0.7–0.8(–1) mm long. Lodicules regularly toothed or with two straight acute lobules. Anthers 1.9–2.3 mm long. Figure 6.

Chromosome Number—Unknown.

Phenology—Flowering and fruiting from June to August.

Distribution and Habitat—Endemic to the Western Caucassus, from Eastern Turkey to Northern-Eastern Iran; at 1280-2000 m elevation; in acid rocks, under middle mountain forest canopy. Figure 7.

Specimens Examined—**GEORGIA. Samegrelo-Zemo Svaneti:** Caucasus centralis, in vicinitate oppidi Mestia, ad septentrionem versus, 43º2’N, 42º43’E, 28 Jul 1979, *Vasak s.n.* (M); Kutaisi Governorate, the gorge of the Ingur, passage from the commune of Ipari to the commune of Kal, 43º0’N, 42º16’E, 28 Jul 1911, *Shelkovnikov s.n.* (TBI); the upper reach of the Vanistskali river, Khorogonskiy mountain mass, 25 Aug 1980, *Gagnidze s.n. & Mosulishvili* (TBI). **Racha-Lechkhumi and Kvemo Svaneti**: the upper reach of the Lukhuni river, 42º49’N, 43º20’E, 12 Jul 1981, *Chelidze s.n. & Shetekouri* (TBI).

RUSSIA. Karachay-Cherkessia: Teberda district, Teberda, 43º26’N, 41º44’E, 15 Jul 1981, *Mosulishvili s.n.* (MO); Teberda village, Karakul Lake, 43º26’N, 41º45’E, 30 Jul 2010, *Soreng 8009 & al.* (US); Teberda reserve, Teberda valley, 43º26’N, 41º44’E, 30 Jun 1993, *Onipchenko s.n.* (MW); Zelenchuk district, Arkhyz, Abishira-Akhuba Ridge, 43º33’N, 41º16’E, 15 Jul 1981, *Zernov 6527* (MW). **Kuban:** shore of Kara-gel Lake, 43º26’N, 41º44’E, 1 Jul 1907, *Endaurowa s.n.* (LE).

Notes—Trisetum rigidum is the most polymorphic taxon of the section and displays great morphological variation throughout its distribution area. The size, as well as the degree of indumentum of the leaf-blades and leaf-sheaths of this species, is a quite variable character.

Boissier (1846) named some small specimens from southwest Iran as *Avena daenesis*. Chrtek (1968) described an infraspecific taxon from the Demavand Mountains from northern Iran and named it *T. rigidum* subsp. *demavandense* Chrtek; it was separated from *T. rigidum sensu stricto* for its smaller size [(8)10–20(–38) cm tall], congested panicles, and larger paleas [(5–)6–7.5 mm long]. However, the studied specimens of *T. rigidum* are extremely variable in size (15.5–60 cm tall), as previously noted, and the paleas [(4–)4.5–6(–6.6) mm long] do not differ significantly from those of *T. rigidum* subsp. *demavandense*. In specimens from the Elburz area and Demavand Mountains, size variability also occurs, including the type material of *T. rigidum* subsp. *demavandense* (*T. rigidum* f. *minor* in sched.). The easternmost specimens of *T. rigidum* studied are those collected by Haradjian from the Akher-Dagh Mountains [*Haradjian s.n.* (B-100526547) and *Haradjian 1619* (S)], which are very similar to those from the Demavand Mountains. As previously noted, the size has proved to be a variable character throughout the whole range of the species and has no taxonomic value. For this reason, the smaller specimens have been considered as synonyms of *T. rigidum*.

Chrtek (1968) described *Trisetum persicum* Chrtek from Luristan, in Southwestern Iran. The main characters used to separate this species are stronger panicles and short rachilla indumentum relative to lemma length. *Trisetum persicum* has lemmas that are 8.7 mm long and rachilla hairs that are 3.4–3.7 mm long, while *T. rigidum* has lemmas that are (5.3–)6.4–8.2(–9.3) mm long and rachilla hairs that are (3.2–)4–4.7(–5.7) mm long. It is important to note the morphological distinctiveness of the specimen collected by *Archibald 2984* (K) in Eastern Iran (the Bakhtiari region) with regard to the type of *T. persicum*, which has straight and pubescent leaf-blades with hairy margins and spikelets that are 8 mm long. Although these characters are distinctive, they fall well within their variation range in the species, and therefore we consider *T. persicum* to be a synonym of *T. rigidum.*

Trisetum rigidum var. *teberdense* Litv. has taller culms, wider leaves with hairs along the margins, and larger spikelets than *T. rigidum* subsp. *rigidum*. Kharadze (1938) combined it at the specific level, and after Tzvelev (1971), it has been considered a subspecies. *Trisetum rigidum* subsp. *teberdense* specimens have top leaf-blades that are (2.6–)3.3–5.7(–6.4) mm wide and pilose along the margins, whereas the studied specimens of *T. rigidum* subsp. *rigidum* have top leaf-blades that are (1–)1.8–3(–5.6) mm wide, abaxially and adaxially glabrous, and sometimes slightly pubescent, with short hairs along the margins. Because of that, we also consider it a subspecies of *T. rigidum*. Moreover, those specimens considered *T. teberdense* present similarities in the disposition of the leaves (parallel to the culm) with *T. buschianum* subsp. *buschianum*, which are more or less pubescent and with hairy margins; the rest of the characters of the panicle and, more precisely, those of the rest of the spikelets (ratio -- lower glume/upper glume, callus indumentum, etc.) are the same as in *T. rigidum*.

Owing to the polymorphism of this species, Kharadze (1938) described a new variety, *T. teberdense* var. *brevifolium,* here included as synonym of *Trisetum rigidum* subsp. *rigidum*. We have only been able to check photos of two of the syntypes. Kharadze's illustration (1938) shows similar traits in the glumes and callus hairs for both taxa. The habit does not differ significantly from specimens of *T. buschianum* subsp. *transcaucasicum*, with short top leaf-blades, and ovate to elliptic-oblong and purplish panicles, but with almost glabrous leaves, and hairs only along the margin as in *T. rigidum* subsp. *teberdense*. Further, more detailed studies are needed to verify the taxonomic value of this variety.

The tendency of this species to vegetative propagation (f. *vivipara* in sched.), with the transformation of floral bracts into true leaves, is noticeable in the specimens collected by *Alexeenko 5623* (LE) (Fig. 8).

5. TRISETUM BUSCHIANUM Seredin, Bot. Mat. (Leningrad) 21: 51. 1961.—TYPE: RUSSIA. Kabardino-Balkar Republic, Besengijskij Czerek, pr. fluminis Besenga, 43º07'N, 43º08'E, 10 Jul 1958, *R.M. Seredin s.n.* (holotype, LE!; isotype, PGFA).

Herbs (10.6–)17.2–28.7(–35) cm tall, not or loosely tufted, short rhizomatous or with stoloniferous rhizomes, culms (0.4–)0.6–0.8(–1.2) mm diam., glabrous; nodes (3)4–6(8), separated along the culm or concentrated in lower part, enclosed or not by the sheaths, glabrous. Basal leaf-sheaths pubescent to densely pubescent, rarely glabrous, with hairs 0.3–0.7(–1) mm long, yellowish to brownish, sometimes greenish; basal leaf-blades (1–)2.5–3.5(–4.7) cm long × (1.9–)2.3–3.2(–5.2) mm wide, flat, sometimes convolute or inrolled, pubescent to densely pubescent abaxially and adaxially, margins with hairs 0.1–0.8(–1.5) mm long, greenish to greyish; top culm leaf-sheaths (3–)4.6–7.6(–10) cm long, shorter or longer than the internodes, glabrous, very rarely with hairs on the upper part, without cilia; top culm leaf-blades (1.3–)1.8–5.7(–8) cm long × (1.8–)2.5–3.4(–5.2) mm wide, flat, sometimes conduplicate, parallel or pendicular to the culm, glabrous to slightly pubescent adaxially and abaxially, margins with hairs (0.05–)0.1–1(–1.3) mm long, greenish to greyish; inner collar region glabrous, margins with hairs (0.6–)0.9–1.3(–1.8) mm long; ligules (1.2–)1.5–2.1(–3) mm long, laciniate, rarely denticulate, glabrous, sometimes puberulous on the apex, rarely on the surface, with hairs 0.2–0.4(–1.2) mm long. Basal node of the panicle glabrous. Panicles (3.4–)4–7(–8.6) cm long × (1.3–)1.7–2.5(–3.4) cm wide, elliptic to oblong or ovate in outline, rarely lanceolate, lax to slightly dense; rachis glabrous to slightly pubescent, with hairs up to 0.1 mm long; longest basal branches (0.5–)0.8–1.3(–2.6) cm. Spikelets (5.5–)6.8–7.5(–8.5) mm long × (1.7–)2.7–4.3(–5) mm wide, 2-3-flowered; pedicels (1.5–)2–2.8(–4.7) mm long, glabrous to slightly pubescent, with hairs up to 0.1 mm long. Glumes unequal to subequal [ratio -- lower glume length/upper glume length = (0.69–)0.72–0.86(–0.94)]; lower glume (4–)4.7–5.5(–6.2) mm long × (0.8–)1–1.4(–1.8) mm wide, narrowly elliptic to narrowly lanceolate [ratio -- lower glume width/lower glume

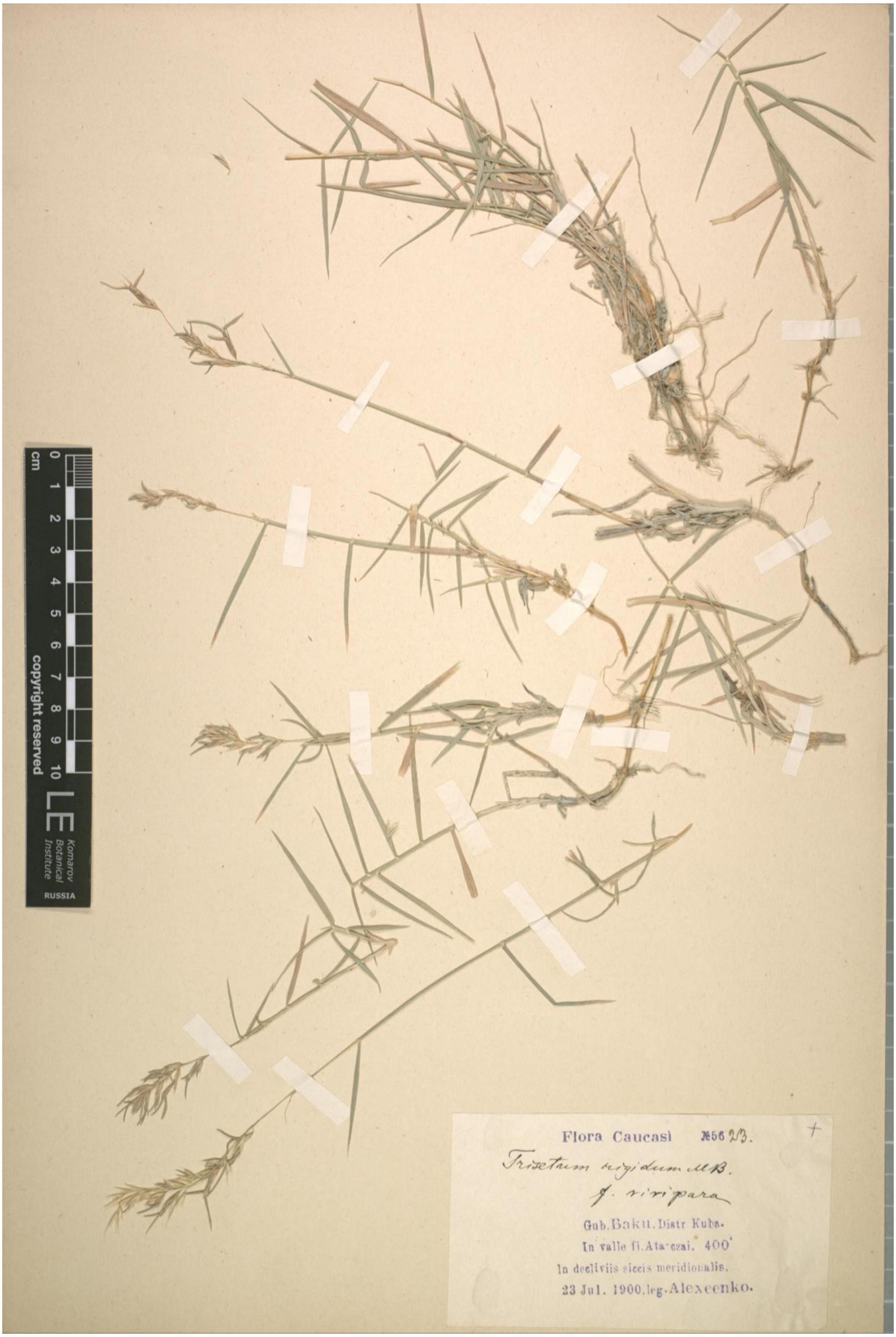

Figure 8. *Trisetum rigidum* subsp. *rigidum*. Specimen with proliferating spikelets, as a possible pseudoviviparous mechanism (*Alexeenko 5623*, LE).

length = (0.15–)0.21–0.29(–0.31)], acuminate, sometimes acute or long acuminate, 1–2(3)-nerved, glabrous, usually with hairs 0.05(–0.2) mm long on the upper part and margins, greenish to purplish; upper glume (5.2–)5.8–6.7(–7.1) mm long × (1.4–)1.8–2(–2.2) mm wide, narrowly elliptic to oblong, rarely lanceolate [ratio -- upper glume width/upper glume length = (0.21–)0.26–0.32(–0.38)], acuminate, sometimes long acuminate or acute, 3-nerved, glabrous, with very short hairs up to 0.05(–0.2) mm long from the middle to the upper part of the central nerve and upper part of the margins, greenish to purplish; rachilla segments between first and second floret 1–1.3(–1.6) mm long, with hairs (2.3–)3–3.6(–4.2) mm long; rachilla segments to sterile floret (0.6–)1.4–1.8(–2.3) mm long, with hairs (1.3–)1.7–2.3(–2.7) mm long. Lemmas (4.7–)5.6–6.1(–6.5) mm long × (0.8–)1–1.4(–1.8) mm wide, elliptic to oblong or broadly lanceolate, sometimes narrowly elliptic or narrowly lanceolate [ratio -- lemma width/lemma length = (0.18–)0.23–0.28(–0.33)], scabridulous, sometimes glabrous, with hairs up to 0.1(–0.3) mm long on the apex and margins, greenish, sometimes yellowish, surrounded by purple; apical teeth (0.1–)0.3–0.5(–0.9) mm long, with aristules (0.1–)0.4–0.6(–1) mm long; awn (5–)5.6–6.8(–7.8) mm long, inserted (2–)2.5–3.1(–3.3) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.36–)0.43-0.51(–0.53)], geniculate near the base, rarely straight, not or slightly recurved to twisted, with adpressed hairs up to 0.1 mm long; callus 0.2–0.4 mm long, elliptic, sometimes oblong, with hairs (0.5–)1.2–2(–2.3) mm long. Paleas (4–)4.4–5.3(–6) mm long × (0.8–)1–1.4 mm wide [ratio -- palea length/lemma length = (0.7–)0.78-0.91(–0.94)], elliptic, sometimes slightly oblanceolate, rarely narrowly elliptic or oblong, with hairs on the upper part of the outer edges; keels with short hairs from the middle to the upper part, ending in teeth 0.2–0.4(–0.5) mm long. Lodicules (0.4–)0.6–0.8(–1) mm long. Anthers (1.6–)2–2.5(–2.7) mm long. Ovary 0.5–0.7(–1) mm long, glabrous, sometimes with hairs 0.1–0.4 mm long on the apex. Caryopsis 1.8–2.2 mm long × 0.4–0.6 mm wide.

a. subsp. BUSCHIANUM

T. rigidum var. *molle* Somm. & Levier, Trudy Imp. S.-Peterburgsk. Bot. Sada 16: 444. 1900.—TYPE: RUSSIA. Karachayevo-Cherkesiya, monte Elbrus, flumen Kükürtli, 43º21’N, 42º22’E, 10 Sep 1890, *C.P.S. Sommier & E. Levier 1359* (lectotype, here designated, FI!; isolectotypes, G-442508!, LE!).

T. transcaucasicum var. *ciliatifolium* Seredin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 55. 1961.—TYPE: RUSSIA. Digorsky District, Karagom river, 43º9’N, 43º39’E, 11 Aug 1925, *E. Busch & N. Busch 37* (holotype, LE!).

Herbs (17–)23.7–30.7(–35) cm tall, culm diam. 0.6–0.9(–1.2) mm; nodes 4–7, separated along the culm, mostly not enclosed by the sheaths. Basal leaf-sheaths pubescent to densely pubescent, with hairs 0.4–0.8(–1) mm long; basal leaf-blades (1.3–)2.7–3.4(–4.7) cm long × 2.3–3.3(–4.7) mm wide, flat, sometimes convolute when dried, pubescent to densely pubescent adaxially and abaxially, margins with hairs 0.6–1(–1.5) mm long; top culm leaf-sheaths (6–)6.7–9(–10) cm long, shorter than the internodes;

top culm leaf-blades (1.8–)2.5–5.7(–8) cm long × (2.5–)3–4.1(–5.2) mm wide, parallel to the culm, sometimes enclosing it or arriving to the panicle, glabrous to slightly pubescent adaxially and abaxially, with hairs (0.3–)0.7–1.1(–1.3) mm long, also on the margins; ligules (1.4–)1.6–2.1(–2.7) mm long, laciniate, rarely denticulate, glabrous, puberulous on the apex and rarely on the surface with hairs 0.2–0.6(–1.2) mm long. Panicles (4.2–)5.2–7.4(–8.6) cm long × 1.3–2.6(–3.4) cm wide, oblong to elliptic in outline, slightly dense; longest basal branches (0.6–)0.7–1.3(–1.7) cm. Lower glume acuminate, sometimes acute, 1(2–3)-nerved, greenish surrounded by purplish on the laterals; upper glume acuminate, sometimes acute, 3-nerved, greenish surrounded by purplish. Lemma apical teeth (0.3–)0.4–0.6(–0.9) mm long, with aristules (0.1–)0.3–0.6(–0.7) mm long; awn 5–6(–7.2) mm long, slightly or not recurved and more or less geniculate near the base, rarely straight; callus with hairs (0.5–)1–1.8(–2) mm long. Lodicules with apex bilobate. Anthers (2–)2.3–2.7 mm long. Figure 9.

Chromosome Number—Unknown.

Phenology—Flowering and fruiting from June to September.

Distribution and Habitat—Endemic to West and Central Caucassus; at 1980–2900 m elevation; in stony slopes, on moraines. Figure 10.

Specimens Examined—**GEORGIA. Mtskheta-Mtianeti:** Pirikiti Khevsureti, v. Arkhoti Netkhecho, 42º35’N, 44º51’E, 19 Jul 1938, *Grigoraschvli s.n.* (MA); Kasbek, 17 Sep, *Meyer 60* (LE); GroBer Kaukasus, Talweitung des T´ruso-Tales, westlich der Schluchtstrecke, 2.7-3.4 km W bis WNW Zemo Ok´rokana oder 7,2-7,9 km WNW Kobi, 42º35’N, 44º25’E, 23 Jul 1997, *Schönswetter s.n.* & *Tribsch* (WU). **RUSSIA. Kabardino-Balkar Republic:** Sukan River, between Aylangen-tash and Sukan-bashi-tsyfi natural landmarks, 27 Jul 1931, *Bush s.n.* & *Bush* (LE); Sukan, 30 Jun 1927, *Bush s.n.* & *Bush* (LE); Sukan, Altulany-bau-bashi, south slope between Ogary-vtsek and Kysyrtsy-kaya, 23 Jul 1931, *Bush s.n.* & *Bush* (LE); upwards of Mystilyar-agach, 5 Jul 1913, *Bush s.n.* & *Bush* (LE); adjoining Ullu-Guluku plane, 43º4’N, 43º15’E, 10 Jul 1913, *Bush s.n.* & *Bush* (LE); Shaurtu glacier, 43º7’N, 43º1’E, 25 Jul 1913, *Bush s.n.* & *Bush* (LE); Bezengi glacier, 43º6’N, 43º9’E, 5 Aug 1913, *Bush s.n.* & *Bush* (LE); Bezengi glacier, 43º6’N, 43º9’E, 14 Aug 1911, *Bush s.n.* & *Bush* (LE); lower edge of Bezengi glacier, 43º6’N, 43º9’E, 4 Jul 1913, *Bush s.n.* & *Bush* (LE); Bezengi glacier, on the left bank of the Bezengi River, 43º6’N, 43º9’E, 6 Jul 1913, *Bush s.n.* & *Bush* (LE); by Bezengi glacier, 43º6’N, 43º9’E, 25 Jul 1892, *Bush s.n.* & *Bush* (LE); Sukan, moraines of Sukan-bashi-ullu-chiran glacier, 30 Jun 1927, *Bush s.n.* & *Bush* (LE); by the left side of Mizhirgi glacier, 43º3’N, 43º10’E, 8 Jul 1913, *Bush s.n.* & *Bush* (LE); Kulak glacier, upwards of Chegem, 43º9’N, 43º1’E, 27 Jul 1913, *Bush s.n.* & *Bush* (LE); Mizhirgi glacier, 43º3’N, 43º10’E, 16 Aug 1911, *Bush s.n.* & *Bush* (LE). **Karachay-Cherkess Republic:** glacier Kukurtlu, 43º21’N, 42º22’E, 13 Aug 1961, *Macha s.n.* (MW); western foothills of Mount Elbrus, River basin Bitik-tyubyu, near the mineral springs, 43º24’N, 42º21’E, 31 Jul 2008, *Zernov 6934* (MW); Karachai district, River Gorge Kukurtlu, left side, about 200 m from the edge Pednika, 43º21’N, 42º22’E, 3 Aug 2009, *Zernov 7263* (MW). **North Ossetia:** Digoria, the Sanguti glacier, 42º49’N, 43º49’E, 12 Jul 1914, *Gladkov 22* (LE).

b. subsp. TRANSCAUCASICUM (Seredin) Mosul., Zametki Sist. Geogr. Rast. 42: 34. 1991. *Trisetum transcaucasicum* Seredin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 54. 1961.—TYPE: AZERBAIJAN. Quba District, Tufan Dag Mountain, 41º09’N, 47º59’E, 13 Aug 1935, *J. Karjagin s.n.* (holotype: LE!; isotypes: GH!, MW!).

T. buschianum var. *kasbeghi* Seredin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 53. 1961.—TYPE: GEORGIA. Mount Kazbek, near Devdorak glacier, 42º41’N, 44º31’E, 3 Jul 1916, *P. Krylov & E. Steinberg s.n.* (holotype: LE!).

T. rigidum var. *ovale* Somm. & Levier, Trudy Imp. S.-Peterburgsk. Bot. Sada 16: 444. 1900.—TYPE: RUSSIA. Karachayevo-Cherkesiya, monte Elbrus, flumen Kükürtli, 43º20’N, 42º23’E, 10 Sep 1890, *C.P.S. Sommier & E. Levier 1359* (lectotype, here designated, FI!; isolectotype: LE!).

Herbs (10.6–)13.6–18.6(–22.6) cm tall, culm diam. 0.4–0.7 mm; nodes (3)4–5(8), concentrated in lower part of the culm, enclosed by the sheaths. Basal leaf-sheaths densely pubescent with hairs 0.3–0.5 mm long, rarely glabrous; basal leaf-blades (1–)2.3–3(–3.4) cm long × (1.9–)2.1–2.9(–3.8) mm wide, flat, sometimes enrolled when dried, pubescent to densely pubescent abaxially and adaxially, margins with hairs (0.1–)0.2–0.6(–0.7) mm long, greyish to greenish; top culm leaf-sheaths (3–)3.6–6.2(–7.3) cm long, longer than the internodes, sometimes shorter; top culm leafblades (1.3–)1.5–2.1(–2.6) cm long × (–1.9)2.1–2.7(–3.4) mm wide, sometimes conduplicate, perpendicular or parallel to the culm, glabrous to slightly pubescent abaxially and adaxially, margins with hairs (0.05–)0.1–0.6(–1.3) mm long; ligules (1.2–)1.7–2(–3) mm long, laciniate, glabrous, rarely with few hairs up to 0.3 mm on the apex. Panicle (3.4–)3.6–4.6(–7.1) cm long × (1.6–)1.8–2.5 cm wide, ovate to elliptic in outline, rarely lanceolate, lax to slightly dense; longest basal branches (0.5–)0.8–1.2(–2.6) cm. Lower glume acuminate, sometimes long acuminate or acute, 1(2)-nerved, dark purple to purplish, rarely greenish, laterals and upper part hyaline or yellowish; upper glume acuminate, sometimes long acuminate, rarely acute, greenish or purplish on the central part, laterals hyaline or yellowish. Lemma apical teeth (0.1–)0.2–0.4(–0.5) mm long, with aristules (0.2–)0.5–0.8(–1) mm long; awn (5.4–)6–7.3(–7.8) mm long, geniculate and twisted near the base; callus with hairs (1.2–)1.6–2.2(–2.3) mm long. Lodicules apex irregular or regular 2–4-lobed, sometimes with one of them lateral. Anthers (1.6–)2–2.3(–2.6) mm long. Figure 9.

Chromosome Number—Unknown.

Phenology—Flowering and fruiting from July to September.

Distribution and Habitat— Endemic to the Central and Eastern part of the Caucassus; at 1740–3250 m elevation; in alluvial rocks and schists. Figure 10.

Specimens Examined—**AZERBAIJAN. Baku:** Kuba district, mons Tufan-Dag, 41º9’N, 47º59’E, 6 Aug 1935, *Karjagin s.n.* (B, GH, HBG); 6 Aug 1935, *Karjagin s.n.* (HBG); 31 Jul 1830, *Meyer s.n.* (LE); in m. Shach-Dagh, Buldurgan, 41º17’N, 47º59’E, 23 Aug 1929, *Sachokjia s.n.* (LE). **GEORGIA. Kakheti:** Großer Kaukasus, Zentralteil, Tush-Psav-Khevsureti, Omalo, im Bereich der Quellzuflüsse des Pirikita Alazani östlich des Azunta-Passes, 42º31’N, 45º19’E, 8 Sep 2009, *Zündorf 25658* & *Gerth* (JE). **Mtskheta-Mtianeti:** Ermani area, Fidar Volcano, 42º29’N, 44º16’E, 22 Aug 1940, *Dolukhanov s.n.* & *Mandenova* (LE); Greater Caucasus, Khevi, Kazbegi, Karkucha, 42º34’N, 44º40’E, 25 Aug 1997, *Gagnidze s.n.* & *al.* (W); Pirikiti Khevsureti, gorge Arhiele, bottom glacier Kidegana, 42º36’N, 44º52’E, Jul 1937, *Grigoraschvli s.n.* (MA); Großer Kaukasus, linksseitige Alluvionen des Flusses Terek zwischen Ach´khoti, P´anshet´i und Kazbegi, 42º38’N, 44º38’E, 23 Jul 1997, *Schönswetter s.n.* & *Tribsch* (WU); *Schneeweiß s.n.* (WU); Großer Kaukasus T´ruso-Schlucht 0.5-2.7 km WNW Zemo Ok´rokana, d.i. ca.5-7.2 km WNW Kobi, 42º36’N, 44º27’E, 23 Jul 1997, *Schönswetter s.n.* & *Tribsch* (WU); Großer Kaukasus, Zentralteil, Kasbek-(Mkinvarzweri) Massiv westlich Kasbegi, Aufstieg über die Tsminda Sameba, am Fuß des SO-Gletschers am Kasbek, 42º39’N, 44º33’E, 6 Aug 2007, *Zündorf 24247* (JE). **RUSSIA. Dagestan:** Dokuzparinsky district, Gora Shalbuzdag, 41º19’N, 47º48’E, 25 Sep 2006, *Kotseruba 56* (LE).

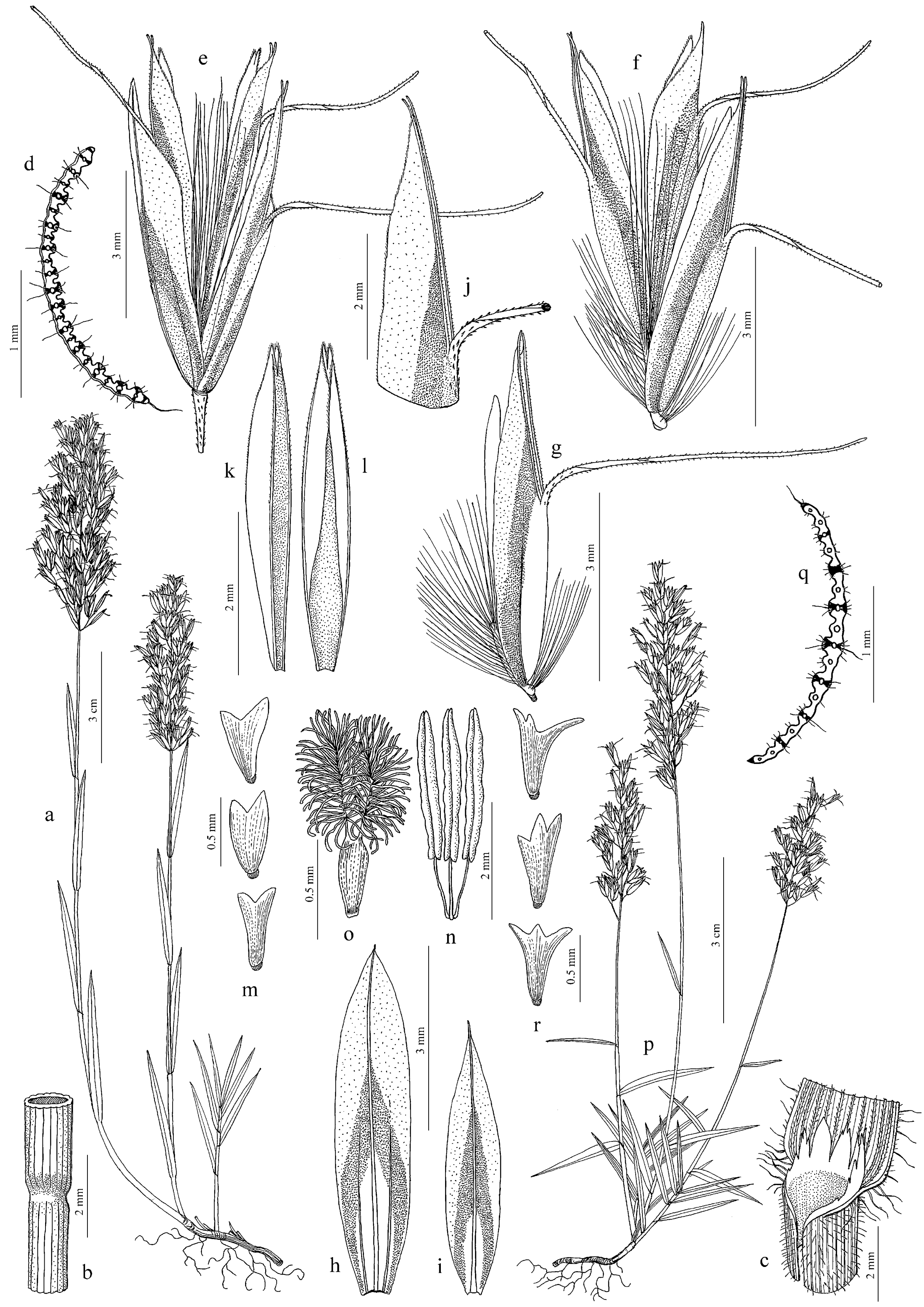

Figure 9. *Trisetum buschianum* subsp. *buschianum.* A. Habit. B. Portions of the culm and node. C. Sheath, ligule, and portion of the blade. D. Transverse section of leaf-blade. E. Spikelet. F. Florets. G. Floret. H. First glume, dorsal view. I. Second glume, dorsal view. J. Lemma, upper part, lateral view. K. Palea, dorsal view. L. Palea, ventral view. M. Lodicules.n. Stamens. O. Pistil. *T. buschianum* subsp. *transcaucasicum*. P. Habit. Q. Transverse section of leaf-blade. R. Lodicules. (*Lipsky s.n.,* LE, A; *Wisniewski s.n.,* K, B-O; *Bush & Bush 11, Meyer s.n.,* LE, M; *Karjagin s.n.,* HBG, P-R; *Meyer 59,* LE, R).

Notes—*Trisetum buschianum* is close to *T. rigidum*, having smaller panicles, usually dark purple, with lower and upper glumes similar in length, longer callus hairs and smaller ligules. *Trisetum rigidum* also has longer hairs on the rachilla segments between the first and second floret than *Trisetum buschianum* [(3.2–)4–4.7(–5.7) and (2.3–)3–3.6(–4.2) mm long, respectively] and longer lemmas [(5.3–)6.4-8.2(–9.3) and 5.6-6.2 mm long, respectively].

We have accepted the criterion of Mosulishvili (1991), and recognize *T. buschianum* and *T. transcaucasicum* at the subspecific level. Tzvelev (1976) commented about the closeness of these species and hinted that perhaps they should be treated as a subspecies. According to Du Riezt (1930), the subspecies of a species are commonly reciprocally intergrading, and their taxonomical delimitation is thus infinitely more arbitrary than that of the species; Stuessy (2014) recognized geography as a fundamental component for recognition of infraspecific taxa. *Trisetum buschianum* subsp. *buschianum* lives in the central Caucasus, and *T. buschianum* subsp. *transcaucasicum* in the central and eastern parts. These two subspecies overlap only in the central part, where there are transitional taxa such as *T. buschianum* var. *kasbeghi* and *T. transcaucasicum* var. *ciliatifolium*. *Trisetum buschianum* subsp. *transcaucasicum* is smaller and has shorter top culm leaf-blades than those of subsp. *buschianum.* The disposition of leaves is normally parallel to the culm and sometimes the leaves reach the panicle in subsp. *buschianum*, whereas the basal leaves are always perpendicular in subsp. *transcaucasicum*. *Trisetum buschianum* subsp. *transcaucasicum* has ovate to elliptic panicles, which are oblong to elliptic in subsp. *buschianum*.

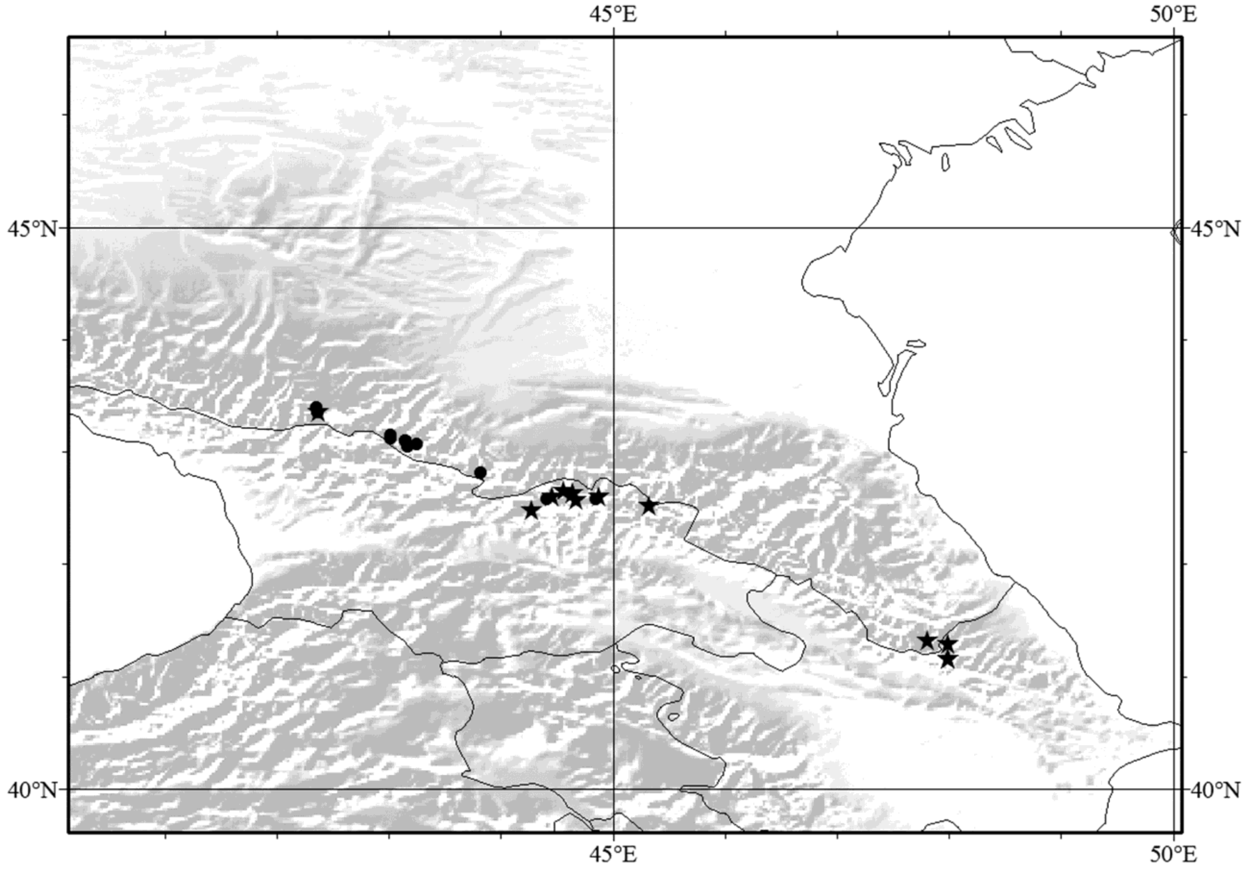

Figure 10. Distribution of *Trisetum buschianum* subsp. *buschianum* (dots) and *T. buschianum* subsp. *transcaucasicum* (stars).

6. TRISETUM VELUTINUM Boiss., Elench. Pl. Nov.: 88. 1838. *Avena velutina* (Boiss.) Nyman, Consp. Fl. Eur.: 812. 1882. *Trisetaria velutina* (Boiss.) Paunero, Anales Jard. Bot. Madrid 9: 512. 1950.—TYPE: SPAIN. Granada, Sierra Nevada, 37º03'N, 3º29'W, Aug 1837, *E. Boissier 187* [lectotype, designated by Burdet & al. (1981: 580), G-176291!; isolectotypes: B-100250154!, G-176292!, G-176293!, G-176294!, G-176295!, G-176296!, G-176297!, G-439749!, GH!, GOET-6971!, H!, JE-18835!, K-808725!, K-808726!, LE!, M-210840!, MA-8011!, NY!, P-2222135!, P-2222141!, P-2222145!, P-2222149!, S-12-12490!, S-13-33131!, SI-30137!, W-1889-0242141!].

T. cavanillesianum Borja & Font Quer, Anales Jard. Bot. Madrid 6: 494. 1946. *Trisetum velutinum* subsp. *cavanillesianum* (Borja & Font Quer) O. Bolòs & Vigo, Fl. Països Catalans 4: 476. 2001.—TYPE: SPAIN. Valencia, sierra de la Murta, cumbres del "Cavall Vernal", 39º9'N, 0º21'W, *J. Borja s.n.* (lectotype, here designated, MA-8010!).

Herbs (16–)25.5–51(–68) cm tall, not or loosely tufted, shortly rhizomatous or with stoloniferous rhizomes, culms (0.25–)0.4–0.8(–1) mm diam., glabrous, rarely slightly puberulous on the upper part, with hairs 0.1 mm long; nodes (4)6–10(11), more or less concentrated in lower part of the culm, enclosed by the sheaths except the upper ones, slightly puberulous or glabrous. Basal leaf-sheaths densely pubescent, with hairs (0.3–)0.8–1.2(–1.5) mm long, greyish to greenish or yellowish to brownish; basal leaf-blades (2.8–)3.3–6.6(–7.4) cm long × (1.3–)2.3–4(–4.8) mm wide, flat to slightly enrolled when dried, densely pubescent abaxially and adaxially, usually longer adaxially, with hairs 0.1–1(–1.2) mm long, greyish to greenish; top culm leaf-sheaths (4.8–)7.2–14(–17) cm long, shorter than the internodes, sometimes longer, glabrous to puberulous, with adpressed hairs, normally with cilia along the margins; top culm leaf-blades (0.3–)1.5–3.4(–4) cm long × (1–)1.2–2(–2.2) mm wide, inrolled along the margins, sometimes parallel to the culm, densely pubescent abaxially, from glabrous to densely pubescent adaxially, with hairs up to 0.2 mm long, greenish to greyish; inner collar region glabrous or with the same indumentum as the leaf-blade, sometimes with hairs 0.1(–0.2) mm long along the margins; ligules (0.5–)1.4–2(–2.5) mm long, laciniate to slightly laciniate, slightly pubescent to pubescent, usually densely on the apex, with hairs (0.05–)0.1–0.4(–0.6) mm long. Basal node of the panicle glabrous or very slightly puberulous, with hairs less than 0.1 mm long. Panicles (4–)5.9–10.5(–15) cm long × (0.7–)1–2.6(–3.6) cm wide, narrowly elliptic to narrowly or broadly lanceolate in outline, sometimes linear, lax to slightly dense with most rachis internodes plainly visible; rachis glabrous to slightly pubescent, with hairs up to 0.1 mm long; longest basal branches (0.4–)0.5–1.4(–3) cm. Spikelets (5–)6.4–8.5 mm long × (1–)2–2.6(–3.2) mm wide, 2(3)-flowered; pedicels (1.7–)2.3–4(–6.5) mm long, pubescent to slightly pubescent, rarely glabrous, with hairs up to 0.1 mm long. Glumes unequal to subequal [ratio -- lower glume length/upper glume length = (0.71–)0.78–0.8(–0.85)]; lower glume (3.5–)4.6–5.6(–6.2) mm long × (0.7–)1–1.1(–1.4) mm wide, narrowly lanceolate, sometimes broadly lanceolate, rarely narrowly elliptic [ratio -- lower glume width/lower glume length = (0.11–)0.17–0.23(–0.29)], acuminate, sometimes long acuminate, 1(3)-nerved, glabrous, with very short hairs on the midrib up to 0.08 mm long, sometimes on the upper part of the margins, greenish to yellowish on the central part, laterals and upper part hyaline; upper glume (4–)5.7–7.2(–8) mm long × (1.4–)1.6–1.7(–2) mm wide, oblong to lanceolate or narrowly elliptic to narrowly lanceolate, rarely slightly oblanceolate or elliptic [ratio -- upper glume width/upper glume length = (0.2–)0.25–0.28(–0.34)], acuminate, usually acuminate, 3-nerved, glabrous, with very short hairs up to 0.05 mm long from the middle to the upper part of the central nerve and upper part of the margins, greenish to yellowish on the central basal part, usually also the central nerve, laterals and upper part hyaline or yellowish; rachilla segments between first and second floret 1–1.8 mm long, with hairs (0.3–)0.7–1.6(–2.4) mm long; rachilla segments to sterile floret (0.8–)1.7–2.4(–3) mm long, with hairs (0.3–)0.6–1(–1.5) mm long. Lemmas (4–)5.4–6.6(–7.8) mm long × (0.7–)1–1.1(–1.4) mm wide, narrowly elliptic or elliptic to narrowly lanceolate, rarely oblong or slightly oblanceolate [ratio -- lemma width/lemma length = (0.14–)0.19–0.27(–0.37)], glabrous to strigulose, yellowish to greenish; apical teeth 0.2–0.4(–0.9) mm long, with aristules (0–)0.3–0.8(–2.5) mm long; awn (5–)6–7.6(–9.3) mm long, inserted (1.3–)2–2.6(–5) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.25–)0.34–0.43(–0.64)], slightly twisted and more or less geniculate near the base, rarely straight, with very short adpressed hairs 0.03 mm long; callus (0.1–)0.2–0.3(–0.4) mm long, elliptic to orbicular or oblong, with hairs 0.25–0.5(–0.7) mm long. Paleas (2.4–)4.2–5.1(–6.1) mm long × (0.6–)0.75–1.5 mm wide [ratio -- palea length/lemma length = (0.36–)0.76–0.83(–0.89)], narrowly elliptic, sometimes elliptic, slightly hairy on the upper part of the outer edges; keels with short hairs mostly on the apex, ending in teeth (0.1–)0.3–0.4 mm long. Lodicules (0.4–)0.5–1(–1.6) mm long, with apex irregularly dentate or 2-lobed, rarely with scattered hairs. Anthers (1.6–)2–3.1(–4) mm long. Ovary (0.4–)0.6–1.2(–1.5) mm long, glabrous, rarely with some hairs on the apex up to 0.2 mm long. Caryopsis 1.9–2 mm long × 0.5–0.6 mm wide. Figure 11.

Chromosome Number—*n* = 14 (Devesa & Romero Zarco, 1984).

Phenology—Flowering from June to August.

Distribution and Habitat— Endemic to South-eastern and Eastern Spain; at 400-2280 m elevation; in fissures of limestones and dolomitic sand soils, on open places. Figure 3.

Specimens Examined—**SPAIN. Albacete:** Ayna, mirador sobre la piscina, 38º33’N, 2º3’W, 20 Jul 1984, *Luceño s.n.* (MA); barrancos del río Mundo, Ayna, 38º33’N, 2º4’W, 11 Jul 1971, *Rivas Goday s.n. & al.* (VAL). **Alicante:** Quatretonda, Serra de Serrella, Les Frares, 38º42’N, 0º17’W, 30 Jun 1997, *Solanas s.n. & al.* (ABH); Sierra de la Safor, Vall de Gallinera, 38º51’N, 0º14’W, 15 Jun 1997, *Soler 7265JXS & Signes* (MA); Castell de Castells (Marina Alta), serra d´Alfaro, 38º44’N, 0º13’W, 7 Jul 1997, *Soler JXS-7339 & Signes* (VAL). **Granada:** Sierra Nevada, Monte Dornajo, 37º7’N, 3º26’W, 15 Jul 1851, *Bourgeau 1519* (G, GOET, K, LE, P, S); Jul 1891, *Porta 648 & Rigo* (B, FI, G, JE, K, M, MA, NY, P, S, W, WU); 30 Sep 1975, *Fernández Casas 963B* (MA); ad Dornajo et Tesoro, 37º26’N, 3º37’W, Jul 1879, *Huter 1171 & al.* (B, K, GB, L, LE, M, MPU, P, PR, WU); Sierra Nevada, pico del Tesoro, 37º5’N, 3º27’W, 14 Aug 2011, *Aedo 18599* (MA); Sierra Nevada, pico Trevenque, 37º4’N, 3º28’W, 13 Jul 1986, *Aedo s.n.* (MA); 37º4’N, 3º28’W, 25 Jul 2013, *Barberá 941 & al.* (MA); *Barberá 942 & al.* (MA); VII, *Del Campo 93* (GB, GH, H, LE, M, MA, MPU, O, P, S, W); 16 Jun 1852, *Del Campo 98* (B, L, MPU, P); 11 Jul 1990, *Wagenitz 4707 & Hellwig* (GOET, JE); Trevenque, Canal de Huenes, 37º5’N, 3º31’W, 20 Jul 1974, *Charpin s.n. & Fernández Casas* (B, C, M, MA, NY); Sierra Nevada, Alayos de Dilar, Corazón de la Sandia, 37º3’N, 3º30’W, Jul 1996, *Bruno Navarro s.n.* (GDA); Sierra Nevada, Barranco de las Víboras, 37º7’N, 3º27’W, 16 Jul 1981, *Romero C170/81* (SEV); Sierra Nevada, Hoya de la Mora, 37º5’N, 3º22’W, 28 Jul 1967, *Segura Zubizarreta s.n.* (MA); Sierra de Alfacar, 37º14’N, 3º33’W, 2 Jul 1878,

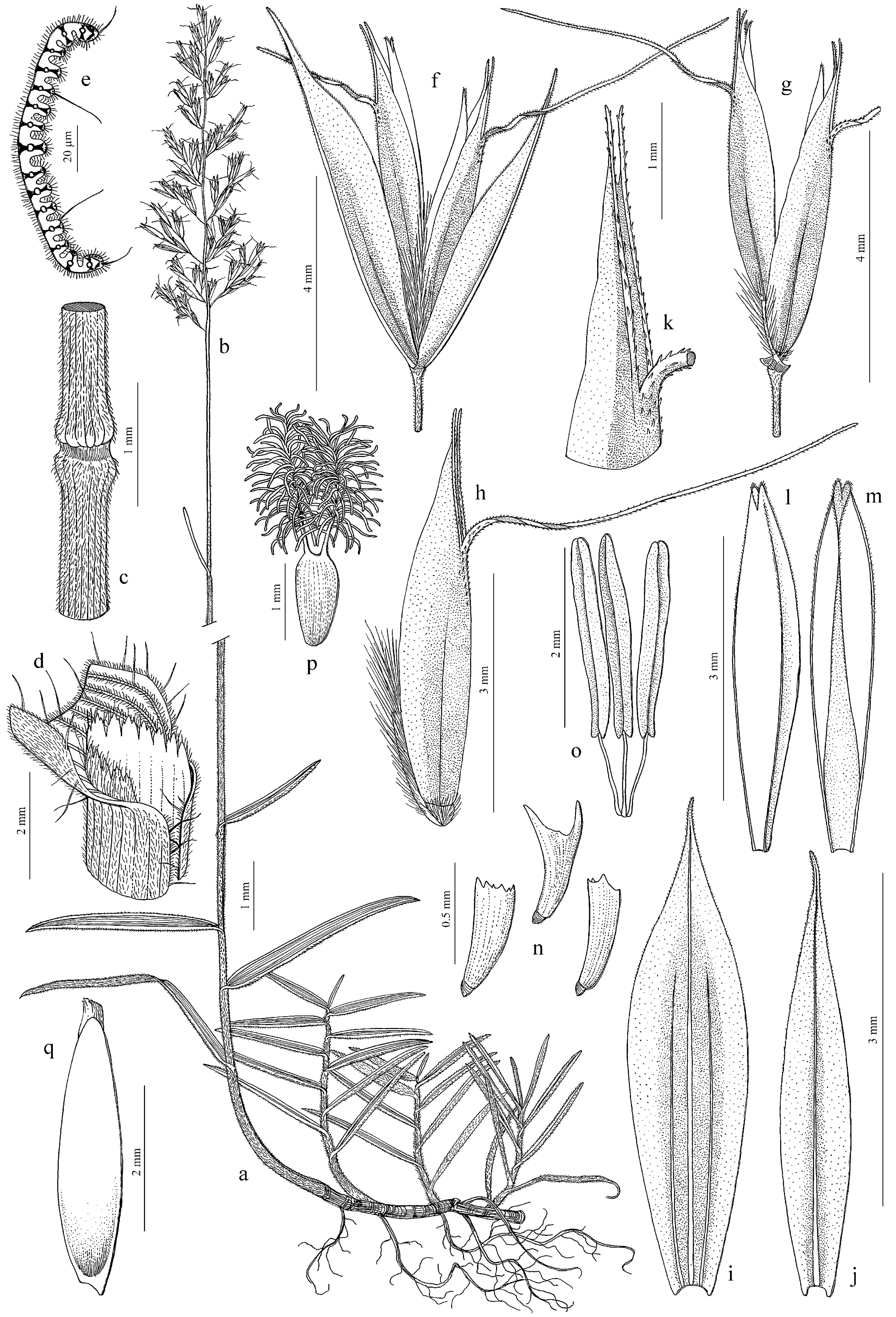

Figure 11. *Trisetum velutinum*. A. Habit. B. Inflorescence. C. Portion of the culm and node. D. Sheath, ligule, and portion of the blade. E. Transverse section of leaf-blade. F. Spikelet. G. Florets. H. Floret. I. First glume, dorsal view. J. Second glume, dorsal view. K. Lemma, upper part, lateral view. L. Palea, dorsal view. M. Palea, ventral view. N. Lodicules. O. Stamens. P. Pistil. Q. Caryopsis. (*Porta & Rigo 648*, B-100526421, MA-8015, A-D, F-M, O-Q; *Signes & Soler 7339*, VAL-218705, E; *Cuatrecasas & Font Quer s.n.*, BC-878863, *Riera 3729*, VAL-37841, N).

Hegelmaier s.n. (JE, P); Sierra de Jatar, 36º56’N, 3º54’W, 13 Jul 1977, *Litzler 77/765E* (MPU); Sierra Almijara, cerro del Lucero, 36º52’N, 3º53’W, 7 Aug 1978, *López 890GF* (MA); Lentegí, Sierra de Cázulas, 36º51’N, 3º47’W, 1 Jul 1978, *Martínez Parras s.n.* (MA); carretera de Murcia a 3 km del Puerto de la Mora, 37º16’N, 3º27’W, Jun 1986, *Morales s.n.* (GDA); Padul, camino de los Gudaris, 37º2’N, 3º34’W, 5 Jul 2000, *Morales s.n. & Baena* (GDA); Sierra del Manar, 37º2’N, 3º36’W, 18 Jun 1980, *Romero s.n. & Morales* (GDA); Sierra de Huetor, Pico Calabozo, 37º17’N, 3º26’W, 25 Jul 1978, *Romero s.n. & Valle* (GDA); Cogollos de la Vega, proximidades a Cortijo de los Asperones, 37º18’N, 3º31’W, 17 Jul 1988, *Socorro s.n. & al.* (GDA). **Málaga:** Cómpeta, Sierra de Cómpeta, 36º50’N, 3º56’W, 7 Jul 1973, *Cabezudo s.n.* & *Valdés* (SEV); 36º50’N, 3º56’W, 7 Jul 1973, *Valdés s.n. & al.* (MA); Sierra de la Tejeda, subida por Canillas del Aceituno, 36º53’N, 4º3’W, 19 Aug 1977, *López s.n.* (MA, SEV); 15 Jul 1981, *Romero s.n.* (B, BC, BCN, G, GDA, H, LE, MA, SEV, VAL, WU). **Valencia:** Serra de la Murta, Cavall Vernat, 39º9’N, 0º21’W, 10 Jul 1946, *Borja s.n.* (ARAN, BC, BCN, F, MA, SEV); Quatretonda, Umbría del Buixcarró, 39º0’N, 0º21’W, 12 Apr 1997, *Herrero-Borgoñón s.n.* (ABH, MA); Villalonga, Sierra de La Safor, 38º51’N, 0º15’W, 11 May 1996, *Herrero-Borgoñón s.n. & al.* (ABH); Buñol, El Fustal, 39º25’N, 0º50’W, 11 Jun 1994, *Laguna s.n.* (ABH); Buñol, Sierra de Malacara, umbría del Fresnal, 39º25’N, 0º38’W, 25 Jul 1991, *Laguna s.n.* (VAL); Fuente Umbría, Collado de Umán, Font de Roses, Buñol, 39º25’N, 0º56’W, 13 Aug 1990, *Laguna s.n. & Crespo* (VAL); Barig, 39º0’N, 0º18’W, Jun 1980, *Monsanet s.n. & Mateo* (VAL); Quatretonda, La Vall d´Albaida, ombria del Buixcarró, 39º0’N, 0º21’W, *Riera 3135* (VAL); Quatretonda (La Vall d´Albaida), els Cuderellets, 38º59’N, 0º22’W, 26 Jun 1996, *Riera 3151* (VAL); Moixent (La Costera), pr. l´Heura, 38º53’N, 0º48’W, 17 Jul 1997, *Riera 3719* (VAL); Moixent (La Costera), bc. De la Falç, 38º53’N, 0º46’W, 17 Jul 1997, *Riera 3729* (VAL); Vilallonga de la Safor, Serra de la Safor, pr. Alt de la Safor, 38º51’N, 0º15’W, 12 Jul 2001, *Riera JRV-4480 & Andrés* (VAL); Simat de Valldigna, entre Les Foies y Mondúver, 39º1'N 0º17'W, 26 Apr 2015, *Barberá 1617 & Quintanar* (MA); Simat de Valldigna (La Safor), Les Foies, 39º1’N, 0º17’W, 2 Aug 1990, *Soriano 0917PS* (VAL); Quatretonda, Pista Els Corrals-Pinet (La Vall d´Albaida), 38º59’N, 0º20’W, 5 Jul 1991, *Soriano 1652PS* (VAL).

Notes—This species is clearly distinguished because of its velutinous leaves. Font Quer (1946) published certain specimens from the Eastern Iberian Peninsula as *Trisetum cavanillesianum*, without making any comparison with *T. velutinum*. The new species may have stood out for its smaller panicle and the general size of the plant, but *T. velutinum* is a highly variable species and we believe that *T. cavanillesianum* does not deserve any taxonomic recognition.

In *Trisetum velutinum* the formation of propagules in the inflorescence by pseudoviviparism has been observed (Pierce et al., 2003) in the specimen collected by *Barberá 1617* & *Quintanar* (MA). *T. velutinum* is one of the three species of the genus with pseudoviviparism; the others are the Canarian endemic *T. tamonanteae* Marrero Rodr. & S. Scholz and *T. rigidum*. According to Marrero & Scholz (2013), this phenomenon becomes intensified and affects the whole inflorescence when the plants bloom in especially humid climatic conditions. This situation is common in the habitat of these species.

7. TRISETUM TAMONANTEAE Marrero Rodr. & S. Scholz, Willdenowia 43: 47, 48 fig. 1, 49 fig. 2. 2013.—TYPE: SPAIN. Canary Islands, Fuerteventura, Pájara, Jandía, Pico de La Zarza, 28º06’02”N, 14º21’27”W, 11 Jun 1987, *A. Marrero s.n.* [holotype: LPA-24804 (image!); isotype: B].

Herbs 19–30(–32) cm tall, densely tufted, shortly rhizomatous, culms (0.5–)0.6–0.7 mm diam., pubescent, with hairs 0.2–0.3(–0.5) mm long; nodes 5–10, separated along the culm, enclosed by the sheaths, rarely exposed, glabrous, rarely with some hairs. Basal leaf-sheaths densely pubescent, rarely the oldest ones glabrous, with hairs 0.4–0.8 mm long, yellowish to brownish, rarely greyish; basal leaf-blades (3.2–)4.7–9.3(–12.2) cm long × (1.3–)1.7–3 mm wide, scattered or distichous in juvenile culms, flat, sometimes enrolled when dried, pubescent abaxially and adaxially, margins with hairs 0.2–0.5 mm long, yellowish to brownish; top culm leaf-sheaths (2.6–)3.8–5.7(–6.5) cm long, longer than the internodes, sometimes shorter, pubescent to densely pubescent, without adpressed hairs and cilia along the margins; top culm leaf-blades (2–)2.7–10(–14) cm long × 2.8–4.5(–6) mm wide, flat, usually reaching or surpassing the panicle, pubescent to densely pubescent abaxially and adaxially, with adpressed and not adpressed hairs, with hairs on the margins up to 0.3 mm long, greenish to greyish, sometimes brownish; inner collar region with the same indumentum as the leaf-blade, with scattered hairs 0.5–1.3 mm long along the margins; ligules (0.8–)1–1.4 mm long, laciniate to slightly laciniate, glabrous. Basal node of the panicle glabrous. Panicles 3–7.7(9.7) cm long × (1.2–)1.4–1.7(–2) cm wide, narrowly to broadly lanceolate in outline, sometimes from narrowly elliptic to oblong, slightly dense, with most rachis internodes plainly visible; rachis densely pubescent, sometimes pubescent, with hairs up to 0.6 mm long; longest basal branches (0.3–)0.5–1.4 cm. Spikelets 4.5–5.8 mm long × 2.7–4 mm wide, (2)3–5-flowered; pedicels (1–)1.7–2.4(–3.7) mm long, pubescent, with hairs up to 0.3 mm long. Glumes unequal to subequal [ratio -- lower glume length/upper glume length = (0.75–)0.77–0.88(–0.91)]; lower glume 3.2-4.5 mm long × 0.7–0.8(–1) mm wide, narrowly lanceolate to narrowly elliptic [ratio -- lower glume width/lower glume length = 0.18–0.22(–0.3)], acute to acuminate, rarely long acuminate, 1(2)-nerved, glabrous, with some hairs on the main nerve up to 0.2 mm long, greenish on the central part, sometimes yellowish, rest hyaline; upper glume 4–5.7(–6) mm long × 1.2–1.4 mm wide, oblanceolate, sometimes elliptic or lanceolate (ratio -- upper glume width/upper glume length = 0.2–0.33), acuminate, sometimes acute, 3-nerved, glabrous, with short hairs up to 0.2 mm long on the central nerve, sometimes also on the margins, greenish on the central part, the remaining hyaline; rachilla segments between first and second floret (0.3–)0.5–0.6 mm long, with hairs 0.1–0.3(–0.7) mm long; rachilla segments to sterile floret 0.4–0.6(–0.8) mm long, with hairs 0.1–0.4 mm long. Lemmas (2.6–)3–4.3(–5.4) mm long × 0.7–0.8(–1) mm wide, oblong to elliptic, sometimes oblanceolate [ratio -- lemma width/lemma length = 0.25–0.38(–0.41)], strigulose, sometimes with short hairs on the aristules, longers on the midrib, up to 0.2 mm long, yellowish to greenish, sometimes brownish; apical teeth 0.2–0.5 mm long, with aristules 0.1–0.7(–0.9) mm long, rarely without aristules; awn (2.8–)3.4–5.1(–6.1) mm long, inserted (0.9–)1.1–2.1 mm from the base [ratio -- awn insertion from the base length/lemma length = (0.26–)0.3–0.4(–0.53)], straight, sometimes slightly twisted on the middle, with very short adpressed hairs 0.05 mm long; callus 0.1–0.2 mm long, elliptic to rounded, with hairs 0.1–0.3 mm long. Paleas 2.3–3 mm long × 0.6–0.8 mm wide [ratio -- palea length/lemma length = (0.56–)0.63–0.74], narrowly elliptic, sometimes oblanceolate, with short hairs along the outer edges; keels with short hairs, ending in teeth (0.1–)0.2 mm long. Lodicules (0.3–)0.4–0.6 mm long, with apex slightly bilobate, one of them lateral. Anthers 0.8–1.6(–1.8) mm long. Ovary 0.3–0.7(–0.8) mm long, glabrous. Caryopsis (1.6–)1.8–2(–2.2) mm long.

Chromosome Number—Unknown.

Phenology—Flowering from April to July.

Distribution and Habitat—Endemic to Jandía massif, Fuerteventura (Canary Islands); at 700–800 m elevation; in volcanic rock fissures and cracks. Figure 12.

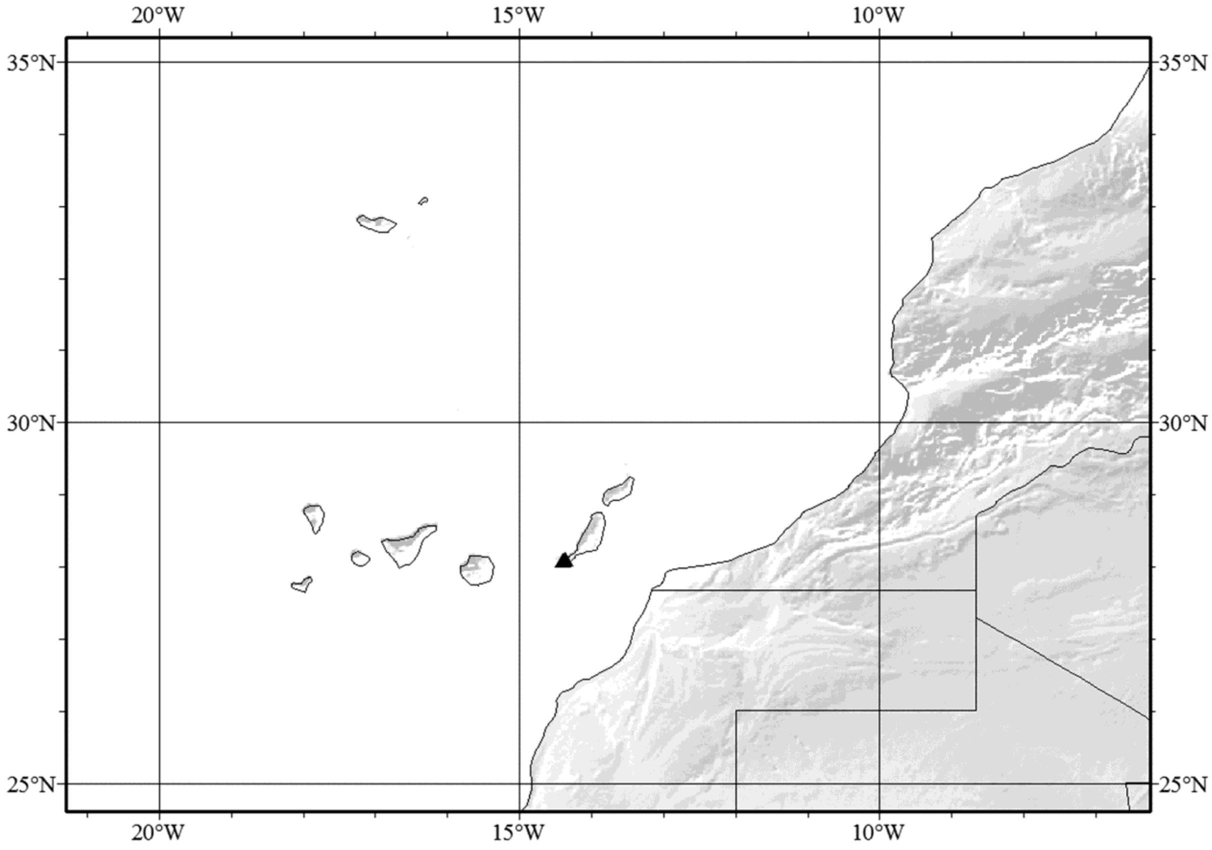

Figure 12. Distribution of *Trisetum tamonanteae*.

Specimens Examined—**SPAIN. Canary Is.:** Fuerteventura, Pájara, Jandía, Pico de La Zarza, 28º6'N, 14º21'W, 30 Mar 1989, *Marrero s.n.* (LPA, MA, P); 28º6'N, 14º21'W, 26 Jul 2000, *Marrero s.n. & Scholz* (LPA); 28º6'N, 14º21'W, 8 Apr 2000, *Marrero s.n. & Scholz* (LPA); entre el Pico de la Zarza y el Pico del Mocán, 28º6'N, 14º21'W, *Marrero s.n. & Scholz* (LPA); 8 Apr 2000, *Marrero s.n. & Scholz* (LPA, P); 8 Jul 2000, *Marrero s.n. & Scholz* (LPA); Pico de la Zarza, andén debajo del paloblanco, 28º6'N, 14º21'W, 8 Apr 2000, *Marrero s.n. & Scholz* (LPA); Pico de La Zarza, 28º6'N, 14º21'W, 17 Jul 1987, *Montelongo s.n.* (LPA); Pico del Fraile, 28º5'N, 14º23'W, Aug 2003, *Scholz s.n.* (LPA); Pico de la Zarza, El Esquinazo, 28º6'N, 14º21'W, Apr 2009, *Scholz s.n.* (LPA); Pico del Fraile, 28º5'N, 14º23'W, 25 Apr 1999, *Scholz s.n. & Almeida* (LPA).

Notes—This species has been included in this section provisionally and with hesitation, because only two specimens with distichous leaves in young shoots and culms have been observed; besides, *Trisetum tamonanteae* has unequal to subequal glumes, another typical character of this section. Marrero & Scholz (2013) separated this species from *T. argenteum*, *T. distichophyllum*, *T. macrotrichum*, and *T. velutinum* because these species present a glaucous-velutinous hairiness and all basal and top leaf-blades are clearly distichous. This is not the case in *T. tamonanteae*.

Doubtful and excluded names

Avena distichophylla Host—The IPNI web attributed to Host (1802) the name *Avena distichophylla.* Host (1802), however, when recorded *Avena distichophylla* repeated the polynomial of Villars and indicated "Vill. delph. 2. p. 144. t. 4", suggesting that he was not publishing a nom. nov. Consequently the name "*Avena distichophylla* Host" should be forgotten. *Avena distichophylla* is also attributed to Schrader by some authors [i.e. Roemer & Schultes 2: 666 (1817)]. The case is similar to the previously mentioned since Schrader in his Flora Germanica 1: 380 (1806) is only indicating the Villar's name, not describing a new species. Therefore, this name should be removed.

Avena distichophylla var. *genuina* Shuttlew., Mag. Zoo. Bot. 2: 17. 1838, nom. inval. (Art. 24.3).

Avena penicillata Willd. ex Steud., Nomencl. Bot., ed. 2, 1: 172. 1840, nom. nud., pro syn.

Avena rotae De Not. ex Parl., Fl. Ital. 1: 264. 1850, nom. nud., pro syn.

Trisetum carpaticum (Host) Roem. & Schult., Syst. Veg. 2: 663. 1817.—This forgotten name is based on *Avena carpatica* Host, Icon. Descr. Gram. Austriac. 4: 18, tab. 31. 1809 which, according to the Host's drawing, belongs to *Avenula pubescens* (Huds.) Dumort.

Trisetum gmelinii ["Gmelini"] Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(2): 15. Mar 1836, nom. inval. *Bromus cinereus* S.G. Gmel. ex Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4: 15. Mar 1836, pro syn. *Avena gmelini* (Trin.) Nyman, Suppl. Syll. Fl. Eur.: 71. 1865.—TYPE: SPAIN. in collibus siccis argillaico-sabulosis madriti, ex hb. Schreb. (lectotype, here designated, LE-TRIN-1893.1!). This specimen was send to Trinius by Schreber and there is no collector indicated in the label. It correspond to *Trisetaria scabriuscula* (Lag.) Paunero, a common species around Madrid.

Trisetum rigidum f. *minor* Kotschy, nom. nud., in sched. (P-2255865!).

Trisetum rigidum f. *colorata* Bornm., nom. nud., in sched. (B!).

Trisetum rigidum f. *major* Bornm., nom. nud., in sched. (BM-1134945!).

Trisetum rigidum f. *vivipara* T. Alex., nom. nud., in sched. (LE!).

ACKNOWLEDGEMENTS

This work was financed by *Flora iberica* CGL2014-52787-C3-1-P, CGL2012-32914 and CGL2015-66161-P, both projects of the Spanish Government. We are indebted to the curators and staff of the herbaria mentioned in Material and Methods for kindly providing specimens. We thank the editor and anonymous reviewers for their critical reviews of the manuscript and for their helpful suggestions during the editing process. We thank A. Quintanar for his revision of an earlier version of this manuscript. Ramón Morales for translations of manuscripts in German. Marta Fernández-Albert and Toni Buira for their technical support. Anne Martin and Maria Morck for their help with the English revision. Robert Vogt, Barina Zoltán, Francesco Zonca, Zbigniew Mirek, Manana Khutsishvili, and Mats Hjertson helped in finding rare literature, type materials, and geographical localities.n. N. Tzvelev, Dmitry Geltman, Roman Ufimov, Elena Glazkova, Denis Melnikov, and the rest of the personal from the Komarov Institute for their help in many aspects and their welcoming attitude during our stay.

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SUPPORTING INFORMATION

Appendix 1. List of the quantitative characters measured.

Plant height (cm); Culm diameter (mm); Culm indumentum length (mm); Nodes number; Basal leaf-sheaths indumentum length (mm); Basal leaf-blades length (cm); Basal leaf-blades width (mm); Basal leaf-blades indumentum length (mm); Top culm leaf-sheaths length (cm); Top culm leaf-blades length (cm); Top culm leaf-blades width (mm); Top culm leaf-blades indumentum length (mm); Iner coller region indumentum length (mm); Ligules length (mm); Ligules indumentum length (mm); Basal nude of the panicle indumentum length (mm); Panicles length (cm); Panicles width (cm); Rachis indumentum length (mm); Longest basal branches length (cm); Pedicels length (mm); Pedicels indumentum length (mm); Spikelets length (mm); Spikelets width (mm); Number of flower per spikelet; Ratio -- lower glume length/upper glume length; Lower glume length (mm); Lower glume width (mm); Ratio -- lower glume width/lower glume length; Lower glume indumentum length (mm); Number of lower glume nerves; Upper glume length (mm); Upper glume width (mm); Ratio -- upper glume width/upper glume length; Upper glume indumentum length (mm); Number of upper glume nerves; Rachilla segments between first and second floret length (mm); Rachilla segments between first and second floret indumentum length (mm); Lemmas length (mm); Lemmas width (mm); Ratio -- lemma width/lemma length; Lemmas indumentum length (mm); Apical teeth length (mm); Aristules length (mm); Awn length (mm); Awn insertion from the base (mm); Awn insertion from the base length/lemma length; Awn indumentum length (mm); Callus length (mm); Callus indumentum length (mm); Palea length (mm); Palea width (mm); Ratio palea length/lemma length; Palea teeth length (mm); Lodicules length (mm); Anthers length (mm); Ovary length (mm); Caryopsis length (mm); Caryopsis width (mm).

Appendix 2. Index to numbered collections cited. The numbers in parentheses refer to the corresponding species in the text. Mixed collections are indicated by a slash (e.g. 1/2).

Abdaladze, O. et al. 332 (4.a), *409* (4.a); *Aedo, C. 18599* (6), *11798* (4.a); *Aellen, P. 1898* (4.a), *1982* (4.a); *Alexeenko, Th. 1101* (4.a), *392* (4.a), *5623* (4.a), *6104* (4.a), *7396* (4.a), *9071* (4.a); *Barberá, P. et al. 941PB* (6), *942PB* (6); *Bobrov, A.E. et N.N. Tzvelev 574* (4.a); *Boissier, E. 187* (6); *Bornmüller, J. 33* (4.a); *Bornmüller, J. et A. Bornmüller 8381* (4.a), *8382* (4.a), *8383* (4.a), *8384* (4.a), *8385* (4.a), *8385b* (4.a); *Borodin, I. 197* (4.a); *Bot. Exk. 447* (1), *740* (1); *Bourgeau, E. 1519* (6); *Castroviejo, S. et al. 11213SC* (1); *Charpin, A. 15786* (2), *19140* (1); *Charpin, A. et R. Salanar AC17607* (1); *Clarke, C.B. 48718* (1); *Danser, B.H. 5050* (1); *Del Campo, P. 93* (6), *98* (6); *Dersch, G. 4488* (2); *Dini-Arazm 12132* (4.a); *Dzens-Litovskaya, N. 99* (4.a); *Eckardt, T. 615* (1), *1056* (1); *Egeröd, K. 9034* (1); *Egorova, T.V. et al. 433* (4.a), *1477* (4.a); *Fernández Casas, F.J. 963B* (6); *Furse, P. 3141* (4.a); *Gagnidze, R. et al. 2524* (4.a), *2941* (4.a); *Gauba, D.E. 1243* (4.a); *Gladkov, I. 22* (5.a); *Grossheim, A. 76* (4.a); *Herrero, A. 2718* (4.a); *Holmberg, O.R. 974* (4.a); *Holtz, F. et al. 978* (4.a); *Hörandl, E. 1739* (1); *Huter, R. 1171* (2); *Huter, R. et al. 1171* (6); *Jacobs, J. 3893* (1); *Kalheber, H. 96-1385* (2); *Kolenati, F.A. 2204* (4.a); *Kotschy, TH. 391* (4.a), *393* (4.a); *Kotseruba, V.V. 30* (4.a), *56* (5.b); *Lachashvili, N. 189* (4.a); *Lippert, W. 26158* (2); *Litwinow, D.I. 257* (4.a), *2809* (4.a); *Litzler, P. 77/765E* (6); *López, G. 890 GF* (6); *Lütkemüller, J. 2253* (1); *Merxmüller, H. et W. Wiedmann 5533* (2), *5534* (2); *Meyer, C.A. 60* (5.a); *Milne-Redhead, E. 2316* (1); *Moutin, R. et J. Bernard 475* (1); *Müller, J. 10983* (2); *Nakhutsrishvili, G. et O. Abdaladze 103* (4.a); *Novopokrovskiy, I.V. 681*

(4.a); *Podlech, D. 42147* (1); *Poretskiy, A. et G. Shults 543* (4.a); *Porta, P. et G. Rigo 648* (6); *Prokhanov, Y.I. 339* (4.a); *Prokhanov, Y.I. et N.T. Cheldyshev 163* (4.a); *Raus, T. 4431* (4.a); *Rechinger, K.H. 40731* (4.a), *48369* (4.a), *57178* (4.a), *5891* (4.a), *6091* (4.a); *Rechinger, K.H. et F. Rechinger 6447* (4.a), *6509* (4.a); *Reverchon, E. et A. Derbez 255* (1); *Riera, J. 3135* (6); *Riera, J. 3151* (6), *3719* (6), *3729* (6); *Riera, J. et J.V. Andrés JRV-4480* (6); *Rigo, G. 1411* (2); *Romero, C. C170/81* (6); *Schiffers, E.V. et T.A. Moreva 5* (4.a); *Soler, J.X. et M. Signes 7265 JXS* (6), *JXS-7339* (6); *Sommier, S. et E. Levier 1359* (4.a/5.a/5.b); *Soreng, R.J. 8009* (4.b); *Soriano, P. 0917PS* (6), *1652PS* (6); *Stebler, F.G. et C.J. Schröter 114* (1); *Tatli, A. 4865* (4.a); *Tzvelev, N.N. et S. Cherepanov 160* (4.a); *Vasilchenko, I.T. et al. 668* (4.a); *Wagenitz, G. 1738* (1/2); *Wagenitz, G. et F. Hellwig 4707* (6); *Wendelbo, P. 1218* (4.a); *Woronow, G. 6256* (4.a); *Zernov, A.S. 6527* (4.b), *6934* (5.a), *7263* (5.a); *Zündorf, H.J. 24247* (5.b); *Zündorf, H.J. et A. Gerth 25658* (5.b).

CAPÍTULO III

Taxonomic revision of *Trisetum* section *Sibirica* (Poaceae: Pooideae: Aveninae)

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Published in *Systematic Botany* 42(4): 782-806 (2017)

***Abstract*—**A taxonomic revision of *Trisetum* sect. *Sibirica* is presented. We include descriptions and synonyms of each taxon from a study of 450 vouchers from 35 herbaria. Detailed morphometric descriptions, illustrations, distribution maps, identification key, and habitat data are given for each taxon. An identification key for all taxa of sect. *Sibirica* is provided. Morphometric variation of the main characters is shown by box-plots. Six names are lectotypified. We recognize six species of *Trisetum* into the section: *T. aeneum, T. bifidum*, *T. henryi*, *T. scitulum*, *T. sibiricum*, and *T. turcicum*. Two infraspecific taxa of *T. sibiricum* are recognized (*T. sibiricum* subsp. *sibiricum* and *T. sibiricum* subsp. *litorale*), while *T. pauciflorum*, *T. sikkimense*, and *T. umbratile* are reduced to synonymy of *T. sibiricum* subsp. *sibiricum*. Four of the six species of *Trisetum* sect. *Sibirica* are endemic to Eastern Asia and New Guinea, while *T. turcicum* grows in Turkey, Caucasus and North Iran, and *T. sibiricum* is widespread from Eastern Europe to Alaska and Canada.

Resumen—Se presenta una revisión taxonómica de *Trisetum* sect. *Sibirica*. Incluimos descripciones y sinónimos de cada taxon tras el estudio de 450 pliegos de 35 herbarios. Se proporcionan descripciones morfométricas detalladas, ilustraciones, mapas de distribución, clave de identificación y hábitat de cada taxon. Se proporciona una clave de identificación para todos los táxones de *Trisetum* sect. *Sibirica*. Se muestran las variaciones morfométricas de los principales caracteres en diagramas de caja. Se han lectotipificado seis nombres. Se reconocen seis especies de *Trisetum* en la sección: *T. aeneum*, *T. bifidum*, *T. henryi*, *T. scitulum*, *T. sibiricum* y *T. turcicum*. Se reconocen dos táxones infraespecíficos de *T. sibiricum* (*T. sibiricum* subsp. *sibiricum* y *T. sibiricum* subsp. *litorale*), mientras que *T. pauciflorum*, *T. sikkimense* y *T. umbratile* se reducen a sinónimos de *T. sibiricum* subsp. *sibiricum*. Cuatro de las seis especies de *Trisetum* sect. *Sibirica* son endémicas del este de Asia y Nueva Guinea, mientras *T. turcicum* crece en Turquía, el Cáucaso y norte de Irán, y *T. sibiricum* está distribuido desde el este de Europa hasta Alaska y Canadá.

INTRODUCTION

Trisetum Pers. is a perennial genus of grasses which belongs to the tribe Poeae R. Br. (Tzvelev, 1989; GPWG, 2001; Soreng et al., 2003, 2007, 2015), and to subtribe Aveninae J. Presl, which comprised 13 genera (Soreng et al., 2015). In recent studies, two new genera have been added to subtribe Aveninae, the genera *Trisetopsis* Röser & A. Wölk (Wölk & Röser, 2013), and *Tzveleviochloa* Röser & A. Wölk (Wölk & Röser, 2017). *Trisetum*, characterized by bifid, awned lemma, and mostly glabrous ovary, is comprised of approximately 70 species that inhabit temperate and cold regions, mainly in the Northern hemisphere, but are also found in South America, Australia, and New Zealand. Typically, they live in weedy places, forests, meadows, mountain slopes, and alpine and tundra grasslands (Hultén, 1959; Chrtek, 1965; Clayton & Renvoize, 1986; Randall & Hilu, 1986; Watson & Dallwitz, 1992; Finot et al., 2004, 2005b). Detailed taxonomical revisions of American taxa, as well as taxa from New Zealand, have been made (Edgar, 1998; Finot et al., 2004, 2005a, 2005b); however, only partial revisions exist for Europe and Asia. All the species of *T.* sect. *Sibirica* are endemic to Asia, two of them reaching to New Guinea and North America.

As in the previous study (Barberá et al., in review), we continue the traditional separation of the two genera based on their perennial (*Trisetum*) versus annual (*Trisetaria*) life-cycles (e.g., Chrtek, 1965; Rechinger,1970; Tzvelev, 1976; Pignatti, 1982; Finot et al., 2004, 2005a, 2005b); therefore, the proposal of Quintanar & Castroviejo (2010) to conserve *Trisetum* against *Trisetaria* is followed.

Trisetum has been traditionally divided into two sections: *T.* sect. *Trisetum*, with lax, open panicles and culms glabrous below the inflorescences, and *T.* sect. *Trisetaera* Asch. & Graebn., with dense, spiciform panicles, and culms pilose below the inflorescences. A review of the history of the genus in America and Europe can be found in Finot et al. (2005a) and Barberá et al. (2017).

Chrtek (1965) deeply studied the European species of *Trisetum*, dividing them into four subgenera (*T.* subg. *Trisetum*, *T.* subg. *Distichotrisetum*, *T.* subg. *Glaciotrisetum*, and *T.* subg. *Graciliotrisetum*), mainly based on the anatomy of the leaves and roots. At the same time, Chrtek divided the subgenus *Trisetum* in five sections (*T.* sect. *Trisetum*, *T.* sect. *Trisetaera*, *T.* sect. *Rigida*, *T.* sect. *Hispanica*, and *T.* sect. *Carpatica*). *Trisetum* sect. *Trisetum* is characterized by its lax panicles and leaves with the sclerenchyma clearly developed in young leaves. This section, defined by Chrtek (1965), includes the species of *T. sibiricum* group.

Chrtek (1968) described one new species from Nepal, Sikkim, southeastern Tibet and China, *Trisetum scitulum*, and divided sect. *Trisetum* into two new series: *T.* ser. *Trisetum*, and *T.* ser. *Sibirica*. *Trisetum* ser. *Trisetum* (including *T. flavescens*, *T. turcicum* from Turkey and Caucasus, *T. thospiticum* from Van Lake in Turkey, the Chinese species *T. henryi*, and *T. scitulum*) was characterized by its geniculate awns, sometimes twisted at the lower part. On the other hand, *Trisetum* ser. *Sibirica* (including *T. sibiricum*, the Central Asian *T. altaicum*, and two Himalayan species *T. aeneum*, and also *T. micans* with some doubts) was diagnosed by its recurved and not geniculate awns, not clearly twisted at the lower part. About the Eastern Asiatic species *T. bifidum*, Chrtek (1968) indicated that it is a species close to sect. *Trisetum*, but it is not included in either series.

Tzvelev (1976) in his treatment of *Trisetum* for the Soviet Union recognized three sections (*T.* sect. *Rigida*, *T.* sect. *Trisetum*, and *T.* sect. *Trisetaera*). He simplified Chrtek´s classification, not accounting for the anatomical characters used by Chrtek (1965). Tzvelev characterized the sections by the type of growth of underground and vegetative shoots, the leaf disposition, the panicle density, and the rachilla and callus hairs length. He included seven species and eight subspecies within *T.* sect. *Trisetum* (*T. ciliare*, *T. turcicum*, *T. sibiricum* subsp. *sibiricum*, *T. sibiricum* subsp. *litorale*, *T. sibiricum* subsp. *umbratile*, *T. flavescens* subsp. *flavescens*, *T. flavescens* subsp. *parvispiculatum*, *T. flavescens* subsp. *tatricum*, *T. alpestre* subsp. *alpestre*, *T. alpestre* subsp. *glabrescens*, *T. altaicum*, and *T. agrostideum*), and did not discuss the series.

Later, Probatova (1979) in her study of the genus from Caucasus arranged *Trisetum* sect. *Trisetum* in four subsections: the monotypic *T.* subsect. *Carpatica* (Chrtek) Probat. (including *T. ciliare*), subsect. *Trisetum* (including *T. flavescens s. l.*, *T. parvispiculatum* and *T. alpestre*), subsect. *Sibirica* (Chrtek) Probat. (including *T. sibiricum* and *T. turcicum*), and subsect. *Agrostidea* Probat. (including *T. altaicum* and *T. agrostideum*). The different subsections are characterized by the type of growth of underground and vegetative shoots, lemma apex, callus, awn and palea keel hairs length and anthers length.

Two other relevant recent floristic accounts cover species of *Trisetum* subsect. *Sibirica*. Wu & Phillips (2006), in their treatment of Flora of China, did not recognize any sections, and considered the subspecies of *T. sibiricum* as species. Enushchenko (2011), in his revision of *Trisetum* in the Northern Asia, also considers the subspecies of *T. sibiricum* as species, but recognized the subsection *Sibirica* of Probatova (1979).

Therefore, the main points of controversy of this group of *Trisetum* concern the divisions of *T. sibiricum*, sometimes divided into many taxa, and the circumscription and rank of the series or subsection *Sibirica*. In this work, Probatova criteria (1979) of classification and our unpublished molecular data are followed to characterize *Trisetum* sect. *Sibirica*.

We present a taxonomic revision of *Trisetum* sect. *Sibirica* based on review of herbarium material, as part of a monograph of *Trisetum* in Eurasia. The synopses mentioned above were all partial works, not providing a detailed view of the entire section. The present work provides a comprehensive study of this section.

MATERIALS AND METHODS

This revision is based on the study of 450 herbarium specimens from the following herbaria: AAH, B, BEOU, BM, C, E, F, FI, G, GB, GH, GOET, H, IFP, JE, K, KYO, KUN, L, LE, LIV, M, MO, MPU, MW, NY, P, PE, PH, PR, PRC, RO, S, TI, UPS, US, W, and WU [acronyms according to Thiers (2017)]. Photos of specimens from CDBI, HHBG, HNWP, PE, and QTPM were also examined on the website of Chinese Virtual Herbarium (CVH; <www.cvh.org.cn>).

Ninety specimens were used for the morphometric analyses, as operational taxonomic units (OTUs), selected to represent as far as possible, the geographical range and the morphological variability of the taxa. Fifty-nine quantitative characters were recorded using a Mitutoyo CD–15DCX digital vernier caliper on 20 specimens of each species when available. Commonly used characters in *Trisetum* taxonomy were selected, as well as those observed to be variable and diagnostic in herbarium specimens. Spikelet measurements were taken on the distal spikelet from the longest branch of the second node of the panicle; floret measurements were taken from the proximal branches. Leaf-blade width was measured one cm above the ligule insertion. The rachilla segment between first and second flower is also referred to as "rachilla". Each character was analyzed for its minimum, maximum, and lower and upper quartiles, using STATISTICA package (www.statsoft.com). Quantitative and qualitative characters are also used in the identification key and descriptions. Minimum and maximum values are noted in brackets and the lower and upper quartile values (between the 25th and 75th percentiles) are noted outside. A combination of morphological characters was employed to distinguish species. Transverse sections of top leaf-blades were prepared by hand, stained with Fasga (Tolivia & Tolivia, 1987), and photographed with a Nikon SMZ1000 optical microscope. For leaf anatomy, the terminology defined by Ellis (1976, 1979) was used.

Additional data on the habitat, distribution, and chromosome numbers were checked from literature and collection labels. Chromosome numbers were summarized from the literature, but the extant vouchers, if any, were not revised. The list of numbered collections, examined specimens, and coordinates used to produce distribution maps were generated by a Microsoft ACCESS database (Microsoft, Seattle, Washington). Species distribution maps were made using ArcGis v.9.3 (ESRI, 2008). The material studied is listed under each species in the taxonomic treatment below. The data for establishing coordinates was completed in almost all cases, using www.geonames.org database.

RESULTS

Morphology

HABIT AND STEM—*Trisetum* sect. *Sibirica* are perennial grasses, short rhizomatous, sometimes with stoloniferous rhizomes (in *T. sibiricum* subsp. *sibiricum*), with well-isolated shoots or loosely tufted habit, normally densely tufted in *T. bifidum*.

The stems are straight, and usually shorter than 90 cm, except *T. henryi*, which can reach more than 150 cm, followed by *T. sibiricum* subsp. *sibiricum,* which can rarely also reach these sizes. *Trisetum sibiricum* subsp. *sibiricum* is the most widespread species of the section, and the taxon with the greatest variation in culm length, (12.7–)57 cm to 100(–150) cm long.

The species of this section present extravaginal growth in the lower and upper nodes, except *T. henryi*, whose upper ones are enclosed by the sheaths. The culms are glabrous in all the species (rarely pubescent on the upper part in *T. turcicum*), with (2–)3–6(–7) nodes. The culm internodes are elongated and separated along the culms in all the species, although sometimes *T. sibiricum* subsp. *litorale* has shorter internodes concentrated in the lower part.

LEAVES—As in the rest of the genus *Trisetum*, the indumentum, shape, and size of ligules, leaf-sheaths, and leaf-blades are variable characters in the same plant, depending on whether they are the basal or the top culm-leaf. Notable heterophylly occurs between young and mature leaf-blades in genus *Trisetum*, as well as in the closely related genus *Koeleria* (Quintanar & Castroviejo, 2013; Barberá et al., 2017).

LEAF-SHEATHS—Basal leaf-sheaths are glabrous to slightly, rarely densely, pubescent. Top culm leaf-sheaths are shorter than their respective internodes, rarely longer in *T. bifidum*, *T. henryi*, and *T. scitulum*; they are always glabrous in *T. aeneum*, *T. bifidum*, and *T. scitulum*, sometimes pubescent in *T. henryi*, *T. sibiricum*, and *T. turcicum*.

Sheath margins are glabrous, except for those of *T. bifidum*, *T. henryi* and, sometimes, *T. sibiricum* subsp. *sibiricum* and *T. turcicum*, which are ciliate.

LEAF-BLADES—The species of *Trisetum* sect. *Sibirica* have flat and non-rigid leaf-blades. The indumentum of leaf-blades has traditionally been used as a distinctive character for taxa delimitation (Tzvelev, 1976; Jonsell, 1980). However, leaf-blade features (mainly indumentum and width) have been considered less important than those linked to spikelet morphology for the taxonomy of the widespread species, due to the high variability of leaf-blade traits. Most of the species of this section have leaves varying from glabrous to pubescent adaxially and abaxially, usually with short hairs on the margins.

The species of *Trisetum*, including sect. *Sibirica*, are mesophytic or xerophytic grasses. While the abaxial surface of the leaf-blades often has a regular surface, the adaxial one has ribs of varying depth (Metcalfe, 1960; Watson & Dallwitz, 1992). In xerophytic species of *Trisetum* sect. *Sibirica*, the depth of the intercostal zones and associated ribs is more pronounced, and the sclerenchyma girders and strands are well-developed. The midrib is not readily distinguishable in all of the species of the section, being conspicuously marked in *T. henryi*, and sometimes in *T. sibiricum* and *T. turcicum*. Among the species of this section, all the vascular bundles are accompanied by more or less developed sclerenchyma girders and strands that attach to both the abaxial and adaxial sides of the leaf-blade. *Trisetum sibiricum* subsp. *litorale*, and sometimes *T. sibiricum* subsp. *sibiricum*, have vascular bundles with well-developed sclerenchyma strands abaxially and small strands adaxially, and nerves with no sclerenchyma present or with small girders in both sides. *Trisetum sibiricum* subsp. *litorale*, and sometimes *T. sibiricum* subsp. *sibiricum*, are mesophytic grasses, which explains their less developed sclerenchyma girders and strands. *Trisetum aeneum*, *T. bifidum*, *T. henryi*, *T. scitulum*, *T. turcicum*, and usually *T. sibiricum* subsp. *sibiricum* have well-developed sclerenchyma girders, anchor shaped or relatively wide and deep bands, and leaf margins with cap of sclerenchyma.

LIGULES—The ligules are membranous, with a truncate, denticulate to laciniate apex, glabrous or pubescent abaxially in *T. bifidum, T. henryi*, and *T. sibiricum* subsp. *sibiricum*, usually with some hairs on the upper part. The shape and size of ligules are variable, with those of basal leaves being shorter than those of top culm leaves. The ligule measurements used in this study were taken from the top culm leaf-blades. *Trisetum scitulum* has the longest ligules (2.2–3.5 mm), while *T. bifidum* has the shortest [0.4–1.1(–1.6) mm].

INFLORESCENCES—Inflorescences are usually lax panicles, but are sometimes dense in *T. aeneum, T. sibiricum* subsp. *litorale,* and *T. turcicum,* oblong to elliptic or lanceolate in outline, and sometimes ovate in *T. sibiricum* subsp. *litorale*. *Trisetum henryi* has the longest panicles [(16–)19–23(–28) cm long], followed by *T. bifidum* and *T. sibiricum* subsp. *sibiricum* [(8.5–)11–19(–27) cm and (5–)11.7–16(–23) cm long, respectively], whereas *T. sibiricum* subsp. *litorale* has the smallest ones [(3.3–)5–7.4(–9) cm long]. *Trisetum henryi* and *T. scitulum* are characterized by having the longest basal branches, while *T. aeneum, T. sibiricum* subsp. *litorale*, and *T. turcicum* have the shorter ones. Fig. 1A–B.

Trisetum sect. *Sibirica* usually has a glabrous rachis, but is sometimes slightly pubescent on the upper part in *T. bifidum, T. sibiricum,* and *T. turcicum*, with hairs up to 0.1 mm long.

SPIKELETS—Spikelet length in *Trisetum* sect. *Sibirica* varies according to the lemma length, spikelets being longest in *T. scitulum, T. turcicum*, and *T. bifidum*; having a broad range of length in *T. sibiricum* subsp. *sibiricum*; and being slightly shorter than average in *T. sibiricum* subsp. *litorale, T. aeneum,* and *T. henryi* (Fig. 1C). The awn is not included in the length of the spikelet.

Rachilla segments are always pubescent, with fairly constant hair length at the species level, although it is not useful as a diagnostic character in this section. The number of florets is usually 2–3 per spikelet, sometimes 1 or 4 in *T. sibiricum* subsp. *sibiricum*, and also 4 in *T. bifidum*.

GLUMES—In the section *Sibirica*, *Trisetum bifidum* glumes are always markedly unequal [ratio -- lower glume length/upper glume length = (0.11–)0.48–0.59(–0.67)], also pronounced in *T. henryi,* and sometimes in *T. sibiricum*. The glumes are less markedly unequal in the rest of species, being subequal in *T. aeneum*, and rarely in *T. sibiricum* (Fig. 1D). Lower and upper glumes are acuminate, sometimes acute or long acuminate, with some short hairs from the middle part to the top of the main nerve and along the margins. The lower glume is almost always shorter than the upper one, as indicated before, with a single nerve extending to the tip. The upper glume always has three nerves, the central one reaching the tip, the lateral ones extending to the middle or the upper half.

LEMMA—The lemma of the species of *Trisetum* sect. *Sibirica*, as well as that of the rest of the genus, is characterized by having a dorsal awn and a bifid apex with two apical teeth normally ending in two aristules separated by a more or less deep sinus. Aristules are the intermediate nerves protruding beyond each tooth apex (Nicora, 1978; Koch, 1979; Finot et al., 2006). In this section, the aristules of *T. scitulum* are longer than the rest of species, having the ones of *T. bifidum* a broader range of their length [0.5–1.3 mm, and (0.1–)0.6–1(–1.3) mm long, respectively] (Fig. 1G). The length of the lemma, without taking the awn into account, is longer in *T. turcicum, T. scitulum*, and *T. bifidum* (6.5–8.7 mm, (6.5–)7.4–7.8(–8.4) mm, and (6–)6.5–7.5(–8.2) mm long, respectively), having a broader range of its length in *T. sibiricum* subsp. *sibiricum* [(4–)5.4–6.8(–7.8) mm long], and *T. sibiricum* subsp. *litorale* and *T. henryi* the shorter ones [(3.8–)4.7–5.7(–6.2) mm and (4.2–)4.8–6.1 mm long, respectively]. The lemma is laterally compressed, elliptic to oblong or lanceolate, golden brown or brownish to yellowish at maturity, punctate

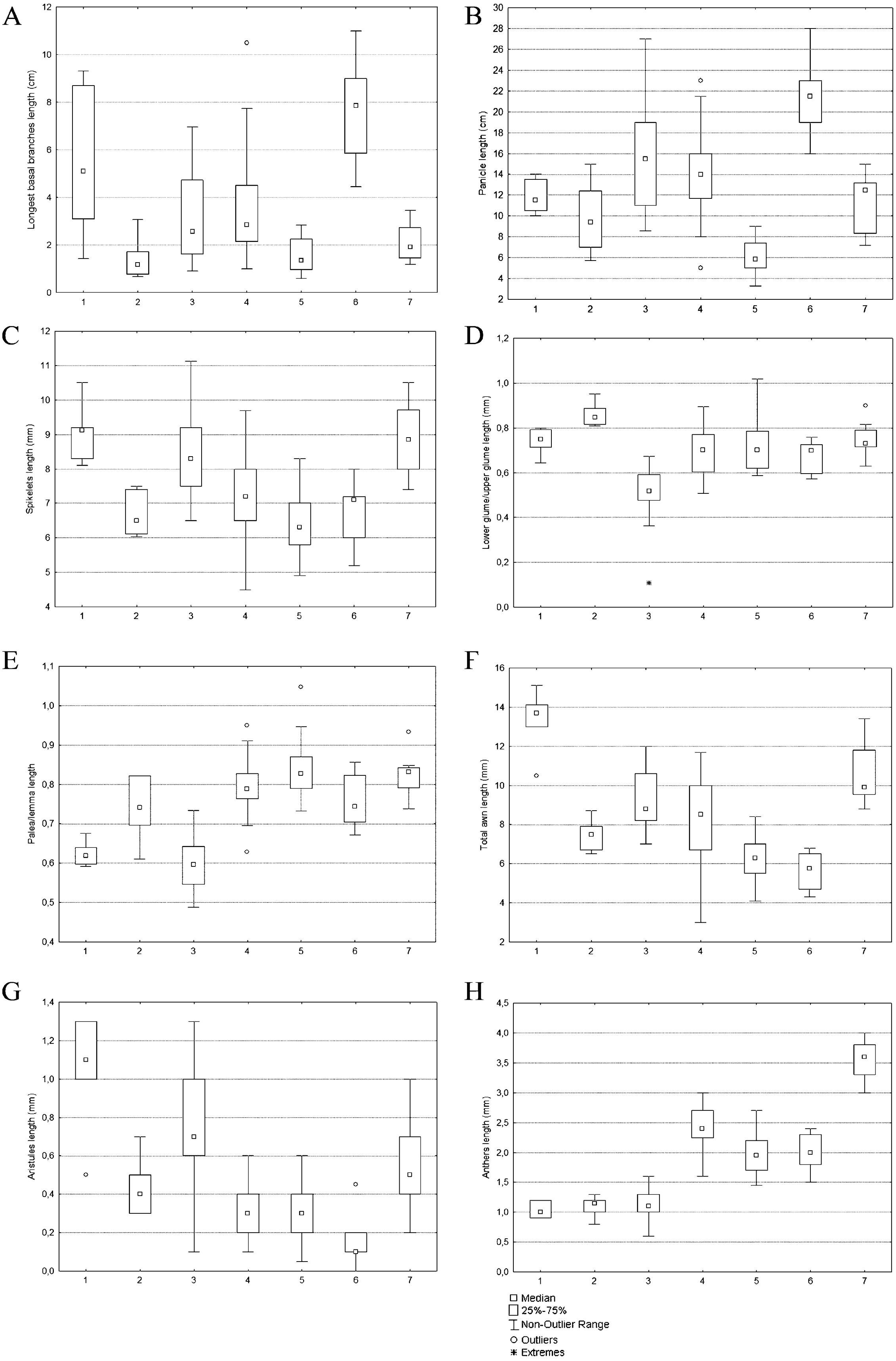

Figure 1. Box plots of a selection of studied variables. A. Longest basal branches length. B. Panicle length. C. Spikelets length. D. Lower glume/upper glume length. E. Palea/lemma length. F. Total awn length. G. Aristules length. H. Anthers length. Numbers along the x-axis correspond to the studied taxa: 1. *T. scitulum*. 2. *T. aeneum*. 3. *T. bifidum*. 4. *T. sibiricum* subsp. *sibiricum*. 5. *T. sibiricum* subsp. *litorale*. 6. *T. henryi*. 7. *T. turcicum*.

to scabridulous, with short hairs from the central to the upper part of the midrib (being the hairs slightly longer in *T. bifidum*).

CALLUS—The callus is elliptic to rounded, or sometimes oblong. The callus is always glabrous in *Trisetum scitulum* and *T. henryi*, and sometimes in *T. sibiricum* and *T. turcicum*, while the rest of species of the section have short and scattered or sparse indumentum. *Trisetum bifidum* is the species with the longest callus hairs (0.3–0.7 mm long).

PALEA—The palea disposition and its shape are the same as in the rest of the species of the genus (Barberá et al., 2017). In this section, the palea of *T. turcicum* is longer than the rest of species [(5–)5.7–7(–7.2) mm long]. The length of both the palea and the lemma is a good taxonomic character for some species, being always markedly unequal in *T. bifidum*, and *T. scitulum*, with the palea reaching to about half the length of the lemma [ratio -- palea length/lemma length = (0.49–)0.55–0.64(–0.73), and 0.6–0.68, respectively]. *Trisetum aeneum*, *T. henryi*, and *T. turcicum* have a slightly less marked unequal difference between these structures [ratio -- palea length/lemma length = (0.61–)0.7–0.82, 0.67–0.82(–0.86), and 0.74–0.84(–0.93), respectively]; they are more variable in *T. sibiricum* [(0.63–)0.77–0.85(–1)] (Fig. 1E).

LODICULES—As in the rest of the genus *Trisetum*, the two lodicules flank the dorsal sides of the ovary or caryopsis, having a more or less oblanceolate shape. The apex is irregular to regularly lobulated (2–3-lobate), rarely laciniate or denticulate, and always glabrous.

AWN—The length and shape of the awn are important taxonomic characters for the classification of this section. The awn shape is basally recurved and usually slightly twisted near the base, although *T. turcicum* and *T. scitulum* has geniculate awns below the middle, and a twisted column up to the geniculate part. *Trisetum scitulum* has the awns significantly longer [(10.5–)13–15 mm long], but the length does not differ greatly in the rest of the species of the section (Fig. 1F). The awn is dorsal, inserted near the middle of the lemma, except *T. bifidum*, species with the awn always inserted closer to the apex.

STAMENS—The anthers length is a good diagnostic character, being fairly constant within the species level. *Trisetum turcicum* is the species with the longest anthers [(3–)3.3–4 mm long], followed by *T. sibiricum* and *T. henryi* [(1.4–)2–2.5(–3) mm long]; the rest of the species of the section have relatively short ones [(0.6–)1–1.3(–1.6) mm long] (Fig. 1H).

OVARY AND CARYOPSIS—The ovary and caryopsis are very similar in all species, being always glabrous. The mature caryopsis is narrowly elliptic to oblong in shape, narrowly elliptic to elliptic in transversal section, not sulcate, with puctiform hilum. The endosperm is soft-liquid.

Taxonomic treatment

TRISETUM sect. SIBIRICA (Chrtek) Barberá, **stat. nov.** *T.* ser. *sibirica* Chrtek, Acta Univ. Carol., Biol. 1967: 107. 1968. *T.* subsect. *Sibirica* (Chrtek) Prob., Novosti Sist. Vyssh. Rast.15: 20. 1979.—TYPE: *T. sibiricum* Rupr.

Herbs shortly rhizomatous, rarely with stoloniferous rhizomes; panicles from lax to dense; spikelets goldish-brown, rarely pale yellowish; callus glabrous or with short hairs up to 0.7 mm long; awns recurved or basally slightly twisted, not or rarely geniculate.

Key to the taxa of Trisetum sect. Sibirica

1. Panicle branches single or paired; awn (10.5–)13–14(–15) mm long.................................... ***T. scitulum***
1. Panicle branches in whorls of 3 or more; awn (3–)6.5–9.5(–13.4) mm long.. 2
  2. Anthers (0.6–)1–1.3(–1.6) mm long.. 3
    3. Panicle dense; glumes subequal [ratio -- lower glume length/upper glume length = (0.8–)0.82–0.89(–0.95)]; lemma 5.6–6(–6.6) mm long; ratio -- palea length/lemma length = (0.61–)0.7–0.82; callus hairs 0.1–0.3 mm long .... ***T. aeneum***
    3. Panicle lax; glumes unequal [ratio -- lower glume length/upper glume length = (0.11–)0.48–0.59(–0.67)]; lemma (6.1–)6.6–7.6(–8.2) mm long; ratio -- palea length/lemma length = (0.49–)0.55–0.64(–0.73); callus hairs 0.3–0.7 mm long.. ***T. bifidum***
  2. Anthers (1.5–)2–3.3(–4) mm long... 4
    4. Top culm leaf-blades 17.5–29.5 cm long, reaching to the panicle, with the central nerve conspicuously marked; lemmas pale yellowish or brownish, with broad hyaline margins......***T. henryi***
    4. Top culm leaf-blades (1.5–)5.6–13(–34.3) cm long, rarely reaching to the panicle, with the central nerve similar to the lateral ones; lemmas golden brownish or yellowish, rarely greenish, with narrow hyaline margins... 5
      5. Awn geniculate, slightly twisted to twisted near the base; anthers (3–)3.3–4 mm long ***T. turcicum***
      5. Awn slightly recurved, sometimes slightly twisted at the base; anthers (1.5–)2–2.5(–3) mm long 6
        6. Herb (12.7–)57–100(–146) cm high; panicles (5–)11.7–16(–23) cm long...................................
        .... ***T. sibiricum*** subsp. ***sibiricum***
        6. Herb (12.8–)23.8–37.7(–58.4) cm high; panicles (3.3–)5–7.4(–9) cm long..................................
        .... ***T. sibiricum*** subsp. ***litorale***

1. TRISETUM SIBIRICUM Rupr., Beitr. Pflanzenk. Russ. Reiches 2: 65. 1845. *Avena ruprechtii* Griseb. in Ledeb., Fl. Ross. 4(13): 418. 1852. *Trisetum ruprechtii* (Griseb.) Steud., Syn. Pl. Glumac. 1: 226. 1854. *Trisetum flavescens* var. *sibiricum* (Rupr.) Ohwi, Bot. Mag. (Tokyo) 45: 192. 1931. *Trisetum bifidum* subsp. *sibiricum* (Rupr.) T. Koyama, Grass. Jap. Neighb. Reg.: 533. 1987. *Trisetaria sibirica* (Rupr.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 385. 1996.—TYPE: RUSSIA. Bashkortostan Republic, Belaja river, 55º53’N 53º36’E, *F.J.I. Ruprecht s.n.* [lectotype, designated by Tzvelev (1976: 262): LE!].

Herb (12.7–)28.8–79(–146) cm high, not or slightly tufted, shortly rhizomatose, sometimes with stoloniferous rhizomes, culm (0.45–)0.9–1.3(–2) mm diam., glabrous; nodes (2)3–5(7), separated along the culm, sometimes concentrated in lower part of the culm, exposed or enclosed by the sheaths, glabrous. Basal leaf-sheaths glabrous to pubescent, with hairs 0.03–0.2(–1.8) mm long, frayed into fibers, yellowish to brownish; basal leaf-blades (1.2–)2.7–7(–17.5) cm long × (2–)2.5–3.6(–7.7) mm wide, flat, rolled when dried, glabrous to pubescent, mostly adaxially, with hairs 0.05–0.8(–1.2) mm long, greenish to greyish, sometimes brownish; top culm leaf-sheaths (4.2–)7.8–17(–25) cm long, shorter than the internodes, glabrous to pubescent on the upper part, without cilia on the margins, rarely with; top culm leaf-blades (1.5–)5.2–13(–34.3) cm long × (2.5–)3.8–6(–11) mm wide, flat, usually parallel to the culm, rarely arriving to the panicle, with the central nerve similar to the lateral ones, from glabrous to pubescent abaxially and adaxially, with hairs up to 1.7 mm long along the nerves and margins, greenish to greyish, rarely brownish; inner collar region glabrous, usually with hairs (0.05–)0.2–1(–2.2) mm long externally and on the margins; ligules (0.5–)1.3–2(–2.7) mm long, denticulate to laciniate, glabrous to slightly pubescent abaxially and on the apex, with hairs 0.1–0.3(–1) mm long. Basal node of the panicle glabrous. Panicles (3.3–)6–15(–23) cm long × (1.2–)2–4(–10) cm wide, elliptic to lanceolate in outline, sometimes ovate or oblanceolate; rachis glabrous, sometimes slightly pubescent, with hairs up to 0.1 mm long; branches in whorls of 3 or 6, longest basal branches (0.6–)1.3–3.5(–10.5) cm long. Spikelets (4.5–)6–7.6(–9.7) mm long × (1.3–)2.2–3.4(–5.5) mm wide, (1)2–3(4)–flowered; pedicels (0.5–)2–5.2(–10.5) mm long, glabrous to slightly pubescent, with hairs up to 0.2 mm long. Glumes unequal, rarely subequal [ratio -- lower glume length/upper glume length = (0.5–)0.6–0.77(–1)]; lower glume (2.5–)3.3–4.4(–5.6) mm long × (0.4–)0.8–1(–1.4) mm wide, narrowly to broadly lanceolate [ratio -- lower glume width/lower glume length = (0.15–)0.2–0.28(–0.35)], acuminate, sometimes acute or long acuminate, 1-nerved, glabrous, with hairs up to 0.15 mm long on the midrib and margins, greenish on the central part, laterals yellowish or sometimes purplish; upper glume (3.7–)5–6(–7.8) mm long × (1–)1.7–2(–2.5) mm wide, elliptic to oblanceolate [ratio -- upper glume width/upper glume length = (0.25–)0.3–0.37(–0.5)], acuminate to long acuminate, sometimes acute, 3-nerved, glabrous, with hairs up to 0.2 mm long from the middle to the upper part of the midrib, greenish on the central part, surrounded by yellowish, sometimes purplish; rachilla segments between first and second floret (0.6–)1–1.5(–2) mm long, with hairs (0.2–)1–1.4(–2.2) mm long; rachilla segments to sterile floret (0.5–)1–1.5(–2.2) mm long, with hairs (0.2–)0.5–0.7(–1.3) mm long. Lemmas (3.8–)5.2–6.2(–7.8) mm long × (1–)1.5–1.8(–2) mm wide, elliptic to oblong, sometimes lanceolate [ratio -- lemma width/lemma length = (0.2–)0.25–0.33(–0.4)], scabridulous, with scattered hairs up to 0.1 mm long on the upper part of the midrib, golden brownish or yellowish, rarely greenish, with narrow hyaline margins; apical teeth (0.07–)0.2–0.5(–1) mm long, with aristules (0.05–)0.2–0.4(–0.6) mm long; awn (3–)6.2–9(–11.7) mm long, inserted (2.2–)2.8–3.7(–4.4) mm from the base [ratio -- awn insertion from the base length/lemma length = 0.5–0.6(–0.78)], slightly recurved and sometimes slightly twisted at the base, with adpressed hairs up to 0.05 mm long; callus 0.2–0.3 mm long, elliptic to orbicular, glabrous or with hairs 0.1–0.2(–0.3) mm long. Paleas (3.3–)4–5(–6.7) mm long × (1–)1.3–2 mm wide [ratio -- palea length/lemma length = (0.63–)0.77–0.85(–1)], elliptic, rarely oblanceolate, margins with scattered hairs on the upper part, rarely glabrous; teeth 0.1–0.3(–0.4) mm long, with short hairs. Lodicules (0.4–)0.6–0.8(–1.1) mm long. Anthers (1.5–)2–2.5(–3) mm long. Ovary (0.3–)0.5–0.8(–1.3) mm long. Caryopsis 2.7–3.7(–4) mm long × 0.5–1(–1.2) mm wide.

a. subsp. SIBIRICUM

Avena rufescens Pančić, Fl. Serbiae, Add.: 238. 1884. *Trisetum rufescens* (Pančić) Adamovic, Index Sem. Hort. Bot. Belgradensi 1903, n. v.—TYPE: SERBIA. Vlasina lake, 42º42'N 20º22'E, Aug 1880, *J. Pančić 1150* [lectotype, here designated: BEOU–13316 (image!)].

Avena sikkimensis Hook. f., Fl. Brit. India 7: 280. 1897. *Trisetum sikkimense* (Hook. f.) Chrtek, Acta Univ. Carol., Biol. 1967: 104. 1968.—TYPE: INDIA. Sikkim, Lachoong Valley, 27º45'N 88º30'E, 9 Jun 1849, *J.D. Hooker s.n.* [lectotype, here designated: K–808691!; possible isolectotypes: E–393839 (image!), GOET!, K–32272!, K–32273!, M–210837!, P–2255848!, P–3351084!, P–3351085!, S!].

Trisetum homochlamys Honda, Bot. Mag. (Tokyo) 43: 293. 1929.—TYPE: JAPAN. Hokkaido Island, Hidaka Province, Samani distr., foot of Mt. Apoi, 42º6'N 143º1'E, 1928, *T. Nakai s.n.* [holotype: TI–21896 (image!)].

Trisetum flavescens f. *senanense* Ohwi, Bot. Mag. (Tokyo) 45: 192. 1931.—TYPE: JAPAN. Honshu Island, Nagano, Senjo Mountain, 35º43'N 138º11'E, 28 Aug 1925, *J. Ohwi s.n.* [holotype: KYO–78671 (image!)].

Trisetum sibiricum var. *umbratile* Kitagawa, Rep. Inst. Sci. Res. Manchoukuo 4: 77. 1940. *T. umbratile* (Kitagawa) Kitagawa, J. Jap. Bot. 31: 302. 1956. *Trisetum sibiricum* subsp. *umbratile* (Kitagawa) Tzvelev, Spisok Rast. Gerb. Fl. S.S.S.R. Bot. Inst. Vsesojuzn. Akad. Nauk 18: 6. 1970.—TYPE: CHINA. Manchuria, Jilin Province, Jingyue Lake, 43º42'N 126º12'E, 6 Jul 1939, *M. Kitagawa s.n.* [holotype: TI–21898 (image!)].

Trisetum pauciflorum Keng, Fl. Tsinling. 1(1): 441. 1976.—TYPE: CHINA. Shaanxi, Xianyang, 34º20'N 108º42'E, 29 Jul 1952, *K.T. Fu 5281* [holotype: WUK?; isotypes: CDBI (image!), PE!].

Herb (12.7–)57–100(–146) cm high, loosely tufted, shortly rhizomatous; nodes (2–)4–5(–7), separated along the culm. Basal leaf-blades (3–)5.3–10.5(–17.5) cm long × (2–)2.7–4.3(–7.7) mm wide; top culm leaf-sheaths (8–)13–20(–25) cm long, glabrous to puberulous or pubescent on the upper part, without, rarely with, cilia on the margins; top culm leaf-blades (1.5–)8.2–20(–34.5) cm long × (2.5–)4–7.2(–11) mm wide. Panicles (5–)11.7–16(–23) cm long × (1.6–)3–5(–10) cm wide, elliptic to oblong in outline, lax to slightly dense; longest basal branches (1–)2–4.5(–10.5) cm long. Pedicels (1.3–)3–6.3(–10.5) mm long. Lemmas (4–)5.4–6.8(–7.8) mm long; awn (3–)6.7–10(–11.7) mm long. Figure 2.

Chromosome Number—2*n* = 14 (Ono & Tateoka, 1953; Tateoka, 1978; Frey, 1992).

Phenology—Flowering and fruiting from June to October.

Distribution and Habitat—*Trisetum sibiricum* subsp. *sibiricum* is present in eastern Europe (Poland, and Serbia), and widespread throughout Asia, arriving in its southern part to Sikkim, and southern China (Sichuan), and in its eastern to Japan, and Kamchatka Peninsula; 0–4,200 m of elevation; at open steppe or marshy meadows, open and sparse forests, among shrubs. Figure 3.

Specimens Examined—**CHINA. Gansu:** Xiahe County, near the Labu, 35º2'N, 102º29'E, 25 Jul 1937, *Fu 1386* (PE); Minxian County, Mawu, 35º27'N, 106º33'E, 26 Jun 1936, *Wang 4559* (PE). **Hebei:** Laiyuan county, 39º20'N, 114º40'E, 13 Jul 1959, *[illegible] 2096* (HNWP). **Heilongjiang:** Mishan county, 45º33'N, 131º53'E, 15 Jul 1980, *Lishuxin 3118* (IFP); Khingai Mountains, Saltanovka, 48º45'N, 127º0'E, 16 Aug 1902, *Litvinov 768* (AAH, GH, NY). **Inner Mongolia:** Bayan Obo, 41º46'N, 109º58'E, 24 Jul 1962, *Meng ning Team 1262* (PE). **Jilin:** vallis Badaochesa, fluvium Sui-fum, 43º11'N, 127º27'E, 21 Jun 1896, *Komarov s.n.* (P). **Qinghai:** Tongde, Hebei, Gongma, 36º26'N, 98º9'E, 29 Jul 1990, *[illegible] 5226* (HNWP). **Shanxi:** Ba ji ling, Ma jia zhuang, Ning wu dong zhai, 13 Sep 1953, *Shanxi Team 246* (PE); Nigwu, 38º50'N, 112º9'E, 29 Jul 1957, *Shanxi Team 1938* (MO, PE); Chiao-ch´eng distr., Pa-shui-kou-shan, 38º30'N, 111º0'E, 24 Aug 1924, *Smith 7173* (BM, PE, S); Ning-wu Hsien, 38º50'N, 112º9'E, 21 Aug 1929, *Tang 1433* (US); Fangshan, 37º53'N, 111º14'E, 3 Aug 1955, *Wenzhong Wang 141* (PE); Guandi mountain, 37º52'N, 111º32'E, 5 Jul 1955, *Yellow river Team 2552* (PE); Li cai shan, cong town, 9 Sep 1955, *Yellow river Team 2614* (PE). **Sichuan:** 22 Jul 1908, *Legendre 391* (P); prope Sung-p´an, 32º40'N, 103º35'E, 14 Jul 1922, *Smith 2772* (BM, PE); San-ch´a-tzü [Sanchazi], 32º47'N, 103º16'E, 10 Aug 1922, *Smith 3447* (MO, PE); Tongolo, 30º3'N, 101º29'E, 22 Aug 1894, *Soulié s.n.* (P); Jinchuan, 27º11'N, 102º17'E, 15 Jun 1983, *Xiaoen Tian 1089* (PE); Seda, Zhamatang, 32º27'N, 100º19'E, 7 Sep 1983, *Xiaozong Tang 1903* (PE). **Tibet Autonomous Region:** Nyingchi county, 29º39'N, 94º22'E, 8 Aug 1983, *[illegible] 6249* (PE). **Xinjiang:** Eastern Tian Shan, left tributary of the Kunges river, 43º8'N, 83º30'E, 7 Aug 1958, *Yunatov 361* (LE); Eastern Tian Shan, Aksu, 50 km from Kalmal-Kure, 41º11'N, 80º16'E, 24 Aug 1957, *Yunatov 1517* & *al.* (LE). **JAPAN. Hokkaido Island:** Kunajiri, Veslovsky Peninsula, Golovnino, 43º41'N, 145º32'E, 6 Aug 1960, *Czerniawa s.n.* (C); côte de Saruru, 44º26'N, 143º13'E, 20 Jul 1893, *Faurie 10523* (FI, G, P); Saruru, 44º26'N, 143º13'E, 20 Jul 1893, *Faurie 10524* (WU); Ile de Rebunshiri, 44º58'N, 147º47'E, 1 Aug 1892, *Faurie 8456* (FI, G); Nemuro prov., Bekkaido-choo, Notsuke-gun, Bekkai, 43º23'N, 145º7'E, 20 Jul 1975, *Furuse 9171* (K); Nemuro prov., Bekkaido-choo, Notsuke-gun, Okuyukiusu, 43º18'N, 145º12'E, 21 Jul 1975, *Furuse 9176* (K); Rishiri Island, 45º10'N, 141º14'E, 20 Jul 1929, *Saito s.n.* (B). **Honshu Island:** côte d´Iwanoi [Chiva pref.], 35º36'N, 140º7'E, 7 Jul 1892, *Faurie* (P); Kai Prov., Nagano pref., near summit Mt. Kita-dake, Ashi-yasu-son, Naka-koma-gum, 35º40'N, 138º14'E, 31 Jul 1969, *Furuse 47899* (K); Suruga prov., Shidzuoka pref., near summit from half way Mt. Semmai-dake, 35º25'N, 138º13'E, 28 Aug 1958, *Furuse s.n.* (AAH, K, S); Suruga prov., Shidzuoka pref., Igawa-mura, Abe-gun, Mt. Shiwomi-dake, 35º34'N, 138º10'E, 23 Aug 1957, *Furuse s.n.* (AAH, S); Shinano prov., Nagano pref., Karuizawa-machi, Minami-karuizawa, 36º21'N, 138º35'E, 16 Jul 1962, *Furuse s.n.* (AAH, S); Mt. Ibukiyama, 35º25'N, 136º24'E, 5 Jul 1942, *Hashimoto 9721* (US); Tochigi pref., Nikko city, Akanagisan, 36º48'N, 139º34'E, Jul 1904, *Makino s.n.* (AAH); Nagano pref., Kirigamine, 36º6'N, 138º10'E, 1 Aug 1935, *Ohwi 8305* (US); Yamanashi pref., Kitadake mountain, 35º40'N, 138º14'E, 23 Aug 1929, *Ohwi s.n.* (GH, US); Kirigamine, 36º6'N, 138º10'E, 23 Jul 1952, *Tateoka s.n.* (B); Shizuoka pref., Shimoda, 34º40'N, 138º57'E, *Wright s.n.* (NY, P). **KAZAKHSTAN. Almaty Oblysy:** Dzungar Alatau, Northern slope of Mount Chemuldyk, 44º45'N, 79º20'E, 19 Aug 1948, *Goloskokov s.n.* (LE); vicinity of of Lepsinsk, Bel-Terek natural landmark, 45º31'N, 80º36'E, 20 Jun 1928, *Lipshits 249* (LE); Kopal uyezd, gorge of the Baskana river, 45º8'N, 79º3'E, 24 Jul 1909, *Lipshits 3044* (LE); Dzhungar Alatau, upper reaches of the Chin-bulak river, 43º17'N, 77º9'E, 24 Aug 1930, *Shipchinskiy 529* (LE); Tian Mountains, in montibus Transiliensibus ad fl. Almatinka Minorem, 43º15'N, 76º55'E, 19 Jul 1933, *Popov 501* (G, K, MA, MW, NY, RO). **East Kazakhstan:** ad fl. Ishar and Ulba, 49º57'N, 82º35'E, *Bunge 101* (P); Zyryanovsk distr., 49º43'N, 84º16'E, 24 Jul 1936, *Temnoev 62* (LE). **KIRGIZSTAN. Bishkek:** gorge of the Karagaydy-Bulak river, 42º52'N, 74º35'E, 20 Jul 1916, *Sovetkina 2706* & *Chausova* (LE). **Issyk-Kul Region:** Central Tian-Shan, southern slope of the Kungei-Alatau range, basin of the Cholpan-ata river, [Keshch]-kurgan natural landmark, 42º43'N, 77º25'E, 30 Jul 1935, *Gomolitskiy 716* & *Semenikhina* (LE); between the Tyupka and the Karkara rivers, 42º10'N, 78º28'E, 27 Jul 1950, *Medvedeva 641* & *al.* (LE); Karkar River Gorge, 42º0'N, 77º30'E, 21 Jul 1962, *Vintergoller s.n.* (FI). **Jalal-Abad Region:** Takhtalyk, 41º32'N, 73º21'E, 10 Aug 1911, *Nestruev 1871* (LE). Naryn Region: North-western slope of Maliy Kalgar mount to the Cholpan-ata river, 41º5'N, 76º45'E, 15 Jul 1936, *Semenikhina 183* (LE). **MONGOLIA. Arkhangai:** northern slope of Orkhon–Selenga watershed, 47º33'N, 102º49'E, 21 Oct 931, *Desiatkin 502* (LE); Khan-Kokshun mount, the Baga-Targyl gorge, 47º30'N, 100º0'E,

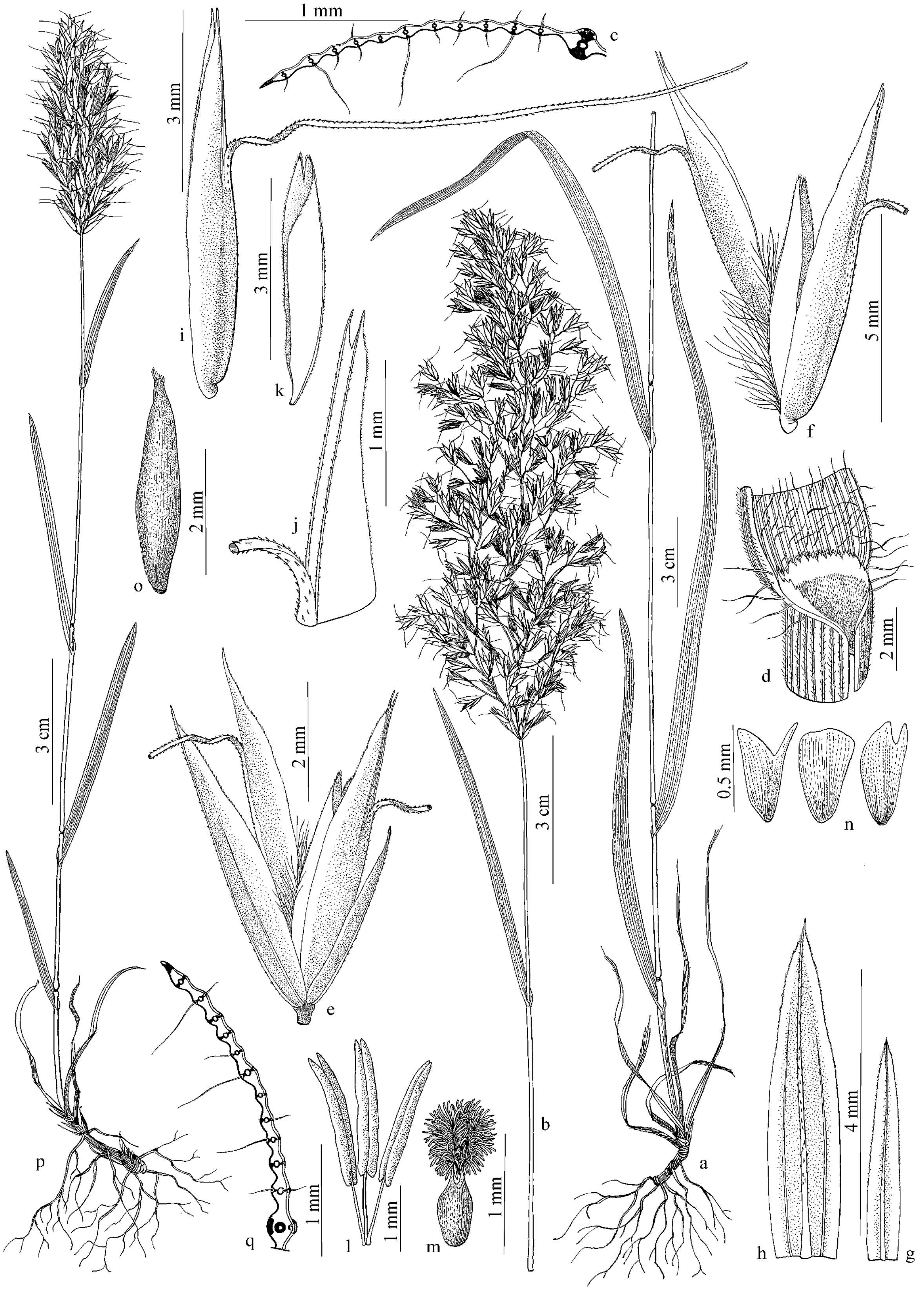

Figure 2. *Trisetum sibiricum* subsp. *sibiricum*. a. Basal habit. b. Inflorescence. c. Transverse section of leaf-blade. d. Sheath, ligule, and portion of the blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Lemma, upper part, lateral view. k. Palea, lateral view. l. Stamens. m. Pistil. n. Lodicules. o. Caryopsis. *Trisetum sibiricum* subsp. *litorale*. p. Habit. q. Transverse section of leaf-blade. (*Sojak s.n.*, PR–807346, a-b; *Popov 501*, G–442513, c; *Sojak s.n.*, PR–807345, d-n; *Deyl & Sojak 4090*, PR–807035, o; *Koroleva & Petrovsky 5703*, M–223301, p; *Solstad & Elven 04_0266A*, O, q).

17 Aug 1926, *Gusev 256* (LE). **Bulgan:** a vico Uňt, 49º8’N, 102º49’E, 11 Aug 1965, *Deyl 2917* & *Sojak* (PR). **Khentii:** Montes Kentei, ad fontes fluviorum Tola, Mensa et Iro, 48º53’N, 109º10’E, 13 Aug 1929, *Ikonnikov-Galitzky 3426* & *Ikonnikov-Galitzky* (AAH); Khentei range,Tsenkher gol opposite to Tsenkheriin dugang, 47º45’N, 109º3’E, 22 Jul 1949, *Yunatov 15678* (LE). **Khövsgöl:** vicinity of Kosogol lake, near Khatkhyl, 50º26’N, 100º9’E, 10 Aug 1925, *Burdukova s.n.* (LE); a vico Tarialan [Tarjalang], inter oppida Bulgan et Muren, 49º37’N, 102º3’E, 13 Aug 1965, *Deyl 3268* & *Sojak* (PR); lacus Chubsugul versus septentrionem a vico Chadchal, 51º6’N, 100º30’E, 16 Aug 1965, *Deyl s.n.* & *Sojak* (PR). **Övörkhangai:** Altai Gobicus, Baga-Bogd-úl [Baga-Bogdo], 44º57’N, 101º35’E, 20 Aug 1966, *Sojak 7177* & *Vasak* (PR). **Selenge:** Kentei mountains, on the way to Dulan Khan daban, 49º57’N, 106º12’E, *Ikonnikov-Galitzky 3426* & *Ikonnikov-Galitzky* (LE). **Töv:** montes Chentej, ad viam ex urbe Ulánbátar ad riv. Terelz, 48º10’N, 107º12’E, 6 Sep 1966, *Vasak 9247* (PR). **Ulaanbaatar:** in valle Nucht ad declivia montium Bogdúl, 47º54’N, 106º52’E, 24 Jul 1965, *Deyl 344* & *Soják* (PR); ad ripam dextram rivi Tola apud vicum Songino (25 km austro-occid. ab opp. Ulan-Bator), 47º54’N, 106º52’E, 31 Jul 1965, *Deyl s.n.* & *Soják* (PR); on Mount Bogdo-ula, 47º49’N, 107º0’E, 27 Jul 1927, *Ikonnikov-Galitzky 119* (LE); Ulan Bator, 47º54’N, 106º52’E, 1 Aug 1961, *Soják s.n.* (PR). **POLAND. Kuyavia-Pomerania:** 80 km NW Torun (Thorn), zwischen Kesowo und Stawecin bei Obrowo nach Süden, 53º33’N, 17º42’E, 13 Jun 1991, *Angerer s.n.* (M); **Podlaskie:** Bialystok province, Białowieża National Park, meadows on the Narewka river, 52º42’N, 23º52’E, 7 Jul 1982, *Frey s.n.* (L). **RUSSIA. Altai Krai:** Biysk okrug, system of the Katun river, Chuiskiy tract, Shabolin vicinity, 52º32’N, 85º12’E, 6 Jul 1904, *Klements 275* (LE); Shebalino area, 3 km W of Cherga, 51º33’N, 85º31’E, 16 Aug 1985, *Alanko 52917* & *al.* (H); Gorno-altaisk, west side of Yabogan Pass, 50º54’N, 85º4’E, 31 Aug 1978, *Elias 4847* & *al.* (NY); Ondugay distr., Eloman, Ailiagushi river valley, 50º45’N, 86º9’E, 14 Oct 1936, *Kalinina s.n.* & *al.* (LE); Shebalinskiy Rayon, Sarlyk river valley, 10 km ESE Topuchaya, 51º6’N, 85º39’E, 31 Jul 2008, *Martins 2301* (JE); in valle fl. Taschte, in fl. Czebdar influent, 11 Aug 1927, *Schischkin s.n.* (NY); in jugum Sajlügem, fl. Bugusum, 49º55’N, 88º59’E, 18 Aug 1931, *Schischkin s.n.* & *Chilikina* (NY); Ausläufer des Seminskij Rückens, etwa 50 km S Cherga, 51º10’N, 85º34’E, 25 Jul 1996, *Sukopp 1658* (B). **Amur:** vicinity of the Zeia-Pristan, Pikan meteorological station, 53º42’N, 127º20’E, 14 Jul 1910, *Evstifeeva 360* (LE); Amur-Zeia plateau, 1.5 km south-west of the mouth of the Belyi stream, 53º44’N, 127º15’E, 5 Jul 1958, *Isachenko 219* & *al.* (LE); Blagoveshchensk, 50º17’N, 127º24’E, Jul 1899, *Karo s.n.* (G). **Arkhangelsk:** Tschurkina, 64º32’N, 40º32’E, 18 Aug 1891, *Kihlman s.n.* (H); Jarnema, 62º57’N, 39º21’E, 17 Aug 1899, *Liro s.n.* & *Cajander* (H); Boljsjezemelskaja, 64º32’N, 40º32’E, 24 Jul 1964, *Rebristaja 553* & *Gokorevskich* (GB); left side between the Khudaya Sarova and Verkhnyaya rivers, 64º16’N, 41º20’E, 25 Jul 1928, *Zubkov s.n.* (LE). **Bashkortostan Republic:** Mesyagutov, Lakly, Lasyn-tash mount, 55º11’N, 58º32’E, 29 Jun 1928, *Noskov 291* & *al.* (LE); Beloretsk distr., Bekhta range, 53º58’N, 58º24’E, 18 Aug 1940, *Sokolova s.n.* (LE); Southern Ural, Bashkir State Nature Reserve, Bolshoy Shatak mount, 53º30’N, 58º12’E, 11 Aug 1946, *Selivanova-Gorodkova 1521* (LE). **Buryatia Republic:** Lake Baikal, North-western shore, Cape Kotelnikovskiy, 55º2’N, 109º6’E, 26 Jul 1967, *Egorova s.n.* & *Siplivinskiy* (LE); Barguzin distr., basin of the Vitim, vicinity of the Polivtsev winter hut, 53º37’N, 109º38’E, 1908, *Iarygin 147* (LE); Barguzin distr., basin of the Vitim river, the vicinity of Endonginskoe winter hut, 53º37’N, 109º38’E, 1908, *Khutov 130* (LE); Selenginsk uyezd, weather station of Verkhnyaya Mishikha, 50º49’N, 103º53’E, 8 Aug 1903, *Litvinov 898* (LE); montes Sajany, mont. Tunkinskie golcy supra pag. Arsan, 51º54’N, 102º25’E, 20 Jul 1961, *Soják s.n.* (PR); Barguzin distr., Ust-Barguzin, near Makarinina, 53º24’N, 109º1’E, 13 Jul 1916, *Larin s.n.* & *Kanevskiy* (LE); selo of Verkhne-Angarskoe, 55º50’N, 109º58’E, 30 Jun 1912, *Shipchinskiy 145* (LE). **Chelyabinsk:** Verkhniy Ufalei, above the Ufalei river, 56º3’N, 60º14’E, 27 Jun 1939, *Igoshina s.n.* (LE). **Irkutsk:** Baikal station (Cape Baranchik), 51º52’N, 104º48’E, 24 Jul 1902, *Borodin 278* (LE); Kirenskuyezd, Okunaika river, near Dushekanskaia path, 56º6’N, 107º39’E, 14 Jul 1914, *Drobov 384* (LE); Cherski Peak, confluence of Angara River with Lake Baikal, ca. 2 km E of Listvyanka, 51º51’N, 104º54’E, 8 Jul 1979, *Iltis 561* & *al.* (NY); Polovinca, 53º7’N, 105º39’E, Aug 1902, *Lönnbohm s.n.* (H); Lake Baikal, near the mouth of the Snezhnaya river, 51º28’N, 104º37’E, 26 Jul 1915, *Sukachev 2577* & *Poplavskaya* (LE); Kulenga river Valley, 54º5’N, 105º35’E, 2 Jul 1908, *Tomin 153* (LE). **Kamchatka Krai:** Olyutorskiy distr., Korfa Bay, Kultushnoe, 60º28’N, 166º17’E, 2 Aug 1960, *Vasilkova s.n.* & *al.* (LE); Yelizovsky distr., 50 km S from Petropavlovsk-Kamchatsky, Zhirovaya bay, 52º36’N, 158º24’E, 7 Jul 2010, *Vislobokov s.n.* (MW); Karaginsky distr., shore of Penzhinskaia Guba, 2–3 km NE of Cape Kingi, 61º48’N, 163º33’E, Aug 1989, *Dorofeev 73* (LE); Penzhinskiy distr., Penzhina river, 12 km down Kamenskoe, 54º39’N, 21º33’E, 25 Jul 1960, *Dragulenko 26/1* (LE); Koryakskaya volcano, 53º19’N, 158º42’E, 14 Aug 1928, *Eyerdam s.n.* (F); basin of the Penzhina river, upper reaches of

the Palmatkina river, 62º24’N, 167º13’E, 14 Aug 1932, *Gorodkov s.n.* & *Tikhomirov* (LE); Toporkov Island, Sarannaja Bay, 55º12’N, 165º56’E, 8 Aug 1920, *Hultén 798* (GB); Kamchatka river, left side of the Belaya river, 15 km away from the mouth, 59º49’N, 163º23’E, 14 Aug 1930, *Karev 669* (LE); Karaginsky distr., near Ossora, 59º14’N, 163º4’E, 6 Aug 1976, *Kharkevich s.n.* & *Buch* (GH); Penzhinskiy distr., Penzhina river, 25 km away from the mouth, 62º28’N, 165º6’E, 14 Aug 1960, *Kuldiushevskiy 110/2* (LE); Olyutorskiy distr., Korfa Bay, vicinity of the poselok of Kultushnoe, 60º28’N, 166º17’E, 2 Aug 1960, *Vasilkova s.n.* & *al.* (LE). **Karelia Republic:** Porog, 63º49’N, 38º28’E, 17 Jul 1875, *Elfving s.n.* (H); Munjärvi, Lettonütylla, 62º14’N, 33º49’E, 3 Jul 1942, *Tuomikoshi s.n.* (H). **Komi Republic:** systema fl. Vyczegda, distr. Kortkeros, prope pag. Konscha, 61º48’N, 51º34’E, 26 Jul 1909, *Andreev 4906a* (C, G, JE, M); 28 Jun 1909, *Andreev 4906b* (C, F, G, JE, M, MO, NY). **Krasnoyarsk Krai:** Yeniseysky distr., Manzia river, 58º29’N, 96º15’E, 12 Jul 1908, *Blagoveshchenskiy 532* (LE); Minusinsk distr., Potroshilovo, Enisei river, 53º55’N, 91º30’E, 9 Jul 1931, *Iliin 28* & *Ovchinnikov* (LE); near Kargino, 58º0’N, 92º58’E, 19 Jul 1914, *Kuznetsov 78* (LE); Minusinsk distr., between the Gal’zey river and mount of Izyk Erbinskiy, 55º43’N, 92º49’E, 28 Jul 1910, *Smirnov 542* (LE). **Kuril Islands:** Kunashir Island, 44º8’N, 145º52’E, 15 Aug 1892, *Faurie 8504* (P); Paramushir, ca. 3 km south of Severo-Kurilsk, 50º37’N, 156º7’E, 1 Aug 1996, *Gage SG1814* & *Semsrott* (NY); Shikotan Island, 43º47’N, 146º44’E, 30 Jul 1931, *Ohwi 378* (US); Kunashir Island, Furukamapp, 44º8’N, 145º52’E, 12 Aug 1923, *Ohwi 5261* (US). **Leningrad:** Podporozh´e distr., Munduksa, 60º54’N, 34º10’E, Jul 1898, *Cajander s.n.* & *Lindroth* (H); 19.5 km of poselok of Volosovo, Bolshoe Zarech’e, 59º23’N, 29º47’E, 9 Jul 1983, *Khaare s.n.* (LE); Lake Onega, S of Svir River, Juksovo, 61º41’N, 35º39’E, 1942, *Sarvela s.n.* (H). **Lipetsk:** Donskoye distr., Vodopyanovo, Galich´ya Gora Reserve, 51º2’N, 43º52’E, 23 Jun 1951, *Vorobyeva s.n.* (K). **Magadan:** Staritskiy peninsula, Shelikhov Gulf, 59º33’N, 150º47’E, 1 Sep 1964, *Iurtsev s.n.* (LE). **Moscow:** Lushki ad Occam, Reservatum publicum, flum. Tadenka, 54º53’N, 37º35’E, 1 Aug 1963, *Smirnow 49* (B, F, G, JE, L, P, S, US). **Novosibirsk:** ca. 7 km S of village Yevsino, 54º20’N, 83º18’E, 27 Jul 1979, *Iltis 1321* & *al.* (NY, S); 3 km SO Chebula, 55º33’N, 84º8’E, 14 Jul 1996, *Sukopp 1523* (B). **Omsk:** Tara distr., Ciany, 56º53’N, 74º22’E, 12 Jul 1922, *Seludjakova s.n.* (PR). **Primorsky Krai:** Imansk distr., E of Evgenievka station, Odarka river (basin of Khanka lake), 44º41’N, 132º48’E, 17 Jun 1911, *Cherskiy 86* (LE); Mongugai river, Ovchinnikovo village, 43º14’N, 131º23’E, 21 Jun 1913, *Diukina 539* (LE); Muravyev Amurskiy peninsula, Okeanskaya station, Sadgorod, 43º15’N, 132º2’E, 7 Jul 1929, *Transhel 153* (LE); 4 km left of the road from Khvalynka to Konstantinovka, 44º40’N, 132º59’E, 4 Jul 1929, *Zhirov 223* (LE). **Sakhalin:** Vladimirof, 50º33’N, 142º36’E, 30 Jul 1908, *Faurie 804* (G, P); Soriofka, 50º33’N, 142º36’E, Aug 1908, *Faurie 805* (G, P); 60 km NW of Okha, at "Judith Bog", mouth of Antonovka River, Pomr Bay, 54º1’N, 142º43’E, 13 Aug 2003, *Legler 1246* (NY); W coast 5 km N of Krasnogorsk, S of Lake Aynskoye, 48º27’N, 142º3’E, 21 Jul 2003, *Legler 773* (NY); Okha distr., Shmidta peninsula, Kuegda Bay, 54º19’N, 142º35’E, 16 Aug 1998, *Sabirova s.n.* & *Sabirov* (LE). **Sverdlovsk:** Elovskiy Ural range, 60º35’N, 59º24’E, 24 Aug 1940, *Tikhomirov 73* (LE). **Tomsk:** Kuznetsk distr., Salair Ridge, between Gavrilovskiy factory and Biryulinskie vysoty, 54º15’N, 85º30’E, 30 Jun 1916, *Utkin s.n.* (LE). **Tula:** pr. Melechowska, 54º11’N, 37º37’E, 7 Jul 1899, *Zinger 796* (G, MW). **Tuva Republic:** Kurtushibinskiy range, upper reaches of Ozhu river, 52º14’N, 94º31’E, 9 Jul 1979, *Shaulo 1562* & *Saya* (LE); 10 Jul 1979, *Shaulo 1561* & *Belskaya* (LE); northern slope of Tannu-Olarange, Khovu-Aksy, 51º7’N, 93º42’E, 22 Jul 1973, *Khanmimchun 2207* & *Amelchenko* (LE). **Tyumen:** Mire behind the village of Vorogushina, north of Tobolsk, 58º11’N, 68º15’E, 2 Jun 1910, *Mameev 675* (K, LE, US); Yalutorovsk distr., 56º39’N, 66º18’E, 14 Jun 1912, *Svitich s.n.* (LE). **Ulyanovsk:** Karsunskiy distr., Staraya Zinov’evka, Barysh river, 54º15’N, 46º55’E, 25 Jun 1916, *Shennikov s.n.* (LE). **Vladimir:** Yriev-Polskiy distr., 5 km S-SE of Shorodoga, Nerl’ river, 56º46’N, 39º51’E, 11 Jul 2007, *Seregin 3135* (MW). **Vologda:** road from Kharino to Ledensk, Prelaya river, 59º58’N, 43º44’E, 17 Aug 1926, *Korchagin 169* & *Gaze* (LE).**Voronezh:** Khoper Nature Reserve, Bogdanovskiy forest, 12–14 km NE Novokhopersk, 51º5’N, 41º37’E, 9 Jun 1980, *Tsvelev 266* (LE). **Zabaykalsky Krai:** Nerchinsko-Zavodsky distr., between Davenda and Kudecha rivers, 53º33’N, 119º19’E, 19 Jul 1909, *Blagoveshchenskiy 1248* & *Poplavskaia* (LE); Aginskoe, Anzhi river, 55º15’N, 94º54’E, 16 Jul 1949, *Fedorov s.n.* & *al.* (LE); Kyrinskiy distr., 17 km S of Kyra, 49º34’N, 111º58’E, 12 Aug 2005, *Golovina 310* (LE); Nertschinsk, 51º59’N, 116º35’E, 1889, *Karo 270* (G, GOET, WU); prope pag. Taptanai, 51º5’N, 114º15’E, 12 Jul 1931, *Krylov s.n.* (NY); Chitinskiy Rayon, 52º0’N, 113º30’E, 14 Jul 1913, *Poplawska 1743* (K); Akshinsk distr., mountains along Bukukun river, near poselok of Bukukunskiy, 49º19’N, 111º15’E, 21 Jul 1913, *Smirnov 70* (LE). **SERBIA.** Vlasina lake, 42º42’N, 20º22’E, 1881, *Pančić s.n.* (W). **SOUTH KOREA. Gangwon:** Ouen-San mountain, 37º30’N, 128º15’E, Jul 1906, *Faurie 1246* (AAH, P). **Gyeongsang:** Mt. Chiisan, 35º20’N, 127º43’E, 18 Jul 1942, *Nakashima s.n.* (US). **Jeju:** Quelpart Island, Hallasan crater, 33º24’N, 126º32’E, 13 Aug 1908, *Taquet 1891* (G, K, NY); Jul 1909, *Taquet 3423* (AAH, NY). **UKRAINE. Poltava:** terrace above the Udoy river near Kalinoviy most, 50º16’N, 32º28’E, 29 Jun 1927, *Poretskiy 298* (LE).

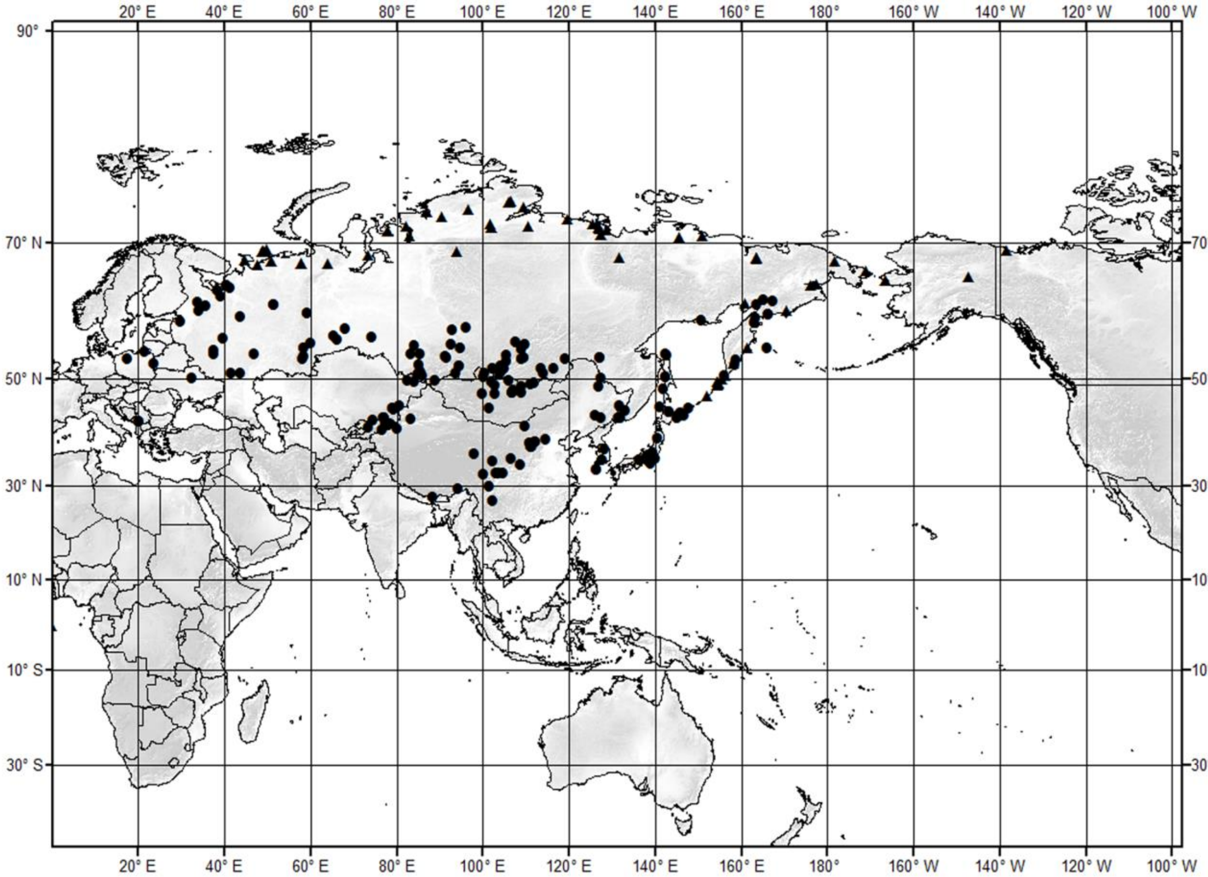

Figure 3. Distribution of *Trisetum sibiricum* subsp. *sibiricum* (dots) and *T. sibiricum* subsp. *litorale* (triangles).

b. subsp. LITORALE Rupr. ex Roshev., Izv. Glavn. Bot. Sada R.S.F.S.R. 21: 90. 1922. *Trisetum sibiricum* var. *litorale* (Rupr. ex Roshev.) Rupr. ex Roshev. in V.L. Komarov (ed.), Fl. URSS 2: 254. 1934. *Trisetum litorale* (Rupr. ex Roshev.) Khokhr. Botan. Zhurn. 63 (3): 395. 1978, nom. illeg., non Phil. 1858. *Trisetaria sibirica* subsp. *litoralis* (Rupr. ex Roshev.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 385. 1996. *Trisetum ruprechtianum* Tzvelev, Novosti Sist. Vyssh. Rast. 42: 89. 2011.—TYPE: RUSSIA. Kanin Peninsula, 67º27’N 47º32’E, 13–14 Aug, *F.J.I. Ruprecht s.n.* [lectotype, designated by Tzvelev (1976: 262): LE!].

Herb (12.7–)23.8–37.7(–58.4) cm high, not tufted, shortly rhizomatous or with stoloniferous rhizomes; nodes 3–4(–5), separated or sometimes concentrated in lower part of the culm, enclosed or not by the sheaths. Basal leaf-blades (1.2–)2–4.3(–10.5) cm long × (2–)2.3–3.4(–4.8) mm wide; top culm leaf-sheaths (4.2–)6–9(–13.7) cm long, glabrous, rarely with hairs on the nerves and upper part, without cilia on the margins; top culm leaf-blades (3.2–)4.5–7.5(–13.7) cm long × (2.7–)3.6–4.4(–7) mm wide. Panicles (3.3–)5–7.4(–9) cm long × (1.2–)1.8–2.6(–3.8) cm wide, ovate, sometimes elliptic or oblong in outline, dense; longest basal branches (0.6–)1–2.3(–2.8) cm long. Pedicels (0.5–)1.5–2.8(–4) mm long. Lemmas (3.8–)4.7–5.7(–6.2) mm long; awn (4–)5.5–7(–8.4) mm long. Figure 2.

Chromosome Number—2*n* = 14 (Zhukova, 1967).

Phenology—Flowering and fruiting from July to September.

Distribution and Habitat—This subspecies is distributed along the Russian coast, from Kanin Peninsula to Kamchatka Peninsula and Kuril Archipelago, extending to Alaska and Artic coast of Yukon territory in Canada; 0–900 m of elevation; in meadows, sandy or rocky riversides, and also in tundra. Figure 3.

Specimens Examined—**CANADA. Yukon:** Arctic Coast west of Mackenzie River delta, between King Point and Kay Point, 69º12’N, 138º30’W, Jul 1934, *Porsild 7122* (S). **RUSSIA. Arkhangelsk:** Bolshezemelskaya tundra, Vangurei range (Pytkov Kamen), Pelekoptama river basin, 67º30’N, 58º0’E, 16 Aug 1930, *Andreev 692* & *Savkina* (LE); Bolshezemelskaya tundra, Vangurei range (Pytkov Kamen), Khylchou river basin, 67º30’N, 58º0’E, 28 Aug 1930, *Andreev 898* & *Savkina* (LE); ad ostia fl. Lena, Bulum, Bach-Ufer, 31 Aug 1901, *Cajander 2074* (H); Bolshezemelskaya tundra, right side ot the Sabrei-Yaga, 67º30’N, 58º0’E, 3 Aug 1938, *Kuznetsov s.n.* (LE); Pai-Khoi, Mount Khunt-Pe, 64º32’N, 40º32’E, 8 Aug 1965, *Rebristaya 702* & *Tokarevskikh* (LE); Bolshezemelskaya tundra, 2 km west of the Iunku-Shor river, 67º30’N, 58º0’E, 8 Aug 1938, *Zubkova s.n.* (LE). **Chukotka Autonomous Okrug:** Olenek river, 72º58’N, 119º48’E, 27 Aug 1875, *Czekanowski s.n.* (LE); prope pagum Kustur, in valle fl. Bytantaj, 68º10’N, 131º40’E, 4 Aug 1959, *Jurtzev s.n.* (C); Anyui Highlands, Pogynden River, 68º12’N, 163º32’E, 21 Jul 1976, *Petrovskyi s.n.* & *Koroleva* (K); near the mouth river Chegitun, 66º33’N, 171º4’W, 7 Aug 1971, *Sekretareva s.n.* & *al.* (BM); Anadyr Krai, the basin of the Belaya river, left tributary of the Anadyr, near the mouth of Belaya river, 64º37’N, 176º14’E, 26 Jul 1929, *Sochava s.n.* (LE); Chukchi National Okrug, Anadyr distr., southern parth of the Ust-belskie mountains, 64º44’N, 177º30’E, 14 Aug 1977, *Vasilieva s.n.* (LE); right side of the Malyi Aniuy river, the middle reaches of the Machvaam river, 68º12’N, 163º32’E, 12 Jul 1952, *Vikulova s.n.* (LE); the middle reaches of the Ekiatap river (left side), the Pastbishchnaya river, 67º44’N, 178º18’W, 12 Aug 1973, *Zubakova s.n.* & *Razzhivin* (LE). **Kamchatka Krai:** Olyutorskiy distr., 61º0’N, 170º30’E, 27 Jul 1974, *Kharkevich s.n.* & *Buch* (H, MO, NY); Olyutorskiy distr., Vyerkhoutourov, 55º16’N, 161º31’E, 25 Jul 1975, *Kharkevich s.n.* & *Buch* (K, MO, MW); Yelizovsky distr., 50 km south from Petropavlovsk-Kamchatsky, Vilyuchinskaya bay, 52º39’N, 158º23’E, 15 Jul 2010, *Vislobokov s.n.* (MW). **Krasnoyarsk:** Taimyr Lake, Bikada-Nguoma river, 74º50’N, 106º30’E, 18 Aug 1974, *[unknown] 57* (LE); the basin of the Kheta river, the Khatanga river, right side of the Khatanga river near the mouth of the Zhdanikha river, 71º54’N, 102º6’E, 8 Aug 1934, *Aleksandrova 134* & *Tiulina* (LE); basin of the Kheta river, the Khatanga river, 71º54’N, 102º6’E, 16 Aug 1934, *Aleksandrova 242* & *Tiulina* (LE); Western Taimyr, right side of the Piasina river (middle reaches) the vicinity of the poselok of Tareia, 73º15’N, 90º28’E, 18 Jul 1965, *Matveeva s.n.* & *al.* (LE); Turukhan Krai, the Piasina river, the mouth of the Pura river (Kuria), 150 verst as away from the mouth of the Piasina, 73º50’N, 87º9’E, 14 Jul 1922, *Pushkarev s.n.* (LE); Khatanga river, the basin of the Novaya river; moraine ridge on the left side of the Novaya river, 10 km away from its mouth, 74º17’N, 109º30’E, 19 Aug 1934, *Tiulina 223* (LE); south-eastern Byrranga, 15 km upstream the mouth of the Malakhaitari, 74º58’N, 106º35’E, 28 Jul 1928, *Kozhevnikov 154* (LE); Taimyr National Okrug, Khatanga distr, right side of the Kotui river, between the Tompoko and Saamoidin rivers, north-western slope, 71º55’N, 102º5’E, 16 Aug 1955, *Kozlitina s.n.* (LE); slope of the bank of the Yenisei river near Sarikha sands, 72º3’N, 82º23’E, 17 Aug 1914, *Kusnezow 2276* & *Reverdatto* (LE); Nasonovskiy island at the mouth of the Yenisei river, 70º54’N, 83º11’E, 24 Aug 1914, *Kusnezow 4043* & *Reverdatto* (LE); Taimyr, the basin of the Novaya river, Ary-mas natural landmark, 70º50’N, 145º33’E, 15 Jul 1969, *Norin s.n.* (LE); SE Taimyr, N Anabar plateau, fusion area rivers Fomich and Popigaj, 72º7’N, 110º33’E, 11 Jul 2008, *Pospelov 08–0466* (MW); central Taimyr, out of the mountains Byrranga p. Fadyukuda, 74º5’N, 96º50’E, 16 Jul 1997, *Pospelov 97–376* (MW); Piasina river, the mouth of the Pura river (Kuria), 73º50’N, 87º9’E, 14 Jul 1922, *Pushkarev s.n.* (LE); "Ary-Mas" nature reserve, c. 50–60 km NNW Khatanga, right riverside of Novaya, 72º27’N, 101º51’E, 27 Jul 2004, *Schönswetter s.n.* & *Tribsch* (WU); Minusinsk uyezd, Abakanskaya Inorodnaya Uprava, upper reaches of the Uybata river, 31 Jul 1909, *Titov s.n.* (LE); Eastern Taimyr, the lower reaches of the Yamu-Nera (the basin of Taimyr Lake), 74º50’N, 106º0’E, 14 Aug 1928, *Tolmachev 770* (C, LE, S); Putorana Mountains, Sirkiuarvit Lake, 69º2’N, 94º9’E, 22 Aug 1969, *Vodopianova s.n.* (LE). **Magadan:** basin of the Medvezhaia river, downstream of the Chapko river, 61º58’N, 160º56’E, 13 Aug 1935, *Sambuk s.n.* & *Zdanevich* (LE); Bilibinsky distr., fontes fl. Lelvergyrgyn, 68º3’N, 163º32’E, 21 Jul 1976, *Koroleva 5703* & *Petrovsky* (C, JE, K, LE, M, MW, NY, US). **Nenets Autonomous Okrug:** Kanin Peninsula, the Pae-khoi range; source of the Tarcho-Yaga river, 16 Aug 1928, *Andreev 1418* (LE); Kolguev Island, valley of the Velikaya river, upstream of the mouth of the Pyrdiu river, 69º20’N, 49º50’E, 31 Aug 1936, *Bogdanovskaya-Gienef s.n.* & *Verlichenko* (LE); Northern part of Malozemelskaya Tundra, near sopka [Liadak], 67º50’N, 51º0’E, 29 Jul 1930, *Igoshina s.n.* (LE); Northern part of Malozemelskaya Tundra, along the bank of the Khorey-Yaga, 67º50’N, 51º0’E, 7 Jul 1930, *Igoshina s.n.* (LE); Kanin, northern part, the middle riches of the Peschanka river, 67º19’N, 47º48’E, 12 Jul 1945, *Matveev s.n.* (LE); Kolguyev Island, 69º5’N, 49º15’E, 1902, *Pohle s.n.* (C, LE); Kanin Peninsula, Krimka, 67º51’N, 44º49’E, 6 Aug 1903, *Poppius s.n.* (FI, P); Kolguev Island, on a slope with meadow on the right side of the Oltsovaya Yakha, left tributary of the Peschanka river, 69º0’N, 49º58’E, 7 Sep 1930, *Smirnova s.n.* (LE); Kolguev Island, right side of the Krivaya river, 69º0’N, 48º46’E, 31 Jul 1930, *Smirnova s.n.* (LE). **Republic of Karelia:** Uusiselkä, Kuivahko niitty, 61º43’N, 34º29’E, 26 Jul 1942, *Kalela s.n.* (H). **Sakha Republic:** lower reaches of the Indigirka, the middle reaches of the Shandrin river, 70º55’N, 151º3’E, 10 Jul 1974, *Korobkov s.n.* & *al.* (LE); Tigija, 71º25’N, 8 Jul 1898, *Nilsson s.n.* (S); Kumach Sor, 71º30’N, 7 Aug 1898, *Nilsson s.n.* (S); Balaganach, 71º35’N, 15 Jul 1898, *Nilsson s.n.* (S); lower reaches of the Lena river, Western spurs of the Tuora-Sis range, mouth of the Sietchan river, 71º5’N, 127º30’E, 7 Jul 1956, *Norin s.n.* & *al.* (LE); north end of the Kharaulakhskiy range, right side of the Bykovskaya canal of the Lena river, vicinity of Sokol, 72º20’N, 125º40’E, 15 Aug 1956, *Polozova s.n.* & *Yurtsev* (LE); Tiksi Bay, NW part of the Buorkhaia Guba (arctic Yakutia), near the airport Tiksi-3, flood-plain of the Khorogol river, 71º41’N, 128º54’E, 4 Aug 2004, *Sekretareva s.n.* & *Sytin* (LE); Lena R. west bank, Chekurovka village, surroundings of settlement, 71º3’N, 127º31’E, 12 Jul 2004, *Solstad 04/0266A* & *Elven* (O); lower reaches of the Lena river, Tit-Ary Island, 71º58’N, 127º0’E, 4 Aug 1956, *Tolmachev s.n. & al.* (LE); lower reaches of the Lena river between Tit-Ary Island and Stolb Island, right side of the Lena, 10 km downstream of Tit-Ary, 71º50’N, 127º20’E, 31 Jul 1955, *Vasilkova s.n.* & *al.* (LE); lower reaches of the Lena river, Polar station Sokol, Bykovskaya Canal, 72º24’N, 126º48’E, 28 Jul 1955, *Vasilkova s.n.* & *al.* (LE). **Sakhalin:** Kuril Islands, 30 Aug 1929, *Bergman 237* (GH); Kuril Archipelago, Simushir Island, inland coastal margin of Malaya Bay, 47º5’N, 152º8’E, 18 Aug 1995, *Gage SG1427* (NY); Kuril Archipelago, Onekotan Island, Kol´tsyevoi Spine, rim of crater, Lake Kol´tsyevoi, 49º22’N, 154º44’E, 7 Aug 1996, *Gage SG1976* (NY); Kuril Archipelago, Kharimkotan, Severgina Bay, ca. 1 km inland from shoreline, 49º9’N, 154º28’E, 8 Aug 1996, *Gage SG2021* (NY); Kuril Archipelago, Onekotan Island, southern end of island, near Trudny River, 49º16’N, 154º44’E, 9 Aug 1996, *Gage SG2117* (NY); Kuril Archipelago, Paramushir, NE corner of the island, environs of lake fed by Savushkina River, 50º44’N, 156º8’E, 4 Aug 1997, *Gage SG4139* (NY); Kuril Archipelago, Shumshu, inland from Babushkina Bay, environs of Luzhanka river, 50º38’N, 156º24’E, 10 Aug 1997, *Gage SG4274* (NY); Kuril Archipelago, Paramushir, inland from eastern Tukharka, Cape Baklanyi, 50º10’N, 155º38’E, 17 Aug 1997, *Gage SG4492* (NY); Kuril Archipelago, Kharimkotan, Severgina Bay, 49º9’N, 154º28’E, 8 Aug 1996, *Semsrott BS0173* (NY); Kuril Archipelago, Makanrushi island, inland from Zakat Bay, environs of Cape Poludennyi, 49º44’N, 154º24’E, 18 Aug 1997, *Semsrott BS1487* (NY). **Yamalo-Nenets Autonomous Okrug:** Yamal Peninsula, the shore of Obskaya Guba, 30 km to the N of Cape Kamennyi, 68º30’N, 73º34’E, Aug 1971, *Gaev s.n.* & *Fediakov* (LE); Gydansk Peninsula, the lower reaches of the Khalmeriakha river, 71º30’N, 78º5’E, 18 Jul 1988, *Khitun 8120* (LE); 23 Jul 1988, *Khitun 8151* (LE); Gydansk Peninsula, the lower reaches of the Khalmeriakha river,valley wall of Lang-to lake, 71º30’N, 78º5’E, 30 Jul 1988, *Khitun 8234* (LE). **USA. Alaska:** White Mountain between the headwaters of Sheep and Mascot Creeks, 65º44’N, 147º6’W, 1 Jul 1953, *Gjaerevoll 294* (S); Norton Sound, behind Pastolik, 63º8’N, 163º18’W, 21 Jul 1926, *Porsild 893* & *Porsild* (H); Seward Peninsula, Port Clarence, Teller, 65º16’N, 166º20’W, 24 Aug 1926, *Porsild 1414* & *Porsild* (S); Bering Strait, Port Clarence, Teller, 65º15’N, 166º21’W, Aug 1949, *Scamman 5410* (S).

Notes—Trisetum sibiricum is the most polymorphic and widespread taxon of the section. This species presents a great morphological variability throughout its distribution area. The panicle shape, as well as the size of the individuals, is a quite variable character.

Although *T. sibiricum* is a distinct species, it has been constantly confused with *T. flavescens*. *Trisetum flavescens* is another of the species of the genus with a wide distribution, covering the whole Europe and the Maghrebian Mountains of North Africa, being introduced in many other temperate zones. *Trisetum flavescens* belongs to *T.* sect. *Trisetum*, and it is characterized by having green (rarely purple shiny) panicles, twisted and geniculate awns, and leaves narrower and with a more compact venation that *T. sibiricum*. However, *T. sibiricum* belongs to *T.* sect. *Sibirica*, and it is differentiated from *T. flavescens*, apart from the characters mentioned before, by its golden brownish or yellowish panicles and twisted but not geniculate awns (Tzvelev, 1976; Frey, 1992).

The westernmost specimens of *T. sibiricum* are those from Poland and Serbia, the ones from Serbia named *Avena rufescens* by Pančić (1884). Some authors (i.e. Roshevitz, 1922; Tzvelev, 1976; Jonsell, 1980) also placed this species in Romania. In the Flora of Romania by Sãvulescu (1972), this species is not cited. Moreover, we have not identified any of the herbarium material from this country as *T. sibiricum*.

Owing to the polymorphism of *T. sibiricum*, some subspecies or varieties have been described by different authors. Kitagawa (1940) described a new variety, *T. sibiricum* var. *umbratile* from Manchuria, characterized by its smaller 2-flowered spikelets (5 mm long) and shorter awns (6.5 mm long). Later, according to these characters, Kitagawa (1956) and Wu & Phillips (2006) recognized it as a species, whereas Tzvelev (1976) identified it as a subspecies, separating it from *T. sibiricum* subsp. *sibiricum* by its wider leaves, and also leaves and basal leaf-sheaths indumentum. Keng described a new species from central China, *T. pauciflorum*, indicating that it was close to *T. henryi* (Anonymous, 1976). This species has small spikelets, as *T. umbratile*, but with recurved awns and a different distribution. Wu & Phillips (2006) indicated that it was not a well-known species, close to *T. umbratile*. This range of variation in the spikelets size and awn length falls well within the variation range of *T. sibiricum* subsp. *sibiricum*; along its distribution, specimens with smaller and 2-flowered spikelets have been studied, mainly in material from Mongolia. For this reason, and also following Stuessy et al. (2014), who recognized geography as a fundamental component for recognition of infraspecific taxa, *T. umbratile* and *T. pauciflorum* have been considered as synonyms of *T. sibiricum* subsp. *sibiricum*.

However, another recognized subspecies, *T. sibiricum* subsp. *litorale*, is a smaller plant with shorter and denser panicles, usually ovate in outline, distributed along northern Russia, arriving to Alaska. In the studied material, specimens from Altai show more contracted panicles, but not as much as those of the coastal regions, and also without shorter culms. This subspecies has a constant morpho-geographic pattern, which overlaps with the morphology of *T. sibiricum* subsp. *sibiricum* in Kuril Archipelago and Kamchatka Peninsula (where both subspecies overlap). As did Roshevitz (1922) and Tzvelev (1976), we have recognized it at subspecific rank.

Hooker (1897) described the species *Avena sikkimensis* from the Himalayan Mountains of Sikkim state in India, synonymized into *Trisetum flavescens* by Bor (1956). Chrtek (1968) indicated that *A. sikkimensis* is different from *T. flavescens*, mainly by its not geniculate awns, combining it as *Trisetum* *sikkimensis*, and including it in serie *Sibirica*. As indicated before, the identification between *T. flavescens* and *T. sibiricum* have been frequently confused, and the specimens from Sikkim, corresponds to *T. sibiricum*. Apart from its slightly smaller stamens, which has been also appreciated in specimen from Mongolia [*Komarov s.n.* (LE)], we did not find more differences between *T. sikkimensis* and *T. sibiricum* subsp. *sibiricum*. For this reason, *T. sikkimensis* has been considered as synonym of *T. sibiricum*.

2. TRISETUM TURCICUM Chrtek, Bot. Not.119: 487. 1966. *Trisetaria turcica* (Chrtek) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 386. 1996.—TYPE: TURKEY. Lazistan, Djimil valley, 40º40'N 39º40'E, Aug 1866, *B. Balansa 1551* [holotype: PRC–454965 (image!); isotypes: G–176299!, G–176300!, GH!, GOET–6970!, JE–18873!, K–808699!, LE–9412!, LE–9413!, P–3644578!, P–3645245!, P–3351081!, P–3351082!, P–3351137!, P–2248780!, P–2248781!, RO (image!), US–1064357!, W–1889–0033667!].

Trisetum thospiticum Chrtek, Bot. Not.119: 489. 1966. *Trisetaria thospitica* (Chrtek) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 386. 1996.—TYPE: TURKEY. Bitlis province, Suphan Dag, 38º57’N 42º50’E, 28 Sept 1954, *P. H. Davis 24763a & O. Polunin* [holotype: E–196474 (image!); isotypes: BM–959386!, K–808700!].

Herb (13.4–)43.7–87.7(–102) cm high, laxly caespitose, shortly rhizomatous, culm 0.7–1.3 mm diam., glabrous, rarely pubescent on the upper part; nodes 4–5, separated along the culm, enclosed or not by the sheaths, puberulous. Basal leaf-sheaths glabrous to slightly pubescent, with hairs up to 0.2 mm long, decaying in fibers, yellowish to greenish or brownish; basal leaf-blades (6–)7.5–10 × 2.6–3.3 mm, flat, usually rolled when dried, from glabrous to pubescent abaxially and adaxially, margins with hairs 0.1–0.8(–1.2) mm long, greenish to brownish; top culm leaf-sheaths (1–)1.4–1.8(–2) cm long, shorter than the internodes, rarely the same length, glabrous to pubescent, with or without cilia on the margins; top culm leaf-blades (6.3–)7–12(–14) cm long × 3–4.2(–5.5) mm wide, flat, pubescent abaxially and adaxially, ciliolate, with hairs 0.1–0.7(–0.9) mm long, greenish to greyish, sometimes brownish; inner collar region hairy, with scattered hairs 0.05–0.3 mm long, also on the margins, rarely glabrous; ligules 1.5–2.8(–3.4) mm long, slightly laciniate to laciniate, glabrous, with scattered hairs 0.1–0.3 mm long on the upper part. Basal nude of the panicle glabrous. Panicles (7.2–)8.2–13.4(–15) cm long × 2–3.6(–4) cm wide, elliptic to oblong, sometimes narrowly to broadly elliptic, dense, sometimes more or less lax; rachis glabrous to slightly pubescent, with hairs up to 0.08 mm long; branches in whorls of 3 or 4, longest basal branches 1–3.2(–3.5) cm long. Spikelets 7.4–9.7(–10.5) mm long × (2–)2.7–4.4(–4.6) mm wide, 2–3-flowered; pedicels 2.7–5.7 mm long, slightly pubescent to pubescent, with hairs up to 0.1 mm long. Glumes unequal [ratio -- lower glume length/upper glume length = (0.63–)0.7–0.82(–0.9)]; lower glume (4–)5–7.2 mm long × 0.9–1.2(–1.5) mm wide, narrowly lanceolate to lanceolate [ratio -- lower glume width/lower glume length = 0.16–0.22(–0.24)], acuminate to long acuminate, 1(–2)-nerved, glabrous, usually with hairs up to

0.08 mm long on the upper part of the margins and central nerve, greenish on the central part surrounded by yellowish; upper glume (6.5–)7.2–8(–8.7) mm long × (1.6–)1.8–2.2 mm wide, elliptic to oblanceolate, sometimes lanceolate [ratio -- upper glume width/upper glume length = (0.23–)0.25–0.28(–0.3)], acuminate to long acuminate, 3-nerved, glabrous, with hairs up to 0.08 mm long from the middle to the upper part of the midrib and margins, greenish with yellowish; rachilla segments between first and second floret 1.7–2.2 mm long, with hairs 1–2 mm long; rachilla segments to sterile floret 1.5–2 mm long, with hairs 0.3–1.2 mm long. Lemmas 6.5–8.7 mm long × 1.6–2 mm wide, narrowly elliptic to lanceolate, sometimes slightly oblanceolate (ratio -- lemma width/lemma length = 0.19–0.28), scabridulous, with hairs up to 0.1 mm long, brownish to greenish, sometimes yellowish; callus 0.2–0.3 mm long, orbicular, rarely elliptic, glabrous or with scattered hairs 0.1–0.2 mm long; apical teeth 0.2–0.9 mm long, with aristules 0.8–1.5(–2) mm long; awn (8.8–)9.5–12.5(–13.4) mm long, inserted (3.8–)4–4.8 mm from the base (ratio -- awn insertion from the base length/lemma length = (0.57–)0.6–0.68), geniculate below the middle, slightly twisted to twisted near the base, with adpressed hairs 0.05 mm long. Paleas (5–)5.7–7(–7.2) mm long × 1.5–1.8 mm wide [ratio -- palea length/lemma length = 0.74–0.84(–0.93)], elliptic, sometimes oblanceolate, margins with short hairs from the middle till the upper part; teeth 0.3–0.4(–0.7) mm long, with short antrorse hairs. Lodicules 0.5–1 mm long, with two bifid lobules, glabrous. Anthers (3–)3.3–4 mm long. Ovary 0.4–1(–1.4) mm long. Caryopsis 3.3–4 mm long × 0.6 mm wide, narrowly elliptic to oblong. Figure 4.

Chromosome Number—2*n* = 28 (Tzvelev, 1976).

Phenology—Flowering and fruiting from July to September.

Distribution and Habitat—It is distributed from the mountains of south and eastern Turkey to the Caucasus and north-west Iran; 2,000–2,800 m of elevation; in forest or among shrubs in subalpine meadows. Figure 5.

Specimens Examined—**ARMENIA. Gegharkunik:** Nor-Bajazet distr., prope pag. Alekssandrovka, 40º30’N, 44º58’E, 8 Jul 1929, *Zedelmejer & Hejdemann s.n.* (LE). **Kotayq:** vicinity of Gokcha Lake, Darachichag, 40º23’N, 45º19’E, 1 Jul 1923, *Smirnov 119* (MW). **Shirak:** Alagez, Karnalykh gorge, south-east of Ziarat mount, 40º32’N, 44º4’E, 9 Aug 1932, *Busch s.n.* (LE). **Syunik:** on a slope to the valley of the Vargavar-chay River, 38º53’N, 46º15’E, 1 Jul 1956, *Egorova 1685* & *al.* (LE); along a slope to the bed of a right tributary of the Megriget River upwards of Vardanadzor, 38º53’N, 46º15’E, 4 Jul 1956, *Egorova 1844* & *al.* (LE). **Yerevan:** Ketan-Dag, 40º21’N, 44º41’E, 18 Aug 1930, *Acheev s.n.* (MW). **AZERBAIJAN. Nakhichevan:** monte Arazhon, 39º17’N, 45º47’E, 3 Aug 1933, *Gadzhiev s.n. et al.* (LE); inter p. Aravsa et monte Arazhon, 39º17’N, 45º47’E, 29 Jul 1933, *Gadzhiev s.n. et al.* (LE); 5–7 km ad NO Urmis, 39º4’N, 45º58’E, 4 Aug 1933, *Karjagin s.n. & Isaev* (F). **GEORGIA.** Akhmetis Raioni, m. Diklo, 42º23’N, 45º41’E, 29 Jul 1861, *Ruprecht s.n.* (LE). **IRAN. Āžārbāyjān-e Gharbī:** Zanjan distr., Tachte Balküns, 36º36’N 47º16’E, 18 Aug 1884, *Knapp s.n.* (WU). **RUSSIA. Dagestan:** Maara mountain, ad pagum Akusha, 42º16’N, 47º20’E, 16 Jul 1898, *Alexeenko s.n.* (LE). **Kabardino-Balkar Republic:** Bashil-Auz, the upper reaches of the Chegem, 43º17’N, 43º8’E, 20 Jul 1913, *Bush s.n. & Bush* (LE); Karasu, Kara-Chiran glacier, 43º17’N, 43º24’E, 29 Jul 1925, *Bush 34 & Bush* (LE). **North Ossetia-Alania:** on Tsadanzerta by the lower edge of Chefanzara, 43º11’N, 44º14’E, 14 Aug 1925, *Bush 42* & *Bush* (LE); Terek oblast, Aday-khokh, 42º56’N, 44º39’E, 28 Jul 1900, *Markovich s.n.*; Terek oblast, Daj-chveh, 42º56’N, 44º39’E, 29 Jul 1900, *Markovich s.n.* (JE). **TURKEY. Bitlis:** Süphan Dag, 38º57’N, 42º50’E, 30 Jul 1966, *Stileman 17* (E, image!). **Erzincan:** Sipikordagh [Sipikor], 39º52’N, 39º35’E, 5 Jul 1889, *Sintenis 1142* (JE). **Erzurum:** between Erzurum and Ispir, East of Rirekent village, Halbogari valley, 40º28’N, 40º59’E, 14 Aug 1976, *Tatli 5331* (GOET). **Kahramanmaraş:** Beryt Dagh, 38º3’N, 36º46’E, 9 Aug 1865, *Haussknecht s.n.* (JE). **Karaman:** près Ermenek, 36º38’N,

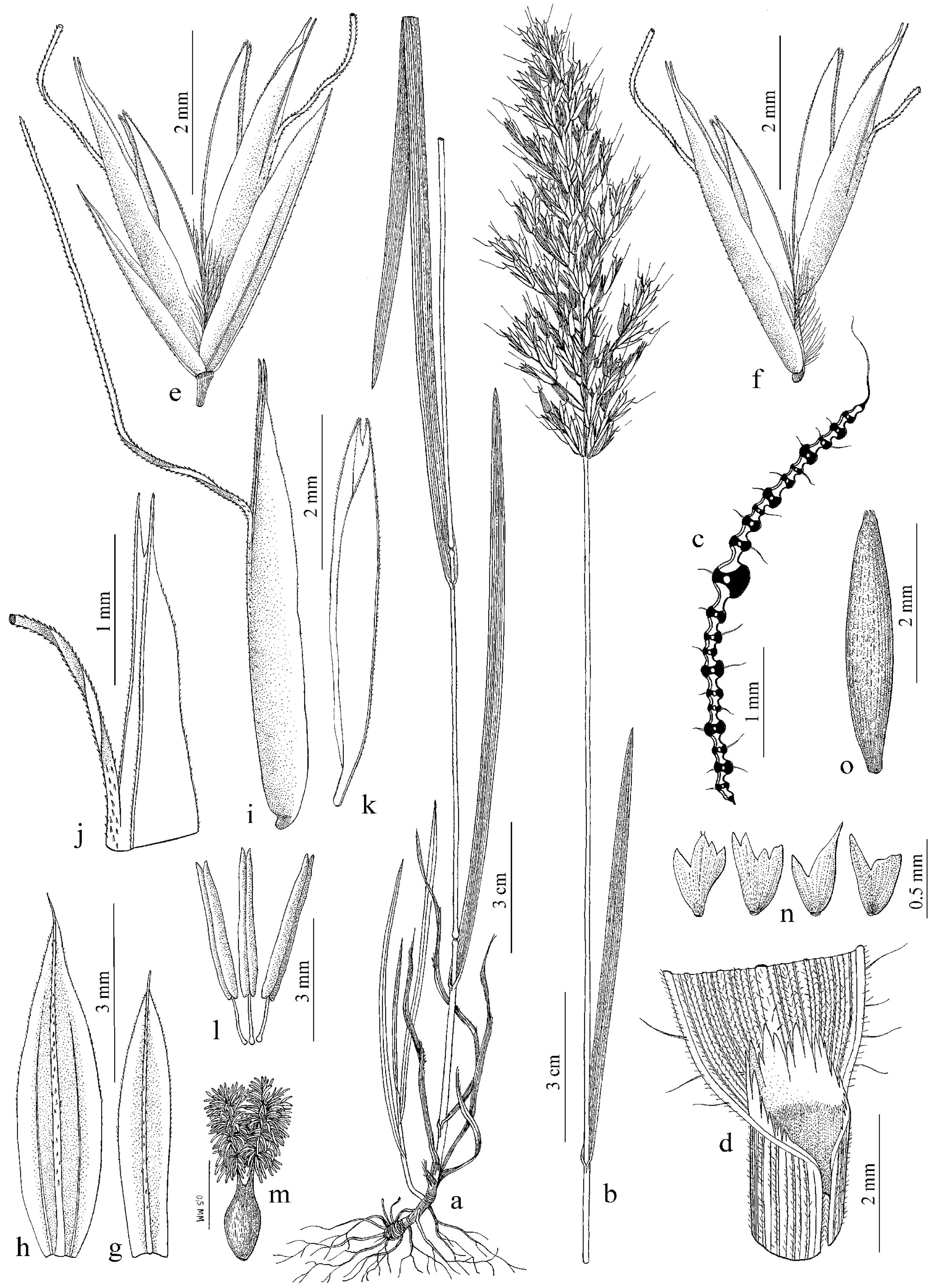

Figure 4. *Trisetum turcicum*. a. Basal Habit. b. Inflorescence. c. Transverse section of leaf-blade. d. Sheath, ligule, and portion of the blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Lemma, upper part, lateral view. k. Palea, lateral view. l. Stamens. m. Pistil. n. Lodicules. o. Caryopsis. (*Balansa 1551*, G–00176299, a-b; *Davis 46563*, K, c; *Balansa 848*, P–02243990, d-f, i-m; *Sintenis 1142*, JE, g-h, o).

32º53'E, Jul 1872, *Péronin 214* (MPU, P, S). **Kars:** 6 km from Sarikamis to Karakurt, 40º9'N, 42º36'E, 15 Jul 1966, *Davis 46563* (K, US). **Kayseri:** Mount Argée [Erciyes], 38º32'N, 35º27'E, 9 Jul 1856, *Balansa 848* (G, GOET, L, P). **Malatya:** inter urbem Malatja et vicum Kjachta, in declivibus opimis montis Gök Tepe versus Kumik, 38º3'N, 38º2'E, 16 Jul 1910, *Handel-Mazzetti 2279* (W). **Rize:** Djimil valley, 40º40'N, 39º40'E, 21 Aug 1866, *Balansa s.n.* (L).

Notes—The Caucasian specimens of *T. turcicum* have been sometimes confused with *T. sibiricum*. *Trisetum turcicum* is mainly differentiated from *T. sibiricum*, and also from the rest of species of *T.* sect. *Sibirica*, by its longer anthers and its awns geniculate below the middle.

Apart from *T. turcicum*, Chrtek (1966) described another species of *Trisetum* from Eastern Turkey, *T. thospiticum*. This species was separated from *T. turcicum* by its habit, smaller spikelets, and shorter anthers. The habit of the type specimen studied [*Davis 24763 & Polunin* (K–808700)] has been also appreciated in specimens of *T. turcicum* from Azerbaijan [*Karjagin s.n. & Isaev* (F)], which are slightly densely caespitose. The length of spikelets and anthers of the type specimen of *T. thospiticum* (9.7 mm and 3.5 mm long, respectively) fall into the variability of *T. turcicum* [7.4–9.7(–10.5) mm and (3–)3.3–4 mm long, respectively)]. For those reasons, *T. thospiticum* has been considered as synonyms of *T. turcicum*.

As indicated before, Chrtek (1968) separated the Asiatic species of *Trisetum* section *Trisetum* in two series (ser. *Trisetum* and ser. *Sibirica*) according to the awn shape. He included *T. turcicum* and *T. thospiticum* in ser. *Trisetum*, because of its geniculate awn. In this work, *T. turcicum* has been included in *T.* sect. *Sibirica* because it shows the rest of characters of the section, being very close to *T. sibiricum*.

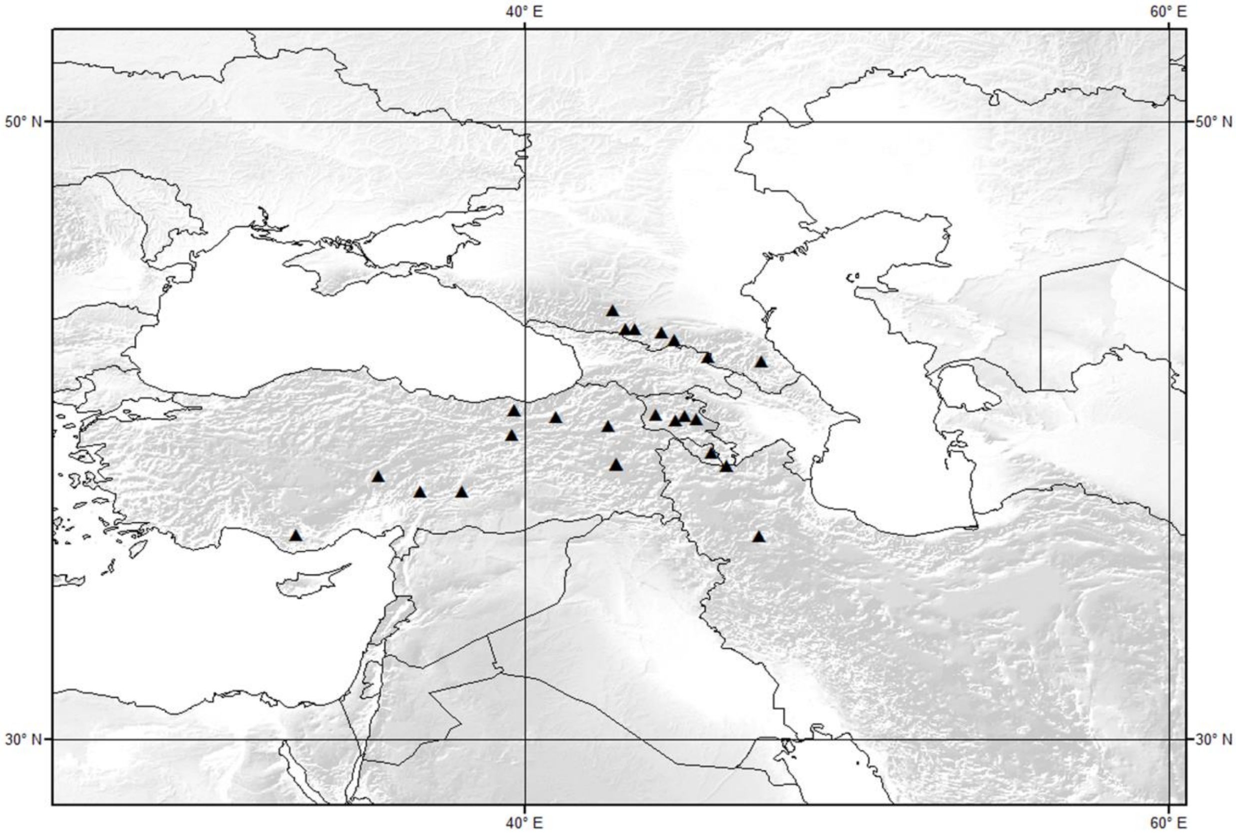

Figure 5. Distribution of *Trisetum turcicum*.

3. TRISETUM BIFIDUM (Thunb.) Ohwi, Bot. Mag. (Tokyo) 45: 191. 1931. *Bromus bifidus* Thunb., Syst. Veg. ed. 14: 119. 1784. *Avena bifida* (Thunb.) P. Beauv., Ess. Agrostogr.: 89, 155. 1812. *Trisetum flavescens* var. *bifidum* (Thunb.) Makino, Bot. Mag. (Tokyo) 26: 215. 1912 [“bifidus”].—TYPE: JAPAN. probably near Nagasaki, *C.P. Thunberg s.n.* [lectotype, designated by Veldkamp & van der Have (1983: 129): UPS-THUNB–002576 (image!); isolectotypes: L–50296!, P–2255904!, S–13–31156!, S–13–31784!].

Bromus avenaeformis Steud., Syn. Pl. Glumac. 1: 326. 1854.—TYPE: JAPAN. [without locality], *H. Bürger s.n.* [lectotype, designated by Veldkamp & van der Have (1983: 129): L–908.98–239 (image!); isolectotype: P–740331!].

Trisetum flavescens var. *macranthum* Hack., Bull. Herb. Boissier 7: 703. 1899. *Trisetum macranthum* (Hack.) Keng, Sinensia 11: 411. 1940. *Trisetum bifidum* var. *macranthum* (Hack.) Ohwi, J. Jap. Bot. 17: 445. 1941.—TYPE: JAPAN. Hokkaido Island, Ishikari Prov., Sapporo, 43º03’N 141º20’E, *U.J. Faurie 7191* (lectotype, here designated: P–2255899!; isolectotypes: FI!, W–1916–0031816!).

Trisetum flavescens var. *papillosum* Hack., Bull. Herb. Boissier 7: 702. 1899. *Trisetum sibiricum* subsp. *papillosum* (Hack.) Roshev., Izv. Glavn. Bot. Sada R. S. F. S. R. 21: 2. 1922. *Trisetum bifidum* var. *papillosum* (Hack.) Ohwi, J. Jap. Bot. 17: 445. 1941.—TYPE: JAPAN. Tokyo, 35º41’N 139º41’E, 6 Jun 1888, *U.J. Faurie 2359* [lectotype, designated by van Royen (1980: 1158): P–2255912!; isolectotypes: P–3351083!, US–101513!].

Trisetum taquetii Hack., Repert. Spec. Nov. Regni Veg. 12: 386. 1913.—TYPE: SOUTH KOREA. Jeju region, Quelpaert Island, forest of Hallasan, 33°24′N 126°32′E, Jul 1909, *T. Taquet 3403* [holotype: W–1916–0042226!; isotypes: AAH!, C!, LE–1001930!, NY!, TI–21900 (image!), TI–21901 (image!), US–1128818!, US–3619058!].

Trisetum biaristatum Nakai, Bot. Mag. (Tokyo) 35: 150. 1921. *Trisetum bifidum* var. *biaristatum* (Nakai) Ohwi, J. Jap. Bot. 17: 445. 1941.—TYPE: JAPAN. Izu province, Aogashima Island, 32º28’N 139º46’E, 16 Jun 1920, *N. Matsuzaki s.n.* [holotype: TI–21892 (image!)].

Trisetum bifidum f. *contracta* Ohwi, Bot. Mag. (Tokyo) 45: 192. 1931.—TYPE: NORTH KOREA. P'yŏngan province, Nampo, 38º44’N 125º24’E, Jul 1901, *U.J. Faurie 883* (lectotype, here designated: P–2255887!; isolectotypes: G–443048!, P–2255946!, W–1916–0031813!).

Trisetum bifidum var. *oshimense* Honda, Bot. Mag. (Tokyo) 49: 697. 1935.—TYPE: JAPAN. Honshû Island, Izu province, Ôshima, Sashikiji, 34º41’N 139º25’E, 22 May 1933, *Y. Jôtani s.n.* [holotype: TI–21893 (image!)].

Trisetum bifidum var. *viride* Honda, Bot. Mag. (Tokyo) 49: 697. 1935.—TYPE: JAPAN. Honshû Island, Izu province, Ôshima, Motomura, 34º45’N 139º21’E, 12 Jun 1932, *Y. Jôtani s.n.* [holotype: TI–21894 (image!)].

Herb (32.8–)44–64.5(–114) cm high, densely tufted, shortly rhizomatous, culm (0.4–)0.7–1.2(–1.5) mm diam., glabrous; nodes (2–)3–5, separated along the culm, not enclosed by the sheaths, glabrous. Basal leaf-sheaths glabrous to pubescent, with hairs (0.05–)0.5–1(–1.5) mm long, decaying into fibers, yellowish to brownish; basal leaf-blades (0.38–)0.53–1.4(–1.85) × (0.21–)0.28–0.41(–1.15) mm, flat, sometimes slightly rolled when dried, glabrous adaxially, glabrous to puberulous mainly on the nerves abaxially, margins with hairs 0.05–1 mm long, greenish and brownish, sometimes yellowish; top culm leaf-sheaths (11.2–)12–20(–27) cm long, shorter than the internodes, rarely longer, glabrous, ciliolated, with hairs up to 1 mm long; top culm leaf-blades (2.6–)4–10(–13) cm long × (0.2–)0.27–0.53(–0.78) cm wide, flat, sometimes parallel to the culm, rarely arriving to the panicle, with the central nerve similar to the lateral ones, glabrous to pubescent adaxially and abaxially, with short, rarely long hairs 0.05–0.1(–1.1) mm long, greenish to greeyish; inner collar region glabrous to hairy, with scattered hairs (0.1–)0.25–0.5(–0.8) mm long; ligules 0.4–1.1(–1.6) mm long, apex denticulate, rarely slightly lobulate, glabrous, sometimes slightly pubescent or with scattered hairs abaxially, with hairs 0.05–0.1(–0.2) mm long. Basal node of the panicle glabrous. Panicles (8.5–)11–19(–27) cm long × (2.3–)2.8–3.5(–5) cm wide, oblong to oblong–lanceolate in outline, sometimes elliptic–oblong; rachis glabrous to slightly pubescent on the upper part, with patent and antrorse hairs up to 0.1 mm long; branches in whorls of 3 or 4, longest basal branches (0.9–)1.6–4.7(–7) mm long. Spikelets (6.5–)7.5–9.2(–11.1) mm long × (1.8–)3–4.3(–5) mm wide, 2–3(–4)–flowered; pedicels (2.3–)3.2–5.4(–7.5) mm long, with scattered hairs or pubescent, with hairs up to 0.1 mm long, rarely glabrous. Glumes unequal [ratio -- lower glume length/upper glume length = (0.11–)0.48–0.59(–0.67)]; lower glume (0.7–)2.8–3.6(–4.3) mm long × (0.2–)0.6–0.9 mm wide, narrowly lanceolate, rarely broadly lanceolate [ratio -- lower glume width/lower glume length = (0.16–)0.19–0.25(–0.29)], acute to acuminate, rarely long acuminate, 1-nerved, glabrous, with hairs 0.05–0.1(–0.2) mm long from the center to the upper part of the nerve, greenish on the center, rarely with some purplish on the upper part; upper glume (5.3–)5.5–6.5(–7.7) mm long × (1.6–)1.8–2(–2.2) mm wide, lanceolate to elliptic, sometimes oblong [ratio -- upper glume width/upper glume length = (0.25–)0.29–0.33(–0.37)], acute to acuminate, 3-nerved, glabrous, with hairs 0.1–0.2 mm long from the middle to the upper part of the central nerve, sometimes also on the upper part of the margins, greenish with a yellowish border, sometimes with purplish on the margins to the top; rachilla segments between first and second floret 1.1–1.5(–1.8) mm long, with hairs (0.2–)1.2–1.4(–1.8) mm long; rachilla segments to sterile floret (1–)1.6–1.8(–2.1) mm long, with hairs (0.1–)0.35–0.7(–1) mm long. Lemma (6–)6.5–7.5(–8.2) mm long × (0.2–)0.6–0.9 mm wide, narrowly lanceolate to narrowly oblong [ratio -- lemma width/lemma length = (0.18–)0.2–0.24(–0.27)], punctate-scabrid, with longer hairs up to 0.2 mm long on the central and upper part, brownish to yellowish, sometimes greenish; callus 0.2–0.3 mm long, orbicular to elliptic, with hairs 0.3–0.7 mm long; apical teeth 0.1–0.4(–0.8) mm long, with aristules (0.1–)0.6–1(–1.3) mm long; awn (7–)8.2–10.6(–12) mm long, inserted (3.5–)4.1–5.3(–6) mm from the base [ratio -- awn insertion from the base length/lemma length = (0.56–)0.62–0.74(–0.83)], strongly recurved near the base, not twisted, with adpressed hairs up to 0.1 mm long. Paleas (3.7–)4–4.5(–4.8) mm long × 1.3–2(–2.5) mm wide [ratio -- palea length/lemma length = (0.49–)0.55–0.64(–0.73)], elliptic, rarely narrowly elliptic, margins with hairs from the middle till the upper part; teeth 0.1–0.4(–0.8) mm long, densely hairy, with hairs up to 0.2 mm long. Lodicules (0.4–)0.6–0.8(–0.9) mm long, with 2(–3) lobules of the same or different length, sometimes slightly denticulate. Anthers (0.6–)1–1.3(–1.6) mm long. Ovary (0.3–)0.8–1.6(–2.2) mm long. Caryopsis (2.4–)2.6–3.3(–3.5) mm long × (0.2–)0.3–0.5 mm wide, narrowly elliptic, sometimes linear. Figure 6.

Chromosome Number—2*n* = 28 (Ono & Tateoka, 1953; Tateoka, 1978), 42 (Hsu, 1972).

Phenology—Flowering and fruiting from April to August.

Distribution and Habitat—This species is distributed from eastern China (Sichuan and Yunnan) to South Korea, Japan and Taiwan, and also in New Guinea; 0–3,225 m of elevation; in moist roadsides and meadows, well-drained slopes, and shady forests. Figure 7.

Specimens Examined—**CHINA. Guangdong:** Tsengshing distr., Naam Kwan Shan, 23º17’N, 113º49’E, 23 Apr 1932, *Tsang 20309* (K, NY, US). **Hubei:** Da Mai Ling, 29º53’N, 113º55’E, 5 May 1957, *[unknown] 411* (PE). **Hunan:** Yi Chang distr., P´ing T´ou Shan, T´ang Wan village, 26º23’N, 110º50’E, May 1934, *Tsang 23765* (C, G, GH, LE, PH, PR, US). **Jiangsu:** Nanking, Spirits Valley, 32º3’N, 118º46’E, 11 Jun 1929, *Keng 2314* (US); Tangchuan, 32º5’N, 118º30’E, 6 May 1922, *Steward 2516* (US). **Sichuan:** Pujiang Xian, Ganxi, Jikongdong, 30º15’N, 103º21’E, 25 Apr 1986, *Naito 15 & al.* (PE). **Yunnan:** Long-Ky, 23º37’N, 104º43’E, Jul 1911, *Maire s.n.* (AAH, NY); Hsi-lung-tang, Cheng-kiang, 24º39’N, 102º56’E, 1939, *Tsiang 16458* & *Wang* (AAH). **Zhejiang:** Hangchow, jiu xi shi ba jian kou, 30º17’N, 120º9’E, 3 May 1935, *Keng 2977* (PE); on the road of Lao Dian to Xi Mao Ling, west Tian Mu Mt., 30º20’N, 119º24’E, 22 May 1957, *Huang Deng 4031* (PE). **INDONESIA. Western New Guinea:** Lake Habbema, 4º8’S, 138º40’E, Aug 1938, *Brass 9118* (AAH, L, US). **JAPAN. Hokkaido Island:** Hokkaido pref., collines d´Yesashi, 44º56’N, 142º35’E, 22 Jul 1890, *Faurie 5711* (G, P); Hokkaido pref., environs de Sapporo, 43º4’N, 141º21’E, 1 Jul 1892, *Faurie 8104* (P). **Honshu Island:** Shizuoka pref., Izu Peninsula, Shuzenji, 34º58’N, 138º55’E, 12 May 1929, *Beattie 10622* & *Kurihara* (US); Wakayama pref., Koya-san, 34º13’N, 135º35’E, 23 Jun 1929, *Beattie 10832* & *Kurihara* (US); Kyoto pref., Kyoto city, Sakyo-ku, Kyoto University campus, southeast of the intersection of Imadegawa-dori and Higashiyo jidori (Hyaku-man-ben), 35º15’N, 135º26’E, 15 May 1977, *Boufford 18987a* & *Wood* (AAH, MO); Kanagawa pref., Chigasaki, 35º20’N, 139º24’E, 15 May 1954, *Dahlstrand s.n.* (GOET); Tokyo pref., near Kichijoji, 35º42’N, 139º34’E, 12 Jun 1929, *Dorsett 483* & *Morse* (LE, P); Aomori pref., Aomori, 40º49’N, 140º44’E, 23 Jul 1897, *Faurie 1212* (WU); Ibaraki pref., 36º17’N, 140º25’E, May 1900, *Faurie 4469* (US); Niigata pref., environs de Shirosaki, 37º42’N, 139º22’E, 29 May 1886, *Faurie 499* (G, P); Yezo [North Hoshu], circa Hakodake, 44º39’N, 142º24’E, Jul 1902, *Faurie 5214* (BM); Aomori pref., plaine de Shichinohe, 40º41’N, 141º9’E, 17 Jun 1886, *Faurie 689* (FI, P); Kanagawa pref., Yokoska [Yokosuka], 35º17’N, 139º40’E, 1866–71, *Franchel 1472* (LE, P, W); Tochigi pref., foot of Mt. Kogashi-yama, Ashigaru, Utsunomiya-shi, 36º37’N, 139º46’E, 22 Jun 1956, *Furuse s.n.* (S); Kanagawa pref., Hakone, 35º11’N, 139º1’E, 18 Jul 1921, *Hitchcock 18318* (US); Tochigi, Nikko to Chuzenji Lake, 36º45’N, 139º37’E, 24 Jul 1921, *Hitchcock 18344* (US); Mizusawa-shi, in Rikuchu, 39º7’N, 141º10’E, 19 Jun 1938, *Iwabuchi s.n.* (US); within the town limits of Yatsuo, 17 km south of the city of Toyama, 36º35’N, 137º7’E, 8 Jun 1955, *Kirino 652* (US); Tohoku distr., Miyagi pref., Sendai-shi, Aoba-ku, Aoshita, 38º18’N, 140º38’E, 10 Jun 1994, *Kondo 227* & *Kurosawa* (AAH); Shizuoka pref., Higashitanaka, Gotenba city, E foot of Mt. Fuji, 35º19’N, 138º56’E, 25 May 1977, *Konta 1184* & *Murata* (AAH); Miyagi pref., Tohoku distr., Sendai-shi, S foot of Mt. Izumigatake, Yoshinodaira Bog, 38º23’N, 140º44’E, 11 Jul 1992, *Kurosawa 5063* (AAH); Fukshima pref., Tohoku distr., Fukushima-shi, in the campus of Fukushima University, 37º40’N, 140º28’E, 18 Jun 1997, *Kurosawa 10102* & *al.* (AAH); Chiba pref., Ichikawa, Kônodai, 35º43’N, 139º55’E, 29 May 1898, *Makino s.n.* (AAH, LE); Musashi prov., Sekido, 35º15’N, 139º36’E, 3 Jun 1946, *Mizushima s.n.* (S); Shizuoka pref., Gendouji, Fujinomiya city, SW foot of Mt. Fujji, 35º13’N, 138º37’E, 21 Apr 1977, *Murata 11739* & *al.* (AAH); Gunma pref., Tano-gun, Nakazato-mura, Mt. Kanoosan, 36º4’N, 138º50’E, 29 May 1976, *Murata 1821* & *al.* (AAH); Tokyo pref., Shinagawa-ku, Oifuto, 35º36’N, 139º43’E, 17 Jun 1984, *Nakamura s.n.* (M); Chiba pref., Mt. Kiyosumi, Amatsukominato-machi, Awa-gun, 35º9’N, 140º9’E, 9 May 1988, *Ohba s.n.* & *al.* (AAH); Kyoto pref., Ogura, prope Kyoto, 34º53’N, 135º46’E, 16 May 1931, *Ohwi 58* (B, GOET, H, LE, UPS); Tsuruga, 35º38’N, 136º3’E, 27 May 1928, *Ohwi 6739* (NY); Shimohsa [Shizuoka], Matsudo, 35º46’N, 139º54’E, 27 May 1926, *Ohwi s.n.* (NY); Gunma pref., Shima Tone-gun, along the Shinyu river,

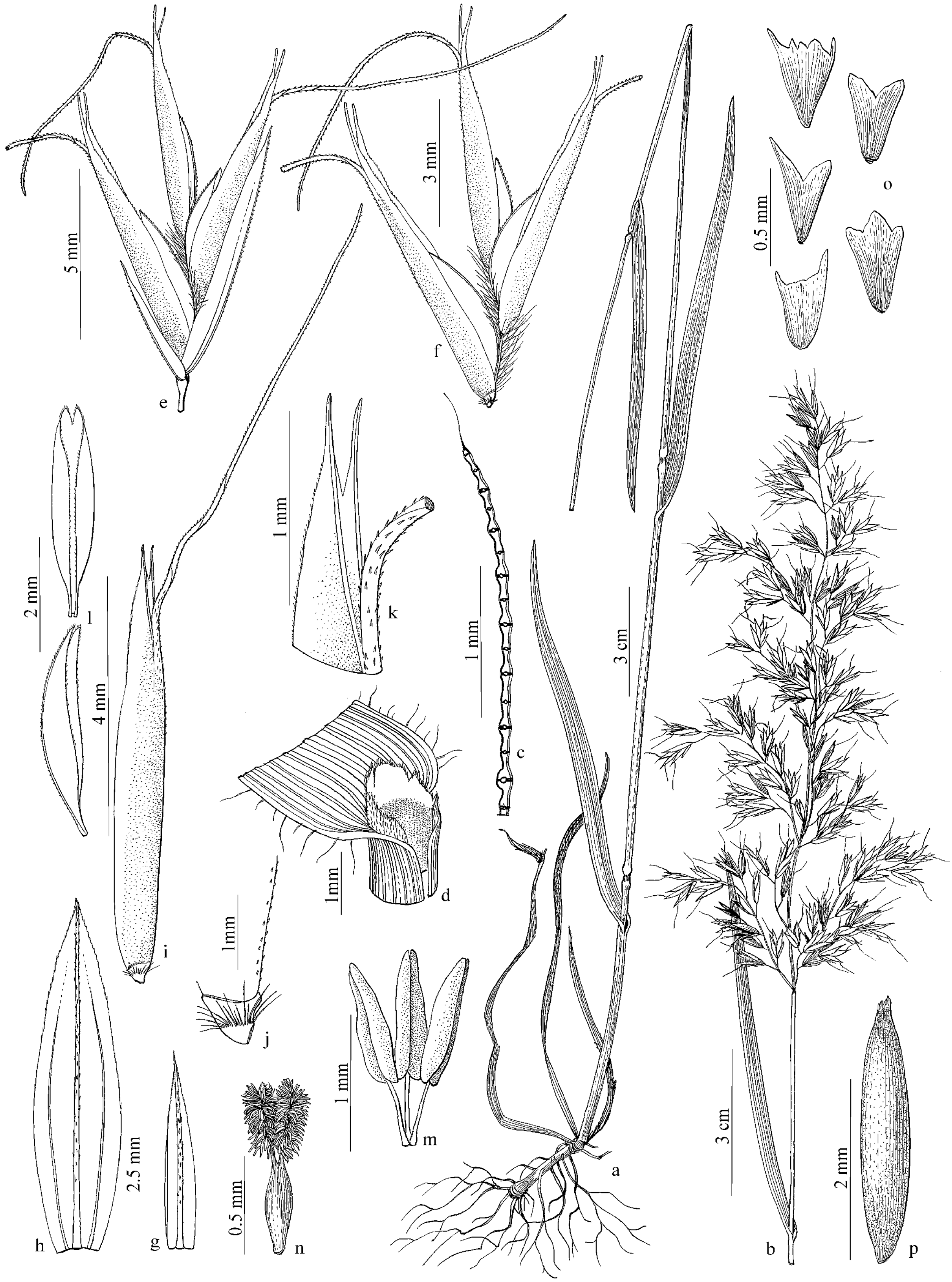

Figure 6. *Trisetum bifidum*. a. Basal habit. b. Inflorescence. c. Transverse section of leaf-blade. d. Sheath, ligule, and portion of the blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Callus, lateral view. k. Lemma, upper part, lateral view. l. Palea, ventral and lateral view. m. Stamens. n. Pistil. o. Lodicules. p. Caryopsis. (*Ohwi 2326*, US–1647265, a-b, o-p; *Koponen 15299*, H, c; *Keng 2977*, PE–718646, d-o).

36º41'N, 138º46'E, 20 Jun 1964, *Ono s.n.* & *Kobayashi* (LE, US); Hirosima pref., Sandankyo, 34º37'N, 132º11'E, 3 Jun 1933, *Sato s.n.* (US); Hoshu, 35º47'N, 137º3'E, 28 May 1930, *Shiota 5579* (GH); Tokyo pref., Edogawa, 35º41'N, 139º52'E, 22 May 1955, *Tanaka s.n.* (K); Kanagawa pref., Hakone, 35º11'N, 139º1'E, 13 Jun 1954, *Tateoka s.n.* (UPS); Tokyo pref., Suginami, 35º41'N, 139º38'E, 15 May 1952, *Tateoka s.n.* (B, C, UPS); Kyoto pref., Ikejiri, Umaji-cho, Kameoka-shi, 35º0'N, 135º32'E, 22 May 1997, *Tsugaru 24822* & *Takahashi* (AAH); Kyoto pref., N foot of the Mt. Ponpon-yama, Oharanoishidzukuri-cho, Kyoto-shi, 34º56'N, 135º37'E, 6 Jun 1997, *Tsugaru 25044* & *Takahashi* (AAH); Fukushima pref., Bandai, 37º36'N, 140º4'E, 9 Jul 1918, *Yasuda s.n.* (L); Saitama pref., Chichibu-gun, Ohtaki-mura, Kawamata, 35º56'N, 138º50'E, 23 May 1989, *Yokota 958* (AAH); Miyagi pref., Sendai-shi, Aoba-ku, Aramaki, Nitayachi, 38º16'N, 140º49'E, 15 Jun 1992, *Yonekura 448* (AAH). **Kyushu Island:** Oita pref., Mt. Yufu, 33º16'N, 131º23'E, 12 May 1928, *Kondo s.n.* (B); Miyazaki pref., Nichinan-shi, Kamishirakimata, valley of Sakatanigawa, 31º38'N, 131º20'E, 25 Apr 1970, *Koponen 15299* (H); Nagasaki pref., Nagasaki, 32º45'N, 129º53'E, 1863, *Maximowicz s.n.* (BM, P); Fukuoka pref., Kasuya, Tatara, Najima, 33º38'N, 130º25'E, 14 Jul 1925, *Schikama 209* (PH); Fukuoka pref., Katsukimura, Ongagun, 33º51'N, 130º38'E, 5 Jun 1930, *Takenouchi s.n.* (B). **Shikoku Island:** Kochi pref., prope Tokushima, 34º4'N, 134º34'E, Jun 1900, *Faurie 4468* (US); Tokushima pref., Inakochimura in Nanishigun, 34º4'N, 134º34'E, 1 Jun 1940, *Inobe s.n.* (US); Kôchi pref., Kôchi, 33º33'N, 133º32'E, May 1893, *Makino s.n.* (AAH). **Tsushima island:** 34º20'N, 129º20'E, 1859, *Wilford 938* (GH, K). **PAPUA NEW GUINEA. Western Province:** Mount Victoria area, Iswan Swamp, c. 2 km SSW of Mount Service, on bank of Koma Creek, 8º55'S, 147º32'E, 19 May 1976, *van Royen 10867* (L). **Hela:** West Sepik, Star Mts., Camp 1, Tel Basin, 5º0'S, 141º5'E, 2 May 1975, *Veldkamp 6248* (L). **SOUTH KOREA. Gyeonggi:** Seoul, 37º33'N, 126º58'E, May 1901, *Faurie 807* (BM); Kyongii-Do, Namhansan, 37º29'N, 127º10'E, 6 Jun 1948, *Yongsok 10030* (F); Kyongii-Do, Kwangnung, 37º44'N, 128º6'E, 3 Jun 1949, *Yongsok 7613* (S). **Jeju:** Quelpaert Island, 33º29'N, 126º29'E, Jun 1907, *Faurie 2228* (AAH, BM, G, LE, W); Quelpaert Island, Hallasan, 33º21'N, 126º31'E, Jul 1909, *Taquet 3423* (AAH, NY); Quelpaert Island, Yengsil [Yeongsil], 36º32'N, 126º51'E, Aug 1911, *Taquet 5096* (AAH, NY). **TAIWAN.** Chiayi Co., A-li-shan, 23º30'N, 120º48'E, 19 May 1969, *Chien-chang Hsu 5394* & *Kuo* (S); 17 Aug 1957, *Ream 589* (US); Chiayi Co., A-li-shan to Tungpu, 23º30'N, 120º48'E, 19 Jun 1970, *Chien-chang Hsu 7293* & *Kuo* (G); Taihoku, Mt. Taiheizan, 24º29'N, 121º32'E, May 1933, *Ohwi 2326* (US); Taipei, prope Pianan-anbu, 25º2'N, 121º38'E, Jun 1933, *Ohwi 2720* (UPS, US).

Notes—*Trisetum bifidum* has a disjunctive range, occurring in the continental part of Asia and Taiwan, and in the mountains of New Guinea. This particular distribution happens also in other species, as indicated by Veldkamp & van der Have (1983).

Chrtek (1968) noted that *T. bifidum* is closely related to the species from *T.* sect. *Trisetum*, differentiated mainly by its palea with longer and sharpest hairs on the keels than *T.* sect. *Trisetum*, which has shorter ones. As Veldkamp & van der Have (1983) said, it has been considered that this species is closely related to *T. flavescens* (generic type of *T.* ser. *Trisetum*), being very close to *T. sibiricum*. Consequently, and because of its characters, these authors included *T. bifidum* in the series *Sibirica* following Chrtek (1968) or in subsection *Sibirica* according to Probatova (1979). Both of the species, *T. bifidum* and *T. sibiricum*, share part of their distribution, but they can be easily differentiated. *Trisetum bifidum* is separated from the other species of *T.* sect. *Sibirica*, and more specifically of *T. sibiricum*, mainly by having a palea about half the length of the lemma [ratio -- palea length/lemma length = (0.49–)0.55–0.64(–0.73)], the awn inserted more apically [ratio -- awn insertion from the base length/lemma length = (0.56–)0.62–0.74(–0.83)], and longer callus indumentum (0.3–0.7 mm long).

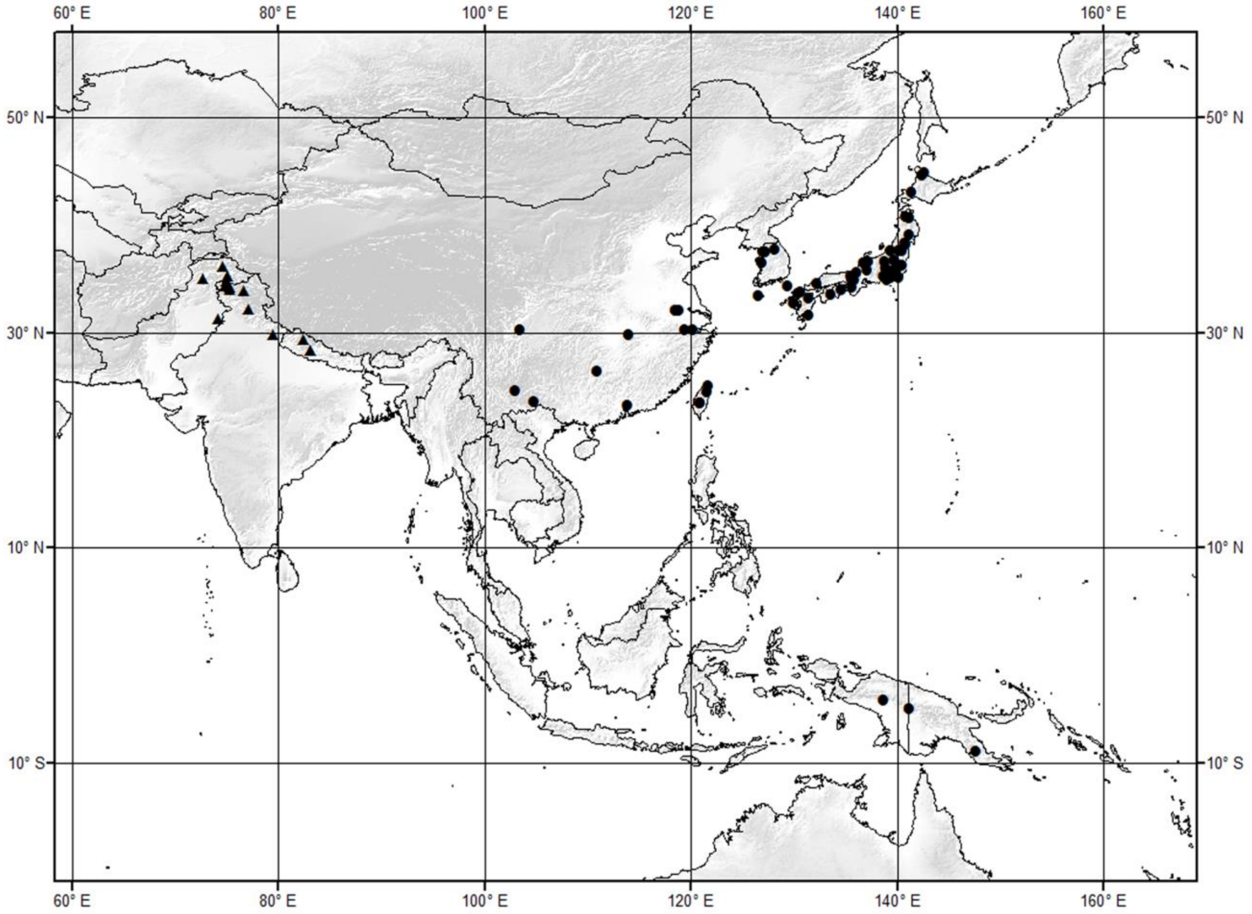

Figure 7. Distribution of *Trisetum bifidum* (dots) and *T. aeneum* (triangles).

4. TRISETUM HENRYI Rendle, J. Linn. Soc., Bot. 36: 400. 1904.—TYPE: CHINA. Hubei, Fang Xian, 32°05′N 110°35′E, 1885–1888, *A. Henry 6643* (lectotype, here designated: K–808693!; isolectotypes: B–10_0279997!, BM–959387!, GH–24560!).

Herb (110–)121–150(–165) cm high, shortly rhizomatous, culm 1.5–4 mm diam., glabrous; nodes (6)7–10(12), separated along the culm, enfolded or not by the sheaths, glabrous. Basal leaf-sheaths glabrous, sometimes very slightly pubescent, with hairs less than 0.1 mm long, decaying into fibers, yellowish to brownish; basal leaf-blades 14–18(–20) mm long × 6–8 mm wide, flat, rolled when dried, glabrous abaxially and adaxially, usually with long hairs on the nerves abaxially, sometimes with hairs on the margins 0.05–1 mm long, brownish to dark green; top culm leaf-sheaths (12.5–)17–23(–25) cm long, longer than the internodes, involving most of the culm, glabrous, normally pubescent on the upper part, with cilia on the margins; top culm leaf-blades 17.5–29.5 cm long × (5.2–)6–8(–10) mm wide, flat, not envolving the culm and arriving to the panicle, with the central nerve conspicuously marked, with hairs abaxially along the nerves and margins, glabrous to slightly pubescent adaxially, with hairs, also along the nerves, dark green to brownish; inner collar region pubescent, also on the margins, with hairs (0.1–)0.8–1 mm long; ligules (1.5–)2–2.8(–3.4) mm long, laciniate or irregular dentate, pubescent to slightly pubescent abaxially, with hairs 0.1–1(–1.4) mm long. Basal node of the panicle glabrous. Panicles (16–

)19–23(–28) cm long × (4–)5–8.5 cm wide, elliptic to narrowly elliptic–oblong in outline, lax to slightly dense; rachis glabrous; branches in whorls of 3 to 7, longest basal branches (4.4–)5.8–9(–11) cm long. Spikelets (5.2–)6–7.2(–8) mm long × (2–)2.3–3.7(–5.6) mm wide, 2–3-flowered; pedicels (2–)3.3–5(–6.8) mm long, glabrous, rarely with hairs up to 0.05 mm long. Glumes unequal [ratio -- lower glume length/upper glume length = 0.6-0.73(–0.76)]; lower glume (2.8–)3.2–4.5 mm long × 0.6–0.8 mm wide, narrowly lanceolate [ratio -- lower glume width/lower glume length = 0.17-0.21(–0.25)], acuminate, sometimes acute, 1-nerved, glabrous, with hairs up to 0.05 mm long from the middle to the upper part of the midrib, greenish to yellowish; upper glume 4.6–6.2 mm long × 1.4–1.6 mm wide, narrowly elliptic to oblanceolate (ratio -- upper glume width/upper glume length = 0.23–0.3), acuminate, rarely acute, 3-nerved, glabrous, with hairs up to 0.05 mm long from the middle to the upper part of the central nerve, greenish to yellowish, sometimes brownish; rachilla segments between first and second floret 1.1–1.7 mm long, with hairs (0.5–)0.7–1(–1.2) mm long; rachilla segments to sterile floret 1.1–1.4 mm long, with hairs 0.4–0.6(–0.8) mm long. Lemmas (4.2–)4.8–6.1 mm long × 0.6–0.8 mm wide, narrowly to broadly lanceolate [ratio -- lemma width/lemma length = 0.21–0.28(–0.36)], scabridulous, with hairs on the midrib up to 0.05 mm long, pale yellowish or brownish, with broad hyaline margins; apical teeth (0.05–)0.1–0.4 mm long, without or with aristules 0.1–0.45 mm long; awn (4.3–)4.7–6.5(–6.8) mm long, inserted 2.5–3.5(–4) mm from the base [ratio -- awn insertion from the base length/lemma length = 0.55–0.60(–0.66)], recurved and not twisted or sometimes slightly twisted at the base, with adpressed hairs up to 0.05 mm long; callus 0.2–0.3 mm long, orbicular to elliptic, glabrous. Paleas (3.6–)4–4.5 mm long × 1.2–1.5(–1.7) mm wide [ratio -- palea length/lemma length = 0.67–0.82(–0.86)], elliptic, margins with hairs from the middle till the upper part; teeth (0.2–)0.3–0.4(–0.6) mm long, with short antrorse hairs. Lodicules 0.4–0.8 mm long, with 2 lobules of the same length. Anthers (1.5–)1.8–2.4 mm long. Ovary (0.5–)0.8–1.3 mm long. Caryopsis 3–3.4 mm long × 0.3–0.6 mm wide, oblanceolate. Figure 8.

Chromosome Number—Unknown.

Phenology—Flowering and fruiting from February to September.

Distribution and Habitat—Endemic from eastern and central China; 1,000–2,400 m of elevation; at open meadows, shady forests. Figure 9.

Specimens Examined—**CHINA. Anhui:** Li Shan, NW Chemen, 30º45'N, 119º20'E, Aug 1925, *Ching 8767* (US). **Henan:** Huopenjin, Lushi, Dalindi, 33º58'N, 110º59'E, 7 Jul 1959, *[unknown] 34437* (PE); Chimanmeizijian, Haoxian, 34º21'N, 111º58'E, 17 Aug 1959, *[unknown] 34986* (PE); Funyu Shan, Xiangshuitai, Tongbaitaohuadong, 32º22'N, 113º23'E, 15 Aug 1956, *Forestry Administration Henan 465* (PE); Laoxiang-ling, Huangshi Xiang, Xixia, 33º20'N, 111º25'E, 12 Jul 1960, *Henan Team 1023* (PE); 17 Jul 1960, *Henan Team 1179* (PE). **Hubei:** Ichang, 30º42'N, 111º17'E, Feb 1887, *Henry 2558* (LE, P); Mars 1889, *Henry 6706* (K, US). **Jiangxi:** Lu Shan, 29º3'N, 116º57'E, 10 Aug 1922, *Steward 2559* (C, G, K, LE, MO, NY, US); Kuling, mountains south of Kiukiang, 29º42'N, 116º0'E, 16 Aug 1921, *Hitchcock 18534* (US), *18551* (US); 17 Aug 1921, *Hitchcock 18558* (US). **Shaanxi:** Taibai County, Baiyun, 33º58'N, 107º12'E, 11 Jul 1938, *Liou & al. 2042* [PE–718810 (image!)]. **Zhejiang:** Changhua, Lin´an city, 30º14'N, 119º43'E, 13 Aug 1957, *He Yinyu 25309* [HHBG–HZ38395 (image!)].

Notes—Rendle studied the grasses of China and its neighboring regions in the article published by Forbes & Hemsley (1904). In this study, he described *T. henryi* as closely allied to *T. sibiricum* (identified

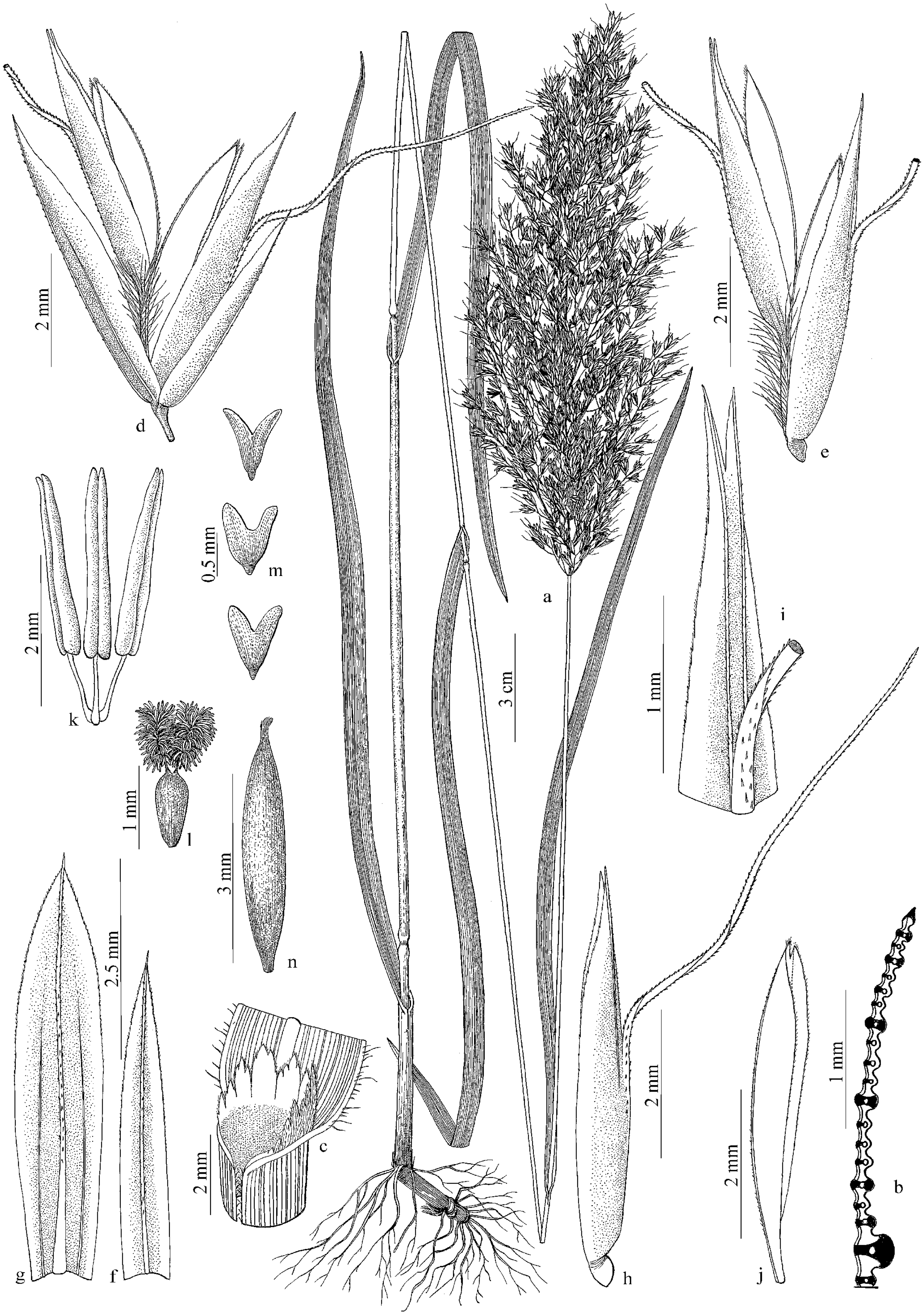

Figure 8. *Trisetum henryi*. a. Habit. b. Transverse section of leaf-blade. c. Sheath, ligule, and portion of the blade. d. Spikelet. e. Florets. f. Lower glume, dorsal view. g. Upper glume, dorsal view. h. Floret. i. Lemma, upper part, lateral view. j. Palea, lateral view. k. Stamens. l. Pistil. m. Lodicules. n. Caryopsis. (*Henry 6643*, K–808693, a, m; *Ching 8767*, US, b; *Steward 2559*, US–1346322, c-j; *[unknown] 34986*, PE–718805, k-n).

as *T. flavescens*), clearly differentiated by being taller and more robust, with more dense panicles and silvery-brown spikelets, and lower glume less acute. Apart from those characters, this species is also characterized by having longer panicles, with longer branches than *T. sibiricum*, always long leaves, the upper one usually exceeding the panicle, with marked central nerves, and longer ligules. It has also spikelets with broad hyaline margins, and lemmas with shorter awns than *T. sibiricum* subsp. *sibiricum*.

One of the studied specimens from the mountains of Zhejiang [*Yao Kan 79429* (MO–3690121)] is exceptional by its smaller panicle and spikelets (11 cm long, and up to 5 mm long, respectively). However, it has a thick culm and long leaves with a marked central nerve, as in *T. henryi*.

Wu & Phillips (2006), in the Flora of China, noted that *T. henryi* is also present in the provinces Jiangsu, Shanxi and South-Eastern Sichuan, from where we have not seen material, but it is surely present there.

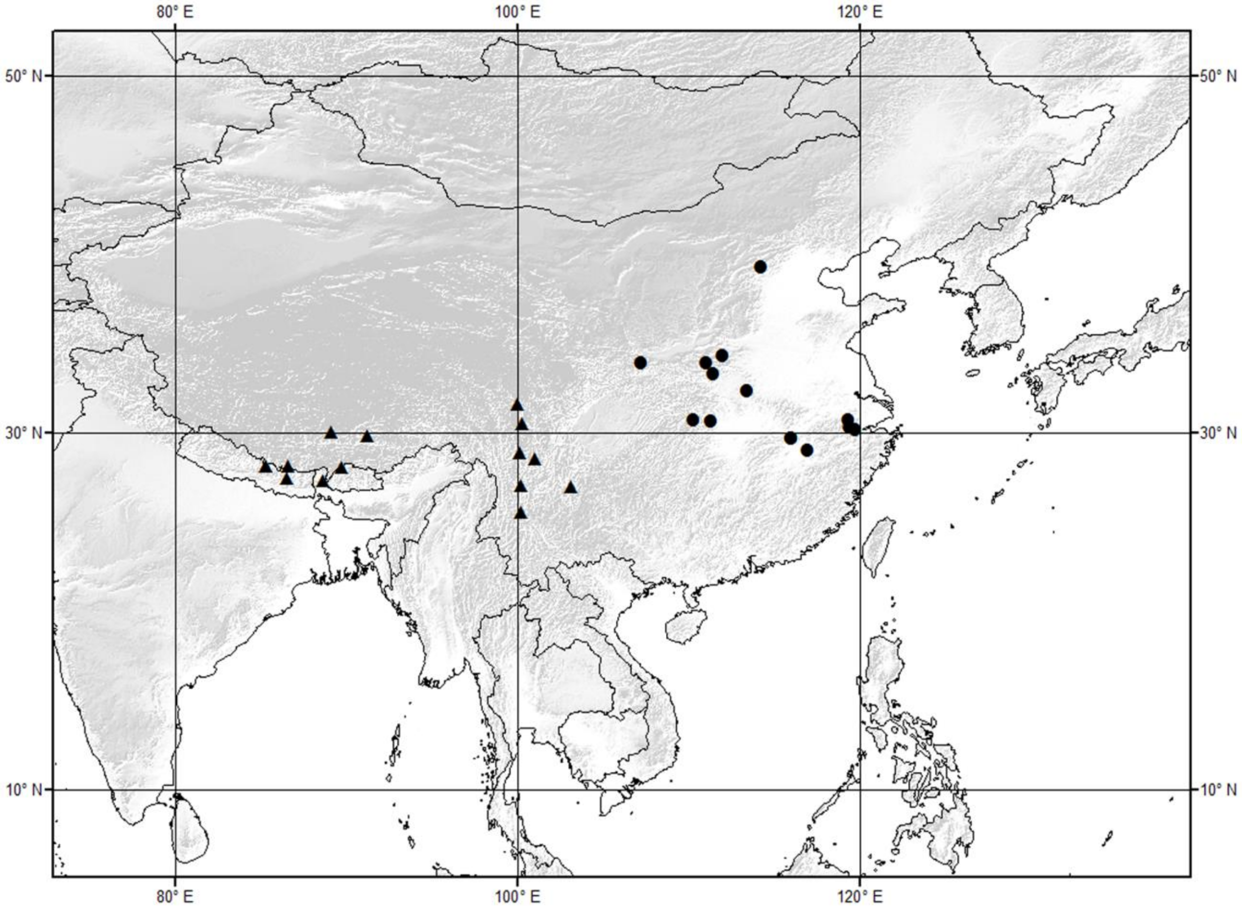

Figure 9. Distribution of *Trisetum henryi* (dots) and *T. scitulum* (triangles).

5. Trisetum aeneum (Hook. f.) R. R. Stewart, Brittonia 5: 431. 1945. *Trisetum aureum* Nees ex Steud., Syn. Pl. Glumac. 1: 225. 1854, nom. illeg., non Ten. 1820. *Avena aenea* Hook. f., Fl. Brit. India 7: 279. 1896. *Trisetum sibiricum* subsp. *aenea* (Hook. f.) Roshev., Izv. Glavn. Bot. Sada R.S.F.S.R. 21: 91. 1922.—TYPE: INDIA. Himachal Pradesh, Shimla distr., Buran Pass, Kedarkanta, 31º23’N 78º8’E, *J.F. Royle 94* [lectotype, here designated: LIV–1952.121.10949 (image!); isolectotypes: LIV–1952.121.10948 (image!), LIV–1952.121.10950 (image!)].

Herb (45–)53–70 cm high, not or loosely tufted, shortly rhizomatous, culm 0.8–1.2(–2) mm diam., glabrous; nodes (3–)4–6, separated along the culms, not enfolded by the sheaths, glabrous. Basal leaf-sheaths glabrous, rarely shortly pubescent, with hairs up to 0.08 mm long, decaying into fibers, brownish to yellowish, sometimes greenish; basal leaf-blades 6–12(–13.5) cm long × (2.3–)2.8–3.8(–4) mm wide, flat, rolled when dried, pubescent with longer hairs abaxially, glabrous to slightly pubescent adaxially, margins with hairs (0.05–)0.1–0.8 mm long, yellowish to brownish, sometimes greenish; top culm leaf-sheaths (10–)12–18.5 cm long, shorter than the internodes, glabrous; top culm leaf-blades (7–)8.5–14.5(–16) cm long × 4–5.6 mm wide, flat, sometimes paralele to the culm and arriving to the panicle, with the central nerve similar to the lateral ones, glabrous abaxially and pubescent adaxially, with adpressed hairs along the nerves in both sides, longers adaxially, with hairs on the margins (0.05–)0.1–1(–1.3) mm long, greenish to greeyish, sometimes brownish; inner collar region glabrous, with hairs on the margins 0.4–1 mm long; ligules (1–)1.3–3 mm long, laciniate, rarely denticulate, glabrous, rarely with scattered hairs on the apex (0.05–)0.1–0.2(–0.4) mm long. Basal node of the panicle glabrous. Panicles (5.7–)7–12.5(–15) cm long × 1.4–2.5(–3) cm wide, oblong to elliptic in outline, rarely oblanceolate, dense, with the rachis visible in some parts; rachis glabrous; branches in whorls of 3 or 4, longest basal branches (0.7–)0.8–1.7(–3.1) cm long. Spikelets 6–7.5 mm long × (2–)2.4–3.7(–4.3) mm wide, 2–3–flowered; pedicels 2–4(–5) mm long, slightly pubescent, with hairs up to 0.08 mm long. Glumes subequal [ratio -- lower glume length/upper glume length = (0.8–)0.82–0.89(–0.95)]; lower glume (4.5–)4.8–5.5(–6) mm long × 1–1.2(–1.4) mm wide, narrowly lanceolate, rarely broadly lanceolate (ratio -- lower glume width/lower glume length = 0.2-0.24), acuminate, rarely long acuminate, 1-nerved, glabrous, with hairs up to 0.1 mm long on the upper part of the nerve and margins, brownish to yellowish, sometimes greenish; upper glume 5.4–6.3 mm long × 1.7–2 mm wide, narrowly elliptic to oblong, sometimes narrowly to broadly lanceolate [ratio -- upper glume width/upper glume length = (0.27–)0.29–0.34(–0.36)], acuminate, rarely long acuminate, 3-nerved, glabrous, with hairs up to 0.1 mm long, from the middle to the upper part of the central nerve and sometimes on the upper part of the margins, brownish to yellowish, sometimes greenish on the central part; rachilla segments between first and second floret 1–1.8 mm long, with hairs 0.7–1.4 mm long; rachilla segments to sterile floret 0.8–1.7 mm long, with hairs 0.1–0.7 mm long. Lemma (5–)5.6–6(–7.8) mm long × 1–1.2(–1.4) mm wide, oblong to broadly lanceolate [ratio -- lemma width/lemma length = (0.24–)0.25–0.32(–0.36)], scabridulous, with hairs on the midrib up to 0.1 mm long, brownish to yellowish, rarely greenish; callus 0.3–0.4 mm long, elliptic to oblong, with hairs 0.1–0.3 mm long; apical teeth 0.1–1.1(–1.5) mm long, with aristules 0.3–0.5(–0.7) mm long; awn 6.5–8(–8.7) mm long, inserted 3–3.3(–5) mm from the base (ratio -- awn insertion from the base length/lemma length = 0.5-0.64), recurved at the base, not or very slightly twisted, with adpressed hairs up to 0.05 mm long. Paleas (3.6–)4.2–4.6 mm long × 1.5–1.8 mm wide [ratio -- palea length/lemma length = (0.61–)0.7–0.82)], elliptic, sometimes narrowly elliptic, margins with short antrorse hairs; teeth 0.1–0.5 mm long, with short antrorse hairs from the middle to the upper part. Lodicules 0.6–0.7 mm long, with 2–3 irregular lobules, rarely laciniate. Anthers (0.8–)1–1.2(–1.3) mm long. Ovary 0.6–1.3 mm long. Caryopsis 2.7–3.7 mm long × 0.5–0.8 mm wide, oblong to narrowly elliptic. Figure 10.

Chromosome Number—Unknown.

Phenology—Flowering and fruiting from July to September.

Distribution and Habitat—It is distributed from north Pakistan and India to central Nepal; at 3,000–4,200 m of elevation; in alpine meadows and grasslands. Figure 7.

Specimens Examined—**INDIA. Himachal Pradesh:** Manali, 32º15'N, 77º10'E, 2 Aug 1941, *Bor 15560* (K). **Jammu and Kashmir:** Sonamarg, Tajivaz, 34º18'N, 75º17'E, 18 Aug 1893, *Duthie 13646* (W); Kashmir, 33º55'N, 76º40'E, *Levinge 27424* (LE); Kun Patthar, Masjid Gali, 34º24'N, 74º51'E, 13 Aug 1939, *Stewart 18448* (NY); Tulian above Pahlgam, 34º0'N, 75º21'E, 30 Aug 1945, *Stewart 21829* (K, NY, US). **Uttarakhand:** Kumaon, above Tola, 29º50'N, 79º30'E, *Strachey 1* & *Winterbottom* (P); Chitona, Tehri, 30º23'N, 78º28'E, 29 Sep 1948, *Koelz 22048* (US). North-West India, *Royle s.n.* (K–808692, LE). **NEPAL. Karnali:** Jumla distr., Maharigaon, 5 miles NE, 29º20'N, 82º23'E, 22 Jul 1952, *Polunin 281* & *al.* (K, UPS). **Dhawalagiri:** Baglung distr., near Dogadi Khola, 28º25'N, 83º10'E, 7 Aug 1954, *Stainton 3785a* & *al.* (UPS); 29 Sep 1954, *Stainton 4648* & *al.* (UPS). **PAKISTAN. Azad Cachemira:** Kashmir, Sind Valley, 3 Sep 1876, *Clarke 31034* (K); Kamri Pass, 34º47'N, 74º56'E, 18 Aug 1939, *Stewart 18700* (NY, US). **Gilgit-Baltistan:** Kamri Valley, near Kalapani, 35º18'N, 75º7'E, 25 Aug 1892, *Duthie 12548* (W); Kalapani, Kamri Pass, 35º18'N, 75º7'E, 25 Aug 1892, *Duthie 12562* (W); Baghrot Valley, 36º8'N, 74º35'E, 20 Sep 1990, *Miehe 3891* & *Miehe* (K). **Khyber Pakhtunkhwa:** beyond Bishigram, 35º4'N, 72º39'E, 10 Jul 1953, *Stewart 25001* & *Rahman* (K).

Notes—*Trisetum aeneum* was already included by Chrtek (1968) in *T.* ser. *Sibirica*, because of its basally recurved and slightly twisted awns. This species is distinguished from the rest of species by its dense and usually contracted panicles, subequal glumes, and small anthers.

In its eastern distribution, this species overlaps with the westernmost *T. scitulum*, in central Nepal; both species have a similar habitat but they are really easy to differentiate, because of their different habit, *T. scitulum* having lax panicles, and branches single or paired instead of being in whorls of more than three in the rest of species of the section.

From *Trisetum sibiricum* subsp. *sibiricum*, present just north and east of the range of *T. aeneum*, it is mainly differentiated by the anthers length, panicle shape, and by its subequal glumes. Roshevitz (1922) considered *Trisetum aeneum* to be a subspecies of *T. sibiricum*, only taking into account its dense panicles and bright bronze spikelets. We consider *T. aeneum* a good species having a separate distribution, and dense panicles, and smaller stamens that are a consistent character in the species of the section.

Steudel (1854) when described *Trisetum aureum* mentioned Royle's collection as follows: “Royle hrbr. nr. 44. Nepal”. According to G. Reid (pers. comm.), there was a misprint or a transcription error because the type material is actually *Royle 94*, not *Royle 44*. An additional fact to support this conclusion is that the specimen *Royle 44* corresponds to *Panicum vestitum* Kunth.

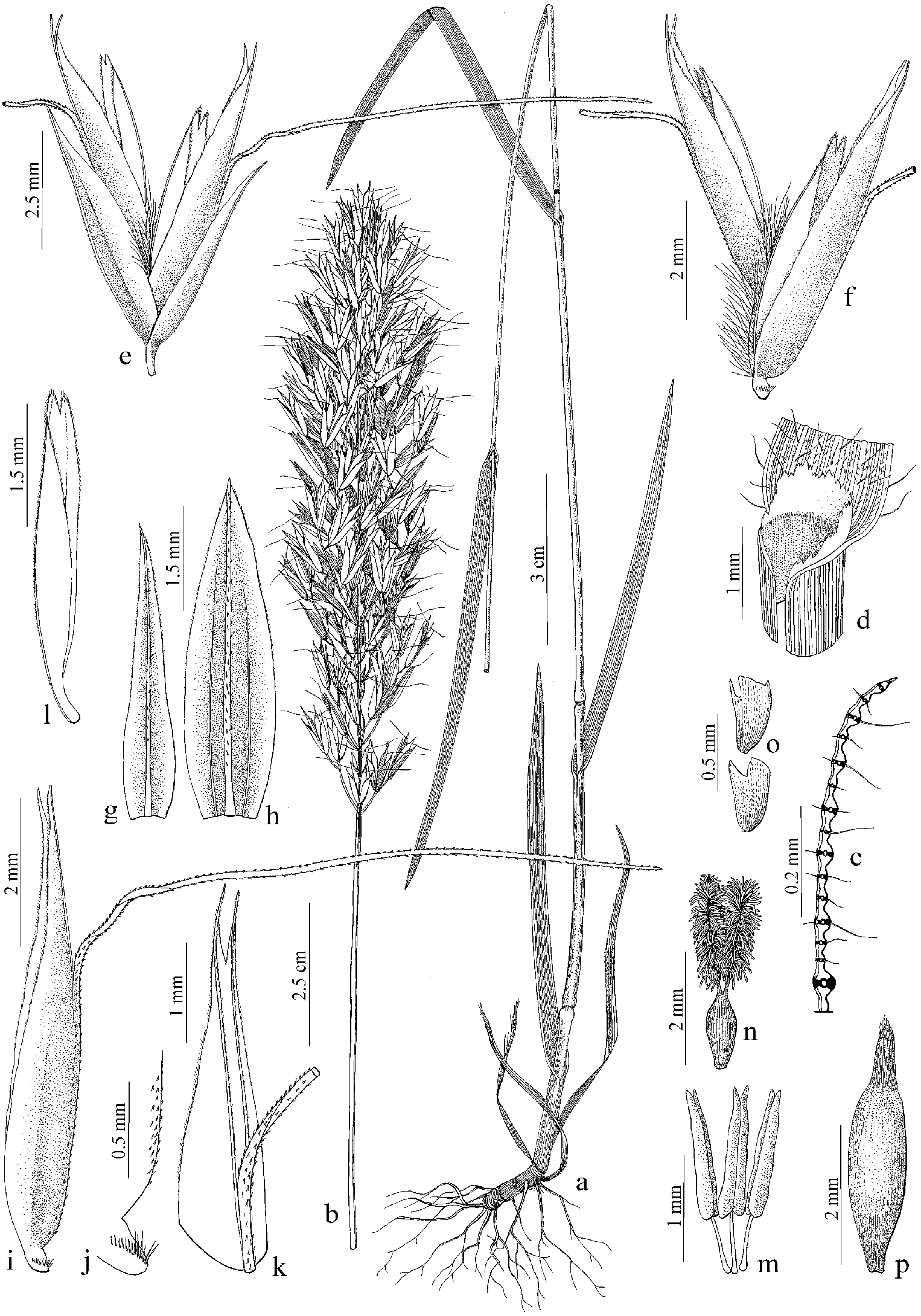

Figure 10. *Trisetum aeneum*. a. Basal habit. b. Inflorescence. c. Transverse section of leaf-blade. d. Sheath, ligule, and portion of the blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Callus, lateral view. k. Lemma, upper part, lateral view. l. Palea, lateral view. m. Stamens.n. Pistil. o. Lodicules. p. Caryopsis. (*Royle s.n.*, K–808692, a-b; *Polunin et al. 281*, UPS-V–644757, c-d; *Jaquemont 1214*, P–2243981, e-l; *Duthie 12548*, W, m-p; *Stewart 18700*, US–2044501, o).

6. TRISETUM SCITULUM Bor ex Chrtek, Acta Univ. Carol., Biol. 1967: 105. 1967.—TYPE: INDIA. Sikkim, 27º20’N 88º37’E, *J.D. Hooker s.n.* [holotype: K–32269!; isotypes: GH!, K!, L–50297 (image!), P–2255859!, W–25045!].

Herb 12–80 cm high, loosely tufted, shortly rhizomatous, culm (0.4–)0.5–2 mm diam., glabrous; nodes 2–3(–4), separated along the culm, not enfolded by the sheaths, glabrous. Basal leaf-sheaths glabrous, sometimes slightly to densely pubescent, with hairs up to 0.3 mm long, decaying into fibers, yellowish to brownish; basal leaf-blades (5.8–)7–13(–15.5) cm long × 1.5–3.7 cm wide, flat to rolled when dried, not rigid, glabrous abaxially, sometimes densely pubescent, pubescent adaxially, also with hairs on the margins (0.05–)0.2–0.8(–1) mm long, greenish-greeyish to brownish; top culm leaf-sheaths 12–13.5(–16) cm long, shorter than the internodes, rarely longer, glabrous, without cilia on the margins; top culm leaf-blades (9–)10–20 cm long × (–0.6)0.8–8 cm wide, flat, usually parallel to the culm, with the central nerve similar to the lateral ones, with short adpressed hairs along the nerves abaxially, pubescent with longer hairs alternate with short ones adaxially, hairs (0.05–)0.1–1.2(–1.6) mm long, with short hairs on the margins, greenish to greeyish; inner collar region glabrous; ligules 2.2–3.5 mm long, laciniate, glabrous. Basal node of the panicle glabrous. Panicles 7–15 cm long × 3–5 cm wide, lanceolate, rarely oblong to elliptic in outline, lax, rarely slightly dense with the rachis visible; rachis glabrous; branches single or paired, longest basal ones (1.4–)3–9(–9.3) cm long. Spikelets 6.5–9.2–(–10.5) mm long × (2.7–)4.7–5.2 mm wide, 1–2(3)–flowered; pedicels (3.3–)3.6–6(–6.2) mm long, slightly pubescent, up to 0.1 mm long. Glumes unequal (ratio -- lower glume length/upper glume length = (0.64–)0.7–0.8); lower glume 4.5–5.4(–5.7) mm long × (0.7–)0.9–1.2 mm wide, narrowly lanceolate, rarely narrowly elliptic (ratio -- lower glume width/lower glume length = (0.14–)0.17–0.22), acuminate, sometimes acute, 1(3)-nerved, glabrous, with hairs on the midrib and margins up to 0.08 mm long, greenish to greeyish or yellowish; upper glume 6–7.6 mm long × 1.2–1.6(–1.8) mm wide, narrowly lanceolate to narrowly elliptic (ratio -- upper glume width/upper glume length = 0.16–0.25), acuminate, rarely acute, 3-nerved, glabrous, with hairs up to 0.1 mm long from the middle to the upper part of the central nerve and upper part of the margins, greenish, sometimes yellowish or greyish; rachilla segments between first and second floret 1.6–2.2 mm long, with hairs 0.9–1.5(–2) mm long; rachilla segments to sterile floret (0.3–)1.5–1.8 mm long, with hairs 0.3–2 mm long. Lemmas (6.5–)7.4–7.8(–8.4) mm long × (0.7–)0.9–1.2 mm wide, narrowly elliptic to narrowly lanceolate, rarely oblong (ratio -- lemma width/lemma length = 0.2–0.3), scabridulous on the central part, with hairs up to 0.1 mm long, golden brown; callus 0.3–0.4 mm long, elliptic, glabrous; apical teeth (0.2–)0.4–1.2 mm long, with aristules 0.5–1.3 mm long; awn (10.5–)11–14(–15) mm long, inserted 4–4.8 mm from the base (ratio -- awn insertion from the base length/lemma length = 0.56–0.63), geniculate below the middle, twisted up to the geniculate part, with adpressed hairs up to 0.05 mm long. Paleas (4.2–)4.6–5.2 mm long × 1.2–1.8 mm wide (ratio -- palea length/lemma length = 0.6–0.68), elliptic to oblong, rarely lanceolate, margins with short antrorse hairs; teeth 0.3–0.6 mm long, with antrorse hairs up to 0.6 mm long from the middle to the upper part. Lodicules 0.7–0.9 mm long,

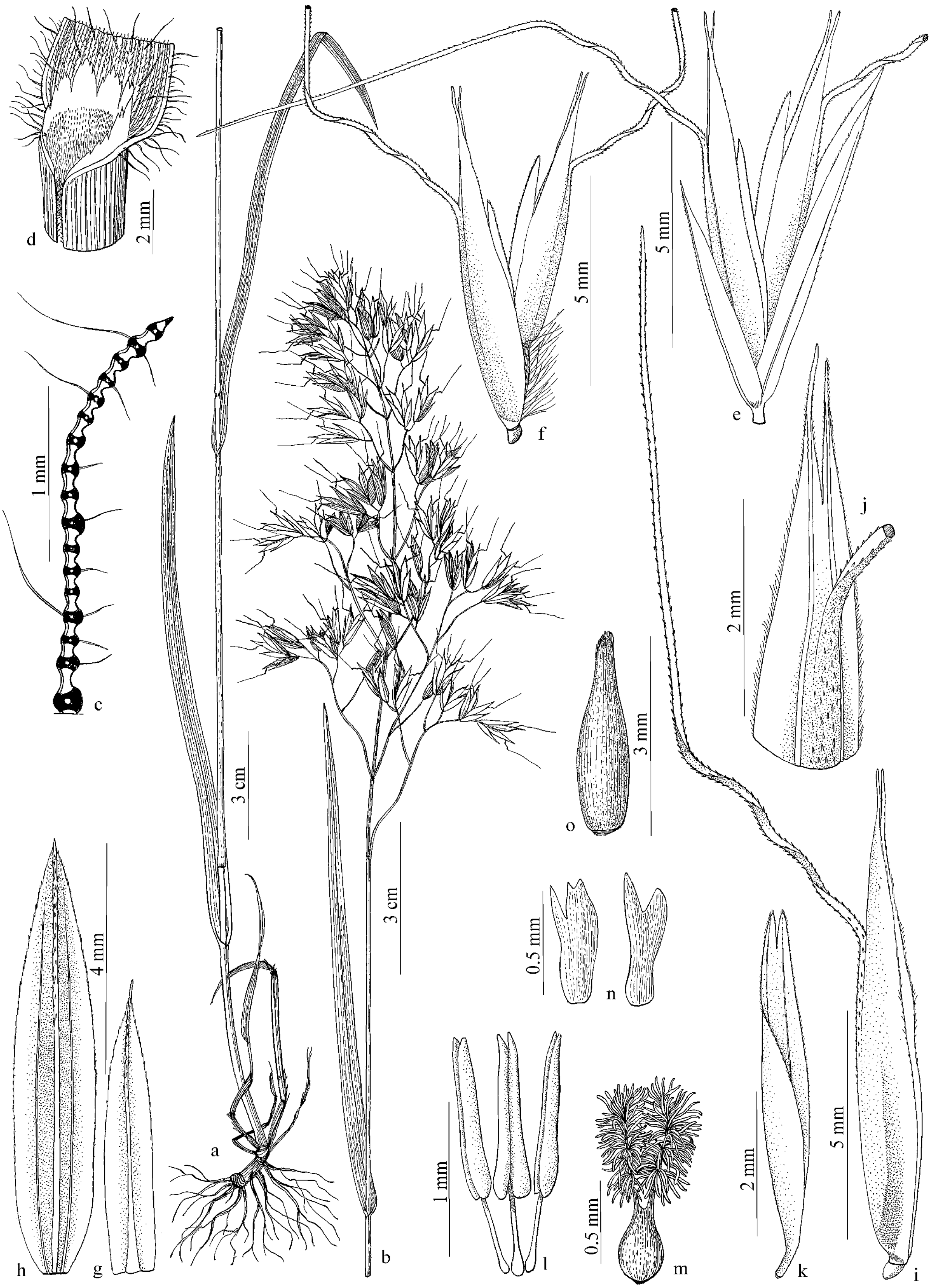

Figure 11. *Trisetum scitulum*. a. Basal Habit. b. Inflorescence. c. Transverse section of leaf-blade. d. Sheath, ligule, and portion of the blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Lemma, upper part, lateral view. k. Palea, lateral view. l. Stamens. m. Pistil. n. Lodicules. o. Caryopsis. (*Delavay 3365*, P–2255919, a-b, d-n; *Stainton 1143*, K, c, n-o).

irregularly or regularly 2–3 lobulate. Anthers 0.9–1.5 mm long. Ovary 0.8–1.8 mm long. Caryopsis 3 mm long × 0.6–0.7 mm wide, narrowly elliptic to elliptic. Figure 11.

Chromosome Number—Unknown.

Phenology—Flowering and fruiting from May to September.

Distribution and Habitat—This species occurs from central Nepal, Sikkim and Bhutan, to south-central China (Eastern Yunnan and Sichuan); 2,800–5,000 m of elevation; in alpine meadows and shrubs, and river banks. Figure 9.

Specimens Examined—**BHUTAN.** Upper Mo Chu Dist, 28º7'N, 89º44'E, 20 Sep 1984, *Sinclair 5199* & *Long* (K). **CHINA. Sichuan:** Daocheng county, 28º54'N, 100º8'E, 1 Aug 1982, *Dong Jian 29060* (CDBI (image!)); Ganzi distr., 31º37'N, 99º59'E, 29 Jul 1961, *Junsheng 9847* (PE (image!)); Ji pu lang, Zhengxi farm, 28º34'N, 100º59'E, 9 Sep 1983, *Qing 13824* (PE); 4.5 km northeast from the city Langtang, 29º52'N, 91º12'E, 27 Aug 1983, *Tang 1836* (PE); Samake, na ta, chang tai, bai yu town, 30º31'N, 100º17'E, 18 Aug 1982, *Tang 768* (PE). **Tibet:** Nanmulin county, Rendui distr., 30º4'N 89º6'E, 2 Sep 1975, *Qinghai-Tibet Team 7430* (KUN (image!), PE, QTPM (images!)). **Yunnan:** au-dessus du Col de Yen Tze hay, 25º35'N, 100º12'E, 6 Aug 1888, *Delavay 3686* (P); Lijiang county, Yulong Snow Mountain, 27º5'N 100º10'E, 29 Jul 1981, *Hengduan Team 2218* (PE (image!)); Qiaojia county, 27º1'N 103º6'E, 13 May 1973, *Kunming Group 8* (KUN (image!)). **INDIA. Sikkim:** Northeast Sikkim, 14 Jun 1894, *Cummins s.n.* (K); Lonok Valley, 27º20'N, 88º40'E, 28 Jul 1903, *Younghusband 187* (K). **NEPAL.** Central Region, Langtang, 28º10'N, 85º20'E, 16 Sep 1986, *Miehe 11878* & *Miehe* (K); Central Region, ob. Langtang, 28º10'N, 85º20'E, 19 Sep 1986, *Miehe 12324* & *Miehe* (K); Central Nepal, Bagmati Zone, Rasuwa Distr., Langtrang Khola-Pirgona-Pyung-a pass-Base Camp, 28º12'N, 86º38'E, 20 Jul 1992, *Miyamoto 20288* (AAH); Eastern Region, Tamur Valley, Ghunsa, E of Lalungchung Gola, 27º30'N, 86º31'E, 27 Jul 1956, *Stainton 1143* (K).

Notes—*Trisetum scitulum* is easily differentiated from the rest of the species by the combination of slender habit, lax panicles, and long awns.

In his Flora of British India, Hooker (1897) identified as *Avena flavescens* material that corresponds to *Trisetum scitulum*, indicating the different characters in the description: "spikelets larger than in most other species of this section, the awn longer; rachilla nodose below the fl. gls., penicillate with long hairs". Bor (1956) dealt with the problems of Hooker´s misapplied concept of the species, and gave a new name to it, *T. scitulum*, without describing it, only making reference to Hooker´s English description of *T. flavescens*. Chrtek (1968) validated the name with a Latin description, and also citing this species from China for the first time.

As happens with *T. turcicum*, Chrtek (1968) included *Trisetum scitulum* in ser. *Trisetum*, because of its geniculate awn. In this work, for the same reasons indicated for *T. turcicum*, *T. scitulum* has been included in *T.* sect. *Sibirica*. Moreover, in recent molecular works (Barberá et al., unpublished), *T. scitulum* appears in *T. sibiricum* sensu lato clade, with the rest of species included in this section.

Doubtful and excluded names

Aira ruprechtii Griseb. ex Hook. f., Trans. Linn. Soc. London 23: 346. 1862, nom. inval., pro syn.

Trisetum flavescens var. *genuinum* Hack., Bull. Herb. Boiss. 7: 702.1899, nom. inval. (Art. 24.3)

Trisetum sibiricum var. *alpinum* Reverd., Fl. Krasnoyarsk Kraya 2: 49. 1964, nom. inval. (Art. 39.1)

Trisetum sibiricum var. *bifidum* (Thunb.) Makino ex T. Koyama, Grass. Jap. Neighb. Reg.: 533. 1987, nom. inval.

Trisetum sibiricum subsp. *glabrum* Galanin, Fl. Daurii 2: 125 (& 138). 2009, nom. inval. (Art. 39.1)

Trisetum sibiricum f. *litorale* Rupr., Beitr. Pflanzenk. Russ. Reiches 2: 65. 1845, nom. nud.

ACKNOWLEDGEMENTS

This work was financed by *Flora iberica* CGL2014–52787–C3–1–P, CGL2012–32914 and CGL2015–66161–P, projects of the Spanish Government, supported by FEDER funds. We are indebted to the curators and staff of the herbaria mentioned in Material and Methods for kindly providing specimens. We thank the editor and anonymous reviewers for their critical reviews of the manuscript and for their helpful suggestions during the editing process. We thank Ramón Morales for translations of manuscripts in German. Toni Buira for his technical support. A. Quintanar for his revision of an earlier version of this manuscript. David Boufford for helping with Chinese translations. H. Nagamasu, Geraldine Reid, and Snežana Vukojičić helped in finding rare literature, type materials, and geographical localities. Roman Ufimov for Russian translations and helped in finding rare literature, and in many aspects. And for the rest of personal from the Komarov Institute, N. N. Tzvelev, Dmitry Geltman, Elena Glazkova, Denis Melnikov, for their help and their welcoming attitude during our stay.

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SUPPORTING INFORMATION

Appendix 1. Index to numbered collections cited. The numbers in parentheses refer to the corresponding species in the text.

Alanko et al. 52917 (1.a); *Aleksandrova, V. D. et L. N. Tiulina 134* (1.b), *242* (1.b); *Andreev, V. N. 1418* (1.b), *4906a* (1.a), *4906b* (1.a); *Andreev, V. N. et Z. Savkina 692* (1.b), *898* (1.b); *Balansa 848* (2), *1551* (2); *Beattie, R. et Y. Kurihara 10622* (3), *10832* (3); *Bergman, S. 237* (1.b); *Blagoveshchenskiy, N. V. 532* (1.a); *Blagoveshchenskiy, N. V. et G. I. Poplavskaia 1248* (1.a); *Bor, N. L. 15560* (5); *Borodin, I. 278* (1.a); *Boufford, D. E. et E. W. Wood 18987a* (3); *Brass, L. J. 9118* (3); *Bunge, A. 101* (1.a); *Bush et Bush 34* (2), *42* (2); *Cajander, A. K. 2074* (1.b); *Cherskiy, A. I. 86* (1.a); *Chien-chang Hsu et Kuo 5394* (3), *7293* (3); *Ching, R. C. 8767* (4); *Clarke, C. B. 31034* (5); *Davis, P. H. 46563* (2); *Davis, P. H. et Polunin 24763a* (2); *Delavay, J. M. 3686* (6); *Desiatkin, N. L. 502* (1.a); *Deyl, M. et J. Sojak 344* (1.a), *2917* (1.a), *3268* (1.a); *Diukina, N. 539* (1.a); *Dong Jian 29060* (6); *Dorofeev, V. I. 73* (1.a); *Dorsett, P. H. et Morse, W. J. 483* (3); *Dragulenko, G. V. 26/1* (1.a); *Drobov, V. P. 384* (1.a); *Duthie, J. F. 12548* (5), *12562* (5), *13646* (5); *Egorova, T.V. et al. 1685* (2), *1844* (2); *Elias, T. S. et al. 4847* (1.a); *Evstifeeva, M. 360* (1.a); *Faurie, U. J. 499* (3), *689* (3), *804* (1.a), *805* (1.a), *807* (3), *883* (3), *1212* (3), *1246* (1.a), *2228* (3), *2359* (3), *4468* (3), *4469* (3), *5214* (3), *5711* (3), *7191* (3), 8104 (3), *8456* (1.a), *8504* (1.a), *10523* (1.a), *10524* (1.a); *Forestry Administration Henan 465* (4); *Franchel, A. 1472* (3); *Fu, K. T. 1386* (1.a), *5281* (1.a); *Furuse, M. 9171* (1.a), *9176* (1.a), *47899* (1.a); *Gage, S. SG1427* (1.b), *SG1976* (1.b), *SG2021* (1.b), *SG2117* (1.b), *SG4139* (1.b), *SG4274* (1.b), *SG4492* (1.b); *Gage, S. et B. Semsrott SG1814* (1.a); *Gjaerevoll, O. 294* (1.b); *Golovina, E.O. 310* (1.a); *Gomolitskiy, P. et T. Semenikhina 716* (1.a); *Gusev, V. A. 256* (1.a); *Handel-Mazzetti, H. F. 2279* (2); *Hashimoto, CH. 9721* (1.a); *He Yinyu 25309* (4); *Henan Team 1023* (4), *1179* (4); *Hengduan Team 2218* (6); *Henry, A. 2558* (4), *6643* (4), 6706 (4); *Hitchcock, A.S. 18318* (3), *18344* (3), *18534* (4), *18551* (4), *18558* (4); *Huang Deng, Y. Y. 4031* (3); *Hultén, E. 798* (1.a); *Iarygin, I. I. 147* (1.a); *Ikonnikov-Galitzky, N. 119* (1.a); *Ikonnikov-Galitzky, N. P. et V. A. Ikonnikov-Galitzky 3426* (1.a); *Iliin, M. et B. Ovchinnikov 28* (1.a); *Iltis, H. H. et al. 561* (1.a), *1321* (1.a); *Isachenko, T. I. et al. 219* (1.a); *Junsheng, Y. 9847* (6); *Karev, G. I. 669* (1.a); *Karo, F. 270* (1.a); *Keng, Y. L. 2314* (3), *2977* (3); *Khanmimchun, V. et V. Amelchenko 2207* (1.a); *Khitun, O.V. 8120* (1.b), *8151* (1.b), *8234* (1.b); *Khutov, N. A. 130* (1.a); *Kirino, S. 652* (3); *Klements, E. 275* (1.a); *Koelz, W. 22048* (5); *Kondo, K. et T. Kurosawa 227* (3); *Konta, F. et K. Murata 1184* (3); *Koponen, T. 15299* (3); *Korchagin, A. et O. Gaze 169* (1.a); *Koroleva, T. et V. Petrovsky 5703* (1.b); *Kozhevnikov, Y. P. 154* (1.b); *Kuldiushevskiy, I. D. 110/2* (1.a); *Kunming group 8* (6); *Kurosawa, T. 5063* (3); *Kurosawa, T. et al. 10102* (3); *Kusnezow, N. I. et W. W. Reverdatto 2276* (1.b), *4043* (1.b); *Kuznetsov, I. V. 78* (1.a); *Legendre, A. F. 391* (1.a); *Legler, B. 773* (1.a), *1246* (1.a); *Levinge, H. C. 27424* (5); *Liou, T. N. et al. 2042* (4); *Lipshits, S. Y. 249* (1.a); *Lipshits, V. 3044* (1.a); *Lishuxin 3118* (1.a); *Litvinov, D. 768* (1.a), *898* (1.a); *Mameev, S. 77* (1.a), *675* (1.a); *Martins, L. 2301* (1.a); *Medvedeva, L. I. et al. 641* (1.a); *Mengning Team 1262* (1.a); *Miehe, G. et S. Miehe 3891* (5), *11878* (6), *12324* (6); *Miyamoto, F. 20288* (6); *Murata, K. et al. 11739* (3); *Murata, J. et al. 1821* (3); *Naito, T. et al. 15* (3); *Nemoto, T. et al. 9574036* (1.a); *Nestruev, S. S. 1871* (1.a); *Noskov, A. K. et al. 291* (1.a); *Ohwi, J. 58* (3), *378* (1.a), *2326* (3), *2720* (3), *5261* (1.a), *6739* (3), *8305* (1.a); *Pančić, J. 1150* (1.a); *Péronin, A. 214* (2); *Polunin, O. et al. 281* (5); *Poplawska, H. 1743* (1.a); *Popov, M. G. 501* (1.a); *Poretskiy, A. 298* (1.a); *Porsild, A. E. 7122* (1.b); *Porsild, A. E. et R. T. Porsild 893* (1.b), *1414* (1.b); *Pospelov, I. N. 08–0466* (1.b), *97–376* (1.b); *Qing, Z. T. 13824* (6); *Qinghai-Tibet Team 7430* (6); *Ream, R. R. 589* (3); *Rebristaja, O. V. et S. A. Gokorevskich 553* (1.a); *Rebristaya O. V. et Tokarevskikh 702* (1.b); *Scamman, E. 5410* (1.b); *Schikama, K. 209* (3); *Selivanova-Gorodkova, E. 1521* (1.a); *Semenikhina, T. 183* (1.a); *Semsrott, B.*

BS0173 (1.b), *BS1487* (1.b); *Seregin, A. 3135* (1.a); *Shan Hanrong et al. 8043* (4), *8389* (4), *9014* (4); *Shanxi Team 246* (1.a), *1938* (1.a); *Shaulo, D. et I. Belskaya 1561* (1.a); *Shaulo, D. et D. Saya 1562* (1.a); *Shiota, K. 5579* (3); *Shipchinskiy, N.V. 145* (1.a), *529* (1.a); *Sinclair, I. W. et D. G. Long 5199* (6); *Sintenis, P. 1142* (2); *Smirnov, V. I. 70* (1.a), *542* (1.a); *Smirnov, P. A. 49* (1.a), *119* (2); *Smith, H. 2772* (1.a), *3447* (1.a), *4276* (6), *7173* (1.a); *Soják, J. et V. Vasak 7177* (1.a); *Solstad, H. et Elven 04/0266A* (1.b); *Sovetkina, M. et S. Chausova 2706* (1.a); *Stainton, J. D. 1143* (6); *Stainton, J. D. et al. 3785a* (5), *4648* (5); *Steward, A. N. 2516* (3), *2559* (4); *Stewart, R. R. 18448* (5), *18700* (5), *21829* (5); *Stewart, R. R. et A. Rahman 25001* (5); *Stileman, R. 17* (2); *Strachey, R. et J. E. Winterbottom 1* (5); *Sukachev, V. et G. Poplavskaya 2577* (1.a); *Sukopp, U. 1523* (1.a), *1658* (1.a); *Tang, T. 1433* (1.a); *Tang, X. 768* (6), *1836* (6); *Taquet, E. 1891* (1.a), *3403* (3), *3423* (1.a), *5096* (3); *Tatli, A. 5331* (2); *Temnoev, N. I. 62* (1.a); *Tikhomirov, B.A. 73* (1.a); *Tiulina, L. N. 223* (1.b); *Tolmachev, A. I. 770* (1.b); *Tolmachev, A. I. et al. 245* (1.b); *Tomin, M. P. 153* (1.a); *Transhel, V. 153* (1.a); *Tsang, W. T. 20309* (3), *23765* (3); *Tsiang, Y. et H. Wang 16458* (3); *Tsugaru, S. et T. Takahashi 24822* (3), *25044* (3); *Tsvelev, N. 266* (1.a); *van Royen, P. 10867* (3); *Vasak, V. 9247* (1.a); *Veldkamp, J. F. 6248* (3); *Wang, T. P. 4559* (1.a); *Wenzhong Wang 141* (1.a); *Wilford, C. 938* (3); *Xiaoen Tian 1089* (1.a); *Xiaozong Tang 1903* (1.a); *Yao Kan 79429* (4); *Yellow river Team 2552* (1.a), *2614* (1.a); *Yokota, A. 958* (3); *Yonekura, K. 448* (3); *Yongsok, O. 7613* (3), *10030* (3); *Younghusband, F. E. 187* (6); *Yunatov, A. A. 361* (1.a), *15678* (1.a); *Yunatov, A. A. et al. 1517* (1.a); *Zhirov, I. 223* (1.a); *Zinger, N. 796* (1.a).

CAPÍTULO IV

Taxonomic revision of *Trisetum* section *Trisetum* (Poaceae: Pooideae: Aveninae) from Eurasia and North Africa

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Annals of the Missouri Botanical Garden, in revision

Abstract—A taxonomic revision of *Trisetum* sect. *Trisetum* is presented. We include descriptions and synonyms of each taxon from a study of 894 vouchers from 45 herbaria. Detailed morphometric descriptions, illustrations, distribution maps, identification key, and habitat data are given for each taxon. Morphometric variation of the main characters is shown by box-plots. Twenty-four names are lectotypified. Two neotypes are designated. We recognize eight species of *Trisetum* in the section: *T. alpestre*, *T. altaicum*, *T. bertolonii*, *T. flavescens*, *T. fuscum*, *T. glaciale*, *T. gracile*, and *T. laconicum*. Two infraspecific taxa of *T. flavescens* are recognized (*T. flavescens* subsp. *flavescens* and *T. flavescens* subsp. *griseovirens*). Six of the eight species of *Trisetum* sect. *Trisetum* are endemic to the different European mountain ranges, while *T. altaicum* grows in Altai and Tian Shan Mountains, and in the mountains of Northern Mongolia and Southern Russia, and *T. flavescens* is widespread in temperate regions of Europe, Western Asia and North Africa. Vegetative propagation by pseudoviviparism is observed for the first time in specimens of *T. flavescens* subsp. *flavescens*.

Resumen—Se presenta una revisión taxonómica de *Trisetum* sect. *Trisetum* en Eurasia y norte de África. Se incluyen descripciones y sinónimos de cada táxon tras el estudio de 894 pliegos de 45 herbarios. Se proporcionan descripciones morfométricas detalladas, ilustraciones, mapas de distribución, clave de identificación y datos de hábitat de cada táxon. Se muestran las variaciones morfométricas de los principales caracteres en diagramas de caja. Se han lectotipificado 24 nombres. Se han designado dos neótipos. Reconocemos ocho especies de *Trisetum* en la sección: *T. alpestre*, *T. altaicum*, *T. bertolonii*, *T. flavescens*, *T. fuscum*, *T. glaciale*, *T. gracile* y *T. laconicum*. Se reconocen dos táxones infraespecíficos de *T. flavescens* (*T. flavescens* subsp. *flavescens* y *T. flavescens* subsp. *griseovirens*). Seis de las ocho especies de *Trisetum* sect. *Trisetum* son endémicas de las diferentes cadenas montañosas europeas, mientras que T. altaicum crece en Altai y en las montañas Tian Shan, y en las montañas del norte de Mongolia y sur de Rusia, y *T. flavescens* está disperso en las regiones templadas de Europa, oeste de Asia y norte de África. Se ha observado por primera vez propagación vegetativa por pseudoviviparismo en especímenes de *T. flavescens* subsp. *flavescens*.

INTRODUCTION

Trisetum Pers. is one of the 18 genera of perennial grasses classified in the Aveninae J. Presl subtribe (Poeae tribe, subfamily Pooideae Benth.; cf. Tzvelev, 1989; GPWG, 2001; Soreng et al., 2003, 2007, 2015, 2017). This genus includes about 50 species that often form a significant part of the temperate and cold grasslands of the northern hemisphere, although they are also found in South America, Australia and New Zealand. Their habitat varies according to their wide distributional range, and its species live from open grasslands to shady areas of forests, high mountain meadows and even the tundra (Hultén, 1959; Chrtek, 1965; Clayton & Renvoize, 1986; Randall & Hilu, 1986; Watson & Dallwitz, 1992; Finot et al., 2004, 2005a, 2005b; Barberá et al., 2017a, 2017b). *Trisetum flavescens* (L.) P. Beauv., one of the species included in the section studied here, is of great economic interest as a fodder plant for both wild and domestic livestock.

To date only detailed taxonomic revisions of the American and New Zealand species of this genus have been carried out (Edgar, 1998; Finot et al., 2004, 2005a, 2005b), in addition to those recently published by us on two Eurasian sections, *T.* sect. *Acrospelion* (Besser) Pfeiff. and *T.* sect. *Sibirica* (Chrtek) Barberá (Barberá et al., 2017a, 2017b). Six of the species of the section to which we dedicate the present work, *Trisetum* sect. *Trisetum*, are endemic to Europe, while *T. altaicum*, and the most ubiquitous *T. flavescens*, both reach eastern Asia, and *T. flavescens* also reaches North Africa, and is introduced into North and South America and into New Zealand.

Trisetum has been traditionally divided into two sections: *T.* sect. *Trisetum*, and *T.* sect. *Trisetaera* Asch. & Graebn. A review of the history of the genus can be found in Finot et al. (2005a) and Barberá et al. (2017a). Chrtek (1965, 1967a, 1968) carefully studied the European species of *Trisetum*, proposing new infrageneric divisions of the genus. Chrtek (1965) divided the European species into four subgenera (*T.* subg. *Trisetum*, *T.* subg. *Distichotrisetum* Chrtek, *T.* subg. *Glaciotrisetum* Chrtek, and *T.* subg. *Graciliotrisetum* Chrtek), mainly based on the variation in vernation (conduplicate or convolute), and on anatomical characters of leaves and roots. At the same time, Chrtek (1965) divided the subgenus *Trisetum* in five sections (*T.* sect. *Trisetum*, *T.* sect. *Trisetaera*, *T.* sect. *Rigida* Chrtek, *T.* sect. *Hispanica* Chrtek, and *T.* sect. *Carpatica* Chrtek). Apart from the anatomical characters, *Trisetum* sect. *Trisetum* was separated by its lax panicles and short ligules, including *T. flavescens*, *T. alpestre* (Host) P. Beauv., *T. sibiricum* Rupr., *T. agrostideum* Fr., and *T. baregense* Laffitte & Miégev. The monotypic *T.* sect. *Carpatica*, established for *T. fuscum* (Kit. ex Schult.) Schult. of the Carpathian Mountains, was characterized by its longer ligules and by the hairiness of lemmas, palea keels, and awns.

Tzvelev (1976) simplified the classification of *Trisetum* by not addressing the anatomical characters used by Chrtek. Tzvelev (1976) recognize three sections (*T.* sect. *Rigida*, *T.* sect. *Trisetaria*, and *T.* sect. *Trisetum*) in his treatment of *Trisetum* for the Soviet Union. He characterized the different sections by the type of growth of underground and vegetative shoots, leaf disposition, panicle density, and the rachilla and callus hair length. He included seven species within *T.* sect. *Trisetum* [*T. ciliare* (Kit. ex

Schult.) Domin, *T. turcicum* Chrtek, *T. sibiricum, T. flavescens, T. alpestre, T. altaicum* Stephan ex Roshev., and *T. agrostideum*].

Later, Probatova (1979) in her study of the genus from the Caucasus arranged *Trisetum* sect. *Trisetum* in four subsections: the monotypic *T.* subsect. *Carpatica* (Chrtek) Probat. (including *T. ciliare*); subsect. *Trisetum* (including *T. flavescens s. l.*, *T. parvispiculatum* (Tzvelev) Prob., and *T. alpestre*); subsect. *Sibirica* (Chrtek) Probat. (including *T. sibiricum* and *T. turcicum*), and; subsect. *Agrostidea* Probat. (including *T. altaicum* and *T. agrostideum*). The subsections were characterized by the type of growth of underground and vegetative shoots, lemma apex, callus, awn and palea keel hairs length and anthers length.

Another relevant floristic study, which covers most of the species of *T.* sect. *Trisetum*, is the Flora Europaea treatment by Jonsell (1980). However, he did not recognize any sections.

After studying *T.* sect. *Acrospelion* and *T.* sect. *Sibirica* (Barberá et al., 2017a, 2017b), here we present the taxonomic revision of *Trisetum* sect. *Trisetum*, which is the third of our ongoing monograph on the genus *Trisetum* in Eurasia. *Trisetum* sect. *Trisetum* is here characterized by having panicles lax to somewhat dense or compact, spikelets usually greenish or purplish, callus with short hairs, awns geniculate or bent, rarely straight, and ovaries usually hairy apically. The most serious taxonomic problems of the group have been the delimitation of the section and the treatment given to *T. flavescens*, a very variable species that has been historically split into many taxa. Our final classification is also based on our current studies on molecular data, which will be published in the near future. This study, based on a thorough review of herbarium material and living plants, is the first to provide a detailed taxonomic scheme of the whole section *Trisetum* as we currently understand it based on our morphological and molecular surveys of the whole subtribe Aveninae.

MATERIALS AND METHODS

This revision is based on the study of 894 herbarium specimens from the following herbaria: AAH, ARAN, B, BC, BCN, BM, BOLO, C, F, FI, G, GB, GDA, GH, GOET, H, HBG, JE, K, L, LE, LW, M, MA, MO, MPU, MW, NY, O, P, PE, PR, PRC, RO, S, SEV, UPS, US, W, and WU [acronyms according to Thiers (2017)]. Photos of specimens from HNWP were also examined on the website of Chinese Virtual Herbarium (CVH; <www.cvh.org.cn>), and specimens from CAI, DAO, FR, and KFTA on the website of Global Plants (JSTOR; <www.plants.jstor.org>). An index of numbered collections is presented in Appendix 1.

One hundred and seventy specimens were used for the morphometric analyses, as operational taxonomic units (OTUs), selected to represent as far as possible, the geographical range and the morphological variability of the taxa. Fifty-nine quantitative characters were recorded using a Mitutoyo CD–15DCX digital vernier caliper on 20 specimens of each species when available. Spikelet measurements were taken on the distal spikelet from the longest branch of the second node of the panicle; floret measurements were taken from the basal floret of the selected spikelet. Leaf-blade width was measured one cm above the ligule insertion. The rachilla internode between first and second flower is also referred to as "rachilla". Each character was analyzed for its minimum, maximum, and lower and upper quartiles, using STATISTICA package (www.statsoft.com). Quantitative and qualitative characters are also used in the identification key and descriptions. Minimum and maximum values are noted in brackets and the lower and upper quartile values (between the 25th and 75th percentiles) are noted outside. Transverse sections of leaf-blades were prepared by hand using the uppermost caulinar leaf; they were stained with Fasga (Tolivia & Tolivia, 1987), and photographed with a Nikon SMZ1000 optical microscope. For leaf anatomy, the terminology of Ellis (1976, 1979) was used.

Additional data on the habitat, distribution, and chromosome numbers were checked from literature and collection labels. Species distribution maps were made using ArcGis v.9.3 (ESRI, 2008). The material studied is listed under each species in the taxonomic treatment below. The geographic coordinates were derived, in almost all cases, using the GeoNames database (<www.geonames.org>).

RESULTS

Morphology

HABIT AND STEM—Perennial grasses commonly with loose habit, with short to long rhizomes and thus well-isolated shoots, sometime densely tufted as in *T. glaciale* and *T. gracile*. The stems are straight in most of the species, except *T. gracile*, which has stems often bent at its blackish nodes, and *T. bertolonii*, which sometimes has the upper part of the stems curved. The stems are usually shorter than 60 cm, except *T. laconicum*, which can reach more than 80 cm, and *T. flavescens* subsp. *flavescens*, which can rarely exceed these sizes. Furthermore, *T. glaciale* and *T. gracile* are the shortest species [(3–)8.8–14.4(–19.5) cm, and (4.5–)8.9–12.5(–18.2) cm, respectively]. Most of the species of the section produce extravaginal tillers, being intravaginal in *T. bertolonii* and *T. laconicum*, rarely in *T. fuscum*. *Trisetum glaciale* is the only species that presents always intravaginal branching. The culms are always glabrous in *T. altaicum*, *T. fuscum*, and *T. laconicum*, sometimes puberulous in some parts in *T. alpestre*, *T. gracile* and *T. glaciale*, rarely so in *T. flavescens*. *Trisetum bertolonii* always has pubescent culms. The number of nodes varies between 2 and 6(7). The culm internodes are mostly concentrated in lower part of the culm in most of the species, although *T. flavescens*, *T. fuscum*, and *T. laconicum* have relatively elongated lower internodes and the nodes well separated along the culm.

LEAVES—In *Trisetum* sect. *Trisetum*, as in the rest of the genus, the different characters of the leaf-sheaths and leaf-blades are variable in the same plant, depending on whether they are the basal or top culm leaf-blades, or if they are young or mature (Barberá et al., 2017a, 2017b).

LEAF-SHEATHS—Basal leaf-sheaths are sparsely to densely pubescent, sometimes glabrous in *T. bertolonii* and *T. gracile*, rarely in *T. alpestre* and *T. flavescens*. The oldest basal leaf-sheaths usually decay into fibers in most of the species, forming a dense layer of decomposed sheaths in *T. glaciale* and *T. gracile*. These two species has distinctly veined leaf-sheaths, and are somewhat inflated in *T. gracile*.

Top culm leaf-sheaths are always glabrous in *T. bertolonii*, *T. gracile*, and *T. laconicum*, sometimes pubescent in *T. alpestre*, *T. altaicum*, and T. fuscum, rarely in *T. flavescens*. *Trisetum glaciale* has always pubescent top culm leaf-sheaths. Sheaths margins are glabrous in *T. bertolonii*, *T. glaciale*, and *T. gracile*, always ciliate in *T. altaicum* and *T. laconicum*. Ciliate margins also sometimes develope in *T. alpestre* and *T. fuscum*, and rarely in *T. flavescens*.

LEAF-BLADES—The species of *T.* sect. *Trisetum* have flat leaf-blades in most of the species, although *T. flavescens* have sometimes convolute to revolute or conduplicate ones, rarely filiform. Most of the species of the section have non-rigid leaf-blades, but *T. glaciale* and *T. gracile* have rigid ones with a thickened midrib, as well as the shortest blades (Fig. 1A), with the margins thickened and cartilaginous in *T. glaciale*. The indumentum of leaf-blades has traditionally been used as a distinctive character for taxa delimitation (Tzvelev, 1976; Jonsell, 1980). However, as for *T.* sect. *Acrospelion* and *T.* sect. *Sibirica*, the leaf-blade features have been considered less important than those of the spikelet morphology for the taxonomy of the widespread species, due the high variability of leaf-blade traits (Barberá et al., 2017a, 2017b). The species of *T.* sect. *Trisetum* have leaves varying from glabrous to pubescent adaxially and abaxially, usually with ciliate margins.

The species of *Trisetum* sect. *Trisetum*, as the rest of the genus, are mesophytic or xerophytic grasses. While the abaxial surface of the leaf-blades often has a flat surface, the adaxial one has ribs of varying depth (Metcalfe, 1960; Watson & Dallwitz, 1992). The xerophytic species of the section have deeper intercostal zones and associated ribs than the mesophytic ones, and the sclerenchyma girders and strands are well developed (Barberá et al., 2017a, 2017b). As indicated before, the midrib is not particularly marked in most of the species of the section, but is strongly marked only in *T. glaciale* and *T. gracile*. Chrtek (1965) made the first detailed study on the histology of European *Trisetum*, including some of the species included in our work of section *Trisetum* (*T. fuscum*, *T. glaciale*, and *T. gracile*). The vascular bundles of the species of *T.* sect. *Trisetum* can be accompanied or not by more or less developed sclerenchyma girders or strands that attach to the abaxial or adaxial sides of the leaf-blade, or to both sides. No transversal section of *T. laconicum* has been done, because of the few specimens available. All of the species of the section have cap of sclerenchyma at the margins. *Trisetum altaicum* and *T. fuscum* are mesophytic grasses, which explain their shallow intercostal zones or ribs, and the vascular bundles with no strands and with narrow girders adaxially and abaxially. *Trisetum flavescens* subsp. *flavescens* has vascular bundles with girders as deep as wide in both surfaces, alternating with bundles with only small girders adaxially. The rest of species of the section are more or less xerophytic grasses. *Trisetum glaciale* has girders only on the midrib, which are abaxially well developed, while *T. gracile* has no girders and presents well-developed strands in every vascular bundle in both surfaces. *Trisetum alpestre*, *T. bertolonii* and *T. flavescens* subsp. *griseovirens* present both, girders and strands, more or less developed.

LIGULES—The ligule measurements used in this study were taken from the top culm leaf-blades, which are usually longer than those of basal leaves. *Trisetum fuscum* has the longest ligules

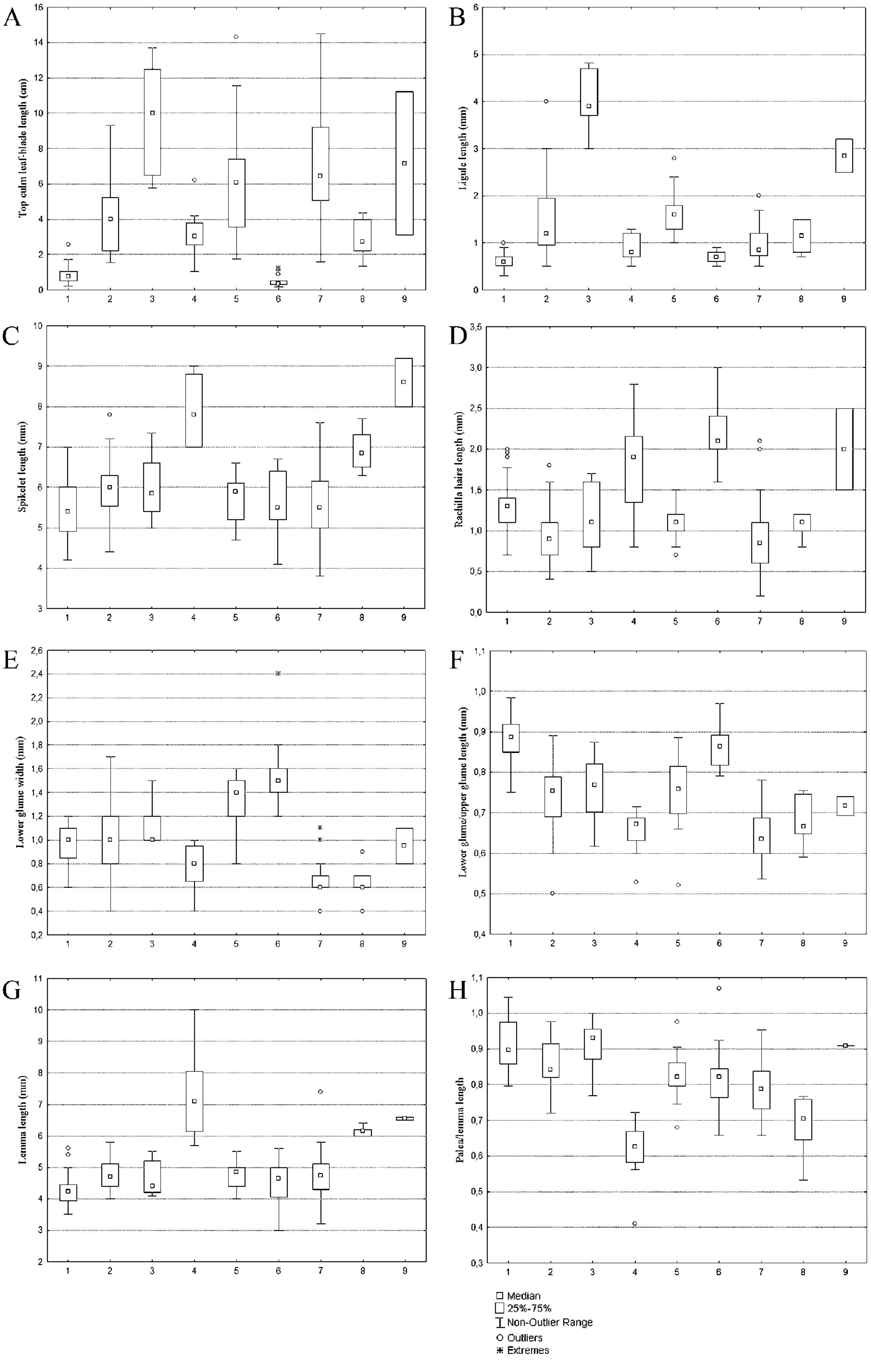

Figure 1. Box plots of a selection of studied variables. A. Top culm leaf-blade length. B. Ligule length. C. Spikelet length. D. Rachilla hairs length. E. Lower glume width. F. Lower glume/upper glume length. G. Lemma length. H. Palea/lemma length. Numbers along the x-axis correspond to the studied taxa: 1. *T. glaciale*. 2. *T. alpestre*. 3. *T. fuscum*. 4. *T. bertolonii*. 5. *T. altaicum*. 6. *T. gracile*. 7. *T. flavescens* subsp. *flavescens*. 8. *T. flavescens* subsp. *griseovirens*. 9. *T. laconicum*.

[(3–)3.7–4.7(–4.8) mm long], followed by *T. laconicum* (2.5–3.2 mm long). The ligules are membranous, truncate or acute, dentate to laciniate, always glabrous in *T. bertolonii* and *T. fuscum*, and usually more or less hairy on the upper part or the surface in the rest of species (Fig. 1B).

INFLORESCENCES**—**Inflorescences are paniculate, lax to somewhat dense or compact, narrowly elliptic to elliptic or lanceolate in outline, sometimes oblong, and always ovate in *T. glaciale* and *T. gracile*. *Trisetum laconicum* has the longest panicles (8–19 cm long), followed by *T. flavescens* and *T. fuscum* [(3.5–)6–10.5(–16.2) cm, and (6.8–)7.9–11.2(–13) cm, respectively], whereas *T. glaciale* and *T. gracile* have the shortest ones [(2.3–)3–4.2(–4.8) cm, and (1.3–)1.6–2.5(–3.1) cm, respectively]. *Trisetum fuscum* is characterized by having the longest basal branches [(1–)2.2–3.8(–5) cm], while *T. glaciale*, and *T. gracile* have the shortest ones [(0.3–)0.4–0.9(–1.1) cm, and (0.2–)0.3–0.9(–1.1) cm, respectively]. The inflorescence rachis is glabrous to sparsely pubescent or always pubescent in *T. bertolonii*, with hairs up to 0.5 mm long.

SPIKELETS**—**Spikelet length in *Trisetum* sect. *Trisetum*, as in the rest of the genus, varies according to the lemma length and the number of florets. *Trisetum laconicum* and *T. bertolonii* have the longest spikelets, followed by *T. flavescens* subsp. *griseovirens* [8–9.2 mm, 7–9 mm, and (6.3–)6.5–7.3(–7.7) mm, respectively] (Fig. 1C). The awn is not included in the length of the spikelet. Furthermore, *T. laconicum* has also the longest pedicels (5–6.3 mm long). Rachilla segments are always pubescent; *T. laconicum*, *T. gracile*, and *T. bertolonii* have the longest hairs [1.5–2.5 mm, (1.6–)2–2.4(–3) mm, and (0.8–)1.3–2.2(–2.8) mm long, respectively]. Therefore, it is a useful diagnostic character for those three species (Fig. 1D).

The number of florets is usually 2–3 per spikelet, except *T. laconicum* which has 3–4 florets, rarely 4 in *T. flavescens* and rarely 1 in *T. glaciale*. Vegetative progagation by pseudoviviparism was observed in a specimen of *T. flavescens* for the first time.

GLUMES**—**In section *Trisetum*, the glumes are unequal, except in *T. glaciale* and *T. gracile*, which have subequal glumes [ratio lower glume length/upper glume length = (0.75–)0.85–0.92(–0.98), and (0.79–)0.82–0.89(–0.97), respectively] (Fig. 1F). *Trisetum altaicum*, *T. gracile*, and usually *T. alpestre*, *T. fuscum* and *T. glaciale* have elliptic to oblong or lanceolate lower glumes, these wider than those of the rest of the section, which have usually narrower ones, sometime linear in *T. bertolonii*. Lower and upper glumes are acuminate to long acuminate, sometimes acute, rarely with the upper one aristulate in *T. alpestre*, with some short hairs from the middle part to the top of the main nerve and along the margins. The lower glume in *T. bertolonii* and *T. laconicum* always has one nerve, other species rarely have one (*T. gracile*) or two lateral nerves (*T. alpestre*, *T. altaicum*, *T. flavescens*, and *T. fuscum*) (Fig. 1E). *Trisetum glaciale* has lower glumes with three nerves, sometimes two. The upper glume has always three nerves, the central one reaching the tip, the lateral ones extending to the middle or the upper half.

LEMMA**—**The lemma structure, as in the rest of the genus, is characterized by having a dorsal awn and a bifid apex with two apical teeth normally ending in two aristules separated by a more or less deep sinus. Aristules are the intermediate nerves protruding beyond each tooth apex (Nicora, 1978; Koch, 1979; Finot et al., 2006; Barberá et al., 2017a, 2017b). Aristules length is a variable character at the species level, being longer in *T. bertolonii* than in the rest of species (1.2–2.3(–4) mm long), followed by *T. flavescens* subsp. *griseovirens* [(0.9–)1–1.4(–1.8) mm long] (Fig. 2B). The length of the lemma, which includes the aristules length and without taking the awn into account, is longer in *T. bertolonii*, *T. laconicum*, and *T. flavescens* subsp. *griseovirens* [(5.7–)6–8(–10) mm, 6.5–6.6 mm, and 6–6.2(–6.4) mm, respectively]. However, the length of the lemma does not differ greatly between the rest of the species of the section (Fig. 1G). The lemma is laterally compressed, from narrowly or broadly lanceolate to elliptic or oblong, greenish to yellowish at maturity in the central part, surrounded by purplish tinges, except in *T. bertolonii* which has hyaline (colorless) margins. Most of the species of *T.* sect. *Trisetum* have glabrous or scabridulous lemmas with very short adpressed hairs up to 0.1 mm long, except *T. fuscum* which sometimes has longer hairs at the awn insertion, and *T. gracile*, which can have pubescent lemmas with hairs (0.05–)0.6–1.4(–2) mm long between its base and the awn insertion.

AWN—The length and shape of the awn are important taxonomic characters for the classification of the species of this section. *Trisetum bertolonii* has the awn significantly longer than the rest of species of the section [(11–)11.5–16(–17) mm long], but the length does not differ greatly in the rest the species. At subspecific rank, the length of the awn is also a good character to differentiate *T. flavescens* subsp. *griseovirens*, with longer awns than *T. flavescens* subsp. *flavescens* [(8–)8.2–9(–10.6) mm, and (4.2–)5.6–7(–8.3) mm, respectively] (Fig. 2A). The awn shape is slightly geniculate to geniculate, and with a twisted column up to the geniculation in *T. flavescens*, *T. glaciale*, and *T. gracile*. *Trisetum altaicum*, *T. fuscum*, and *T. laconicum* have more or less bent awns at the base, while *T. alpestre* and *T. bertolonii* have awns straight or bent at the middle. The awn is dorsal, inserted above or at the middle of the lemma, except for *T. gracile*, where the awn is inserted slightly below the middle [ratio awn insertion from the base length/lemma length = (0.34–)0.41–0.49(–0.51)].

CALLUS—The callus is elliptic to orbicular, or sometimes oblong, and always has short hairs. *Trisetum bertolonii* has the longest callus hairs [1.5–2.2(–2.6) mm], while the rest of species have hairs always shorter than 1.4 mm long (Fig. 2C).

PALEA—The palea disposition and its shape are the same as in the other sections. The surfaces are hyaline. The two keels extend into two fine teeth (Barberá et al., 2017a, 2017b). In this section, the palea of *T. laconicum* is longer than the rest of species (5.8–6 mm long). The upper part of the flange edges and keels of the palea normally have very short hairs, which can reach to 0.4 mm long in *T. fuscum*. The length of both the palea and the lemma is always markedly unequal in *T. bertolonii* [ratio palea length/lemma length = (0.4–)0.58–0.67(–0.7)], followed by *T. flavescens* subsp. *griseovirens* [ratio palea length/lemma length = (0.53–)0.65–0.76(–0.77)] (Fig. 1H). In the rest of species, the difference between the palea and the lemma is more or less subequal to equal.

LODICULES—As in the rest of the sections of *Trisetum*, the two lodicules flank the dorsal sides of the ovary or caryopsis, and have a more or less oblanceolate shape (Barberá et al., 2017a, 2017b). The apices are irregularly dentate to laciniate or with (1)2–3 teeth or lobules of equal or different depth, except in *T. gracile*, which are usually entire.

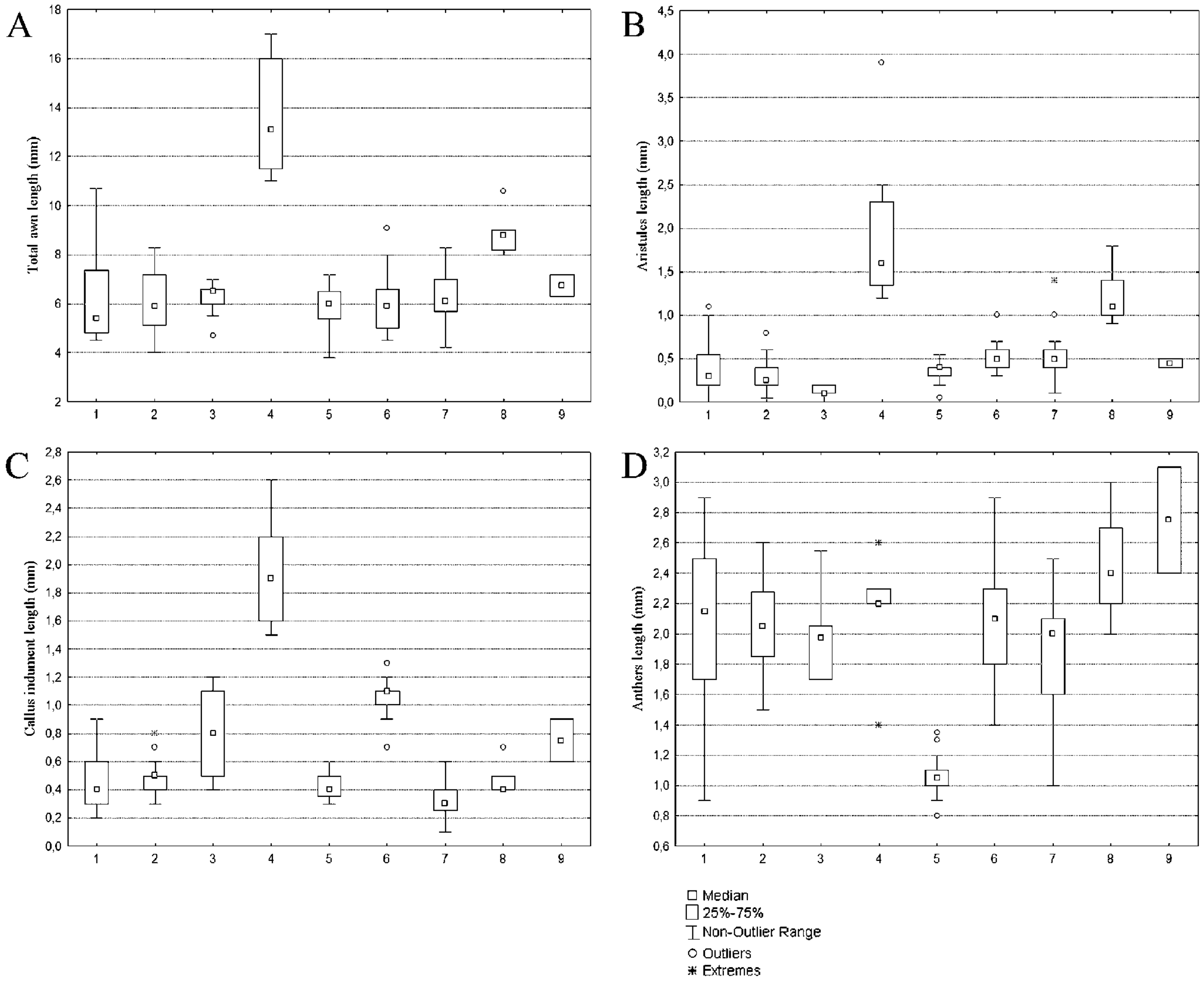

Figure 2. Box plots of a selection of studied variables. A. Total awn length. B. Aristules length. C. Callus indument length. D. Anthers length. Numbers along the x-axis correspond to the studied taxa: 1. *T. glaciale*. 2. *T. alpestre*. 3. *T. fuscum*. 4. *T. bertolonii*. 5. *T. altaicum*. 6. *T. gracile*. 7. *T. flavescens* subsp. *flavescens*. 8. *T. flavescens* subsp. *griseovirens*. 9. *T. laconicum*.

STAMENS—The length of the anthers does not vary much between the species of this section, except for *T. altaicum*, which has the smallest anthers [(0.8–)1–1.35 mm] (Fig. 2D).

OVARY AND CARYOPSIS—In this section, most of the species have a glabrous ovary. However, *T. glaciale* has ovaries from sparsely to more densely puberulous on the upper part, rarely glabrous, and *T. alpestre* usually has an apical tuft of hairs or scattered hairs at the apex. *Trisetum altaicum* rarely has a single hair on the upper part of the ovary. The shape of the mature caryopsis is similar in all species, being narrowly elliptic to oblong, while *T. glaciale* a more or less fussiform one. The transversal section is narrowly elliptic to elliptic and the caryopsis is not sulcate, with a punctiform hilum. The endosperm is semi-liquid.

Taxonomic treatment

TRISETUM Pers. sect. TRISETUM.—TYPE: *Avena flavescens* L. (current name *T. flavescens* (L.) P. Beauv.) [lectotype designated by Hitchcock (1920)].

T. sect. *Carpatica* Chrtek, Bot. Not. 118(2): 222. 1965. *T.* subsect. *Carpatica* (Chrtek) Prob., Novosti Sist. Vyssh. Rast. 15: 19. 1979.—TYPE: *T. fuscum* (Kit. ex Schult.) Schult.

T. ser. *Laconica* Chrtek, Acta Univ. Carol., Biol. 1966: 94. 1967. TYPE: *T. laconicum* Boiss. & Orph.

T. sect. *Gracilia* Chrtek & Jirásek, Webbia 17: 573. 1963. *T.* subg. *Graciliotrisetum* Chrtek, Bot. Not. 118(2): 223. 1965.—TYPE: *T. gracile* (Moris) Boiss.

T. subg. *Glaciotrisetum* Chrtek, Bot. Not. 118(2): 223. 1965.—TYPE: *T. glaciale* (Bory) Boiss.

Herbs with or without tufted habit, rhizomatous, sometimes shortly stooling; panicles lax to somewhat dense or compact; spikelets greenish or purplish, never goldish-brown; callus with short hairs, rarely longer than 1.4 mm; awns distinctly geniculate or slightly bent at the middle or the base, rarely straight; ovaries glabrous, sometimes sparsely to densely pubescent apically.

Distribution and Habitat—Trisetum sect. *Trisetum* occurs from Western Europe and Maghrebian mountains to Western Asia, extending eastward into the mountains of Altai and Tian Shan and northern Mongolia and adjacent Russia, eastern Kyrgyz Republic and Kazakhstan. The richest areas are the different European mountain ranges. It grows on mountain meadows and flood plains, in rock fissures and forests, at elevations from sea level to more than 3000 m.

Key to the taxa of Trisetum sect. Trisetum

1. Callus hairs 1.5–2.2(–2.6) mm long; awn (11–)11.5–16(–17) mm long .... ***T. bertolonii***
1. Callus hairs (0.1–)0.3–0.5(–1.3) mm long; awn (3.8–)5.3–7(–10.7) mm long 2
  2. Plants (3–)8.9–14.1(–19.5) cm high; top culm leaf-blade (0.2–)0.3–1.5(–2.6) cm long; panicles (1.3–)2.2–3.8(–4.8) cm long, ovate in outline 3
    3. Nodes enfolded by the sheaths; basal leaf-sheaths not inflated, densely pubescent; basal leaf-blades with the margins thickened, cartilaginous; callus hairs (0.2–)0.3–0.6(–0.9) mm long .... ***T. glaciale***
    3. Nodes not enfolded by the sheaths, rarely enfolded; basal leaf-sheaths somewhat inflated, glabrous to sparsely pubescent; basal leaf-blades with the margins not thickened; callus hairs (0.7–)1–1.3 mm long .... ***T. gracile***
  2. Plants (14.4–)28–47(–141.5) cm high; top culm leaf-blade (1.3–)2.2–12.5(–14.5) cm long; panicles (3.4–)6–9.4(–19) cm long, not or very rarely ovate 4
    4. Spikelets 8–9.2 mm long; palea 5.8–6 mm long... ***T. laconicum***
    4. Spikelets (3.8–)5.3–6.3(–7.8) mm long; palea (2.2–)3.6–4.3(–5.6) mm long 5
      5. Ligules (3–)3.7–4.7(–4.8) mm long .... ***T. fuscum***
      5. Ligules (0.5–)0.8–1.7(–4) mm long 6

6. Lower glumes (0.8–)1.2–1.6 mm wide; anthers (0.8–)1–1.3 mm long .... ***T. altaicum***

6. Lower glumes (0.4–)0.6–1(–1.7) mm wide; anthers (1–)1.8–2.2(–3) mm long.......................... 7

7. Awn straight or bent, very slightly twisted at the base; ovary usually with an apical tuft of hairs 0.1–0.2(–0.3) mm long or with scattered hairs at the apex .... ***T. alpestre***

7. Awn geniculate to slightly geniculate, more or less twisted at the base, rarely not twisted; ovary always glabrous... ***T. flavescens***

1. TRISETUM ALPESTRE (Host) P. Beauv., Ess. Agrostogr.: 88. 1812. *Avena alpestris* Host, Icon. Descr. Gram. Austriac. 3: 27, tab. 39. 1805. *Trisetaria alpestris* (Host) Baumg., Enum. Stirp. Transsilv. 3: 264. 1816. *Trisetum flavescens* var. *alpestris* (Host) Schrad., Linnaea 12: 443. 1838. *Avena flavescens* var. *alpestris* (Host) DC., Bot. Gall. 1: 512. 1828. *Trisetum flavescens* subsp. *alpestre* (Host) Hack., Magyar Bot. Lapok 2: 106. 1903.—TYPE: AUSTRIA. *N.T. Host s.n.* (lectotype, designated here, W1885-0002400!; isolectotype, W-0024994!).

Trisetum alpestre var. *purpurascens* Schur, Oesterr. Bot. Z. 10: 74. 1860.—TYPE: ROMANIA. Harghita, Őcsem Teteje Mountain, 46º39’N, 25º48’E, 28 Jul. 1853, *P.J.F. Schur s.n.* (lectotype, designated here, W!).

Trisetum alpestre var. *argentoideum* Schur, Oesterr. Bot. Z. 10: 74. 1860.—TYPE: ROMANIA. Harghita, Őcsem Teteje Mountain, 46º39’N, 25º48’E, Jul., *P.J.F. Schur s.n.* (lectotype, designated here, W!).

Trisetum alpestre var. *glabrescens* Schur, Enum. Pl. Transsilv.: 759. 1866. *Trisetum alpestre* subsp. *glabrescens* (Schur) Tzvelev, Novosti Sist. Vyssh. Rast.7: 64. 1971.—TYPE: ROMANIA. Königstein Mt. (Piatra Craiului), 45º38’N, 25º36’E, Aug., *P.J.F. Schur s.n.* (lectotype, designated here, LW-213277 image!).

Trisetum alpestre var. *macranthum* Schur, Enum. Pl. Transsilv.: 759. 1866.—TYPE: ROMANIA. Harghita, Őcsem Teteje Mountain, 46º39’N, 25º48’E, 28 Jul. 1853, *P.J.F. Schur s.n.* (lectotype, designated here, LW-213278 image!).

Trisetum baregense Laffitte & Miégev., Bull. Soc. Bot. Fr. 21: 46. 1874. *Avena subalpestris* subsp. *baregense* [baregensis] (Laffitte & Miégev.) Nyman, Consp. Fl. Eur.: 813. 1882. *Trisetum agrostideum* subsp. *baregense* (Laffitte & Miégev.) Chouard, Bull. Soc. Bot. Fr. 72: 340. 1925. *Trisetum flavescens* subsp. *baregense* (Laffitte & Miégev. ex Miégev.) O. Bolòs, Masalles & Vigo, Collect. Bot. (Barcelona) 17: 96. 1988. *Trisetaria baregensis* (Laffitte & Miégev.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 382. 1996.—TYPE: FRANCE. Haut-Pyrenées, Héas valley, Gabiédou peak, 42º42’N, 0º5’E, 13 Jul. 1862, *J. Miégeville s.n.* (lectotype, designated here, P-2217672!).

Trisetum alpestre f. *calvescens* Hack., Magyar Bot. Lapok 2: 108. 1903.—TYPE: ROMANIA. Harguita district, Nagy Hagymás Mountain, 46º42’N, 25º48’E, 21 Jun. 1901, *A. de Degen, Gram. Hung. 121* (lectotype, designated here, JE!).

Trisetum alpestre f. *anomalum* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 111. 1904.—TYPE: Tatra Mountains, *A. Rehmann s.n.* (Herbarium number: 69/276) (LW?) (no original material found).

Trisetum alpestre var. *aureum* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 111. 1904.—SYNTYPES: POLAND. Tatra Mts., Jaworzynka, 49º34'N 20º0'E, *F.I. Berdau s.n.* (KRAM?) (no original material found); POLAND?. Tatra Mts., *Rogalski s.n.* (no original material found); ROMANIA. Suhard Mts, Bucovina, 47º44'N 26º39'E, *A. Rehmann s.n.* (LW?) (no original material found).

Trisetum alpestre f. *majus* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 111. 1904.—TYPE: Lesser Poland Voivodeship, Tatra Mts., Dolina Kościeliska valley, 49º16′N 19º52'E, *B. Kotula s.n.* (KRAM?) (no original material found).

Trisetum alpestre var. *pulchrum* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 110. 1904.—SYNTYPES: Tatry, *B. Kotula s.n.* (KRAM?) (no original material found);Tatry, *E. Wołoszczak s.n.* (W?) (no original material found); ROMANIA. Suhard Mts., Bucovina, *A. Rehmann s.n.* (LW?) (no original material found).

Trisetum alpestre var. *tatrense* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 111. 1904.—TYPE: POLAND. Lesser Poland Voivodeship, Tatra Mts., Mt. Łysanki, 49º16'N 19º55'E, *B. Kotula s.n.* (KRAM?) (no original material found).

Trisetum flavescens f. *tirolensis* Hack., Allg. Bot. Z. Syst. 9: 189. 1904.—TYPE: ITALY. Trentino-Alto Adige, South Tyrol, Carbonin [Schluderbach], 46º37'N, 12º13'E, 21 Aug. 1903, *A. Kneucker, Gram. Exsicc. 442* [lectotype, designated here, B-10_0366348!; isolectotypes, B-10_0366347!, C!, G-00443036!, G-00443093!, KFTA-0000478 (image!), L-0050287!, L-1346752!, MA-292728, MO-2879843!, MO-3057065!, NY!, O-V2126668!, O-V2126570!, PR-9070!, S!, US-557059!, WU!].

Herb (14.4–)21.5–35.7(–53.5) cm high, slightly cespitose to cespitose, shortly rhizomatous, culm 0.3–0.8 mm diam., straight, glabrous, sometimes puberulous at the middle part or around the nodes, with hairs up to 1.5 mm long; nodes (2–)3–4(–5), mostly concentrated in lower part of the culm, not included in the sheaths, sometimes included, glabrous, yellowish to dark brownish. Basal leaf-sheaths surfaces and margins pubescent, rarely glabrous, with hairs (0.05–)0.3–0.6 mm long, sometimes decaying into fibers, yellowish, sometimes greenish or brownish; basal leaf-blades (1.9–)3–7.5(–12) cm × (1.1–)1.6–2.3(–4) mm, flat, slightly inrolled when dried, from sparsely to densely pubescent abaxially and adaxially, with hairs (0.05–)0.1–0.9(–1.2) mm long, sometimes glabrous, margins also with hairs, yellowish or brownish to greenish; top culm leaf-sheaths (5–)6.3–9.6(–16) cm long, glabrous to pubescent, with or without cilia; top culm leaf-blades (1.5–)2.2–5.2(–9.3) cm × (1–)1.6–3(–4.1) mm, flat, sometimes with margins inrolled, parallel to the culm, glabrous to pubescent adaxially and abaxially, with hairs (0.05–)0.1–0.8(–1.7) mm long, with cilia, greenish to greyish, sometimes yellowish or brownish; inner collar region glabrous to pubescent on the margins, with hairs (0.05–)0.4–0.7(–1.1) mm long; ligules (0.5–)0.9–2(–4) mm long, irregularly dentate, sometimes laciniate, glabrous, sometimes with scattered hairs 0.05–0.3 mm long on the apex. Basal node of the panicle glabrous. Panicles (3.4–)5.4–7.5(–11.5) × (1.2–)1.8–2.5(–3.6) cm, lanceolate in outline, sometimes oblong to elliptic, rather lax; rachis internodes glabrous to sparsely pubescent, mostly on the upper part, with hairs up to 0.2 mm long; longest basal branches (0.4–)0.8–2(–3.3) cm long. Spikelets (4.4–)5.5–6.3(–7.8) × (1.2–)2.2–3.2(–5) mm, 2–3-flowered; pedicels (1.5–)2.4–4.1(–5.2) mm long, glabrous to sparsely pubescent, mostly apically, with hairs up to 0.2 mm long. Glumes unequal [ratio lower glume length/upper glume length = (0.5–)0.69–0.79(–0.9)]; lower glume (2.5–)3.4–4.4(–5.3) × (0.4–)0.8–1.2(–1.7) mm, narrowly to broadly lanceolate, rarely elliptic to oblong [ratio lower glume width/lower glume length = (0.15–)0.19–0.31(–0.4)], acuminate to long acuminate, 1(–3)-nerved, glabrous usually with scattered hairs up to 0.1 mm long on the upper part of the midrib, greenish, surrounded by purplish or with hyaline margins; upper glume (3.6–)4.7–5.8(–7.5) × (1.5–)1.8–2(–2.3) mm, elliptic to broadly lanceolate or oblong, rarely oblanceolate [ratio upper glume width/upper glume length = (0.28–)0.31–0.38(–0.5)], acuminate to long acuminate, rarely acute or aristulate, 3-nerved, glabrous, usually with very short scattered hairs up to 0.1 mm long from the middle to the upper part of the central nerve, greenish rarely purplish, surrounded by yellowish or purplish; rachilla segment between first and second floret (0.7–)1–1.3(–1.7) mm long, with hairs (0.4–)0.7–1.1(–1.8) mm long; rachilla segment to sterile floret (1–)1.2–1.6(–2.2) mm long, with hairs (0.2–)0.4–0.9(–1.3) mm long. Lemmas (4–)4.4–5.1(–5.8) × (0.4–)0.8–1.2(–1.7) mm, oblong to elliptic, sometimes narrowly to broadly lanceolate [ratio lemma width/lemma length = (0.21–)0.29–0.35(–0.5)], scabridulous, with very short hairs up to 0.1 mm long on the midrib, rarely glabrous, greenish to yellowish, sometimes surrounded by a purplish flush; apical teeth (0.05–)0.2–0.45(–0.7) mm long, with aristules (0.05–)0.2–0.4(–0.8) mm long; awn (4–)5–7.2(–8.3) mm long, inserted (2–)2.4–3(–3.5) mm from the base [ratio awn insertion from the base length/lemma length = (0.52–)0.55–0.62(–0.65)], straight or bent, very slightly twisted at the base, with very short adpressed hairs up to 0.05 mm long; callus 0.2–0.3 mm long, elliptic to orbicular, rarely oblong, with hairs (0.3–)0.4–0.5(–0.8) mm long. Paleas (3.3–)3.8–4.5(–5.6) × (0.8–)1–1.4(–1.6) mm [ratio palea length/lemma length = (0.72–)0.82–0.91(–1)], oblong to oblanceolate or elliptic, margins glabrous or with scattered hairs; teeth (0.01–)0.1–0.3 mm long, with short antrorse hairs. Lodicules (0.4–)0.5–0.7(–0.9) mm long, with 2 lobules, of the same or different length. Anthers (1.5–)1.8–2.3(–2.6) mm long. Ovary (0.4–)0.5–0.8(–1.3) mm long, usually densely pubescent with an apical tuft of hairs 0.1–0.2(–0.3) mm long, sometimes glabrous or with scattered hairs at the apex. Caryopsis 2.7–2.8 × 0.6 mm, broadly lanceolate to narrowly elliptic or oblong. Figure 3.

Chromosome number—2*n* = 14 (Frey, 1992).

Additional illustrations—Chrtek (1967b: 4, 5, sub *Trisetum baregense*); Sãvulescu (1972: 289, Planşa 56, 1a-e); Frey (1992: 459, fig. 9).

Phenology—Trisetum alpestre has been collected in flower and fruit from June to September.

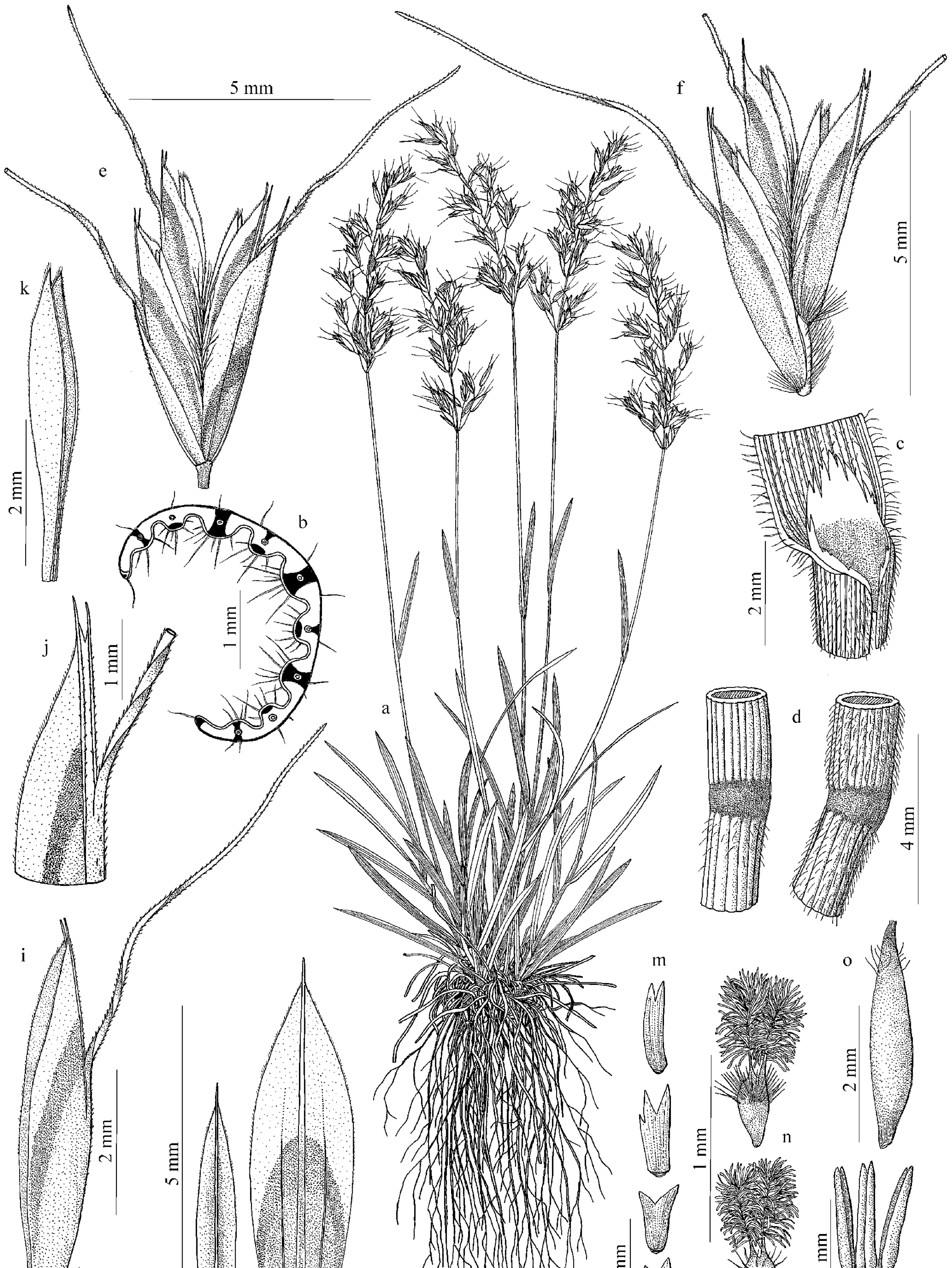

Figure 3. *Trisetum alpestre* (Host) P. Beauv. a. Habit. b. Transverse section of leaf-blade. c. Portion of sheath, ligule, and portion of the blade. d. Portions of the culm and node. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Lemma, upper part, lateral view. k. Palea, lateral view. l. Stamens. m. Lodicules.n. Pistil. o. Caryopsis. a, c-d, e-n based on *Du Rietz s.n.* (UPS-V-644660); b based on *Bornmüller s.n.* (B-10_0526398); m, n based on *Barberá et al. 953PB* (MA-872340); m based on *Barberá & Quintanar 1062PB* (MA-87668) and *Vestergren s.n.* (S); o based on *Neyraut s.n.* (JE).

Distribution and Habitat—Trisetum alpestre is distributed in the mountains from northern Spain (the westernmost in Burgos province), Pyrenees and the Alps, up to the Carpathians. It grows on limestone slopes and rock fissures from subalpine to alpine meadows, at 500–2800 m. Figure 4.

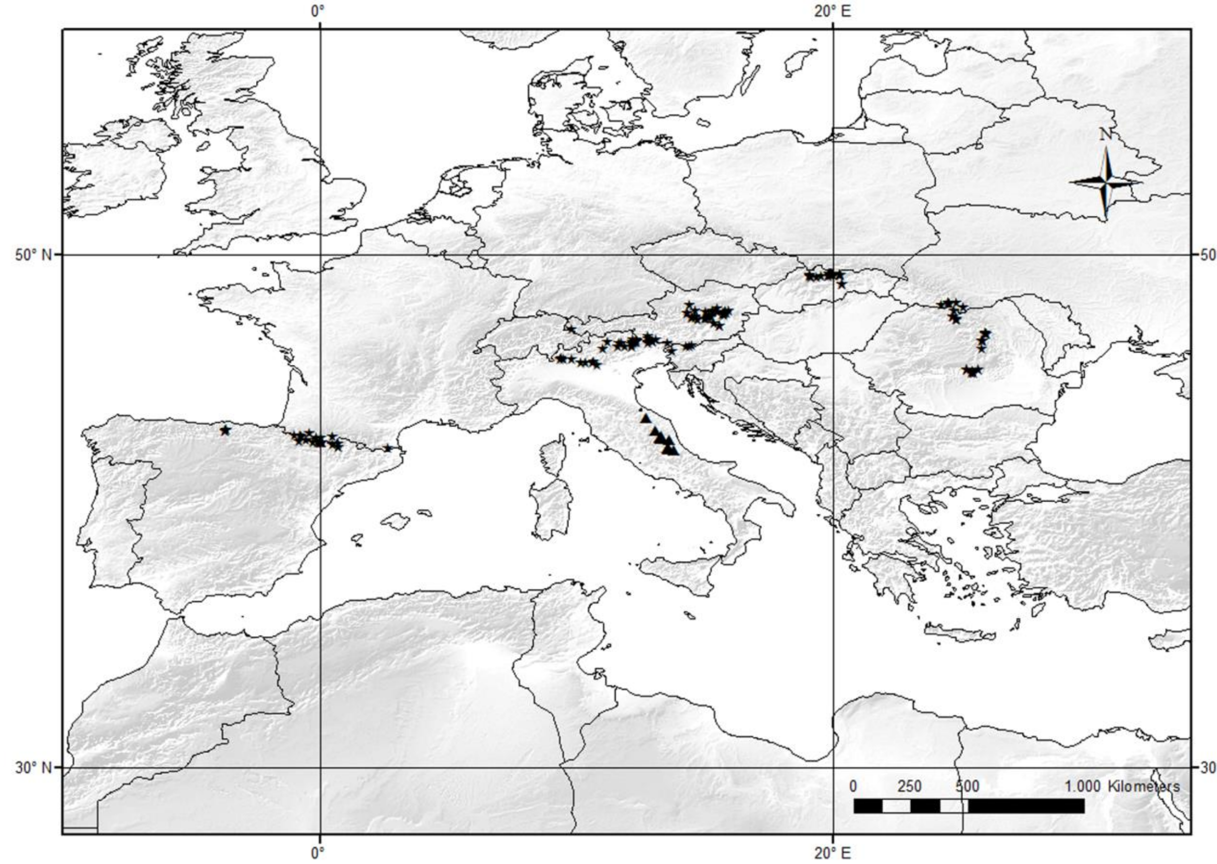

Figure 4. Distribution of *Trisetum alpestre* (stars) and *T. bertolonii* (triangles).

Discussion—Trisetum alpestre has been recognized by some authors as a subspecies or variety of *T. flavescens*. *Trisetum alpestre* is clearly separated from *T. flavescens* by its habit, that is usually more densely tufted, and usually has fewer nodes [(2–)3–4(–5) and (3–)4–5(–7), respectively] which are mostly concentrated in the lower part of the culm and sometimes enfolded by the sheaths, and top culm leaf-blades shorter and parallels to the culm [(1.5–)2.2–5.2(–9.3) cm, and (1.3–)4–9(–14.5) cm, respectively]. Apart from those characters, *T. alpestre* is differentiated from *T. flavescens* by its longer ligules [(0.5–)0.9–2(–4) mm, and (0.5–)0.7–1.2(–2) mm, respectively], wider and usually with purplish lower and upper glumes (lower glumes (0.4–)0.8–1.2(–1.7) mm, and (0.4–)0.6–0.7(–1.1) mm, respectively; upper glumes (1.5–)1.8–2(–2.3) mm, and (1.1–)1.5–1.8(–2.2) mm, respectively), straight or bent awns, and ovaries usually with an apical tuft or scattered hairs at the apex.

Trisetum baregense was described in 1874 from the Pyrenees. Chrtek (1967b) was the first one who wrote about the similarity between *T. baregense* and *T. alpestre*. He stated that these species differ by their awn length, glume width, and mainly by the ovary indumentum being glabrous in *T. baregense* and hairy in *T. alpestre*. Chrtek (1967b) also recorded the existence of intermediate specimens between both species in the Carpathians and in the French Alps. Schur (1866) recognized some Carpathian varieties; one of them is var. *glabrescens*, differentiated by glabrous upper leaf surfaces, leaf-sheaths, and ovaries. Tzvelev (1971) raised it to subspecific rank. Hackel (1904) described *T. alpestre* f. *tirolensis*, which is also differenciated by its glabrous ovaries. Küpfer (1974), in his work about the relationships between the Alpine and Pyrenean floras, considered *T. alpestre* and *T. baregense* as schizoendemics, being the two species diploids (2*n* = 14). He affirmed also that ovary indumentum is not a useful character to separate these taxa. Küpfer (1974) added the lemma apex as another character to differentiate both, *T. alpestre* having the lateral nerves slightly excurrent and *T. baregense* slightly or not excurrent, with a mucro of 0–0.3 mm. However, in the studied material, no difference in the lemma apex has been found. Alejandre et al. (2012) identified the western specimens of *T. alpestre* as "*T.* cf. *baregense*", and they indicated the morphological similarities between *T. alpestre* and *T. baregense*, as for example the ovary indumentum. We agree with Chrtek (1967b) and Küpfer (1974) that the ovary indumentum is a variable character. Most of the specimens from the eastern Alps and the Carpathians have a crown of hairs at the ovary apex, but there are also glabrous specimens or those with scattered hairs at the apex, as in the specimens from the Pyrenees. The same kind of variability, not taxonomically correlated with name taxa, has been observed in leaf and sheath indumentum. However, the awn length is slightly longer in *T. alpestre* than in *T. baregense*, and the glumes width slightly wider in *T. alpestre*. Apart from those characters, no other important differences have been found to differentiate these two species, so we consider *T. baregense* to be a synonym of *T. alpestre*.

Additional specimens examined—**AUSTRIA. Carinthia:** Loibel, 46º26'N, 14º16'E, *Fries s.n.* (UPS); Karawanken, Koschuta, 46º26'N, 14º25'E, 10 Aug. 1949, *Hepp s.n.* (M); Karawanken, Hochobir, 46º30'N, 14º29'E, 5 Aug. 1938, *Hepp s.n.* (M); 16 Aug. 1949, *Merxmüller* & *Wiedmann 5532* (M); Plöcken, am Gipfel des Polinigg, 46º37'N, 12º58'E, 13 Aug. 1949, *Merxmüller* & *Wiedmann 5549* (M); Gailtal, Karnische Alpen, auf steinigen Stellen im Sittmoosergruben bei Mauthen, 46º39'N, 12º57'E, 30 Aug. 1926, *Vierhapper s.n.* (WU); Gailtal, in Alpenmatten der Jauken bei Kötschach, 46º42'N, 13º5'E, 27 Aug. 1926, *Vierhapper s.n.* (WU). **Lower Austria:** under alpinen region des Göller bei St. Egid, 47º47'N, 15º29'E, 20 Jul. 1878, *Fehlner s.n.* (FI, GH, HBG, JE, K, L, MPU, P, US, WU); Nördliche Kalkhochalpen, Rax-Alpe, zwischen den Landesgrenze westl. des Biβkogels und dem Habsburg-Haus, 47º44'N, 15º42'E, 19 Jul. 2007, *Fischer* & *Fischer s.n.* (WU); Mt. Dürrenstein inter Landro et Prags, 47º47'N, 15º3'E, 2 Aug. 1870, *Huter s.n.* (GH, K); Schneeberg, Saugraben, 47º47'N, 15º47'E, 14 Jul. 1994, *Mrkvicka 1109* (WU); Raxalpe, ca. 500 m O vom Ottohaus am Jakobskogel, 47º43'N, 15º46'E, 24 Aug. 1959, *Podlech 5892* (M); in alpe Schneeberg, inter Baumgartner et Saugraben, 47º47'N, 15º47'E, 6 Jul. 1922, *Vestergren s.n.* (GB, S); Raxalpe, oberhalb vom Ottohaus, Beweideter Rasen in der Krummholzstufe, 47º43'N, 15º46'E, 25 Jul. 1956, *Wagenitz s.n.* (GOET). **Styria:** Wienerbruck bei Mariazell, Hintere Tormaner, 47º51'N, 15º18'E, 6 Jun. 1985, *Adler s.n.* (W); Kalbling, 47º33'N, 14º31'E, *Angeli s.n.* (K); Kalwang, am Zeiritzkampel, 47º29'N, 14º43'E, 8 Sep. 1897, *Correns s.n.* (M); Hochschwabgebiet, Tragöss, ober dem Grüner See, 47º32'N, 15º3'E, 22 Jun. 1950, *Eisenzopf s.n.* (H); St. Ilgener Thal am Hochschwab, Thalenge nach St. Ilgen, 47º34'N, 15º7'E, 16 Jul. 1903, *Handel-Mazzetti s.n.* (WU); Hochschwab, Bruck, Trockene Rasenhänge der Roten Wand bei Mixnitz, 47º19'N, 15º21'E, 26 Jul. 1952, *Merxmüller* & *Wiedmann 5546* (M); Weizklamm, 47º15'N, 15º34'E, 18 Jul. 1888, *Preissmann s.n.* (B, UPS); Wegscheid bei Mariazell, 47º46'N, 15º18'E, 8 Jul. 1885, *Preissmann s.n.* (WU); in valle Gesäuse, 47º35'N, 14º37'E, 28 Jun. 1889, *Richter s.n.* (WU); Trenchtling, 47º32'N, 15º0'E, 11 Jul. 1897, *Sartorius s.n.* (M); Kalbling, 47º33'N, 14º31'E, *Somerauer s.n.* (PR); Gesäuse, Hochtor, 47º33'N, 14º37'E, 15 Jul. 1903, *Vierhapper s.n.* (WU). **Tyrol:** Lienz, Kerschbaumer Alpe, 46º46'N, 12º46'E, Aug 1872, *Gander s.n.* (B, JE); 2 Aug. 1869, *Leresche s.n.* (L). **Upper Austria:** Haselgattern, Windischgarsten, 47º43'N, 14º19'E, 13 Jul. 1911, *Aust s.n.* (L); bei

Steyr, 48º2'N, 14º25'E, Aug. 1892, *Dürrnberger s.n.* (WU); Weyer, 47º51'N, 14º39'E, Aug. 1892, *Dürrnberger s.n.* (JE). **Vorarlberg:** Eisernes Tör bei Höhlenhain, 47º6'N, 9º48'E, 12 Aug. 1909, *Vierhapper s.n.* (WU). **FRANCE. Hautes-Pyrénées:** Cirque de Gavarnie, 42º41'N, 0º0'W, Aug. 1880, *Ball s.n.* (MO); Aug. 1868, *Bordère s.n.* (K, H, MO, MPU, NY, O, PR, WU); Aug. 1874, *Bordère s.n.* (GB, JE, NY, PR, RO, WU); 2 Jul. 1870, *Reuter s.n.* (NY); Héas valley, Pic de Gabiédou, 42º42'N, 0º5'E, Aug. 1864, *Bordère s.n.* (O); 11 Aug. 1874, *Bordère s.n.* (NY, WU); 27 Aug. 1876, *Bordère s.n.* (GB, M, WU); 17 Jul. 1865, *Miégeville s.n.* (P); Troumouse, 42º43'N, 0º6'E, Jul. 1878, *Bordère s.n.* (K); Aug. 1877, *Bordère s.n.* (WU); *Lagger s.n.* (WU); près de Baréges, 42º53'N, 0º3'E, 22 Aug. 1948, *Chouard s.n.* (G); Cauterets, abords du sentier qui monte au Péguère par la crète qui sépare le ravin de La Laoune de celui de la Glacière, 42º52'N, 0º7'W, 29 Jul. 1903, *Neyraut s.n.* (MPU); Cauterets, Mont Péguère, 42º52'N, 0º7'W, 18 Aug. 1905, *Neyraut s.n.* (H, JE, MPU, PR); Marboré, 42º41'N, 0º0'E, 27 Aug. 1856, *Zetterstedt s.n.* (GB). **Pyrénées Atlantiques:** base de la Tènèbre d´Isabe, près des Eaux-Chaudes, 42º56'N, 0º29'W, 19 Aug. 1909, *Barrère s.n.* (MPU); cerca de Castet, Macizo de Jaut, 43º4'N, 0º25'W, 4 Aug. 1980, *Vivant s.n.* (ARAN). **Pyrénées-Orientales:** Amelie-les-Bains, 42º28'N, 2º40'E, *Taylor s.n.* (BM). **ITALY. Friuli Venezia Giulia:** Udine prov., Forni Avoltri, 46º35'N, 12º46'E, Sep. 1857, *Ball s.n.* (GH). **Lombardy:** Brescia prov., Campione prope Lecco, 45º49'N, 10º10'E, 14 Aug. 1863, *Ball s.n.* (GH); Lecco prov., Alpe Campei, sur Moggio, 45º55'N, 9º29'E, 5 Aug. 1912, *Braum* (G); Bergamo prov., Bergamasker Alpen, Nordhänge des Pizzo Arera, 45º56'N, 9º48'E, 16 Aug. 1968, *Podlech* & *Lippert 15367* (M); Como prov., Mt. Campione du côté du Val Sassina, 45º59'N, 9º24'E, 14 Sep. 1892, *Saint-Lager s.n.* (G, L, NY). **Trentino-Alto Adige:** Mt. Dürrenstein, 46º38'N, 12º12'E, 29 Aug. 1896, *Bornmüller s.n.* (B, JE); Mt. Piano, 46º36'N, 12º14'E, 22 Aug 1896, *Bornmüller s.n.* (B); Mt. Cristallo, Val Fonda, 46º34'N, 12º11'E, 23 Aug. 1896, *Bornmüller s.n.* (B); Mt. Sarlkofel, 46º42'N, 12º11'E, 7 Sep. 1896, *Bornmüller s.n.* (B); North Wolkenstein, Regensburger Hütte, 46º35'N, 11º45'E, 23 Jul. 1991, *Dersch 4487* (GOET); Sextener Dolomiten, an Weg 100 NW unterhalb des Burgstalls, 46º36'N, 11º12'E, 24 Jul., *Dietrich 4176* (M); Pragser Dolomiten, bei Landro, 46º37'N, 12º13'E, 27 Jul. 1933, *Gross s.n.* (US); Fedaia Pass, Fassatal, 46º27'N, 11º52'E, 15 Jul. 1905, *Handel-Mazzetti s.n.* (WU); Sexten, Altler stein vallis Fischelein, 46º38'N, 12º21'E, 10 Aug. 1872, *Huter s.n.* (B, JE, K, M, MPU, P, RO, W, WU); Rotwandhütte, 46º25'N, 11º37'E, 30 Jul. 1963, *Raabe s.n.* (HBG); Mte. Tombea, 45º48'N, 10º37'E, 1913, *Wettstein s.n.* (M); Valle Gröden, 46º34'N, 11º40'E, 24 Aug. 1896, *Spencer s.n.* (L). **Veneto:** Mt. Baldo, 45º43'N, 10º49'E, 29 Aug. 1858, *Ball s.n.* (GH, US); prope Cortina d´Ampezzo, 46º32'N, 12º8'E, 5 Sep. 1860, *Ball s.n.* (F); Mt. Pelmo, 46º25'N, 12º8'E, 18 Sep. 1857, *Ball s.n.* (GH); Drei Zinnen (Tre Cime di Lavaredo), 46º37'N, 12º18'E, 14 Aug. 1963, *Raabe s.n.* (HBG); Mt. Pelmo, 46º25'N, 12º8'E, 24 Jul. 1895, *Saint-Lager s.n.* (G, L). **POLAND. Lesser Poland Voivodeship:** Zakopane, 49º17'N, 19º56'E, 23 Jul. 1929, *Nilsson s.n.* (JE); 10 Aug. 1888, *Freyn s.n.* (B, PR); Kosninarski Wierd [Kasprowy Wierch], 49º13'N, 19º58'E, 18 Aug. 1860, *Bisse s.n.* (JE); Hala Stoly, 49º13'N, 19º54'E, 27 Jul. 1978, *Frey s.n.* (L); Gladkie Uplazianskie, 49º14'N, 19º53'E, 4 Aug. 1931, *Pawlowska et al. s.n.* (GB, GH, K, S, UPS); Koscielisco, 49º17'N, 19º53'E, Jul. 1868, *Fritze s.n.* (B); Zakopane, Mt. Nosal, 49º16'N, 19º59'E, 12 Jul. 1914, *Sagorski s.n.* (JE). **ROMANIA. Arges:** Montibus Bîrsei, montis Piatra Craiului, 45º31'N, 25º12'E, 11 Jul. 1979, *Parascan s.n.* & *Danciu* (H); 3 Aug. 1979, *Parascan* & *Danciu s.n.* (M). **Bistriţa-Năsăud:** Rodna, Mt. Korongyis [Corongisul], 47º31'N, 24º47'E, 9 Aug. 1902, *Degen s.n.* (PR); 11 Aug. 1902, *Degen s.n.* (B, WU); Rodnaborberek [Rodnei Mt.], Saca, 47º28'N, 24º49'E, 1 Aug. 1909, *Vierhapper s.n.* (WU). **Braşov:** Gebirgsstock des Bucegiul (Bucegi Mts), bei Kronstadt, Bucsoiu, 45º27'N, 25º27'E, 18 Aug. 1910, *Ginzberger s.n.* (WU); Piatra mare, 45º33'N, 25º38'E, 12 Jul. 1895, *Sagorski s.n.* (JE); Bucses Nordhang, Malajester Tal [Malaiesti], 45º27'N, 25º27'E, 27 Jul. 1909, *Vierhapper s.n.* (WU). **Dâmboviţa:** Bucegi Mountains, Ţigăneşti Grat, 45º28'N, 25º25'E, 6 Aug. 1928, *Schwarz 621* (B, JE); Bucegi Mountains, Tiganester Grat, Malajestu Hütte, 45º27'N, 25º27'E, 8 Aug. 1928, *Schwarz s.n.* (B, JE). **Harghita:** Ciuc, Bicaz, 46º21'N, 25º48'E, 6 Jul. 1938, *Nyárády s.n.* (C, MW, O, P, RO); montis "Nagy Hagymás", ad pagum Balánbánya, 46º39'N, 25º48'E, 21 Jun. 1901, *Degen 120* (BM, GB, GH, JE, K, O, WU); Öcsem Teteje Mountain, 46º39'N, 25º48'E, Jul., *Schur s.n.* (W). **Maramureş:** Rodnaer-Alpen [Rodnei Mountains], Cisia, 47º35'N, 24º40'E, 27 Jul. 1903, *Ade s.n.* (M). **Neamt:** Masivul Ceahlău, 46º59'N, 25º56'E, 22 Jul. 1931, *Hayrén s.n.* (H); Ceahalu mountains, Cabana Dochia, 46º57'N, 25º57'E, 1961, *Heinrich s.n.* (JE); Aug. 1961, *Lange s.n.* (JE). **Prahova:** Montis Bucegi, Vale Jepilor, 45º24'N, 25º29'E, 26 Jul. 1959, *Ciocîrlan* & *Todor s.n.* (M). **SLOVAKIA. Košice:** Belianske Tatry, 49º14'N, 20º15'E, 15 Aug. 1968, *Beck 270* (B); Belianske Tatry, above Chata Protcz, 49º13'N, 20º16'E, 31 Jul. 1966, *Dahl* & *Hadac s.n.* (O); von Nesselblösse, Béla Höhlenhain, Bélaer Kalkalpen, 49º14'N, 20º15'E, 23 Jul. 1912, *Korb s.n.* (UPS); comit. Szepes, ad pagum Sztracena [Stratená], 48º52'N, 20º20'E, 10 Jul. 1932, *Lengyel s.n.* (M, S); 14 Jul. 1933, *Lengyel s.n.* (P). **Prešov:** Belianske Tatry, 49º14'N, 20º15'E, 15 Aug. 1968, *Beck 271* (B); Belianske Tatry, Mt. Stierberg, 49º14'N, 20º15'E, 12 Sep. 1905, *Degen s.n.* (G, GB); Belianske Tatry, Chata Protcz, 49º13'N, 20º16'E, 31 Jul. 1966, *Dhal* & *Hadac s.n.* (O); Drechselhäuschen [Belianske Tatry], 49º14'N, 20º15'E, 29 Aug. 1921, *Kionka s.n.* (UPS); Belanske Tatry, Tatranská Kol, 49º13'N, 20º19'E, 14 Jul. 1958, *Rothmaler s.n.* (JE). **Žilina:** Kvácsányi völgy, 49º11'N, 19º32'E, 9 Jun. 1908, *Degen s.n.* (C, GB); montis Velky Choc, prope oppidum Ruzomberok, 49º9'N, 19º20'E, 21 Jul. 1959, *Deyl et al. s.n.* (C, FI, M, MA, NY, P, PH); Suchý Vrch, ubar Turz-St. Martin, 49º10'N, 19º5'E, Jul. 1931, *Hruby s.n.* (H, O); Rozsutec, 49º13'N, 19º5'E, Jul. 1890, *Sagorski s.n.* (JE); Kralovan, 49º9'N, 19º7'E, Jul. 1890, *Sagorski s.n.* (JE); Mala Fatra, montis Rosutec, 49º13'N, 19º5'E, Jun. 1935, *Weber s.n.* (P). **SLOVENIA**. **Gorizia:** Tolmin, Kuk, 46º15'N, 13º45'E, 25 Jul. 1855, *Areschoug s.n.* (UPS). **SPAIN. Burgos:** Espinosa de los Monteros, Macizo de Castro Valnera (Montes de Pas), cabecera del circo de Bernacho, 43º9'N, 3º40'W, 3 Sep. 2013, *Barberá et al. 951PB* (MA); Espinosa de los Monteros, Macizo de Castro Valnera (Montes de Pas), escarpes de la Calleja Honda, 43º9'N, 3º40'W, 3 Sep. 2013, *Barberá et al. 953PB* (MA). **Cantabria:** Soba, Parque Natural de los Collados del Asón, canal entre Mota La Fuente y Monte Primera, 43º11'N, 3º38'W, 3 Sep. 2013, *Barberá et al. 957PB* (MA); Soba, Parque Natural de los Collados del Asón, Mota La Fuente, 43º11'N, 3º38'W, 3 Sep. 2013, *Barberá et al. 958PB* (MA). **Huesca:** Valle de Bujaruelo, Torla, barranco de Lapazosa, 42º42'N, 0º4'W, 16 Sep. 2013, *Barberá* & *Quintanar 1062PB* (MA); Vall de Pineta, sota el Coll d´Añisolo, 42º41'N, 0º3'E, 8 Aug. 1991, *Carrillo* & *Ninot s.n.* (BCN); Candanchú, Tortielle Alto, solana La Zapatilla, 42º47'N, 0º31'W, 12 Aug. 1965, *Montserrat 1339/65* (MA); Benasque, Valle de Astoí, 42º36'N, 0º31'E, 23 Jul. 1955, *Montserrat 761/55* (MA); Bal d´Ansó, Canaletas de Ruzkia, 42º45'N, 0º49'W, 28 Jul. 1993, *Soriano* & *Gomà s.n.* (BCN); Panticosa, Sierra de Tendenera, por debajo del ibon de los Asnos, 42º41'N, 0º16'W, 10 Aug. 1980, *Vivant s.n.* (ARAN). **Lérida:** Vall de Pineta, sota el Coll d´Añisolo, 42º40'N, 0º44'E, 18 Jul. 1997, *Carrillo s.n.* (BCN); Canaleta de Romero, Argia de Lin, Vielha e Mijaran, 42º30'N, 0º43'E, 18 Aug. 1998, *Carrillo s.n.* (BCN); Cap al Coth des Aranesi, Vielha e Mijaran, 42º30'N, 0º43'E, 18 Aug. 1998, *Ninot* & *Carreras s.n.* (BCN). **Navarra:** Isaba, Anielarra, 42º56'N, 0º44'W, 1 Aug. 1987, *Aizpuru* & *Catalán s.n.* (ARAN); Otsagabia, Cima del Orhy, 42º59'N, 1º0'W, 22 Jul. 1987, *Aizpuru* & *Catalán s.n.* (ARAN); Roncal, Anielarra, Puerto de Eraice, 42º56'N, 0º43'W, 19 Aug. 1969, *Montserrat 5690/69* (MA). **UKRAINE. Chernivtsi:** Putila distr., the ChyorniyDol Range, on rocks of Mt. Bolshoy Kamen, 47º59'N, 25º5'E, 20 Jul. 1961, *Artemchuk s.n.* (LE). **Ivano-Frankivsk:** Verkhovina distr., watershed between the Chyorniy Cheremosh and Beliy Cheremosh rivers, 33–36 km SSW of Verkhovina, 48º9'N, 24º47'E, 25 Jul. 1985, *Geltman et al. 2094I* (LE); Kosiv distr., the Chivchin Mountains, Mt. Mokrinskiy Kamen, 47º51'N, 24º42'E, 16 Sep. 1965, *Kharkevich s.n.* (LE). **Zakarpattia:** Rakhiv dist., Mt. Bliznitsya, 48º3'N, 24º12'E, 28 Jun. 1950, *Igoshina s.n.* (LE); Mt. Chyorna Gora, Petrosh, 48º7'N, 24º33'E, 21 Jul. 1946, *Petrov s.n.* (LE); Petros Mt., 48º7'N, 24º33'E, 25 Jul. 1961, *Slyusarenko s.n.* (LE); in dizione alpis Howerla, 48º9'N, 24º29'E, Jul. 1907, *Stockin s.n.* (G); Breskul, 48º9'N, 24º30'E, 1910, *Stockin s.n.* (P).

2. TRISETUM ALTAICUM Stephan ex Roshev., Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 3: 85. 1922.—TYPE: RUSSIA. Siberia, Altai, "Avena altaica Stephan herb. Fisher", probably *Mardovkin s.n.* (lectotype, designated here, LE!).

Trisetum flavescens var. *serotina* Ledeb., Fl. Altaic. 1: 91. 1829.—TYPE: Altai, near Riddersk, 27 Jul. 1826, *C.F. Ledebour s.n.* (lectotype, designated here, LE!).

Herb (15.9–)26.3–38.3(–67.3) cm high, slightly cespitose to cespitose, shortly rhizomatous, culm (0.3–)0.7–0.9(–1.2) mm diam., straight, glabrous; nodes (2–)3–4(–5), mostly concentrated in lower part of the culm, not included in the sheaths, glabrous, yellowish to blackish. Basal leaf-sheaths pubescent, with hairs (0.1–)0.5–0.7(–1.1) mm long also on the margins, sometimes decaying into fibers, yellowish to brownish; basal leaf-blades (1.6)2.3-4.7(13.2) cm × (1.7–)2.3–3.2(–4.5) mm, flat, slightly inrolled when dried, glabrous to sparsely pubescent adaxially and abaxially, with hairs (0.05–)0.1–1(–1.3) mm long also on the margins, yellowish to brownish, sometimes greenish; top culm leaf-sheaths (6–)8–10.3(–15.7) cm long, glabrous to pubescent, with hairs up to 1 mm long, margins ciliate; top culm leaf-blades (1.7–)3.5–7.4(–14.3) cm × (1.8–)2.5–3.3(–4.5) mm, flat, usually parallel to the culm, rarely arriving to the panicle, glabrous to puberulous abaxially and adaxially, with hairs (0.05–)0.1–1(–1.3) mm long on the margins, greenish to greyish, rarely brownish; inner collar region glabrous, with scattered hairs (0.2–)0.6–0.9(–1.2) mm long on the margins; ligules (1–)1.3–1.8(–2.8) mm long, irregularly laciniate or toothed, glabrous, usually with scattered hairs (0.1–)0.2–0.4(–0.8) mm long on the margins and upper part. Basal node of the panicle glabrous. Panicles (4.9–)6–8(–13.8) × (1.1–)1.5–2(–2.4) cm, narrowly oblong to elliptic in outline, sometimes lanceolate, somewhat dense; rachis internodes glabrous, usually with scattered hairs up to 0.2 mm long; longest basal branches (0.6–)0.9–1.7(–2.7) cm long. Spikelets (4.7–)5.2–6.1(–6.6) × (1.5–)1.9–2.3(–3) mm, 2(–3)-flowered; pedicels (1.4–)2.5–3.7(–5) mm long, glabrous, rarely with few scattered hairs up to 0.1 mm long. Glumes unequal [ratio lower glume length/upper glume length = (0.52–)0.7–0.8(–0.89)]; lower glume (2.4–)3.2–3.8(–4.7) × (0.8–)1.2–1.6 mm, broadly lanceolate to elliptic [ratio lower glume width/lower glume length = (0.3–)0.35–0.4(–0.53)], acuminate, sometimes acute or long acuminate, 1(–3)-nerved, glabrous, with scattered hairs up to 0.2 mm long on the upper part of the midrib, greenish surrounded by purplish; upper glume (3.9–)4.4–5(–6) × 1.7–2(–2.2) mm, broadly lanceolate to elliptic, sometimes oblong [ratio upper glume width/upper glume length = (0.36–)0.39–0.4(–0.49)], acute to acuminate, rarely long acuminate, 3-nerved, glabrous, with scattered hairs up to 0.15 mm long on the upper part of the midrib, greenish surrounded by purplish; rachilla segment between first and second floret (0.7–)1–1.2(–1.5) mm long, with hairs (0.7–)1–1.2(–1.5) mm long; rachilla segment to sterile floret (1.1–)1.4–1.8(–2.2) mm long, with hairs 0.4–0.9(–1.3) mm long. Lemmas (4–)4.4–5(–5.5) × (0.8–)1.2–1.6 mm, lanceolate or oblong, sometimes elliptic [ratio lemma width/lemma length = (0.27–)0.3–0.38(–0.4)], scabridulous, with very short hairs on the midrib, up to 0.1 mm long, greenish, surrounded by a purplish flush; apical teeth (0.1–)0.2–0.3(–0.5) mm long, with aristules (0.05–)0.3–0.4(–0.6) mm long; awn (3.8–)5.4–6.5(–7.2) mm long, inserted 2.3–2.8 mm from the base [ratio awn insertion from the base length/lemma length = 0.53–0.58(–0.67)], slightly or strongly curved at the base, rarely not curved, slightly twisted, with adpressed hairs up to 0.05 mm long; callus 0.2–0.3 mm long, elliptic to orbicular, with hairs 0.3–0.5(–0.6) mm long. Paleas (3.4–)3.7–4.3(–4.7) × (0.8–)1–1.2(–1.4) mm [ratio palea length/lemma length = (0.68–)0.8–0.9(–0.97)], elliptic to oblong, sometimes oblanceolate, margins with hairs on the upper part; teeth 0.1–0.2(–0.3) mm long, with short antrorse hairs. Lodicules (0.5–)0.7–0.8(–1.1) mm long, with 2 lobules of the same length, rarely laciniate. Anthers (0.8–)1–1.3 mm long. Ovary (0.4–)0.6–1.1(–2.7) mm long, glabrous, rarely with one hair up to 0.2 mm long on the upper part. Caryopsis (1.5–)1.9–2.5(–2.8) × (0.25–)0.4–0.5(–0.7) mm, narrowly elliptic to oblong. Figure 5.

Chromosome number—2*n* = 14 (Sokolovskaya & Probatova, 1975; Probatova & Sokolovskaya, 1980).

Phenology—Trisetum altaicum has been collected in flower and fruit from June to September.

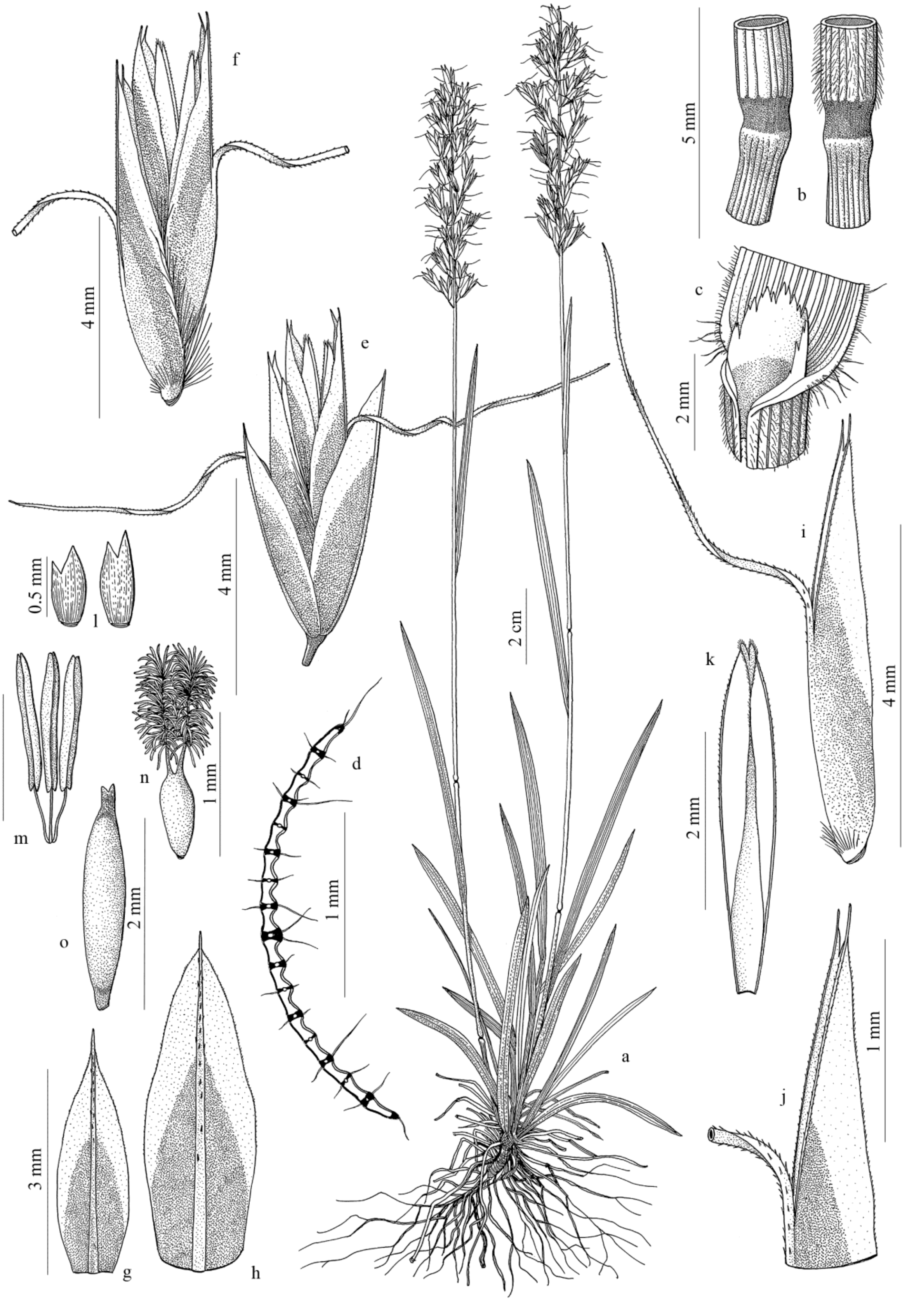

Figure 5. *Trisetum altaicum*. a. Habit. b. Portions of the culm internode and node. c. Portion of sheath, ligule, and portion of the blade. d. Transverse section of leaf-blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Lemma, upper part, lateral view. k. Palea, ventral view. l. Lodicules. m. Stamens.n. Pistil. o. Caryopsis. a, d based on *Albitskaia & Novoseltseba s.n.* (H-1168456); b-c, e-n based on *Kuznetsov & Iljin s.n.* (S); l based on *Igonnikov-Galitzky 465* (S); o based on *Maksimova s.n.* (B-10_0526146).

Distribution and Habitat—*Trisetum altaicum* is distributed in the Tian Shan Mountains (in eastern Kyrgyz Republic and Kazakhstan, and Xinjiang province in China), the Altai Mountains and along the mountains in northern Mongolia and adjacent Russia (eastern part in Zabaykalsky Krai and Buryatia Republic in Russia). This species occurs in alpine meadows and swales, rocky slopes and coniferous forests at 1520–3020 m. Figure 6.

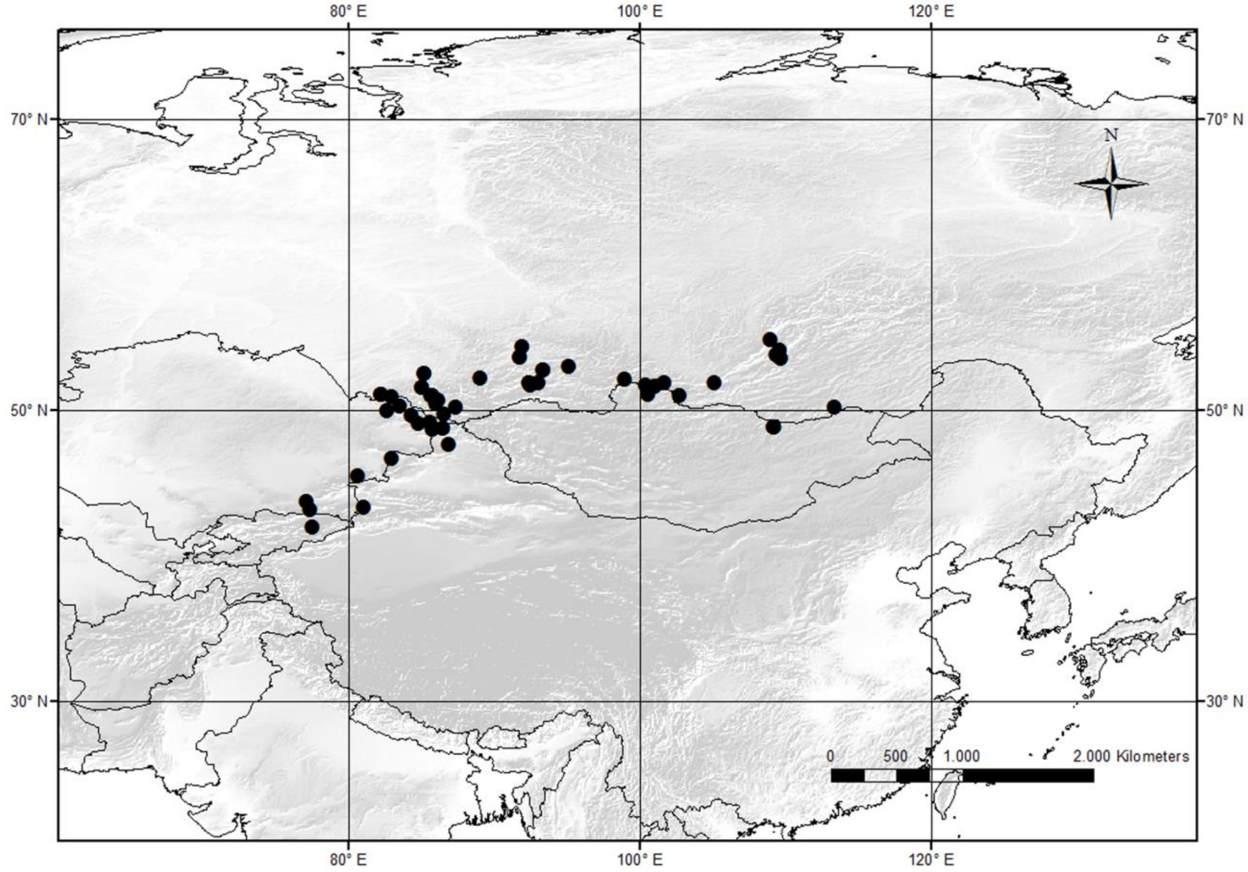

Figure 6. Distribution of *Trisetum altaicum* (dots).

Discussion—Enushchenko (2011: 59) did not follow the requirements of the Art. 7.10 of the ICN for lectotypification. Consequently, a lectotype is formally designated here for *Trisetum altaicum*. According to R. Ufimov and A. Grebenjuk (in litt.), the original collection was probably collected by Mardovkin, who was a Fisher´s collector. The choice of this type was made by R. Roshevitz with a label on the sheet, but it was never published.

Trisetum altaicum is the species of the section with the shortest anthers [(0.8–)1–1.35 mm]. It is also characterized by its cespitose habit, wider lower glumes [(0.8–)1.2–1.6 mm], usually purplish and narrower panicles, from narrowly oblong to elliptic in outline, and awns slightly or strongly curved at the base, rarely not curved.

Probatova (1979) placed *T. altaicum* in subsect. *Agrostidea*, together with *T. subalpestre* Neuman. These species share their cespitose habit, often spiciform panicles, and short callus hairs and anthers. Our unpublished molecular data showed that those species are not closely related, *T. subalpestre* alinging in the *T. spicatum* complex (Barberá et al., unpublished data).

Additional specimens examined—**CHINA. Xinjiang:** north of Tacheng, 46º44'N, 82º57'E, 13 Aug. 1957, *Kejian Gua 2930* (PE); Burqin region, 47º42'N, 86º51'E, 23 Jul. 1972, *[unknown] 2052* (HNWP). **KAZAKHSTAN. Almaty:** Talgarskoe gorge, 43º13'N, 77º17'E, 14 Jun. 1909, *Bogolyubov 343* (LE); Trans-Ili Alatau, gorge of the Malaya Almatinska river, 43º46'N, 77º7'E, 16 Jul. 1927, *Dubiansky* & *Basilevskaja s.n.* (LE); The Ketmenskiy range, upper reach of the Sumbe river, 43º20'N, 81º0'E, 12 Aug. 1931, *Rodin 1108-A* (LE); Lepsinsk uyezd, Tarbagatay range, the Say-asu pass, 45º31'N, 80º36'E, 21 Jun. 1915, *Sapozhnikov* & *Tripolitova s.n.* (LE). **East Kazahstan:** Ust-Kamenogorsk uyezd, a range along the Kuzgunda superior river, 49º58'N, 82º36'E, 2 Jul. 1908, *Sedelnikov s.n.* (LE); Narymskiy range, watershed between the basins of the Bukon and Kurchum rivers, pass from Dira to Terekta, 49º6'N, 84º48'E, 6 Aug. 1914, *Jakowleff 40* (LE); Ridder distr., 5 km south of Ridder, Noth slope of the Ivanovskiy range, 50º20'N, 83º30'E, 5 Aug. 1936, *Matveeva s.n.* (LE); Kaby, Chegan-Daba, Arasankaba, 48º48'N, 86º28'E, Aug. 1920, *Sapozhnikova s.n.* (G, LE); montium Narymensium, pr. pagum Katon-Karagaj, 49º10'N, 85º36'E, 6 Sep. 1930, *Smirnow 10* (JE, MW); Zyryan distr., Tatarskoe saddle, 49º43'N, 84º16'E, 15 Aug. 1936, *Temnoev 123* (LE). **KIRGIZSTAN. Issyk Kul:** The Terskey Alatau range, northern slope, the Chimundusay pass, 42º0'N, 77º30'E, 5 Jul. 1936, *Ovchinnikov* & *Usov 35* (LE). **MONGOLIA. Khentii:** Western Kentey Mountains, Kerulen and Onon rivers, Kentein-khan, 48º53'N, 109º10'E, 23 Jul. 1928, *Ikonnikov-Galitskiy* & *Ikonnikov-Galitskiy 465* (LE); western Kentey Mountains, Kerulen and Onon rivers, hill NNO from Kentein-khan, 48º53'N, 109º10'E, 24 Jul. 1928, *Ikonnikov-Galitskiy* & *Ikonnikov-Galitskiy 478* (LE); western Kentey Mountains, upper reach of the Kerulen river, NE of Kentein-khan golets, 48º53'N, 109º10'E, 26 Jul. 1928, *Ikonnikov-Galitskiy* & *Ikonnikov-Galitskiy 575* (LE); SE slope of Kentein-khan golets, 48º53'N, 109º10'E, 9 Aug. 1928, *Ikonnikov-Galitskiy* & *Ikonnikov-Galitskiy 922* (AAH, LE, NY). **Khövsgöl:** north slope above the saddle between summits of Mt. Sardyk, 51º45'N, 100º20'E, 30 Jul. 1926, *Kuvaev 165-2* (LE, MW); Khangay upland, eastern shore of Khovsgol lake, 51º6'N, 100º30'E, 14 Jul. 1924, *Neyburg s.n.* (LE). **RUSSIA. Altai Krai:** Zmeinogrosk uyezd, 51º9'N, 82º11'E, 15 Jun. 1909, *Ilyin s.n.* (L, LE); Biysk uyezd, Mt. Yantyg-Khat, a pass between the Ak-kaya and Ayryk rivers, 52º32'N, 85º12'E, 22 Jun 1915, *Krylov s.n.* (LE); Biysk uyezd, Katunskie belki, upper reach of the Katun river, 49º46'N, 86º31'E, 11 Jun 1911, *Nekrasowa s.n.* (LE); Biysk Okrug, Chernyiy Anuy, snowed summits Talitskie belki, 51º34'N, 85º0'E, 8 Aug. 1929, *Pobedimova 649* (LE). **Altai Republic:** Gorno-Altayskaya oblast, Onguday area, Mt. Sarlyk, 51º5'N, 85º42'E, 18 Aug. 1985, *Alanko et al. 53269* (H); Terektinskiy range, the Kostakhta river, 50º30'N, 86º0'E, 4 Jul. 1931, *Shishkin et al. s.n.* (LE, NY); Kosh-Agachsky rayon, 17 km SW of Chibit, pass from Baksara to Eshtykol valley, 50º14'N, 87º19'E, 28 Jul. 2008, *Serogin* & *Serogin S-443* (MW); Seminsky Pass, 51º1'N, 85º38'E, 26 Jul. 1996, *Sukopp et al. 1667* (NY); Zmeinogorsk uyezd, Valley of the Chernovaya river, 51º9'N, 82º11'E, 5 Aug. 1910, *Tomin 313* (LE). **Buryatia Republic:** Tunkinsky distr., near the selo of Mondy, bottom of the valley of the Khulugaysha river, 51º40'N, 100º59'E, 2 Aug. 1963, *Alyanskaya et al. s.n.* (LE); Lake Baykal, source of the Muzhinay river, 54º54'N, 108º54'E, Aug. 1967, *Egorova* & *Siplivinskiy s.n.* (AAH, GB, LE); Barguzin uyezd, basin of the Muya river, on top of the Kindikanskiy pass, 53º37'N, 109º38'E, 7 Aug. 1914, *Korotkiy et al. 849* (LE); eastern Sayan, the Pogranichniy range, the Tengisin-Daban, 52º10'N, 98º56'E, 19 Aug. 1959, *Malyshev* & *Pezhemskiy 56* (LE); Hangarulsky range, at the source of the Snezhnaya river, 51º5'N, 102º43'E, 20 Aug. 1912, *Smirnow 615* (LE); Lake Baikal, Chivyrskuy, upper reach of the Khozhalvyy river, 53º52'N, 109º17'E, 1 Aug. 1928, *Sukachev et al. 1652* (LE); Barguzin uyezd, mouth of the Kudalda river, 54º9'N, 109º33'E, 25 Jul. 1939, *Tyulina s.n.* (LE). **Irkutsk:** Lake Baykal, Kulkut, on the way up to Khamar-Daban, 51º55'N, 105º5'E, 14 Jul. 1915, *Tsinzerling s.n.* (LE). **Khakassia Republic:** Abakan river, Mt. Saman, 52º16'N, 88º59'E, 8 Aug. 1927, *Plotnikov s.n.* (PR). **Krasnoyarsk Krai:** Western Sayan, vicinity of the Olenya Rechka station, 52º48'N, 93º17'E, 21 Jul. 1964, *Khabarov* & *Chayka s.n.* (LE); Western Sayan, the Monysh range, 51º54'N, 92º23'E, 25 Jul. 1968, *Krasnoborov* & *Khanminchum 6812* (LE); Western Sayan, Sabinskiy range, at the upper reach of Sambyd river, 51º54'N, 92º23'E, 20 Aug. 1966, *Krasnoborov* & *Kuklina s.n.* (LE); Minusinsk distr., in alpibus Sajanensibus ad fl. Kazyr super, 53º42'N, 91º41'E, 12 Aug. 1913, *Kusnezow* & *Iljyn s.n.* (K, LE, MO, MW, PR, S); basin of the Sydy, the Sisma and the Many rivers (tributaries of Enisey), 54º22'N, 91º51'E, 30 Jul. 1908, *Volkov 397* (LE). **Tuva Republic:** western slope of the Akademika Obrucheva range, basin of the Tapsa river, upper reach of its right tributary the Kara-Khem river, 53º2'N, 95º4'E, 10 Jul. 1974, *Krasnoborov* &

Khanminchun 749 (LE); Western Sayan, Uyukskiy range, upper reach of the Orto-Khem river, eastern part of the Mt. Bedelig, 51º47’N, 92º26’E, 18 Jul. 1974, *Lomosonova 2590* (LE); Western Sayan, Kurtushibinskiy range, interfluve of the Khem and Ozhu rivers, 51º55’N, 93º0’E, 11 Jul. 1979, *Shaulo* & *Belskaya 1520* (LE). **Zabaykalsky Krai:** Khentey-Chikoyskoe upland, the Borshchovochniy range, 51º43’N, 111º58’E, 5 Aug. 1967, *Maksimova s.n.* (AAH, B, G, K, LE, M, S); Aksha uyezd, basin of the Onon river, near the source of the Balidzhi river, 50º16’N, 113º17’E, 1 Aug. 1913, *Smirnow 1433* (LE).

3. TRISETUM BERTOLONII Jonsell, Bot. J. Linn. Soc. 76(4): 320. 1978. *Avena villosa* Bertol., Exc. Re Bot.: 6. 1820 [Opusc. Sci. 4: 222. 1820, n.v.]. *Trisetum villosum* (Bertol.) Schult., Mant. 2: 368. 1824, nom. illeg., non Pers., 1805. *Trisetaria villosa* (Bertol.) Banfi & Soldano in Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 386. 1996.—TYPE: ITALY. Teramo prov., Monte Corno, Arapietra, 42º29’N 13º34’E, 1818, *A. Orsini s.n.* [lectotype, designated by Jonsell (1978: 320), BOLO (image!)].

Trisetum villosum var. *glaberrimum* Ces., Comp. Fl. Ital. 1(3): 64. 1869. *T. villosum* subsp. *glaberrimum* (Ces.) Arcang., Comp. Fl. Ital.: 779. 1882.—TYPE: ITALY. Chiarino, *G. Gussone s.n.* (no original material found).

Herb (16.5–)17.7–27.8(–38) cm high, cespitose, shortly rhizomatous, culm 0.4–07 mm diam., straight, sometimes curved at the upper part, pubescent, with hairs 0.2–0.8 mm long; nodes 2–3(–4), mostly concentrated in lower part of the culm, not included in the sheaths, glabrous, brownish. Basal leaf-sheaths glabrous to pubescent, with hairs 0.1–0.3 mm long, decaying into fibers, yellowish; basal leaf-blades (2–)4.2–7.8(–12) cm × 1.2–1.5(–2) mm, inrolled, glabrous abaxially and pubescent adaxially, with hairs up to 0.2 mm long, also on the margins, greyish to greenish; top culm leaf-sheaths (3.6–)5.3–8.5(–11) cm long, glabrous, without cilia on the margins; top culm leaf-blades (1–)2.5–3.8(–6.2) cm × 1.4–2(–2.4) mm, conduplicate or flat, with margins inrolled, parallel to the culm, pubescent abaxially, glabrous adaxially, with scattered hairs on the margins, with hairs (0.05–)0.2–0.4 mm long, greenish; inner collar region glabrous; ligules 0.5–1.3 mm long, slightly irregularly dentate, glabrous. Basal node of the panicle glabrous to pubescent, with hairs up to 0.5 mm long. Panicles (3.5–)4.6–7.4(–8) × 1.6–3 cm, narrowly elliptic, sometimes ovate to broadly lanceolate in outline, rather lax; rachis internodes pubescent, rarely sparsely puberulous, with hairs up to 0.5 mm long; longest basal branches (0.7–)0.9–1.6(–1.7) cm long. Spikelets 7–9 × 2.5–4(–5) mm, 2–3-flowered; pedicels 3.7–4.7(–8.4) mm long, pubescent, sometimes very sparsely pubescent, with hairs up to 0.2 mm long. Glumes unequal (ratio lower glume length/upper glume length = (0.53–)0.63–0.7); lower glume (3.8–)4.6–5.3(–6) × (0.4–)0.6–1 mm, narrowly lanceolate, rarely linear [ratio lower glume width/lower glume length = (0.11–)0.14–0.17(–0.2)], long acuminate to acuminate, 1-nerved, glabrous, usually with scattered hairs up to 0.1 mm on the upper part of the central nerve, greenish margins hyaline, rarely surrounded by purplish; upper glume 6.8–8(–9) × 1.4–2(–2.4) mm, broadly lanceolate to oblong or elliptic, rarely narrowly lanceolate [ratio upper glume width/upper glume length = (0.19–)0.22–0.28(–0.3)], acuminate to long acuminate, 3-nerved, glabrous, sometimes with scattered hairs up to 0.1 mm on the upper part of the midrib, greenish, sometimes yellowish, with hyaline margins; rachilla segment between first and second floret 1–1.8 mm long, with hairs (0.8–)1.3–2.2(–2.8) mm long; rachilla segment to sterile floret 1.4–2(–2.3) mm long, with hairs 1–1.5 mm long. Lemmas (5.7–)6–8(–10) × (0.4–)0.6–1 mm, oblong to narrowly lanceolate [ratio lemma width/lemma length = 0.13–0.23(–0.3)], glabrous, sometimes scabridulous, yellowish or greenish, with hyaline margins, sometimes surrounded by a purplish flush; apical teeth 0.3–0.5(–0.8) mm long, with aristules 1.2–2.3(–4) mm long; awn (11–)11.5–16(–17) mm long, inserted 2.8–4 mm from the base [ratio awn insertion from the base length/lemma length = (0.56–)0.6–0.68(–0.75)], straight or slightly curved at the middle, twisted, with short adpressed hairs up to 0.05 mm long; callus 0.2–0.3 mm long, elliptic, rarely orbicular, with hairs 1.5–2.2(–2.6) mm long. Paleas (3.2–)3.8–5.2 × 0.8–1.2 mm [ratio palea length/lemma length = (0.4–)0.58–0.67(–0.7)], oblong to oblanceolate, margins glabrous or with scattered hairs; teeth 0.2–0.4(–0.6) mm long, with short antrorse hairs. Lodicules 0.4–0.7(–0.8) mm long, with 2 lobules of the same length, rarely with 3 not deep ones. Anthers (1.4–)2.2–2.3(–2.6) mm long. Ovary 0.5–0.9(–1.1) mm long, glabrous. Caryopsis c. 3.2 × 0.9 mm, oblong. Figure 7.

Chromosome number—$2n = 14$ (Favarger, 1973).

Additional illustrations—Chrtek & Jirásek (1963: 577, fig. 3, 3, sub *Trisetum villosum*); Chrtek (1967c: 176, tab. I, 2; 178, tab. II, 3–4, sub *Trisetum villosum*); Fiori & Paoletii (1895: 27, 231 sub *Trisetum villosum*).

Phenology—Trisetum bertolonii has been collected in flower and fruit from May to August.

Distribution and Habitat—This species is endemic to the Apennines. It is found in limestone rocks on mountain cliffs at 170–1630 m. Figure 4.

Discussion—Trisetum bertolonii is easily differentiated from the rest of species of the section by its habit, with long and convolute leaves or with margins inrolled, and a combination of different characters of the spikelets. This species has the longest callus hairs [1.5–2.2(–2.6) mm], upper glumes [6.8–8(–9) mm], and awns [(11–)11.5–16(–17) mm], which are straight or slightly curved at the middle, and lemmas with hyaline margins.

Chrtek (1967c) considered *T. bertolonii* to be closely related to *T. griseovirens*, from the High Atlas Mountains in Morocco, because of their similar habits, shape and anatomy of the leaves, and awn length. Later, Jonsell (1978) agreed that *T. bertolonii* is close to, but not conspecific with *T. griseovirens*. We consider *T. griseovirens* to be a subspecies of *T. flavescens*. The material studied of both species shows some similarities in habit, and other characters of the spikelets, which are more pronunciated in *T. bertolonii*. *Trisetum bertolonii* and *T. flavescens* subsp. *griseovirens* have narrow leaves (convolute or filiform and inrolled, respectively), longer aristules [1.2–2.3(–4) mm, and (0.9–)1–1.4(–1.8) mm, respectively], longer awns, and a more marked difference between the palea and the lemma length [ratio palea length/lemma length = (0.4–)0.58–0.67(–0.7), and (0.53–)0.65–0.76(–0.77), respectively]. However, both taxa are easy to differenciate, because *T. bertolonii* has longer callus hairs

Figure 7. *Trisetum bertolonii*. a. Habit. b. Portion of the culm internode and node. c. Portion of sheath, ligule, and portion of the blade. d. Transverse section of leaf-blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Lemma, upper part, lateral view. k. Palea, lateral view. l. Lodicules. m. Stamens.n. Pistil. o. Caryopsis. a, l based on *Bertoloni s.n.* (P-03365075); b-c, e-k, m-n based on *Merxmüller & Wiedmann 19570* (M-0223256); d, l based on *Navarro et al. CN4234* (MA-699433); o based on *Orsini s.n.* (P-02320457).

[1.5–2.2(–2.6) mm, and 0.4–0.5(–0.7) mm, respectively] and straight or slightly curved awns, whereas *T. flavescens* subsp. *griseovirens* has geniculate ones. Additionally, our molecular data (Barberá et al., unpublished) show that both taxa are not closely related. Thus, we do not agree with Jonsell (1978) who states that *T. bertolonii* and *T. griseovirens* may constitute an isolated pair of species with an interesting phytogeographical disjunction.

Due to the long aristules of *T. bertolonii*, the aristules were not taken into account for calculating the ratio of the awn insertion from the base length/lemma length.

Additional specimens examined—**ITALY. Acoli Piceno:** Monte Vettore, 42º49’N, 13º16’E, 21 Jul. 1886, *Orsini 863* (L); Monte Volubrio, 42º55’N, 13º16’E, 1847, *Bertoloni s.n.* (P); Furca del Cristo sub monte Vettore, 42º49’N, 13º16’E, 6 Jul. 1856, *Caruel s.n.* (K); Monte della Sibilla, 42º54’N, 13º15’E, 1843, *Marzialetti s.n.* (FI); Monte Vettore, 42º49’N, 13º16’E, Jul. 1856, *Rostan s.n.* (BM). **L´Aquila:** Gran Sasso, Campo Imperatore, Observatory, 42º26’N, 13º33’E, 3 Aug. 1960, *Segelberg s.n.* (GB, S). **Macerata:** in montibus di Camerino, 43º8’N, 13º4’E, 1831, *Bertoloni s.n.* (B). **Pesaro-Urbino:** Gola die Furlo an der Via Flaminia, zw. Fossombrone und Acqualagna, 43º38’N, 12º42’E, 16 May 1964, *Merxmüller* & *Wiedmann 18/64* (M). **Pescara:** Vado di Sole, 42º23’N, 13º47’E, 2 Jul. 2002, *Navarro* & *al. 4234* (MA). **Teramo:** Monte dei Fiori, 42º46’N, 13º35’E, *[unknown] s.n.* (H); Monte Corno, 42º28’N, 13º33’E, *Orsini s.n.* (FI, P); 1833, *Orsini s.n.* (P); Monte Corno ad Arapietra, 42º29’N, 13º34’E, *Orsini s.n.* (FI).

4. TRISETUM FLAVESCENS (L.) P. Beauv., Ess. Agrostogr. 88. 1812. *Avena flavescens* L., Sp. Pl.: 80. 1753. *Trisetaria flavescens* (L.) Baumg., Enum. Stirp. Transsilv. 3: 263. 1816. *Avena flavescens* var. *pratensis* Neilr., Fl. Nied.-Oesterr.: 56. 1859, nom. illeg. *Avenastrum flavescens* (L.) Jess., Deutschl. Gräser: 215. 1863. *Trisetum pratense* Pers., Syn. Pl. 1: 97. 1805, nom. illeg. *Trisetum flavescens* subsp. *pratense* Asch. & Graebn., Syn. Mitteleur. Fl. 2: 265. 1899.—TYPE: Herb. A. van Royen Nº 913. 7-458 [lectotype, designated by Cope in Cafferty et al. (2000: 247), L-221378 image!].

Herb (20.2–)30.9–58.1(–141.5) cm high, not to slightly cespitose or cespitose, rhizomatous or with stoloniferous rhizome, culm (0.3–)0.6–0.8(–1.2) mm diam., straight, glabrous, rarely sparsely pubescent, with hairs 0.1–0.5 mm long; nodes (3–)4–5(–7), separated along the culm, not included in the sheaths, glabrous, yellowish to brownish. Basal leaf-sheaths sparsely pubescent to pubescent, rarely glabrous, with hairs (0.1–)0.4–1(–1.7) mm long, decaying into fibers, yellowish to brownish, sometimes greenish; basal leaf-blades (1.4–)3.9–7(–18) cm × (0.6–)1.5–2.7(–5.6) mm, flat, sometimes convolute, rarely filiform, inrolled when dried, from glabrous to pubescent abaxially, pubescent, rarely glabrous adaxially, with hairs (0.05–)0.1–0.8(–1) mm long, usually with cilia, brownish to yellowish, sometimes greenish or greyish; top culm leaf-sheaths (4.5–)7.5–11(–20) cm long, glabrous, rarely pubescent, rarely with cilia, usually with hyaline margins; top culm leaf-blades (1.3–)4–9(–14.5) cm × (1–)1.8–3.4(–6) mm, from flat to convolute or filiform, rarely parallel to the culm, glabrous to pubescent abaxially, pubescent to densely pubescent adaxially, rarely glabrous, with hairs (0.05–)0.2–1(–1.5) mm long, sometimes with cilia, greenish to greyish; inner collar region glabrous, rarely with scattered hairs or sparsely pubescent, with hairs 0.05–1 mm long; ligules (0.5–)0.7–1.2(–2) mm long, irregularly dentate to laciniate, rarely entire, glabrous, sometimes with adpressed hairs on the surface, glabrous or with hairs (0.05–)0.2–0.4(–0.6) mm long on the upper part. Basal node of the panicle glabrous, rarely sparsely puberulous, with hairs 0.05–0.2 mm long. Panicles (3.5–)6–10.5(–16.2) × (0.9–)1.5–2.8(–5) cm, narrowly elliptic or elliptic to narrowly lanceolate or lanceolate in outline, rarely oblong or ovate, lax to somewhat dense; rachis internodes glabrous to sparsely pubescent, mostly on the upper part and branches, rarely pubescent, with hairs up to 0.2(–0.3) mm long; longest basal branches (0.5–)1.1–2.1(–4) cm long. Spikelets (3.8–)5.2–6.3(–7.7) × (0.8–)1.8–3(–3.8) mm, 2–3(4)-flowered; pedicels (1.5–)2.6–3.7(–5) mm long, sparsely pubescent, sometimes glabrous or pubescent, with hairs 0.05–0.1(–0.3) mm long. Glumes unequal [ratio lower glume length/upper glume length = (0.54–)0.6–0.7(–0.78)]; lower glume (2–)3–3.7(–4.6) × (0.4–)0.6–0.7(–1.1) mm, narrowly lanceolate, sometimes broadly lanceolate [ratio lower glume width/lower glume length = (0.1–)0.17–0.22(–0.37)], acuminate, sometimes long acuminate, rarely acute, 1(3)-nerved, glabrous, usually with short hairs from the center to the upper part of the main nerve, up to 0.1 mm long, greenish, rarely purplish or brownish, with hyaline margins; upper glume (3.2–)4.6–5.3(–7.4) × (1.1–)1.5–1.8(–2.2) mm, elliptic, usually oblong or broadly lanceolate, sometimes slightly oblanceolate [ratio upper glume width/upper glume length = (0.25–)0.3–0.36(–0.47)], acuminate to long acuminate, 3-nerved, glabrous, usually with short hairs from the center to the upper part of the central nerve, with hairs up to 0.1 mm long, greenish, rarely purplish, usually with hyaline margins; rachilla segment between first and second floret (0.6–)0.8–1.1(–1.3) mm long, with hairs (0.2–)0.6–1.1(–2.1) mm long; rachilla segment to sterile floret (0.7–)1–1.2(–1.5) mm long, with hairs (0.2–)0.4–0.7(–1.2) mm long. Lemmas (3.2–)4.4–5.4(–7.4) × (0.4–)0.6–0.7(–1.1) mm, narrowly to broadly lanceolate, sometimes oblong or elliptic, rarely oblanceolate [ratio lemma width/lemma length = (0.19–)0.23–0.3(–0.43)], glabrous to scabridulous, with short hairs up to 0.1 mm long on the upper part and along the midrib, greenish to yellowish on the central part, sometimes with purplish; apical teeth (0–)0.2–0.3(–0.6) mm long, with aristules (0.1–)0.4–0.7(–1.8) mm long; awn (4.2–)5.7–7.2(–10.6) mm long, inserted (1.5–)2.4–3.3(–4) from the base [ratio awn insertion from the base length/lemma length = (0.45–)0.54–0.59(–0.67)], geniculate to slightly geniculate, more or less twisted at the base, rarely not twisted, with hairs up to 0.05 mm long; callus (0.1–)0.2 mm long, orbicular, sometimes rounded or elliptic, with hairs (0.1–)0.2–0.4(–0.7) mm long. Paleas (2.2–)3.4–4.2(–5.5) × (0.6–)0.8–1(–1.3) mm [ratio palea length/lemma length = (0.53–)0.72–0.82(–0.95)], elliptic to narrowly elliptic, sometimes slightly oblanceolate, margins with hairs on the upper part, sometimes glabrous; teeth (0.05–)0.2–0.3(–0.6) mm long, with short antrorse hairs mostly on the upper part, rarely glabrous. Lodicules (0.3–)0.4–0.6(–0.9) mm long, with (1)2–3 teeth or lobules of equal or different depth, sometimes entire. Anthers (1–)1.7–2.2(–3) mm long. Ovary (0.3–)0.4–0.7(–1.1) mm long, glabrous. Caryopsis (2.3–)2.4–2.9(–3.7) × 0.3–0.5 mm, narrowly elliptic, sometimes linear.

Key to the subspecies of Trisetum flavescens

1. Lemma (3.2–)4.3–5.1(–7.4) mm long; aristules (0.1–)0.4–0.6(–1.4) mm long; awn (4.2–)5.6–7(–8.3) mm long.. ***T. flavescens*** subsp. ***flavescens***

1. Lemma 6–6.2(–6.4) mm long; aristules (0.9–)1–1.4(–1.8) mm long; awn (8–)8.2–9(–10.6) mm long...... .... ***T. flavescens*** subsp. ***griseovirens***

a. subsp. FLAVESCENS

Avena purpurascens DC., Cat. Pl. Horti Monsp.: 82. 1813. *Trisetum flavescens* subsp. *purpurascens* (DC.) Arcang., Comp. Fl. Ital.: 779. 1882. *Trisetum flavescens* f. *purpurascens* (DC.) Borza, Consp. Fl. Rom. 1: 24. 1947. *Trisetaria flavescens* subsp. *purpurascens* (DC.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 383. 1996.—TYPE: FRANCE. Savoie, Cenis Mt., 45º15’N 6º54’E, 1809, *J. L. Bonjean s.n.* (lectotype, designated here, G-DC-00418509 image!).

Trisetum splendens C. Presl, Cyper. Gramin. Sicul.: 30. 1820. *Avena splendens* (C. Presl) Guss., Fl. Sic. Prodr. 1: 126. 1827. *Trisetum flavescens* subsp. *splendens* (C. Presl) Arcangeli, Comp. Fl. Ital.: 779. 1882. *Trisetum flavescens* var. *splendens* (C. Presl) Parl., Fl. Ital. 1: 261. 1848. *Trisetaria flavescens* subsp. *splendens* (C. Presl) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 383. 1996.—TYPE: ITALY. Sicily, San Martino, 37º59’N, 15º9’E, Jun. 1817, *C. Presl s.n.* (lectotype, designated here, PRC-450870 image!; possible isolectotypes, PRC-450868 image!, W-1889-0242136!).

Trisetum flavescens var. *biflorum* Gray, Nat. Arr. Brit. Pl. 2: 129. 1821.—TYPE: GREAT BRITAIN. *S.F. Gray s.n.* (no original material found).

Avena flavescens var. *variegata* Gaudin ex Mert. & Koch in Röhl., Deutschl. Fl. 1, ed. 3: 562. 1823. *Trisetum flavescens* var. *alpinum* Parl., Fl. Ital. 1: 261. 1850, nom. illeg. *Trisetum flavescens* var. *variegatum* (Gaudin ex Mert. & Koch) Schur, Enum. Pl. Transsilv.: 758. 1866. *Trisetum flavescens* [b] *variegatum* (Gaudin ex Mert. & Koch) Asch. & Graebn., Syn. Mitteleur. Fl. 2: 266. 1899. *Trisetum flavescens* f. *variegatum* (Gaudin ex Mert. & Koch) Beetle, Phytologia 38(3): 176. 1978.—TYPE: SWITZERLAND. *J.F. Gaudin s.n.* (lectotype, designated here, L-1346419!).

Avena flavescens var. *major* Spenn., Fl. Friburg. 1: 108. 1825.—TYPE: GERMANY. Friburg, *F.C.L. Spenner s.n.* (FB?) (no original material found)

Avena flavescens var. *capillacea* Gaudin, Fl. Helv. 1: 337. 1828. *Trisetum flavescens* var. *capillaceum* (Gaudin) Ducommun, Taschenb. Schweiz. Bot.: 857. 1869.—TYPE: SWITZERLAND. Vaud, Châteaux d´Oex, Jun. and Jul., *J.F. Gaudin s.n.* (no original material found).

Avena flavescens var. *maior* Gaudin, Fl. Helv. 1: 337. 1828, nom. illeg., non Spenn. 1825. *Trisetum flavescens* var. *latifolium* Schur, Enum. Pl. Transsilv.: 758. 1866, nom. illeg.—TYPE: SWITZERLAND. *J.F. Gaudin s.n.* (no original material found).

Avena flavescens var. *lutescens* Rchb., Fl. Germ. Excurs. 1: 51. 1830. *Trisetum flavescens* f. *lutescens* (Rchb.) Buia & Morariu, Fl. Republ. Social. Român. 12: 292. 1972. *Trisetum flavescens* subvar. *lutescens* (Rchb.) Maire, Cat. Maroc.: 48. 1931.—TYPE: Lectotype, designated here, Rchb., Icon. Fl. Germ. Helv. 1, Tab. XCIX, fig. 1695. 1834.

Trisetum burnoufii Req. ex Parl., Fl. Ital. 1: 263. 1850. *Avena burnoufii* (Req. ex Parl.) Nyman, Syll. Fl. Eur.: 413. 1855. *Trisetum flavescens* var. *burnoufii* (Req. ex Parl.) Hack in Briq., Prodr. Fl. Corse 1: 104. 1910. *Trisetum flavescens* subsp. *burnoufii* (Req. ex Parl.) P. Fourn., Quatre Fl. France, ed. 2: 60. 1946. *Trisetaria burnoufii* (Req. ex Parl.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 382. 1996.—TYPE: FRANCE. Corse, Haute-Corse, Corte, 42º18’N, 9º8’E, 7 Oct. 1847, *E. Requien s.n.* (lectotype, designated by Signorini & Ricceri [1996: 215], FI not seen; isolectotypes, G-00100184!, P-03365150!).

Avena candollei M. Serres, Bull. Soc. Bot. France 4: 440. 1857. *Trisetum candollei* (M. Serres) Verlot, Cat. Pl. Vasc. Dauphiné: 365. 1872.—TYPE: FRANCE. Hautes-Alpes, Gap, 44º34’N 6º5’E, *B. Blanc s.n.* (no original material found).

Trisetum flavescens var. *glabratum* Asch., Fl. Brandenburg 1: 830. 1864.—TYPE: GERMANY. Brandenburg, *[unknown collector]* (no original material found).

Trisetum flavescens var. *biflorum* Schur, Enum. Pl. Transsilv.: 757. 1866, nom. illeg., non Gray, 1821.—TYPE: ROMANIA. Kronstadt [Braşov], *P.J.F. Schur s.n.* (no original material found).

Trisetum flavescens var. *triflorum* Schur, Enum. Pl. Transsilv.: 758. 1866.—TYPE: ROMANIA. Sibiu [Hermannstadt], 45º48’N 24º9’E, Jun. 1852, *P.J.F. Schur s.n.* (lectotype, designated here, LW-213271 image!).

Avena flavescens var. *depauperata* Mert. & W.D.J. Koch, Deutschl. Fl., ed. 3, 1: 563. 1823. *Trisetum flavescens* var. *depauperata* (Mert. & W.D.J. Koch) Uechtr., Fl. Schlesien: 512. 1881.—TYPE: GERMANY. Alps, *F.K. Mertens & W.D.J. Koch s.n.* (LE?) (no original material found).

Trisetum bungei Boiss., Fl. Orient. 5: 535. 1884.—TYPE: IRAN. Golestan, Ziarat, 36º41’N, 54º31’E, 13 May 1858, *A.A.v. Bunge 68* (lectotype, designated here, P-03644568!; isolectotypes, B not seen, K image!).

Trisetum pratense var. *villosum* Čelak., Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1887: 180. 1887. *Trisetum flavescens* var. *villosum* (Čelak.) Fiek, Jahresber. Schles. Ges. Vaterl. Cult. 67: 167. 1889.—TYPE: CZECH REPUBLIC. Ptáčkovna, Písek, 49º19’N 14º10’E, *H. Ciboch s.n.* (no original material found).

Trisetum flavescens var. *nodosum* Chabert, Bull. Soc. Bot. France 36: 31. 1889.—TYPE: ALGERIA. Nador supra Medeah, 36º15’N 2º45’E, 1871-1875, *A.C. Chabert s.n.* (FI?) (no original material found).

Trisetum flavescens var. *tenue* Hack. ex Formánek, Verh. Naturf. Vereins Brünn 35: 155. 1897. *Trisetum tenue* (Hack.) Chrtek, Acta Univ. Carol., Biol. 1971: 228. 1973, nom. illeg., non Roem. & Schult., 1817. *Trisetum tenuiforme* Jonsell, Bot. J. Linn. Soc. 76: 320. 1978. *Trisetum flavescens* subsp.

tenue (Hack. ex Formánek) Strid, Mount. Fl. Greece 2: 808. 1991. *Trisetaria tenuiformis* (Jonsell) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 385. 1996.—TYPE: GREECE. Thessalia, Agrapha, Monoster Korona, 39º08'N, 21º38'E, 1 Aug. 1896, *E. Formánek s.n.* (lectotype, designated by Jonsell [1978: 320], W-1916-0031810!).

Trisetum flavescens var. *serbicum* Velen., Fl. Bulg., Suppl. 1: 295. 1898. *Trisetum flavescens subsp. serbicum* (Velen.) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(2): 312. 1933.—TYPE: SERBIA. Vranja, 42º33'N 21º54'E, 1898, *L.L. Adamović s.n.* (lectotype, designated here, PRC-451825 image!).

Trisetum flavescens var. *ponticum* Velen., Fl. Bulg., Suppl. 1: 295. 1898.—TYPE: BULGARIA. Burgas, 42º30'N 27º28'E, 1893, *S. Jablonowsky s.n.* (lectotype, designated here, PRC-451827 image!).

Avena flavescens f. *major* Hausskn., Mitth. Thüring. Bot. Vereins 13: 42. 1899, nom. illeg., non Spenn., 1825.—TYPE: GREECE. Thessaly, Pharsalus, 39º17'N, 22º23'E, Jun. 1885, *C. Haussknecht s.n.* (lectotype, designated here, JE–18858!).

Avena flavescens var. *pindica* Hausskn, Mitth. Thüring. Bot. Vereins 13: 43. 1899.—TYPE: GREECE. Monte Karava, 39º18'N, 21º33'E, Jul. 1885, *C. Haussknecht s.n.* (lectotype, designated here, JE-00018850!; isolectotype, JE-00018851!).

Trisetum corsicum Rouy, Rev. Bot. Syst. Géogr. Bot. 1: 139. 1904. *Trisetum flavescens* var. *corsicum* (Rouy) Briq., Prodr. Fl. Corse 1: 103. 1910. *Trisetum flavescens* subsp. *corsicum* (Rouy) Cif. & Giacom., Nomencl. Fl. Ital., 1: 30. 1950.—TYPE: FRANCE. Corse, Corte, 42º18'N 09º09'E, Jul. 1898, *J. Foucaud 924* [lectotype, designated by Signorini & Ricceri (1996: 216), LY not seen; isolectotypes, G-00100185!, P-319106!, P-2217837!, P-2221569!].

Trisetum flavescens var. *paczoskii* Zapał., Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math. 3: 167. 1904.—TYPE: Tatra Mts., *[collector unknown]* (KRAM?) (no original material found).

Trisetum flavescens f. *scabriusculum* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 107. 1904.—TYPE: UKRAINE. Dublyani, *J.K. Paczoski s.n.* (KRAM?) (no original material found).

Trisetum flavescens f. *subpilosum* Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 107. 1904.—TYPE: POLAND. Lesser Poland Voivodeship, Wola Batorska, 50º03'N 20º15'E, *J. Krupa s.n.* (KRAM?) (no original material found).

Trisetum flavescens var. *barcinonensis* Sennen, Bull. Géogr. Bot. 23: 50. 1913.—TYPE: SPAIN. Barcelona prov., Tibidabo Mountains, Santa Cruz de Olorde, 41º25'N 2º06'E, Jun. 1911, *F. Sennen 1238* (lectotype, designated here, MA-7940!; isolectotypes, B-10_0470051!, BCN-82824!, DAO-000465368 image!, JE-00021246!, JE-00021247!, JE-00021248!, JE-00021249!, FR-0036078 image!, MPU!, NY!, SEV-6701!, W-19120005494 image!, W-19230017014 image!, W-20080017999 image!, WU!).

Trisetum handelii Vierh., Oesterr. Bot. Z. 73: 128. 1924.—TYPE: ITALY. Veneto, Ampezzo, 46º25'N 12º47'E, 1905–1907, *F.K.M. Vierhapper s.n.* (lectotype, designated here, WU-0073386 image!; choice made by W. Till).

Trisetum macratherum Maire & Trab., Bull. Soc. Hist. Nat. Afrique N. 23: 218. 1932. *Trisetum flavescens* var. *macratherum* (Maire & Trab.) Maire & Weiller, Fl. Afrique N. 2: 247. 1953. *Trisetum flavescens* subsp. *macratherum* (Maire & Trab.) Dobignard, J. Bot. Soc. Bot. France 28: 44. 2004.—TYPE: ALGERIA. Near Oran, 35º41'N, 0º37'W, *L.C. Trabut s.n.* (lectotype, designated here, MPU-3029!).

Trisetum flavescens var. *clausonii* Maire, Bull. Soc. Hist. Nat. Afrique N. 23: 219. 1932.—TYPE: ALGERIA. Djelfa prov., Kef Roumia, 34º23'N 3º10'E, 30 May 1855, *Th. Clauson s.n.* (lectotype, designated here, MPU-3030!; isolectotype, P-83440!).

Trisetum flavescens var. *africanum* H. Lindb., Acta Soc. Sci. Fenn., Ser. B, Opera Biol. 1(2): 25. 1932. *Trisetum flavescens* subsp. *africanum* (H. Lindb.) Dobignard, J. Bot. Soc. Bot. France 28: 44. 2004.—TYPE: MOROCCO. Marrakesh-Safi, Amizmiz, 31º13'N 8º13'W, 24 May 1926, *H. Lindberg 2719* [lectotype, designated by Väre (2012: 89), H-1168497!; isolectotype, CAI-000243 image!, H-1168500!].

Trisetum flavescens f. *hirticulmis* H. Lindb., Acta Soc. Sci. Fenn., Ser. B, Opera Biol. 1(2): 25. 1932.—TYPE: MOROCCO. Marrakesh-Safi, Asni, Reraïa river valley, 31º10'N 7º54'W, 2 Jun. 1926, *H. Lindberg 3483* [lectotype, designated by Väre (2012: 89), H-1168498!].

Trisetum flavescens subsp. *tatricum* Chrtek, Čas. Nár. Mus., Odd. Přír. 35(2): 81. 1966.—TYPE: SLOVAKIA. Belanské Tatry, Bujaci, 49º13'N 20º16'E, 15 Aug. 1933, *K. Domin s.n.* (holotype, PRC-454454 image!).

Trisetum flavescens subsp. *parvispiculatum* Tzvelev, Spisok Rast. Gerb. Fl. S.S.S.R. Bot. Inst. Vsesojuzn. Akad. Nauk 18: 6. 1970. *Trisetum parvispiculatum* (Tzvelev) Prob., Bot. Zhurn. (Moscow & Leningrad) 60: 674. 1975.—TYPE: RUSSIA. Dagestan Republic, Makhachkala, Tarkitau Mountain, 42º56'N 47º27'E, 17 May 1953, *J.I. Prokhanov 407* (holotype, LE!).

Herb (20.2–)36.4–63.1(–141.50) cm high. Basal leaf-blades (1.5–)4.2–7(–18) cm × (0.6–)1.5–2.8(–5.6) mm, flat, sometimes convolute, inrolled when dried. Top culm leaf-blades (1.6–)4.9–9.2(–14.5) cm × (1–)2–3.5(–6) mm, from flat to convolute, rarely filiform or paralele to the culm. Panicles (3.6–)6.9–10.6(–16.2) × (0.9–)1.6–2.9(–5) cm. Spikelets (3.8–)5–6.1(–7.6) mm. Lemmas (3.2–)4.3–5.1(–7.4) mm long; aristules (0.1–)0.3–0.6(–1.4) mm long; awn (4.2–)5.6–7(–8.3) mm long. Ratio palea length/lemma length (0.66–)0.73–0.83(–0.95). Anthers (1–)1.6–2.1(–2.5) mm long. Figure 8a, 9a, 10a, and 11a.

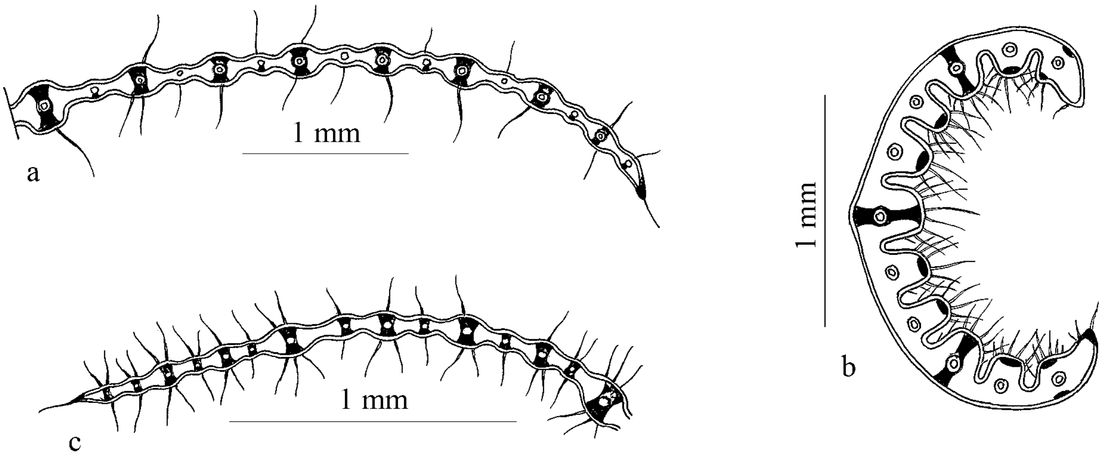

Figure 8. Transverse section of leaf-blade. a. *Trisetum flavescens* subsp. *flavescens*. b. *T. flavescens* subsp. *griseovirens*. c. *T. fuscum*. (a based on *Aedo et al. 8571* (MA-700192); b based on *Jury et al. 8847* (MA-391300); c based on *Rechinger s.n.* (S).

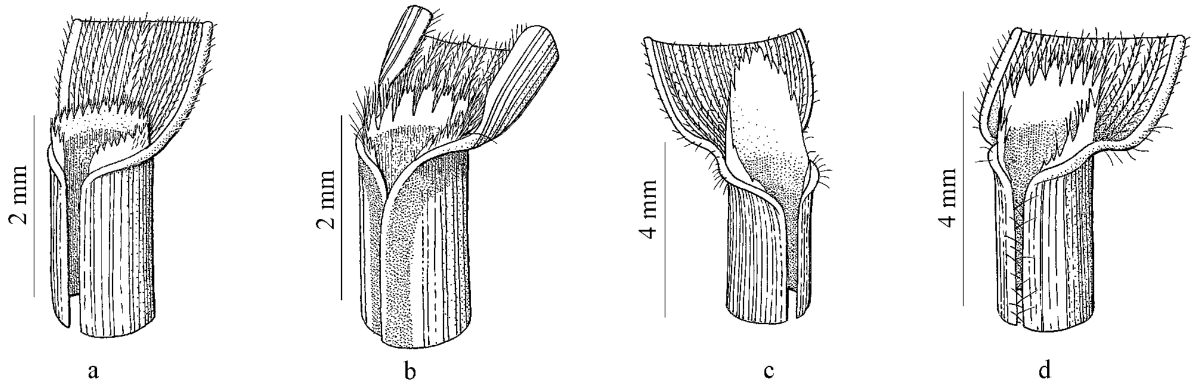

Figure 9. Portion of sheath, ligule, and blade. a. *Trisetum flavescens* subsp. *flavescens*. b. *T. flavescens* subsp. *griseovirens*. c. *T. fuscum*. d. *T. laconicum*. (a based on *Döring & Holtz s.n.* (GOET); b based on *Cabezas et al. FJC419* (MA-746349); c based on *Nyárády s.n.* (L-1346389); d based on *Orphanides 2890*, B-10_0508993).

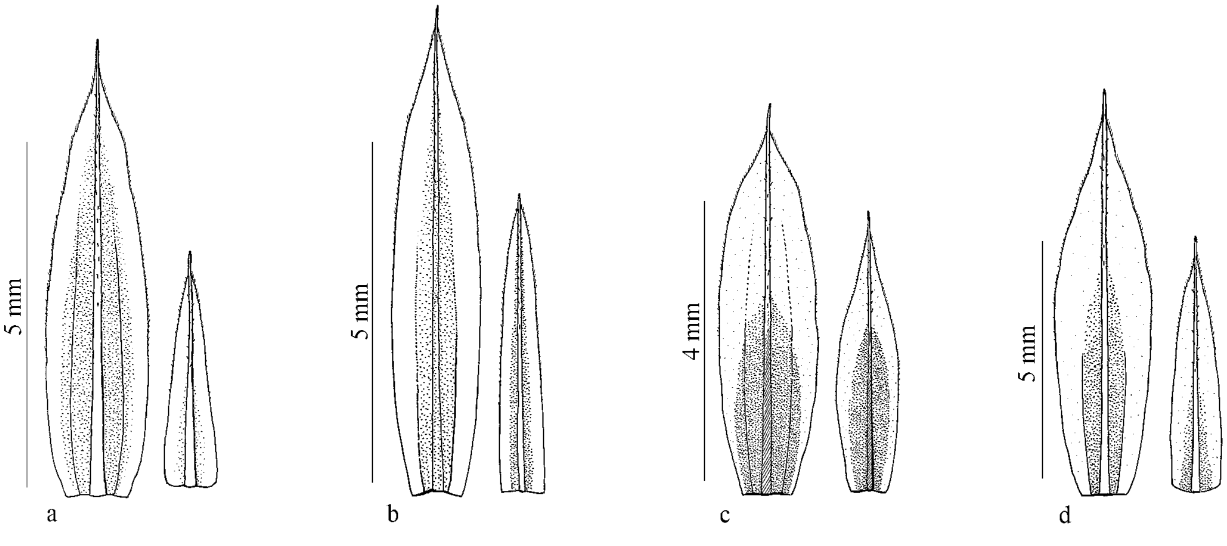

Figure 10. Upper and lower glume, dorsal view. a. *Trisetum flavescens* subsp. *flavescens*. b. *T. flavescens* subsp. *griseovirens*. c. *T. fuscum*. d. *T. laconicum*. (a based on *Barberá & Quintanar 897PB* (MA-871565); b based on *Cabezas et al. FJC419* (MA-746349); c based on *Nyárády s.n.* (L-1346389); d based on *Orphanides 2890* (B-10_0508993).

Chromosome numbers—2*n* = 12 (Sokolovskaya & Probatova, 1975), 24 (Frey, 1992), 28 (Sorokin, 1990), 36 (Strid & Andersson, 1985).

Additional illustrations—Fiori & Paoletii (1895: 28, 234 sub *Trisetum burnoufii*, 235 sub *T. flavescens*); Chrtek & Jirásek (1963: 577, fig. 3, 4); Sãvulescu (1972: 289, Planşa 56, 2a-c); Frey (1992: 453, fig. 6); Signorini & Ricceri (1996: 219, fig. 1, sub *Trisetum corsicum*); Gabrielian (2010: 176, tab. 44, 1, 1a).

Phenology— Trisetum flavescens subsp. *flavescens* has been collected in flower and fruit from May to October.

Distribution and Habitat—*Trisetum flavescens* subsp. *flavescens* is widespread throughout Europe, extending to western Asia, and northern Africa, and it has been introduced in many other temperate zones of Asia, North and South America and also New Zealand; on meadows, forest clearings, among shrubs or on stony places, growing from the sea level to 2900 m. Figure 12.

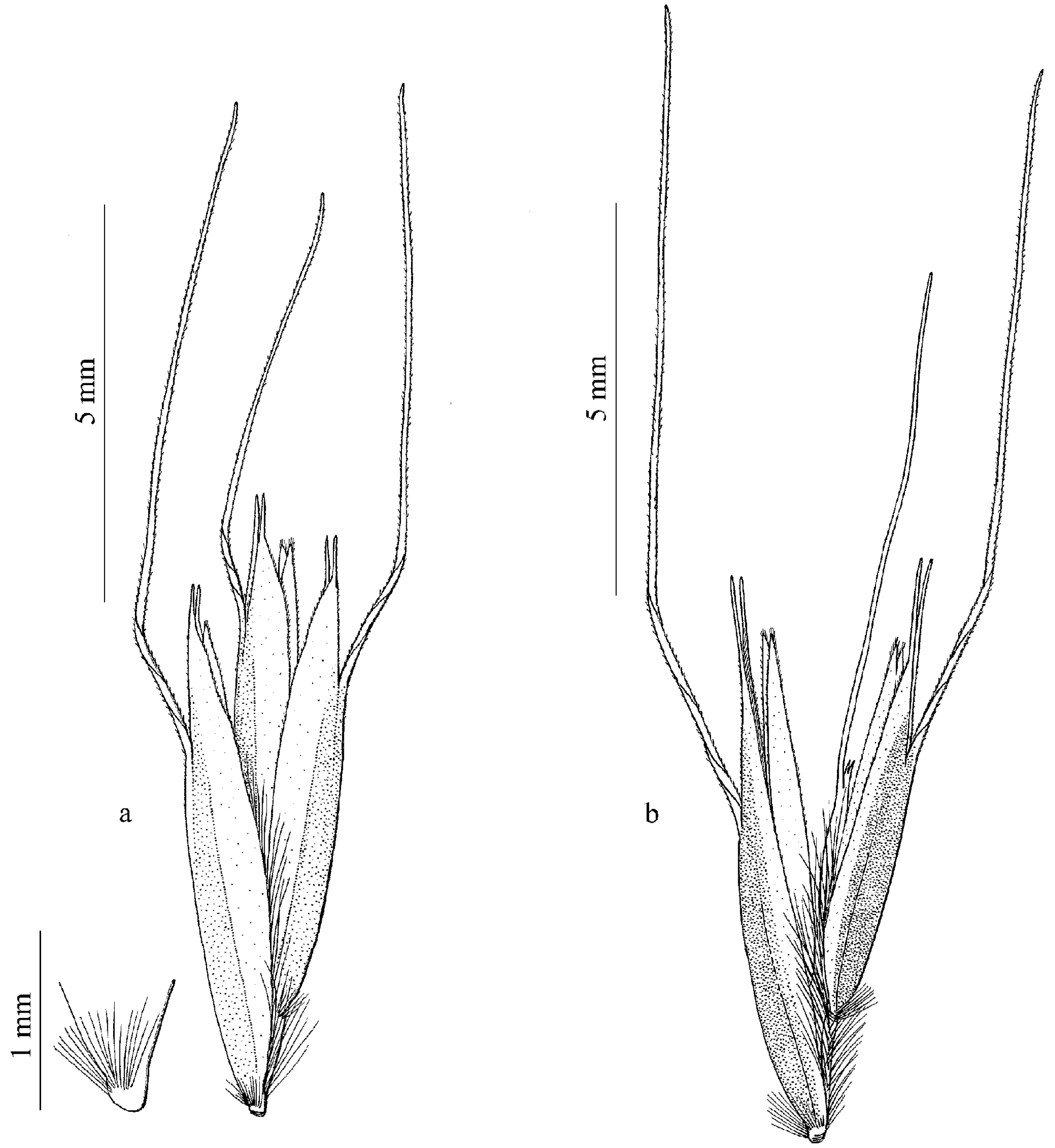

Figure 11. Florets. a. *Trisetum flavescens* subsp. *flavescens*. b. *T. flavescens* subsp. *griseovirens*. (a based on *Barberá & Quintanar 897PB* (MA-871565); b based on *Cabezas et al. FJC419* (MA-746349).

Discussion—Trisetum flavescens is one of the most polymorphic and widespread taxa of the genus. The morphology and hairiness of leaves, as well as the shape and color of the panicles, are highly variable. This species is characterized as having short ligules [(0.5–)0.7–1.2(–2) mm] and short callus hairs [(0.1–)0.2–0.4(–0.7) mm], narrow lower glumes [(0.4–)0.6–0.7(–1.1) mm], and always geniculate awns and glabrous ovaries. Barberá et al. (2017b) pointed out that it has been frequently confused with *T. sibiricum,* which belongs to *T.* sect. *Sibirica*.

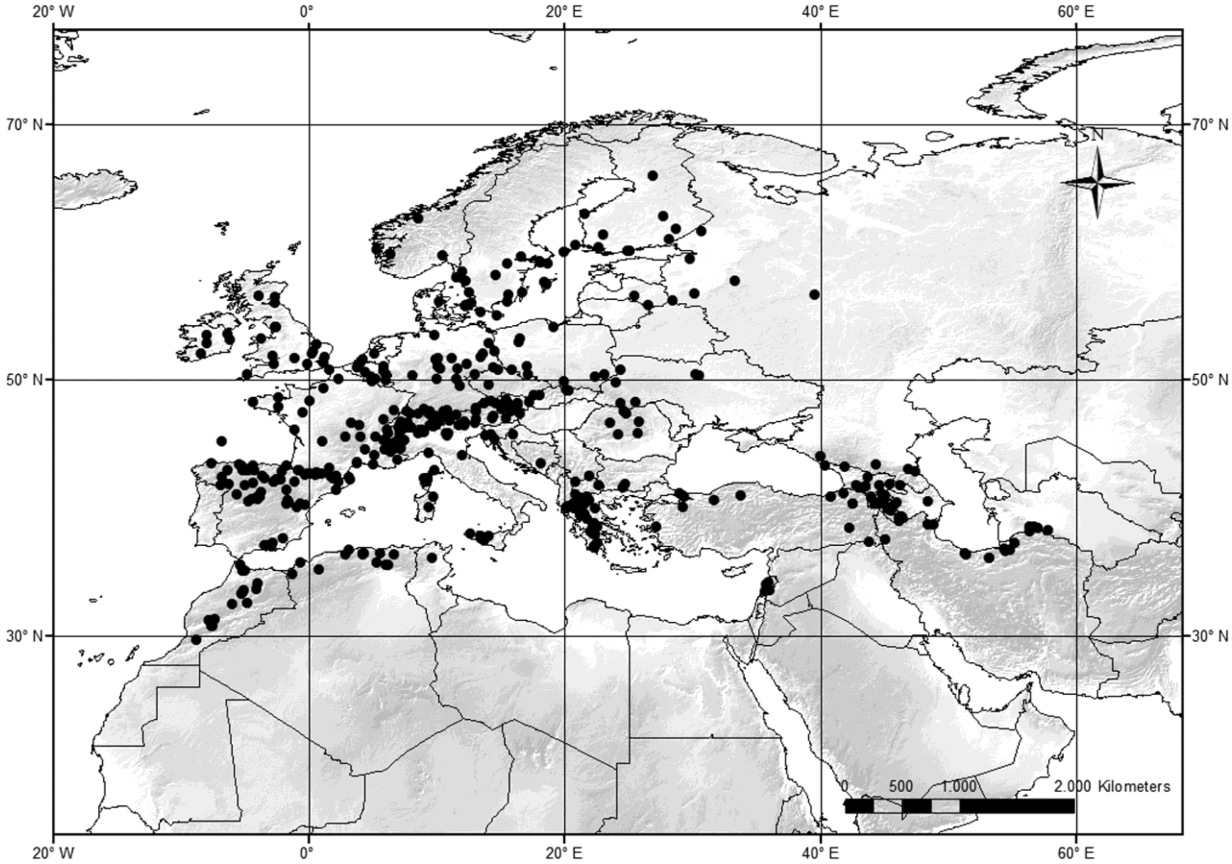

Figure 12. Distribution of *Trisetum flavescens* subsp. *flavescens* (dots) in Eurasia and North Africa.

Due to the polymorphism of *T. flavescens*, many subspecies and varieties have been described by different authors to classify its morphogical variation. Presl (1820) described *T. splendens,* with flat leaves and contracted golden panicle, which was later reduced to the rank of subspecies by Arcangeli (1882); this was also accepted as such by many authors (Jonsell, 1980; Pignatti, 1982; Signorini & Ricceri, 1996). In the same way, *T. purpurascens*, with wider leaves, slightly longer ligules, and dense purplish spikelets, was described by de Candolle (1813) from the Alps and then reduced to subspecies by Arcangeli (1882) and at that rank accepted by Jonsell (1980), Frey (1992) [sub var. *purpurascens*], and Tison & Foucault (2014). Strid & Tan (1991) indicated that the differences between *T. flavescens* subsp. *splendens* and *T. flavescens* subsp. *flavescens* are rather obscure. Chrtek (1966) described *T. flavescens* subsp. *tatricum* the specimens from the Carpathian Mountains, but these are hardly distinguishable from *T. flavescens* subsp. *purpurascens*. Three additional species have been described because of their more or less pubescent and convolute leaves and the culm hairiness, namely *T. tenuiforme*, *T. burnouffi*, and *T. corsicum*. *Trisetum burnouffi* and *T. corsicum* are endemic to Corsica, the second one with intermediate characters between *T. burnouffi* and *T. flavescens*. Signorini & Ricceri (1996) studied these species, including *T. splendens,* and accepted all these taxa at the species rank. Later, Jeanmonod & Gamisans (2007) recognized *T. corsicum* as a subspecies of *T. flavescens*, and *T. burnouffi* as a variety of this subspecies. Apart from these taxa from the Mediterranean region and Europe, other taxa were described from Africa and Asia. Tzvelev (1970) published *T. flavescens* subsp. *parvispiculatum*, with small spikelets and lemmas, from the Caucasus and mountain ranges of Iran and Turkmenistan. The detailed study of the morphology of the specimens belonging to this taxon indicates that these supposed diagnostic characters are not exclusive to them, and that they occur indiscriminately also in other specimens of Europe and the Mediterranean region.

Maire & Trabut (Maire, 1932) and Lindberg (1932) described other species and varieties from North Africa, namely *T. macratherum*, *T. flavescens* var. *africanum*, and *T. griseovirens*. Chrtek (1967c) considered that *T. griseovirens* was the only one well-characterized, mainly by the characters of the spikelet (length of spikelet, lemma, and awn). However, Dobignard (2004) treated these three taxa as subspecies, making clear that he did so only to reflect intraspecific variability of *T. flavescens* and awaiting a more rigorous taxonomic revision in the future.

As has already been commented, the leaf-blade traits of *T. flavescens* and its associated taxa are highly variable, much more than the characters of the spikelets and, therefore, we recommend giving them a secondary diagnostic value. Consequently, we decided to synonymize all these taxa with more labile foliar morphology, and to maintain only two subspecies in *Trisetum flavescens*, *T. flavescens* subsp. *griseovirens* and the typical subspecies.

Vegetative propagation by pseudoviviparism has been appreciated in a specimen of *T. flavescens* subsp. *flavescens* collected by *de Wilde s.n.* (L-1346507) (Fig. 13). Until now, this type of propagation has been observed only in *T. rigidum* (M. Bieb.) Roem. & Schult., *T. tamonanteae* Marrero Rodr. & S. Scholz, and *T. velutinum* Boiss., all belonging to *T.* sect. *Acrospelion* (Marrero & Scholz, 2013; Barberá et al., 2017a).

Additional specimens examined—**ALBANIA. Gjirokastër:** Mali Lunxheris, N-Hänge, 40º4’N, 20º8’E, 13 Jul. 1980, *Krendl s.n.* (C); Nemerçka, über Permet, südwestlich vom Qafa e Dhembelit, 40º12’N, 20º20’E, 12 Jul. 1959, *Meyer s.n.* (JE). **Korçë:** near Ersekë, 40º20’N, 20º40’E, 29 Jun. 1933, *Alston* & *Sandwith 1994* (K). **Vlorë:** Mali i Gjer (Mali Gjinezh), Delvina, zwischen Qafa Gradishtit und Qafa Piloit, 40º0’N, 20º5’E, 26 Jun. 1959, *Meyer s.n.* (JE). **ALGERIA. Algiers:** à Maison Carrée, près d´Alger, 36º43’N, 3º8’E, 31 May 1930, *Faurel s.n.* (P). **Batna:** Pic des Cédres, 35º33’N, 6º2’E, 6 Jul. 1935, *Faurel s.n.* (P). **Blida:** à Chrea, 36º25’N, 2º52’E, 5 Jul. 1930, *Faurel s.n.* (P). **Bouïra:** environs de Tala Rana, versant meridional du Lalla Khelidja, 36º25’N, 4º13’E, 30 Jun. 1875, *Duhamel s.n.* (G). **Constantine:** Djebel Cougour près de Batna, 35º33’N, 6º10’E, 22 May 1899, *Cosson s.n.* (L). **Oran:** pente sud du Djebel-Santo, 35º44’N, 0º43’W, 11 Jun. 1852, *Balansa s.n.* (L). **Sétif:** Massif de Bou-Talef, près de Charène, 35º45’N, 5º19’E, 21 May 1937, *Faurel s.n.* (P). **Tiaret:** Massif de Bélezma, de Bocdem, 35º13’N, 0º45’E, 16 Jun. 1937, *Faurel s.n.* (P). **Tizi Ouzou:** Grande Kabylie, Nationalpark Djurdjura, bei Tala Guilef, 36º27’N, 4º13’E, 30 Jun. 1983, *Scholz* & *Baillargeon s.n.* (B). **Tlemcen:** au-dessus de Tlemcen, 34º52’N, 1º18’W, 19 Jun. 1856, *Bourgeau s.n.* (UPS). **ANDORRA:** pr. Soldeu, 42º34’N, 1º40’E, 29 Aug. 2002, *Aedo et al. 8571* (MA). **ARMENIA. Aragatsotn:** monte

Figure 13. *Trisetum flavescens* subsp. *flavescens*. Specimen with proliferating spikelets based on *de Wilde s.n.* (L-1346507).

Aragat, Ghazaravan, carretera de subida al lago Kari, 40º23’N, 44º15’E, 30 Jun. 2005, *Medina et al. 2606* (MA); Ashtarak distr., in declivibus montis Arailer, in vicinitate pagi Egvart, 40º24’N, 44º28’E, 15 Jul. 1975, *Vasak s.n.* (B, G). **Gegharkunik:** pr. Sevan, 40º35’N, 44º57’E, 19 Jun. 2005, *Aedo et al. 11722* (MA); Vardenis distr., montis Vardenisskij Khrebet, in declivibus montis Kungukh-tar, 40º10’N, 45º43’E, 29 Jul. 1975, *Vasak s.n.* (B, G, MA, NY). **Kotayk:** pr. Tsahkadzor village, Tehenis mountain, 40º32’N, 44º41’E, 22 Jun. 2005, *Castroviejo et al. 17687* (MA). **Lori:** Akhtala, above village Ghochkan (Tchotchkan), 41º11’N, 44º49’E, 24 Jun. 2009, *Vitek et al. 09-1870* (B). **Shirak:** Akhuryan distr., Shirak range, N of the Dzhadzhur pass, 40º51’N, 43º59’E, 23 Jun. 1960, *Tsvelev* & *Cherepanov 215* (LE). **Syunik:** Meghri distr., on a slope to a right tributary of the Mergiget river, near Vardanadzor, 38º58’N, 46º12’E, 29 Jun. 1956, *Egorova et al. 1512* (LE); Pirdaudan, 39º15’N, 46º8’E, 23 Jun. 1893, *Lipskiy s.n.* (LE). **Tavush:** Haghartsin monastery, 40º49’N, 44º53’E, 21 Jun. 2005, *Castroviejo et al. 17555* (MA). **Vayots Dzor:** pr. Ger-Ger, 39º47’N, 45º32’E, 24 Jun. 2005, *Herrero et al. 2841* (MA). **AUSTRIA. Carinthia:** Mauthen im Gailthal, 46º39’N, 12º59’E, 22 Jun. 1934, *Ronninger s.n.* (NY). **Lower Austria:** St. Poelten, 48º12’N, 15º38’E, Jun. 1879, *Hackel s.n.* (B, PR); Gloggnitz, 47º40’N, 15º56’E, 28 Jun. 1861, *Halácsy s.n.* (WU); Semmering ad stationem in prato, 47º38’N, 15º49’E, 29 Jun. 1922, *Vestergren s.n.* (NY, S). **Salzburg:** Gaisberg, 47º48’N, 13º6’E, 22 May 1922, *Pettersson s.n.* (H). **Styria:** in ruderatis prope urbem Graz, 47º4’N, 15º27’E, Jun. 1808, *Fritsch s.n.* (H, L, MA, O, WU). **Tyrol:** Obergurgl, 46º52’N, 11º1’E, 3 Aug. 1992, *Emanuelsson 1319* (S); im Paznauntal bei Galtür am Eingang des Jamtales, 46º58’N, 10º11’E, 27 Jul. 1978, *Holtz 03.892* (GOET). **Upper Austria:** circa Aistersheim, 48º11’N, 13º44’E, Jun. 1875, *Keck s.n.* (B, F, G, GOET, H, MO, MW, NY, WU); Lichtenberg, N v. Ort bei Kaiserberg 5, 48º22’N, 14º15’E, 18 Jun. 1995, *Kleesadl 178* (W, WU). **Vienna:** Neuwaldegg, 48º14’N, 16º17’E, 27 Jul. 1921, *Fiedler s.n.* (B). **Voralberg:** Illufer unter Feldkirch, 47º13’N, 9º36’E, 3 Aug. 1869, *Boetz s.n.* (W). **AZERBAIJAN. Daglig-Shirvan:** road Shemakha-Aksu, 40º34’N, 48º24’E, 1 Jun. 1949, *Beydeman s.n.* (LE). **Ganja-Qazakh:** Dashkasan distr., Khachbulag, 40º28’N, 46º0’E, 16 Jul. 1970, *Lyatifova 24* (LE). **Lankaran:** a pass between Lerik and the village of Bozuchar, 38º46’N, 48º24’E, 3 Jul. 1931, *Shipchinskiy 565* (LE). **BELGIUM. East Flanders:** Gent, "Snepkaai", 51º3’N, 3º43’E, 14 Jun. 1957, *Michiels s.n.* (C). **Liège:** Ardennen, tussen Eupen en Baraque Michel, 50º31’N, 6º3’E, Jun. 1950, *Borssum Waalkes 5114* (L). **Limburg:** prairies à Maeseyck, 51º5’N, 5º47’E, 24 Jun. 1871, *Cogniaux s.n.* (NY). **Namur:** Rochefort, Croise St. Jean, 50º9’N, 5º14’E, 15 Jun. 1934, *Mosseray-Staner s.n.* (C). **Walloon Brabant:** Waterloo, 50º42’N, 4º23’E, 1 Jul. 1923, *Lambert s.n.* (US). **BOSNIA AND HERZEGOVINA:** Homami do pr. cast. Jablan, 43º32’N, 18º8’E, Sep. 1910, *Vandas s.n.* (PR). BULGARIA. **Plovdiv:** Central Rhodopes mts., pr. Kosovo, 41º54’N, 24º42’E, 29 Jun. 2004, *Aedo et al. 10371* (MA). **Smolyan:** Central Rhodope mts., Smolyan distr., Gela village, 41º39’N, 24º33’E, 28 Jun. 2004, *Aedo et al. 10141* (MA). **CROATIA. Zagreb County:** Zagreb, 24 km E of Zagreb, by the road Zagreb-Beograd, 45º48’N, 15º58’E, 13 Jun. 1971, *Suominen 472* (H). **CZECH REPUBLIC. Central Bohemian:** Příbram distr., na lukách pred Novou Hospodou [Nová Hospoda], 49º41’N, 14º2’E, Jun. 1904, *Tocl s.n.* (G, H). **South Moravian:** Strážnice, Velká, locis "na Kukách", supra Vápenky, 48º52’N, 17º37’E, 20 Jun. 1930, *Podpera et al. s.n.* (C, G, H, K, MO, S, UPS, US, WU). **Ústí nad Labem:** Děčín distr., Šluknov, 51º0’N, 14º27’E, 16 Jun. 1964, *Chrtek* & *Pistulková s.n.* (G, H, K, L, MA, MO, S, UPS). **DENMARK. Capital Region:** Bornholm, Rønne Åvangskolen, 55º6’N, 14º42’E, 17 Jun. 1978, *Lütken s.n.* (MO). **Central Jutland:** Aabyhoj, Ruderat ved Frichs fabrikker, 56º9’N, 10º9’E, 21 Jun. 1964, *Øllgaard s.n.* (MO). **Zealand Region:** Bastrup, 55º49’N, 12º16’E, 25 Jun. 1944, *Lange s.n.* (US). **FINLAND. Åland Islands:** Maarianhamina, Badhusberget, 60º6’N, 19º55’E, 21 Sep. 1984, *Hæggström 5224* (H). **Lapland:** Männikkö prope opp. Willmanstrand, 66º3’N, 26º55’E, 12 Jul. 1887, *Sælan s.n.* (H). **Northern Savonia:** Kuopio, Vanhan tulitikkentehtaan puisto, 62º53’N, 27º40’E, 25 Jul. 1931, *Toivanen s.n.* (H). **Ostrobothnia:** Vaasa, Vasklot, 63º5’N, 21º34’E, 28 Jun. 1954, *Malmberg s.n.* (H). **Pirkanmaa:** Satakunta, Karkku, 61º26’N, 23º2’E, 2 Sep. 1870, *Hjelt s.n.* (H). **South Karelia:** Lappeenranta, Linnoitus, 61º3’N, 28º10’E, 20 Jun. 1948, *Eurola s.n.* (H). **Southern Savonia:** Savonlinna, Saaminki, Aholahti, 61º53’N, 28º45’E, 27 Jun. 1920, *Linkola s.n.* (H). **Southwest Finland:** Turku, Paimio, Juntola, E bank of Paimio River at the bridge above the power station, 60º27’N, 22º41’E, 3 Jul. 1982, *Kukkonen 11193* (H). **Uusimaa:** Helsinki, Nordsjö, Rastila, 60º12’N, 25º7’E, 3 Jul. 1964, *Ruotsalo s.n.* (H). **FRANCE. Allier:** Arouer, Les Damariats, 46º41’N, 3º17’E, Jun. 1894, *Lassimonne s.n.* (C). **Alpes-de-Haute-Provence:** Lautaret, 44º26’N, 6º21’E, Jul. 1905, *Jeanpert s.n.* (F). **Alpes-Maritimes:** Cipières village, 43º46’N, 6º57’E, 1 Jul. 1992, *Hepper 9464* (B). **Ardèche:** Saint-Julien-du-Serre, 44º39’N, 4º24’E, 5 Jun. 1902, *Girod s.n.* (G). **Ariège:** Haies à Pamiers, 43º7’V, 1º36’E, 12 Jun. 1877, *Huet s.n.* (UPS). **Bouches-du-Rhône:** Martigues, 43º24’N, 5º3’E, May 1871, *Autheman s.n.* (UPS). **Charente-Maritime:** La Rochelle, 46º10’N, 1º9’W, 6 Jun.

1955, *Galiano s.n.* (SEV). **Corse: Upper Corsica**, Massif du San Petrone, a l´WNW d´Aïti, 42º23'N, 9º14'E, 30 Jun. 1990, *Gamisans 14681* (G); Corte, au dessus de Casanova, ravin de Taola, 42º15'N, 9º10'E, 8 Jul. 1979, *Gamisans s.n.* (G); Upper Corsica, Calacuccia, 42º20'N, 9º0'E, 8 Jul. 1911, *Petry s.n.* (BM, H, O, PR). **Côtes d´Armor:** Côte du Nord, Pléhérel, 48º39'N, 2º22'W, 11 Jun. 1967, *Bakker* & *Beglel s.n.* (L). **Dordogne:** Sainte-Orse, 45º12'N, 1º4'E, 16 Jun. 1891, *Mouillefarine s.n.* (US). **Haute Garonne:** Bagnères-de-Luchon, 42º47'N, 0º35'E, 6 Jul. 1885, *Peyron s.n.* (G). **Hautes-Alpes:** La Monta près Abriès, Chemin de la Traversette, 44º46'N, 6º59'E, 9 Aug. 1913, *Jeanpert s.n.* (F); Tal der Aigue Blanche (Seitental des Val Queyras), SE von St. Vèran, 44º42'N, 6º52'E, 14 Jul. 1970, *Matthei s.n.* (B). **Haute-Saône:** Champagney, 47º42'N, 6º40'E, 6 Jun. 1868, *Vendrely s.n.* (JE). **Haute-Savoie:** Mt. Veyrier, Col des Contrebandiers, east of Annecy, 45º54'N, 6º10'E, 20 Jul. 1967, *Ib Olsen 578* (C). **Hautes-Pyrénées:** Gèdre, 42º41'N, 0º0'W, Jun. 1884, *Bordère s.n.* (JE, L). **Hérault:** St. Felix du Monceau bei Gigean, 43º29'N, 3º43'E, 24 May 1972, *Döring* & *Holtz s.n.* (GOET). **Isère:** Dauphiné, Saint-Pierre-de-Chartreuse, La Scia, 45º20'N, 5º51'E, 28 Jul. 1959, *Segelberg s.n.* (S). **Jura:** prés secs à Salins, 46º56'N, 5º52'E, Jun. 1851, *Garnier s.n.* (B, F, JE). **Loire:** Montbrison, 45º36'N, 4º3'E, Jun. 1887, *Girod s.n.* (G). **Maine-et-Loire:** St. Barthélemy, 47º28'N, 0º29'W, Jun. 1914, *Bioret s.n.* (S). **Morbihan:** prés secs à Saint-Antoine en-Ploërmel, 47º55'N, 2º23'W, 20 May 1953, *Arsène 2317* (G). **Orne:** prope Alençon, 48º26'N, 0º5'E, 22 Jun 1886, *Beaudouin s.n.* (FI, S). **Puy-de-Dôme:** Torr ängsmark i St. Nectaire, 14 km öster om Mont-Dore, 45º34'N, 2º49'E, 4 Jul. 1955, *Een s.n.* (S). **Pyrénées Orientales:** Angostrine, 42º28'N, 1º57'E, 7 Jul. 1927, *Sennen s.n.* (BM, PH, US). **Saône-et-Loire:** chemin des bois de La Motte-Saint-Jean, 46º29'N, 3º57'E, May 1959, *Charpin s.n.* (G). **Savoie:** Col du Petit Mont Cenis, 45º12'N, 6º52'W, 22 Aug. 2013, *Aedo 20920* (MA). **Seine-Maritime:** Bonsecours, 49º25'N, 1º7'E, 19 Jun. 1934, *Tiderstrom s.n.* (NY). **Somme:** Doullens, 50º9'N, 2º20'E, 12 Jul. 1887, *Copineau s.n.* (US). **Vaucluse:** Malaucène, 44º10'N, 5º7'E, 8 Jun. 1876, *Delacour s.n.* (K). **GEORGIA. Abkhazia:** Gagra massif, on Mamdzyshkha Mt., 43º18'N, 40º20'E, 27 Jul. 1905, *Voronov s.n.* (LE). **Imereti:** Adzhar-Imereti range, Zekari pass, 41º49'N, 42º51'E, 29 Jul. 1970, *Menitskiy s.n.* (LE). **Kakheti:** Lagodekhi gorge, in vicinity of a meteorogical station, 41º49'N, 46º16'E, 16 Sep. 1949, *Golubkova* & *Pojarkova 1256* (LE). **Samtskhe-Javakheti:** western part of mountain range of Trialeti, surroundings of Azavreti, 41º36'N, 43º23'E, 15 Jul. 2002, *Schneeweiss s.n.* (B). **Shida Kartli:** above the selo of Khampalgom on Alkhashenda Mt., 42º27'N, 43º45'E, 23 Jul. 1928, *Bush* & *Bush s.n.* (LE). **Tbilisi:** Trialeti, Didgori, 41º47'N, 44º39'E, 8 Jul. 1997, *Gagnidze et al. 2799* (MO). **GERMANY. Baden-Württemberg:** Freiburg, Radolfzell am Bodensee, 47º44'N, 8º58'E, 5 Oct. 1975, *Fritze s.n.* (K). **Bavaria:** Weilheim-Schongau, 47º40'N, 10º48'E, 24 Jul. 2001, *Willing* & *Willing 13363* (B). **Brandenburg:** Kreis Eisenhüttenstadt, Fiederzwenkenhang an den Lossower Bergen, 52º18'N, 14º33'E, 14 Jun. 1974, *Benkert s.n.* (B). **Hamburg:** ad Blankenese, 53º33'N, 9º48'E, Jun. 1840, *Sonder s.n.* (UPS). **Hesse:** Eichenberg, 1 km südöst. Netra, 51º5'N, 10º5'E, 18 Aug. 1988, *Böhle 13551* (B). **Lower Saxony:** Mesobrometum bei Göttingen-Nikolausberg, 51º33'N, 9º58'E, 10 Jun. 1952, *Trautmann s.n.* (GOET). **Saxony:** Erzgebirge, Neudorf, Kretscham, 50º28'N, 12º59'E, 28 Aug. 1965, *Fröhner 3911* (B). **Saxony-Anhalt:** Kreis Quedlinburg, Altenburg bei Quedlinburg, 51º47'N, 11º9'E, 20 Jun. 1952, *Dähnn s.n.* (B). **Thuringia:** Jena, 50º55'N, 11º35'E, 16 Jun. 1927, *Huysman s.n.* (L). **GREAT BRITAIN. East of England:** Cambridgeshire, in fruticetis apud Gog Magog Golf Course, 52º9'N, 0º11'E, 28 Jun. 1961, *Sell 61/299* (H, O, UPS). **North West:** Cumbria, Westmorland, Burton-in-Kendal, Dalton, 54º11'N, 2º43'W, 4 Jul. 1976, *Halliday 36/79* (C). **Scotland:** East Lothian, East Links, near North Berwick, 56º3'N, 2º43'W, 8 Aug. 1956, *Green 18* (H, MO, S, UPS); Angus, East Haven, al sur de Arboath, 56º31'N, 2º40'W, 14 Jul. 1984, *Valdés s.n.* (SEV); Perthshire, Kenmore, grounds of Taymouth Castle, 56º36'N, 3º59'W, 7 Jul. 1953, *Welch 5200* (C, F). **South East:** Surrey, Chipstead valley near Coulsdon, 51º19'N, 0º8'W, 1 Jul. 1954, *Cannon* & *Cannon 2735* (L). **South West:** Somerset, Chedar Gorge, pr. Weston, 51º18'N, 2º48'W, 14 Jul. 1996, *Aedo* & *Gama CA3874* (MA). **West Midlands:** Herefordshire, Kentchurch, 51º55'N, 2º51'W, 13 Jun. 1937, *Hubbard s.n.* (C). **GREECE. Central Greece:** Evrytania, Agrafa area, 5 km WNW of the village of Petrálona, 39º10'N, 21º43'E, 11 Aug. 1981, *Franzén* & *Andersson 640* (G). **Central Macedonia:** Florina, Pellis, Mt. Voras, 1 km NE of marshy area known as Dobro Pole, 40º55'N, 21º47'E, 17 Jul. 1981, *Strid et al. 19163* (C, G). **Epirus:** Central Pindus range, pr. Mount Smolikas, Lake Drakolimni, 40º5'N, 20º54'E, 28 Jun. 2007, *Gonzalo et al. RG789* (MA); Ioannina distr., Montes Pindus, in monte Tsuka Rossa ditionis pagi Vovousa (Viosa), 39º56'N, 21º2'E, 2 Aug. 1956, *Rechinger 18583* (B, MA, MO, S). **Peloponnese:** Lakonia, Taigetos mts., pr. Aghia Marina, 37º3'N, 22º15'E, 24 Jun. 2007, *Aedo et al. 14339* (MA); Korinthia, Kilini, 37º55'N, 22º24'E, 22 Jun. 2007, *Herrero et al. AH3383* (MA). **Thessaly:** Lárisa, Ep. Elassonos, Mt. Olympus, S. foothills, 2 km E of the village of Karya, 39º59'N, 22º23'E, 14 Jun. 1976, *Strid* & *Kjellsson 11406* (G).

Western Greece: von Fteri zum Klokos, 38º9’N, 22º2’E, 8 Jul. 1991, *Burri* & *Krendl s.n.* (B). **Western Macedonia:** Kozani, Askio, macizo Askion, monte Siniatsikon, por encima de Námata, 40º24’N, 21º32’E, 1 Jul. 2007, *Herrero et al. AH3636* (MA); Florina, Melitti, Mount Kajmakcalan, 40º53’N, 21º46’E, 1 Jul. 1999, *Schuler 99/746* (B). **HUNGARY.** Vas: Kőszeg, 47º23’N, 16º32’E, 29 May 1931, *Holmström s.n.* (H, GB, S). **IRAN. Golestan:** Mt. Elburs orient., in valle Zaringol, 36º44’N, 54º48’E, 30 Jun. 1938, *Gauba s.n.* (US); 60 km NE Gonbadghabous [Gonbad-e Kāvūs], 37º15’N, 55º10’E, 14 May 1966, *Pabot 7719* (G). **Mazandaran:** prope Pol-e-Zoghal, 36º30’N, 51º19’E, 31 May 1938, *Gauba s.n.* (US); au dessus de la plus haute des bergeries de Sang-Deh, 36º4’N, 53º13’E, 5 Jul. 1973, *Klein 4832* (G). **West Azerbaijan:** Uromiyeh [Urmia], around Soluk waterfall, 7º33’N, 45º4’E, 27 May 2004, *American-Iranian Botanical Delegation 34291* (MO). **IRELAND. Leinster:** Louth co., Thomastown Bog, 2 1/4 miles W of Duleek, 53º39’N, 6º25’W, 26 Jul. 1969, *Scannell s.n.* (H). **Munster:** Tipperary co., between Borrisokane and Cloughjordan, 52º56’N, 8º2’W, 9 Jul. 1967, *Scannell s.n.* (H). **ITALY. Belluno:** Cortina d´Ampezzo, 46º32’N, 12º8’E, Oct. 1870, *Ball s.n.* (GH). **Cuneo:** Crissolo, 44º41’N, 7º9’E, 13 Jul. 1890, *Bicknell s.n.* (UPS). **Forli-Cesena:** Castrocaro, 44º10’N, 11º56’E, 29 May 1877, *Sommier s.n.* (G). **Genova:** in Wiesen bei Cogorno nördl. Lasagna, 44º19’N, 9º22’E, 5 Jun. 1983, *Nowak It83/319* (B). **Livorno:** Capraia Isola, Sentiero per Monte Arpagna, presso l´inizio dei due sentieri, per punta del trattaio e per Colombia, 43º1’N, 9º48’E, 18 Jun. 1996, *Signorini* & *Miniati s.n.* (FI). **Sardegna:** Isola di Tavolara, 40º54’N, 9º42’E, 12 Jun. 1988, *Arrigoni s.n.* (FI); Nuoro prov., Gruppo del Gennargentu, Nodu ´E Littipori e Mte Bruttu presso Acru Correboi, 40º5’N, 9º21’E, 8 Jul. 1972, *Arrigoni* & *Nardi s.n.* (FI). **Sicily:** Palermo, Riserva di Bosco della Ficuzza, Piano de la Tramontana, Rocca Busambra, 37º51’N, 13º25’E, 31 May 2000, *Castroviejo et al. 15391SC* (MA); Trapani, Mt. San Giuliano, near Erice, 38º2’N, 12º35’E, 31 May 1990, *Raimondo s.n. et al.* (B, G, SEV); Agrigento, Monte delle Rose, Garden "Acqua Bianca", 37º39’N, 13º25’E, 12 Jun. 1964, *Segelberg s.n.* (S). **South Tyrol:** Pustertal, prope Niederdorf, 46º44’N, 12º11’E, *Bornmüller s.n.* (C, F, G, GOET, H, L, MW, MO, PR, S, WU). **Trentino:** Sellajach, Rodella, 46º29’N, 11º44’E, 30 Jul. 1907, *Bornmüller s.n.* (B). **Trieste:** SW-Hang des Monte Lanaro oberhalb Rupingrande, 45º44’N, 13º46’E, 26 Jun. 1980, *Leuschner* & *Sigi 17397* (B). **Turin:** Monastero di Lanzo, tra Monastero e Lanzo, circa 1 km a S-SO di Coassolo, sul lato destro della valle del Torrente Tesso, 45º18’N, 7º26’E, 28 Jun. 1993, *Pistarino* & *Gallo s.n.* (H). **Verbano-Cusio-Ossola:** prati nella compagna di Stresa, 45º52’N, 8º32’E, 25 May 1912, *Boggiani s.n.* (B, G). **Verona:** Monte Baldo, 45º43’N, 10º49’E, Jul. 1931, *Baschant s.n.* (B). **LATVIA. Aizkraukle:** Kokenhusen, ved Fernbandinien, 56º39’N, 25º26’E, 30 Jun. 1929, *Grøntved s.n.* (C). **Daugavpils:** 20 km west of Daugavpils, bank of the Rauda river, 55º52’N, 26º32’E, 13 Jun. 1930, *Birkmane 28952* (LE). **LEBANON. Beqaa:** grès entre Towmat Gezzine et Machghara, 33º31’N, 35º39’E, 29 May 1950, *Mouterde 9853* (G). **Mount Lebanon:** Kesrouan, Chahtoul, 34º2’N, 35º43’E, 5 Jun. 1956, *Mouterde 11697* (G). **North:** Hadet el Djoubbeh, 34º14’N, 35º55’E, 12 Jun. 1933, *Samuelsson 2142* (S). **LUXEMBOURG:** Draufelt, 50º1’N, 6º0’E, Jun. 1963, *Germain 10598* (K). **MACEDONIA. Eastern Region:** Vinica, prope Suhostre, 41º50’N, 22º39’E, 7 Jul. 2004, *Quintanar 1408AQ et al.* (MA). **Polog Region:** Schar-dagh, in cacumine Kobelica, 42º5’N, 20º53’E, 14 Aug. 1917, *Bornmüller 2202* (B, JE, NY). **Southwestern Region:** Ochrid, in montibus Petrina, supra vicum Pestany, 41º3’N, 20º53’E, 19 Jun. 1968, *Weber s.n.* (PR). **MOROCCO. Béni Mellal-Khénifra:** region de El Ksiba, 32º30’N, 6º0’W, 5 Jul. 2006, *Quintanar et al. 2040AQ* (MA). **Drâa-Tafilalet:** Collado de Tamrouit, circo de Jaffar, 32º33’N, 4º53’W, 7 Jul. 2006, *Castroviejo et al. SC17882* (MA). **Fès-Meknès:** refugio de Taffert, Atlas Medio, 33º38’N, 4º9’W, 23 Jun. 1997, *Aedo et al. CA4165* (MA); carretera entre Imouzzèr e Ifrane, pr. Ifrane, 33º33’N, 5º5’W, 24 Jun. 2008, *Andrés Sánchez et al. SA233* (MA). **Marrakesh-Safi:** sous Tizi-n´Tichkat, 31º17’N, 7º22’W, 20 Jun. 1985, *Dobignard 3861* (G); Oukaïmeden, pista por encima de la estación de esquí, 31º13’N, 7º52’W, 11 Jul. 1984, *López* & *Muñoz Garmendia 8979GL* (MA). **Souss-Massa-Drâa:** Col Tizi-Melloul, 30º46’N, 7º36’W, 27 Jun. 1997, *Aedo et al. 4381* (MA); proximidades de la pista que une Askaun y Ansal, 30º46’N, 7º39’W, 10 Jun. 2009, *Quintanar et al. 3630AQ* (MA). **Tanger-Tétouan-Al Hoceïma:** Chefchaouen, Jbel Talamssemtane, c. 38 km from Chefchaouen, 14 km above Bab Taza on track to Jbel Talamssemtane, 35º9’N, 5º12’W, 26 Jun. 1992, *Achhal et al. s.n.* (FI); montis Dj. Dersa, supra Tetauen, 35º35’N, 5º23’W, 20 Jun. 1930, *Maire s.n.* (P). **NETHERLANDS. Limburg:** Slenaken, 50º46’N, 5º51’E, 10 Jul. 1951, *Larsen s.n.* (C). **South Holland:** shoulders of road near Oude Tonge, island Goeree-Overflakkee, 51º41’N, 4º12’E, 10 Jun 1958, *Florschütz et al. s.n.* (K). **Utrecht:** Western vic. of Utrecht, near Amsterdam-Rhine-canal, 52º5’N, 5º7’E, 11 Jun. 1954, *Leeuwenberg s.n.* (H, K, MA, MO, NY). **Zeeland:** Zd. Beveland, Perkpolder, på vallen vid färjeläget, 51º24’N, 4º1’E, 7 Jun. 1959, *Een s.n.* (S). **NORWAY. Akershus:** Asker, 59º50’N, 10º26’E, 20 Jun. 1896, *Werenskiold s.n.* (GH). **Hordaland:** Hardanger, Odda, Lindenes, 59º52’N, 6º21’E, 29 Jun.

1906, *Selland s.n.* (O, S, WU). **Møre og Romsdal:** Sunndal, 62º40’N, 8º33’E, 19 Sep. 1981, *Berg s.n.* (O). **POLAND. Greater Poland:** Schönlanke, 53º2’N, 16º27’E, Jun. 1906, *Bothe s.n.* (B). **Lesser Poland:** Wieliczka, 49º58’N, 19º58’E, 9 Jun. 2004, *Zelazny s.n.* (B). **Lower Silesia:** Liegnitz, Boberau [Bobrów], 50º52’N, 15º50’E, 28 Aug. 1889, *Figers s.n.* (G, JE, S, WU). **Lublin:** inter vicos Na Garbie et Hamernia, 50º27’N, 23º7’E, 19 Jun. 1976, *Palkowa* & *Sidzina s.n.* (B, G, H, MA, MO, NY, PH). **Opole:** Laki k. Otmuchowa pow. Grodków, 50º28’N, 17º10’E, 19 Jun. 1952, *Nikosiewicz s.n.* (B, H). **Pomerania:** Tiegenhof, am Damm in Petershagen, 54º14’N, 19º8’E, Jun. 1902, *Gross s.n.* (B). **Subcarpathia:** Lazów near Lezajsk, 50º20’N, 22º23’E, 30 Jul. 2005, *Nobis* & *Nobis s.n.* (B, H). **West Pomerania:** [illegible], Krone, 53º16’N, 16º28’E, 13 Jun. 1877, *Ruhmer s.n.* (JE). **PORTUGAL. Tras-os-Montes e Alto Douro:** Bragança, inter Castrelos et Conlelas, 41º49’N, 6º54’W, 27 Jun. 1968, *Silva* & *Teles 8348* (US). **ROMANIA. Bistrița-Năsăud:** in pratis montis Cisia ad Rodnam, 47º27’N, 24º49’E, 24 Aug. 1902, *von Degen 119* (BM, K, O, US, WU). **Cluj:** valle "Valea Seaca", prope opp. Cluj, 46º43’N, 23º32’E, 26 Jun. 1970, *Gergely s.n.* (C, G, H, MA, MW, US). **Covasna:** sub colle "Forbic" prope pag. Vîlcele, 45º51’N, 25º41’E, 19 Jul. 1971, *Morariu s.n.* (C, G, H, JE, K, MA, MW, O, US). **Harghita:** Muntele Surdecc, am Lacu Rosu, 46º47’N, 25º47’E, 3 Jul. 1979, *Lippold s.n.* (JE). **Maramureş:** auf Alpentriften des Berges Cisia in den Rodnaer Karpathen in Siebenbürgen, 47º35’N, 24º40’E, 24 Aug. 1902, *von Degen s.n.* (B, C, G, H, L, MA, MO, PR, S, US, WU). **Sibiu:** Hermannstadt [Sibiu], 45º48’N, 24º9’E, 16 Jun. 1912, *Barth s.n.* (JE). **RUSSIA. Kabardino-Balkar Republic:** Sunzhenskiy range, northern slope, 3 verstas SE of the margin on the selo of Verkhniy Kurp, 43º28’N, 44º22’E, 6 Oct. 1924, *Knorring s.n.* (LE). **Karachay-Cherkess Republic:** Teberda distr., Dombai village, Musatcheri Mt., along road S and E from jct of 2nd & 3rd chairlifts, 44º3’N, 40º1’E, 31 Jul. 2010, *Soreng et al. 8024* (US). **Leningrad Oblast:** Gatchina distr., vicinity of Elizavetino station, near the selo of Malye Bornitsy, 59º29’N, 29º46’E, 28 Jun. 1984, *Tsvelev 24* (LE). **Novgorod Oblast:** Valdayskiy distr., the village of Niva (former Nebylitsy), 20 km SE of Valday, 57º46’N, 33º20’E, 27 Jul. 2003, *Sennikov s.n.* (LE). **Pskov Oblast:** 4-5 km SE of Sebezh and 2-2.5 km W of the selo of Cherneya, 56º17’N, 28º28’E, 5 Jun. 2002, *Tsvelev 154* (LE). **Republic of Adygea:** Lago-Naky Nature Reserve, 8.5 km by road S of Bolsahys Azishskaya (Cave), 44º3’N, 40º1’E, 6 Aug. 2010, *Soreng et al. 8041* (US). **Republic of Dagestan:** Makhachkala distr., north-eastern slope of Tarki-Tau Mt., 42º55’N, 47º25’E, 8 Jun. 1925, *Bodanovskaya-Gienef s.n.* (LE). **Republic of Karelia:** Sortavala, 61º42’N, 30º40’E, 21 Jun. 1895, *Mustonen s.n.* (H). **Vladimir Oblast:** Yuryev-Polskiy distr., 31 km N of Yuryev-Polskiy, 1.5 km downstream of the selo of Luchki, right side of the floodplain of the Nerl river, 56º46’N, 39º32’E, 1 Aug. 2010, *Seregin 4697* (LE). **SERBIA:** Vranja, 42º33’N, 21º54’E, Jun. 1896, *Dimitrijevitz s.n.* (WU). **SLOVAKIA. Bratislava:** Bazini [Pezinok], 48º17’N, 17º16’E, 4 Jun. 1917, *Holuby s.n.* (PR). **Prešov:** Belanske Tatry, Kotlina siedmich pramének, Lawinental, 49º13’N, 20º19’E, 17 Aug. 1965, *Fröhner 3868* (B). **Trenčín:** montanis Bosacá, 48º53’N, 18º2’E, Jun. 1887, *Holuby s.n.* (JE). **SLOVENIA. Gorizia:** Bovec, Jusliche Alpen, Predilpass, 46º25’N, 13º34’E, 21 Jul. 1913, *Ronniger s.n.* (G). **Littoral–Inner Carniola:** Postojna, 8 km NW of Postojna, Bukove, Predjamski grad., 45º46’N, 14º12’E, 12 Jun. 1971, *Hämet-Ahti 2440* (H). **SPAIN. Almería:** Sierra Nevada, La Ragua, Bayárcal, 37º3’N, 2º59’W, 6 Jul. 1981, *Segura Zubizarreta s.n.* (MA). **Asturias:** Valles, San Román de Villa, Piloña, 43º21’N, 5º19’W, 24 Jun. 2002, *San Miguel s.n.* (MA). **Ávila:** sierra de Ojos Albos, Los Regajales, 40º42’N, 4º31’W, 3 Jul. 1984, *Burgaz et al. s.n.* (MA). **Barcelona:** Turó d´en Corts, Collserola, 41º25’N, 2º6’E, 11 Jun. 1989, *García Pausas s.n.* (BCN). **Burgos:** San Martín de Ubierna, 42º30’N, 3º42’W, 7 Jul. 1984, *Galán Cela* & *Martín 591* (MA). **Cantabria:** San Vicente de la Barquera, 43º22’N, 4º23’W, 29 Jun. 1986, *Aedo s.n.* (MA). **Castellón:** Vistabella del Maestrat, Al Forí, 40º17’N, 0º17’W, 19 Jun. 1980, *Soriano s.n.* (BCN). **Cuenca:** Mogorrita, Montes Universales, 40º20’N, 1º46’W, 22 Jul. 1979, *López 2085GF* (MA). **Gerona:** prop de Vidrá, Ripollés, 42º7’N, 2º18’E, 23 Jun. 1981, *Papiró s.n.* (BCN). **Granada:** Sierra Nevada, carril del Puerto de la Ragua a Jerez del Marquesado, barranco de los Pasillos, 37º7’N, 3º4’W, 26 Jun. 1997, *Morales* & *Baena s.n.* (MA). **Guadalajara:** entre Alustante y Alcoroche, Los Horcajos, 40º36’N, 1º39’W, 13 Jul. 1965, *Paunero* & *Rivas s.n.* (MA). **Guipúzcoa:** Hondarribia, 43º21’N, 1º48’W, 27 Jun. 1984, *Catalán s.n.* & *Aizpuru* (MA). **Huesca:** Valle de Bujaruelo, Torla, barranco de Lapazosa, 42º41’N, 0º6’W, 16 Sep. 2013, *Barberá et al. 1059PB* (MA); Benasque, prados sobre Cerler, 42º35’N, 0º32’E, 20 Jul. 1955, *Montserrat 702/55* (MA). **León:** Redipollos, 43º0’N, 5º15’W, 3 Jul. 1983, *Andrés s.n.* (BCN). **Lérida:** valle de Arán, pr. Baguergue, 42º43’N, 0º54’E, 8 Oct. 2006, *Aedo et al. 13498* (MA). **Logroño:** Torrecilla de Cameros, 42º15’N, 2º37’W, 15 Jun. 1966, *Segura Zubizarreta s.n.* (MA). **Lugo:** Orol, 43º33’N, 7º38’W, *Merino s.n.* (MA). **Madrid:** Puerto de Rascafría, 40º54’N, 3º52’W, 27 Jun. 1973, *López* & *Valdés Bermejo s.n.* (MA). **Navarra:** Valle del Roncal, Puerto de Arlas, 42º58’N, 0º45’W, 27 Jul. 1969, *Galiano et al. s.n.* (GDA, SEV). **Orense:** Vilardesilva, Serra da Enciña da Lastra, 42º27’N, 6º50’W, 16 Jun. 2017, *Aedo et al. 25040* (MA). **Palencia:** Velilla del Río Carríón, proximidades del Espigüete, por carretera que va a Cardaño de Arriba, 42º57’N, 4º45’W, 15 Jul. 2013, *Barberá* & *Quintanar 897PB* (MA). **Salamanca:** Castellanos de Villiquera, 41º3’N, 5º41’W, 4 Jun. 1979, *Amich s.n.* (MA). **Segovia:** Sepúlveda, Hoz del río Duratón, 41º17’N, 3º45’W, 9 Jul. 1981, *Cebolla et al. s.n.* (MA). **Soria:** Montenegro de Cameros, La Cuerda, 42º6’N, 2º46’W, 22 Jun. 2005, *Molina* & *Montamarta s.n.* (MA). **Teruel:** entre Orihuela y Noguera, 40º27’N, 1º35’W, 14 Jul. 1965, *Paunero* & *Rivas s.n.* (MA). **Valladolid:** Castromonte, 41º46’N, 5º2’W, 28 Jun. 1906, *Sennen s.n.* (MA). **Zamora:** Villardeciervos, 41º56’N, 6º17’W, Jul. 1947, *Bernis s.n.* (MA). **Zaragoza:** Egea de los Caballeros, Erla, orillas del río Arba de Biel, 42º7’N, 1º8’W, 19 Jun. 1955, *Paunero s.n.* (MA). **SWEDEN. Blekinge:** Nättraby par., Agdatorp, 56º12’N, 15º31’E, 5 Aug. 1927, *Arrhenius s.n.* (S). **Bohuslän:** Nösund, 58º6’N, 11º31’E, 21 Jul. 1936, *Fries s.n.* (S). **Dalsland:** Ödeborg, Kyrkskolan, 58º32’N, 11º58’E, 19 Jun. 1925, *Johansson s.n.* (S). **Gotland:** Dalhem, 57º33’N, 18º32’E, 22 Jun. 1974, *Karlsson s.n.* (S). **Halland:** Falkenberg, 56º54’N, 12º29’E, 24 Jun. 1912, *Svenson s.n.* (S). **Jämtland:** Fröso, 63º11’N, 14º32’E, 22 Oct. 1933, *Lange s.n.* (S). **Närke:** Stora Mellösa sn, Göksholm, 59º12’N, 15º30’E, 29 Jun. 1929, *Broddeson s.n.* (S). **Öland:** Borgholm, 56º52’N, 16º39’E, 23 Jun. 1911, *Erdmann s.n.* (S). **Östergötland:** Västra Tollstad, 4.5 km NNW of Alvastra, W side of Omberg by reserve Bokskogen, 58º18’N, 14º38’E, 3 Jul. 1957, *Ahti B426* (H). **Skåne:** Hälsingborg, Sofiero, 56º5’N, 12º40’E, 11 Jul. 1942, *Pettersson s.n.* (S). **Småland:** Algutsboda par., Boda, 56º43’N, 15º34’E, 13 Jun. 1987, *Karlsson 87031* (S). **Södermanland:** Nämdö par., Bunkvik, 59º10’N, 18º40’E, 4 Aug. 1988, *Sundin 57* (S). **Uppland:** Stockholm, Laduvikens NO-hörn, 59º19’N, 18º3’E, 28 May 1998, *Blom* & *Thorán 4497* (S). **Västergötland:** Lerum, Hulan´s park, 57º46’N, 12º16’E, 10 Jul. 1946, *Ohlsén s.n.* (S). **Västmanland:** Tillberga, Hedensberg, 59º41’N, 16º38’E, 29 Jun. 1950, *Almquist s.n.* (S). **SWITZERLAND. Basel-Stadt:** S part of Riehen, Lange Erlen, 47º34’, 7º36’E, 8 May 1948, *Ruotsalo s.n.* (H). **Graubünden:** Engiadina Bassa, Guarda, 46º46’N, 10º9’E, 17 Jul. 1990, *Castroviejo et al. 11464SC* (MA). **Berne:** Ganterland beim Haus Schopen, Ringoldswil ob Gunten am Thunersee, 46º41’N, 7º43’E, 11 Aug. 1954, *Keller s.n.* (G). **Geneva:** environs de Genéve, à Carouge, 46º10’N, 6º8’E, Jun. 1871, *Brown s.n.* (UPS). **Saint Gallen:** St. Gallen-Nest, 47º25’N, 9º22’E, 15 Jun. 1969, *Leenhouts 2037* (L). **Solothurn:** bei Frohburg, 47º22’N, 7º53’E, 25 Jul. 1905, *Fisher-Sigwart s.n.* (B, H, K, L, MA, MO, PR, S, US, WU). **Ticino:** Lugano, 46º0’N, 8º57’E, 1 Jun. 1967, *Leenhouts 1518* (L). **Valais:** La Fouly, pr. Orsieres, 45º54’N, 7º6’E, 17 Aug. 2013, *Aedo 20819* (MA). **Vaud:** Les Plans-sur-Bex, 46º15’N, 7º5’E, 29 Jul. 1972, *Scholz s.n.* (B). **Zürich:** prés sur le Zürichberg, 47º23’N, 8º34’E, 18 Jul. 1890, *Stebler* & *Schröter 31* (S, US). **SYRIA. Rif Dimashq:** Ouadi el Karn, 33º37’N, 36º4’E, 28 May 1953, *Pabot s.n.* (G). **TUNISIA. Siliana:** Dj. Bargou, 36º6’N, 9º36’E, 18 May 1903, *Murbeck s.n.* (H, UPS). **TURKEY. Artvin:** Salalet ad Artwin [Artvin], 41º11’N, 41º49’E, 30 Jun. 1912, *Holmberg 1985* (S). **Bitlis:** Tarvan [Tatvan], 38º30’N, 42º16’E, 27 Jun. 1954, *Davis* & *Polunin 22187* (BM, G). **Bolu:** Aladag-Kartalkaya, 40º36’N, 31º40’E, 1 Jul. 1955, *Alpay 414* (G). **Bursa:** Ulu Dag, Yesil Konak Bölgesi Civari, 40º4’N, 29º13’E, 15 Jul. 1955, *Alpay 112* (G). **Cankiri:** Ilgaz distr., Küçüz Ilgaz Dag, Wiesen 1 km südlich der Passhöhe, 41º2’N, 33º44’E, 12 Jul. 1964, *Huber-Morath 17383* (G). **Hakkari:** Karadag, 37º20’N, 43º48’E, 16 Aug. 1954, *Davis* & *Polunin 24393* (BM, G). **Istambul:** Tchataldagh, près d´Alemdagh, 41º2’N, 29º15’E, 5 Jun. 1892, *Aznavour s.n.* (G). **Izmir:** Yamanlar Dağı, Rastplatz, 38º33’N, 27º10’E, 10 Jul. 1978, *Kesercioglu 101* (GOET). **Kars:** prope opp. Sarykamysch, 40º19’N, 42º35’E, 1 Jul. 1914, *Litvinov s.n* (C, G, H, JE, K, MO, NY,). **Rize:** Vallée d´Khabakhor, 40º55’N, 40º50’E, 30 Aug. 1866, *Balansa s.n.* (L). **TURKMENISTAN**. **Ahal:** Baharly distr., SW Kopetdag, western part of Kecce-Yola, 38º15’N, 57º48’E, 4 Jun. 1974, *Nikitin* & *Ivanov s.n.* (BM, G, H, K, L, MA). **Balkan:** Kara-Kala distr., top of Mt. Khasar, 38º34’N, 56º44’E, 23 Jun. 1931, *Borisova 184* (LE). **UKRAINE. Chernivtsi Oblast:** Vashkivtsi distr., Nyzhni Stanivtsi, valley of the Brusnytsya River, 48º18’N, 25º33’E, 21 Jun. 1952, *Gorokhova s.n.* (LE). **Kiev Oblast:** vicinity of Irpen, 50º31’N, 30º15’E, 6 Jul. 1969, *Kharkevich s.n.* (LE). **Lviv Oblast:** Shevchenkovskiy rayon, 50º26’N, 30º31’E, 24 Jun. 1991, *Tsebryk s.n.* (B). **Volyn Oblast:** Volodymyr-Volyns’kyy, Ostrivok, 50º50’N, 24º20’E, 31 May 1918, *von Hayek s.n.* (WU). **Zakarpattia Oblast:** road Yasinya-Rakhiv, 48º16’N, 24º21’E, 2 Sep. 1968, *Bobrov et al. s.n.* (LE). **WALES.** Denbighshire, Tan Penmaen Head, east side of Colwyn Bay, 53º17’N, 3º43’W, 19 Jun. 1960, *Brummitt 60394* (MA).

b. subsp. GRISEOVIRENS (H. Lindb.) Dobignard, J. Bot. Soc. Bot. France 28: 44. 2004. *T. griseovirens* H. Lindb., Acta Soc. Sci. Fenn., ser. B, Opera Biol. 1(2): 25, fig. 6. 1932. *T. flavescens* var.

griseovirens (H. Lindb.) Maire, Fl. Afrique N. 2: 247. 1953.—TYPE: MOROCCO. Marrakech, Aït Messane, between Fimelil and Arround, 31º07'N, 7º55'W, 10 Jun. 1926, *H. Lindberg s.n.* [lectotype, designated by Väre (2012: 89), H–1088222!].

Herb 20.5–30(–36.5) cm high. Basal leaf-blades (1.4–)2.3–5.5(–6.8) cm × (1.2–)1.5–1.8 mm, inrolled, sometimes filiform. Top culm leaf-blades (1.3–)2.2–4(–4.4) cm × (1.2–)1.4–2 mm, flat or slightly convolute to filiform or inrolled. Panicles (5–)5.5–6.5(–8.5) × 1–2(–3) cm. Spikelets (6.3–)6.5–7.3(–7.7) mm long. Lemmas 6–6.2(–6.4) mm long; aristules (0.9–)1–1.4(–1.8) mm long; awn (8–)8.2–9(–10.6) mm long. Ratio palea length/lemma length (0.53–)0.65–0.76(–0.77). Anthers (2–)2.2–2.7(–3) mm long. Figures 8b, 9b, 10b, 11b.

Chromosome number—2*n* = 12 (Galland, 1985, 1988).

Additional illustrations—Chrtek (1967c: 176, tab. I, 1; 178: tab. II, 1, 2, sub *Trisetum griseovirens*).

Phenology—*Trisetum flavescens* subsp. *griseovirens* has been collected in flower and fruit from June to August.

Distribution and Habitat—This subspecies is endemic to the High Atlas Mountains, in Morocco, at 1900–3250 m, where it grows in sandstone formations and granitic rocky grasslands. Figure 14.

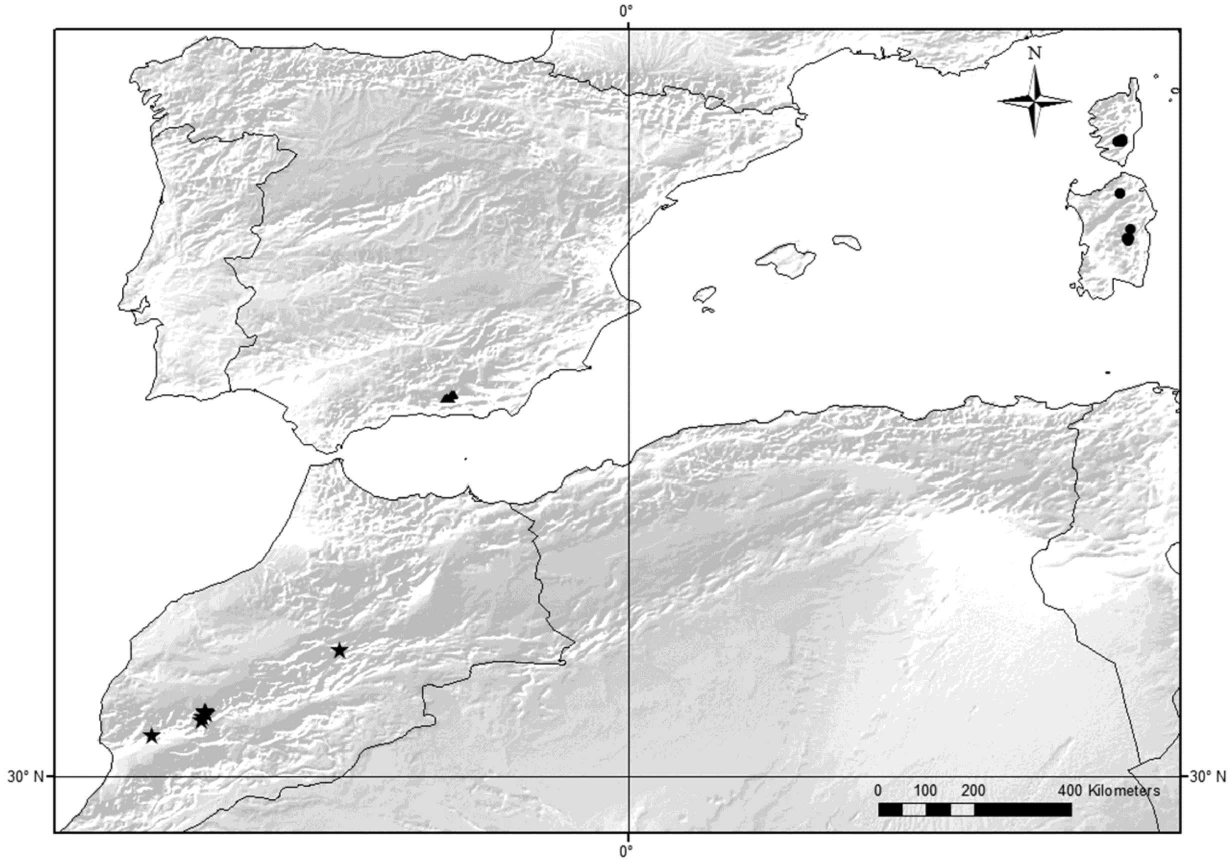

Figure 14. Distribution of *Trisetum glaciale* (triangles), *T. gracile* (dots), and *T. flavescens* subsp. *griseovirens* (stars).

Discussion—When Dobignard (2004) combined *T. griseovirens* under *T. flavescens*, he misspelled the epithet as “griseovirescens”. That is corrected to the original spelling.

Trisetum flavescens subsp. *griseovirens* is separated from subsp. *flavescens* by its habit (having shorter height, usually inrolled and filiform basal and upper leaves, and smaller panicles), and by its longer spikelets, aristules, and awns. Chrtek (1967c) recognized this taxon at specific rank, as did Lindberg (1932). He assigned much importance to the anatomical characters of the leaves. Some of the specimens studied from Morocco possess intermediate characters between subsp. *griseovirens* and subsp. *flavescens*. For example, the specimens *Dobignard 3861* (G-00443134), and *López & Muñoz Garmendia 8979GL* (MA-549691), have a similar habit to that of *T. flavescens* subsp. *flavescens*, but have the long lemmas, aristules, and awns, as in *T. flavescens* subsp. *griseovirens*. The opposite happens with the specimen *Sánchez et al. SA233* (MA-782244), with only the habit similar to that of subsp. *griseovirens*. Moreover, the specimen *Aedo et al. 4381* (MA-593200) has some individuals with character of subsp. *griseovirens*, and others of subsp. *flavescens*, all of them from the same population. It seems that subspecific rank is here appropiate because of its geographical isolation and the presence of some intermediate specimens (Du Rietz, 1930).

As indicated above, Chrtek (1967c) considered that *T. griseovirens* is closely related to *T. flavescens* (sub *T. burnouffi*) but even more so to *T. bertolonii*. However, our molecular data (Barberá et al., unpublished) suggest that *T. griseovirens* belongs to the *T. flavescens* complex, which is also in accordance with the morphology.

Additional specimens examined—**MOROCCO. Khenifra:** Arhbalou canyon n´Oussaka between Jebel Masker and Jebel Bou Ijallabene, S Assaka, 32º22’N, 5º22’W, 2 Jul. 1989, *Lippert 24863* (M). **Marrakesh:** Oukaimeden, Adrar Tizrag, 31º12’N, 7º51’W, 1 Jul. 2006, *Cabezas et al. FJC419* (MA); directly above (N of) Oukaimeden, 31º12’N, 7º52’W, 17 Jul. 1981, *Davis 67647* (M); près d´Isougane-n-Guadouns, 31º3’N, 7º56’W, 1 Aug. 1938, *Faurel s.n.* (MPU, P); Adrar-n-Oukaïmeden, vertiente S, 31º11’N, 7º51’W, 29 Jun. 2006, *Herrero et al. 2985* (MA, MPU); 72 km S from Marrakech, Oukaïmeden, 31º13’N, 7º52’W, 3 Jul. 1987, *Jury et al. 8847* (MA, SEV); surroundings of Oukaimeden, 31º11’N, 7º51’W, 15 Jul. 1989, *Lippert 25525* (M, W); Reraya, Arround, 31º7’N, 7º55’W, 23 Jul., *Litardière s.n.* (MPU); 19 Jul. 1924, *Maire s.n.* (MPU). **Taroudant:** Adrar-n-Dern, Toubkal NP, 30º47’N, 8º52’W, 24 Aug. 1992, *Kreisch 92/0631* (B).

5. TRISETUM FUSCUM Roem. & Schult., Syst. Veg. 2: 664. 1817. *Avena fusca* Schult., Oestr. Fl. ed. 2, 1: 268. 1814, nom. illeg. hom., non Ard., 1789. *Trisetum flavescens* subsp. *fuscum* (Roem. & Schult.) Hack., Magyar Bot. Lapok 2: 111. 1903. *Trisetaria fusca* (Roem. & Schult.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 383. 1996.—TYPE: SLOVAKIA. Carpathians, *P. Kitaibel s.n.* (lectotype selected by B. Jonsell in sched., designated here, M-0210842!; isolectotype, M-0223323!).

Trisetum transylvanicum Steud., Syn. Pl. Glumac. 1: 226. 1855.—TYPE: ROMANIA. Transylvania, *J.C.G. Baumgarten s.n.* (lectotype, designated here, P-219670!).

Trisetum varium var. *violaceum* Schur, Oesterr. Bot. Z. 10: 75. 1860.—TYPE: ROMANIA. Mts. Königstein [Piatra Craiului], 45º30’N 25º13’E, 13 Aug. 1854, *P.J.F. Schur s.n.* (neotype, designated here, LW-213275 image!).

Trisetum flavescens f. *majus* Zapal., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 108. 1904.—TYPE: Tatra Mountains, *J. Krupa s.n.* (KRAM?) (no original material found).

Herb (26.8–)44.9–54(–72) cm high, not to slightly cespitose, stoloniferous rhizome, culm (0.4–)0.6–0.9(–1.1) mm diam., straight, glabrous; nodes 4–5, separated along the culm, not included in the sheaths, rarely included, glabrous, yellowish or brownish. Basal leaf-sheaths sparsely pubescent to pubescent, with hairs (0.2–)0.6–0.8 mm long, decaying into fibers, brownish to yellowish; basal leaf-blades (1.1–)6.1–10(–18) cm × (1.4–)2.5–3.2(–5) mm, flat, sometimes slightly inrolled when dried, sparsely to densely pubescent adaxially and abaxially, sometimes glabrous abaxially, margins with hairs (0.05–)0.3–0.9(–1.2) mm long, yellowish to brownish, sometimes greenish; top culm leaf-sheaths (7–)9–12(–13.7) cm long, not distinctly veined, glabrous, sometimes with hairs on the upper part, with or without cilia on the margins; top culm leaf-blades (5.7–)6.5–12.5(–13.7) cm × (2.1–)3.4–5(–6.1) mm, flat, usually parallel to the culm, sometimes surpassing the panicle, pubescent adaxially and abaxially, sometimes glabrous or less densely pubescent abaxially, with hairs on the margins (0.05–)0.1–1(–1.2) mm long, greenish to greyish; inner collar region glabrous, with scattered hairs (0.2–)0.8–1.3(–2.3) mm long on the margins; ligules (3–)3.7–4.7(–4.8) mm long, irregularly dentate to laciniate, glabrous. Basal node of the panicle glabrous. Panicles (6.8–)7.9–11.2(–13) × (1.5–)1.8–3.5(–4.5) cm, elliptic to oblong in outline, lax to somewhat dense; rachis glabrous, sometimes sparsely pubescent, up to 0.3 mm long; longest basal branches (1–)2.2–3.8(–5) cm long. Spikelets (5–)5.4–6.6(–7.4) × (1.8–)2.2–3.1(–3.2) mm, 2-3-flowered; pedicels (1.7–)2.5–3.3(–4.4) mm long, glabrous to sparsely pubescent, with hairs up to 0.2 mm long. Glumes unequal [ratio lower glume length/upper glume length = (0.62–)0.7–0.82(–0.88)]; lower glume (2.9–)3.5–4.3(–4.5) × 1–1.2(–1.5) mm, broadly lanceolate, sometimes narrowly lanceolate [ratio lower glume width/lower glume length = (0.22–)0.25–0.34], acuminate, sometimes long acuminate, 1(–3)-nerved, glabrous, usually with hairs up to 0.05 mm long on the upper part and margins, greenish to purplish; upper glume (4–)4.7–5.5(–6.3) × (1.8–)2–2.4(–2.6) mm, elliptic to lanceolate, rarely oblanceolate [ratio upper glume width/upper glume length = (0.36–)0.38–0.46(–0.51)], acuminate to long acuminate, 3-nerved, glabrous, with hairs up to 0.1(–0.3) mm long from the middle to the upper part of the midrib and margins, greenish surrounded by purplish and yellowish; rachilla segments between first and second floret 0.9–1.3 mm long, with hairs (0.5–)0.8–1.7 mm long; rachilla segments to sterile floret (1–)1.2–1.8 mm long, with hairs (0.3–)0.7–1.2(–1.5) mm long. Lemma (4.1–)4.2–5.2(–5.5) × 1–1.2(–1.5) mm, oblong to broadly lanceolate, sometimes elliptic [ratio lemma width/lemma length = (0.33–)0.35–0.41(–0.44)], strigulose, with hairs (0.05–)0.1–0.2 mm long, the longest ones at the awn insertion, greenish to yellowish on the central part, surrounded by purplish; apical teeth (0.1–)0.2–0.4(–0.8) mm long, with aristules 0.1–0.2 mm long, rarely without; awn (4.7–)6–6.6(–7) mm long, inserted (2.1–)2.8–3(–3.4) mm from the base [ratio awn insertion from the base length/lemma length = 0.5–0.68(–0.83)], strongly curved basally, not or slightly twisted at the base, with adpressed hairs 0.05–0.2 mm long, the longest ones at the base; callus (0.1–)0.2(–0.3) mm long, elliptic to orbicular, with hairs (0.4–)0.5–1.1(–1.2) mm long. Paleas (3.6–)3.9–4.5(–5.5) × 1–1.5(–

1.7) mm [ratio palea length/lemma length = (0.77–)0.87–0.95(–1)], lanceolate or elliptic to slightly oblanceolate, margins with hairs from the middle to the upper part; teeth 0.2(–0.3) mm long, with short antrorse hairs sometimes up to 0.4 mm long. Lodicules (0.4–)0.5–0.8(–0.9) mm long, with 2-3 lobules or teeth of the same length. Anthers 1.7–2.1(–2.5) mm long. Ovary (0.4–)0.5–0.8(–1.1) mm long, glabrous. Caryopsis 1.6–2.8 × 0.5–0.6 mm, oblong to elliptic. Figure 8c, 9c, 10c, 15a.

Chromosome number—2*n* = 28 (Frey, 1991).

Additional illustrations—Chrtek & Jirásek (1963: 577, fig. 3, 3, sub *Trisetum ciliare*); Chrtek (1965: 213, Abb. 1, 2; 214, Abb. 3, 1; 217, Abb. 4, 1); Sãvulescu (1972: 289, Planşa 56, 3a-c, sub *Trisetum ciliare*); Frey (1992: 464, fig. 12).

Phenology—Trisetum fuscum has been collected in flower and fruit from June to October.

Distribution and Habitat—This species is endemic to the Carpathian Mountains; it grows on scree of mountain meadows and flood plains, in wet rock fissures, at 1500–2000 m. Figure 16.

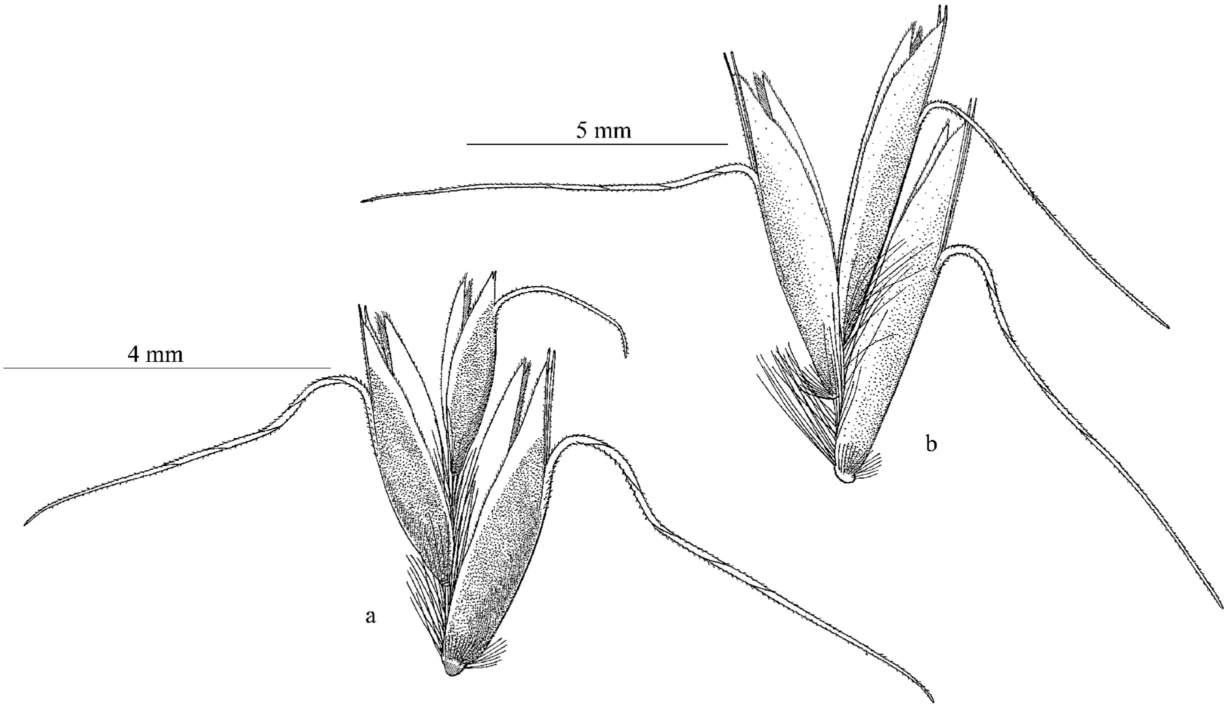

Figure 15. Florets. a. *Trisetum fuscum*. b. *T. laconicum*. (a based on *Nyárády s.n.* (L-1346389); b based on *Orphanides 2890* (B-10_0508993).

Discussion—Trisetum fuscum is mainly differentiated from the rest of species of the section by its longer ligules [(3–)3.7–4.7(–4.8) mm long]. *Trisetum fuscum* is similar to *T. alpestre*, with which it has been frequently confused. Apart from the ligules length, *T. fuscum* is separated from *T. alpestre* by its larger size [(26.8–)44.9–54(–72) cm, versus (14.4–)21.5–35.7(–53.5) cm] and not or more loosely tufted habit, longer and wider top culm leaf-blades [(5.7–)6.5–12.5(–13.7) cm × (2.1–)3.4–5(–6.1) mm, versus (1.5–)2.2–5.2(–9.3) cm × (1–)1.6–3(–4.1) mm], and longer panicles [(6.8–)7.9–11.2(–13) mm, versus (3.4–)5.4–7.5(–11.5) mm]. Concerning spikelet characters, *T. fuscum* has wider upper glumes than *T.*

alpestre [(1.8–)2–2.4(–2.6) mm, versus (1.5–)1.8–2(–2.3) mm], awns strongly curved basally and sometimes with long hairs at the base (up to 0.2 mm), paleas sometimes also with longer hairs (up to 0.4 mm apically), and glabrous ovaries.

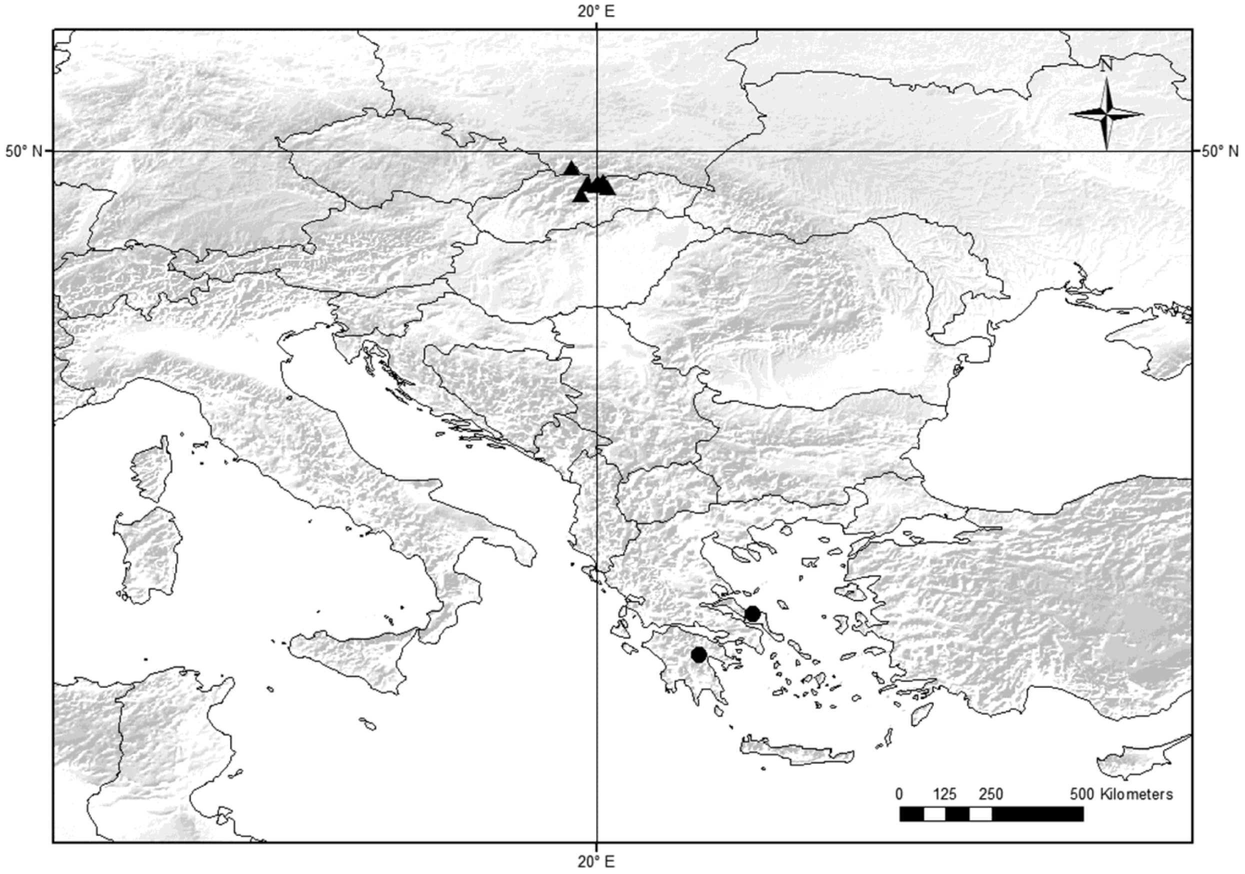

Figure 16. Distribution of *Trisetum fuscum* (triangles) and *T. laconium* (dots).

Trisetum fuscum is easy to differentiate from *T. flavescens*, with which it has sometimes been confused. The ligules are significantly shorter in *T. flavescens* [(0.5–)0.7–1.2(–2) mm]. Some authors, such as Chrtek (1968), Jonsell (1980) and Frey (1992), give much taxonomic importance to the hairiness of the lemma and the palea to differentiate *T. fuscum* from *T. alpestre* and *T. flavescens*. In particular, Chrtek (1968) published a detailed morphological study of *T. fuscum*, comparing each of those characters between the three species. In our study of *T. fuscum*, the hairiness of both, the palea and the lemma, exhibited great variability in length and density, suggesting that this feature is of minor taxonomic utility.

Jonsell (1980) described the ovary of *T. fuscum* as having a few apical hairs. Latter, Frey (1992), also observed 2-3 long papillae (atypical hairs) on the top of the ovary of *T. fuscum*. However, in all the specimens of *T. fuscum* studied by us, the ovaries were glabrous.

Arduino (1789) proposed simultaneously the name *Avena fusca* in an illustration (tab. 4), which was validly published as an alternative name for his *Avena hispanica* according to the art. 36.2 of ICN (McNeill et al., 2012). Consequently the *Avena fusca* Schult. is a later homonym (art. 53.1), being spelled exactly like the Arduino´s name for a taxon of the same rank, but based on a different type. We have decided to conserve the epithet “fuscum”, as a replacement name with the same type as the illegitimate name, in order to avoid disadvantageous nomenclatural changes.

Additional specimens examined—**POLAND. Lesser Poland Voivodeship:** Morskie Oko, 49º11’N, 20º4’E, 19 Jul. 1929, *Nilsson s.n.* (S); Kociol pod Rysami, Rysy, 49º11’N, 20º4’E, 20 Aug. 1931, *Pawlowski s.n.* (GB, GH, K, LE, S, UPS). **SLOVAKIA. Banská Bystrica:** Djumbier [Ďumbier], 48º56’N, 19º38’E, *Gustav s.n.* (MO). **Prešov:** Mlynica, 49º6’N, 20º18’E, 29 Jul. 1966, *Dahl* & *Hadac s.n.* (O); Csorbam, Jégtói völgy valley and Furkota völgy, 49º10’N, 20º1’E, 9 Aug. 1904, *Degen s.n.* (BM, GB, JE, LE, WU); Jégtói, 49º10’N, 20º1’E, Jul. 1904, *Degen s.n.* (BM, GB, JE, WU); Dolina Litworowa valley, 49º10’N, 20º7’E, 29 Aug. 1988, *Frey s.n.* (L); Nowy, 49º15’N, 20º11’E, Aug. 1972, *Fritze s.n.* (K); Jul. 1971, *Fritze s.n.* (JE, M, PR); pr. Jaworina, 49º35’N, 19º24’E, 11 Sep. 1865, *Fritze s.n.* (K); Zelene Pleso, 49º10’N, 20º7’E, 1 Aug. 1964, *Hadac* & *Dahl s.n.* (O); Omladék-völgy valley (Trümmertal), 49º10’N, 20º4’E, 2 Aug. 1932, *Lengyel s.n.* (GB, HBG, M, S); Mengusovský valley, 49º10’N, 20º4’E, 18 Sep. 1910, *Nyárády s.n.* (L, UPS). **Žilina:** Jarzabczy Wierch, 49º11’N, 19º47’E, 10 Aug. 1922, *Pawlowski s.n.* (S); Arva, lacum inferiorem Roháč see, 49º 12’N, 19º 45’E, 25 Jul. 1928, *Rechinger s.n.* (S); Raczkowa sjö, 49º11’N, 19º48’E, 3 Aug. 1813, *Wahlenberg s.n.* (UPS).

6. TRISETUM GLACIALE (Bory) Boiss., Elench. Pl. Nov.: 87. 1838. *Avena glacialis* Bory, Ann. Gén. Sci. Phys. 3: 6. 1820 [“Glacialis”]. *Trisetaria glacialis* (Bory) Paunero, Anales Jard. Bot. Madrid 9: 514. 1950.—TYPE: SPAIN. Granada, Sierra Nevada, Aug 1837, *P.E. Boissier 186* (neotype, designated here, G-00176302 image!; isoneotypes, B-10_0250162!, B-10_0347071!, BM-001134049 image!, G-00176303!, G-00176305 image!, GH!, GOET!, JE!, K!, L-1346396!, L-1346397!, L-1346398!, L-1346399!, L-1346401!, LE!, M-0210838!, MA-8022!, MO-1604193!, MPU!, MW!, NY-431723!, O-V2126600!, O-V2126602!, P-00731516!, P-02219574!, P-02219579!, P-02219569!, P-03364420!, RO image!, US!, W-0025052 image!, W-1889-0242183!.

Trisetum antonii-josephii Font Quer & Muñoz Med., Anales Jard. Bot. Madrid 6: 495. 1946 [“Antonii-Josephii”]. *Trisetaria antonii-josephii* (Font Quer & Muñoz Med.) Paunero, Anales Jard. Bot. Madrid 9: 516. 1950.—TYPE: SPAIN. Granada, Sierra Nevada, Jerez del Marquesado, Barranco del Nacimiento del río Alhorí, 37º07’N 3º14’W, 19 Jul 1923, *P. Font Quer & J.M. Muñoz Medina s.n.* (holotype, BC-81358!).

Herb (3–)8.8–14.4(–19.5) cm high, cespitose to densely cespitose, shortly rhizomatous, culm 0.3–0.7 mm diam., straight, glabrous, with some dispersed hairs mostly on the upper part, sometimes puberulous, with hairs 0.1–0.6(–1.2) mm long; nodes (2–)3(–4), concentrated in lower part of the culm, included in the sheaths, pubescent, yellowish. Basal leaf-sheaths distinctly veined, not inflated, densely pubescent, with hairs up to 1.2 mm long, with a dense layer of the oldest ones decomposed into fibers, yellowish to greenish; basal leaf-blades (0.9–)1.4–4.2(–8.4) cm × (0.7–)1.6–2.5(–3) mm, rigid, flat, sometimes conduplicate, with the central nerve and margins thickened, cartilaginous, densely pubescent, with patents hairs 0.1–0.5(–0.9) mm long, abaxially and adaxially, greyish to greenish; top culm leaf-sheaths (1.8–)2.5–3.7(–4.6) cm long, involving most of the culm, distinctly veined, pubescent, with long and short hairs, without cilia on the margins; top culm leaf-blades (0.2–)0.5–1.5(–2.6) cm × (0.6–)1.2–2(–2.5) mm, flat to conduplicate, densely pubescent abaxially and adaxially, with short and some scattered long hairs

(0.05–)0.1–0.5(–0.6) mm long, greenish to greyish, sometimes slightly yellowish; inner collar region densely pubescent, with hairs 0.1–0.3(–0.7) mm long; ligules (0.3–)0.5–0.7(–1) mm long, acute, laciniate, slightly strigose, puberulous on the upper part, with hairs 0.2–0.4(–0.9) mm long. Basal node of the panicle glabrous, sometimes with dispersed hairs 0.1–0.2(–0.3) mm long. Panicles (2.3–)3–4.2(–4.8) × (0.7–)1–1.4(–1.8) cm, ovate in outline, from compact to somewhat lax; rachis glabrous to sparsely pubescent, with hairs 0.1–0.3 mm long; longest basal branches (0.3–)0.4–0.9(–1.1) cm long. Spikelets (4.2–)4.8–6(–7) × (1–)1.6–2.4(–3.8) mm, (1)2(3)-flowered; pedicels (1–)1.5–2.2(–3.6) mm long, from sparsely pubescent to pubescent, with hairs 0.1–0.3 mm long. Glumes unequal to subequal [ratio lower glume length/upper glume length = (0.75–)0.85–0.92(–0.98)]; lower glume (3.2–)4.2–5(–5.7) × (0.6–)0.8–1.2 mm, broadly lanceolate, sometimes narrowly lanceolate [ratio lower glume width/lower glume length = (0.1–)0.2–0.25(–0.3)], acuminate to long acuminate, (2–)3-nerved, glabrous, sometimes with very short hairs up to 0.06 mm long on the upper part of the margins and central nerve, greenish on the central basal part, sometimes purplish, laterals and upper part purplish, sometimes yellowish; upper glume (4.2–)4.7–5.6(–6.5) × (1–)1.2–1.6(–2.1) mm, broadly lanceolate, sometimes lanceolate [ratio upper glume width/upper glume length = (0.17–)0.24–0.33(–0.48)], acuminate to long acuminate, 3-nerved, glabrous, sometimes with scattered and very short hairs up to 0.07 mm long on the midrib and upper part of the margins, greenish on the central basal part, sometimes purplish, margins and upper part purplish, sometimes yellowish; rachilla segments between first and second floret 1–1.5(–2.2) mm long, with hairs (0.7–)1–1.4(–2) mm long; rachilla segments to sterile floret (1–)1.3–1.7(–1.9) mm long, with hairs (0.5–)0.8–1.1(–1.7) mm long. Lemmas (3.5–)4–4.5(–5.6) × (0.6–)0.8–1.2 mm, broadly lanceolate [ratio lemma width/lemma length = (0.24–)0.28–0.37(–0.45)], glabrous to strigulose, greenish, sometimes yellowish, purplish on the laterals and upper part; apical teeth (0.2–)0.4–1(–2) mm long, with aristules 0.2–0.5(–0.9) mm long, rarely without; awn (4.5–)4.8–7.4(–10.7) mm long, inserted (1.9–)2.3–2.6(–3) mm from the base [ratio awn insertion from the base length/lemma length = (0.45–)0.54–0.63(–0.71)], slightly geniculate, twisted at the base when mature, with very short adpressed hairs up to 0.05 mm long; callus (0.15–)0.2(–0.3) mm long, elliptic, sometimes elliptic-oblong, with hairs (0.2–)0.3–0.6(–0.9) mm long. Paleas (3–)3.6–4.1(–4.6) × (0.6–)0.8–1(–1.4) mm (ratio palea length/lemma length = 0.8–1.05), narrowly elliptic, margins with short antrorse hairs; teeth (0.2–)0.3–0.6(–0.8) mm long, with short antrorse hairs of less than 0.1 mm long. Lodicules 0.4–0.7(–0.9) mm long, irregularly dentate. Anthers (0.9–)1.7–2.6(–2.9) mm long. Ovary (0.3–)0.5–0.8(–2) mm long, from sparsely puberulous to puberulous on the upper part, with hairs 0.1–0.3 mm long, rarely glabrous. Caryopsis 2.5–3.1 × 0.5–0.8 mm, more or less fussiform. Figure 17.

Chromosome number—2*n* = 14 (Küpfer, 1968).

Illustrations—Paunero (1950: 548, lám. XII, sub *Trisetaria glacialis*; 549, lám. XIII, sub *Trisetaria glacialis*; 550, lám. XIV, sub *Trisetaria antoni-josephii*; 551, lám. XV, sub *Trisetaria antoni-josephii*; 552, lám. XVI, sub *Trisetaria antoni-josephii* and *Trisetaria glacialis*; 553, lám. XVII, sub *Trisetaria antoni-josephii* and *Trisetaria glacialis*; 554, lám. XVIII, sub *Trisetaria antoni-josephii* and *Trisetaria*

Figure 17. *Trisetum glaciale*. Image of an isoneotype (B-10_0250162).

glacialis); Chrtek & Jirásek (1963: 575, fig. 2, 4–6); Chrtek (1965: 214, Abb. 2, 1; 215, Abb. 3, 8; 217, Abb. 4, 4–5; 218, Abb. 5, 4–5).

Phenology—Trisetum glaciale has been collected in flower and fruit from June to September.

Distribution and Habitat—Endemic to the Sierra Nevada, in southern Spain; 2400–3400 m of elevation; in mountain pastures, in fissures of schist soils. Figure 14.

Discussion—Burdet et al. (1981: 580) proposed *Boissier 186* as lectotype, which seems to be a mistake as that was not original material. After searching in Bory´s collection, no original material has been found. Nevertheless, the specimens collected by Boissier come from the type locality, and match the current concept of *T. glaciale*. Therefore, it is appropriate to consider Burdet proposal as a neotypification (art. 9.9 of ICN).

The IPNI website has two entries for *Avena glacialis*, one attributed to Bory (1820), and the other to Boissier (1838). However, Boissier (1838) made a combination of Borys´s name in the genus *Trisetum*, not *Avena*, and explicitly referred to the basionym as: "*Avena glacialis Bor. Fl. nº* 20". Consequently, the name "*Avena glacialis* Boiss." has no standing and should be disregarded.

Trisetum glaciale is characterized by its densely tufted habit and short height [(3–)8.8–14.4(–19.5) cm], and by having short and rigid leaf-blades with a thickened midrib and margins, the margins also cartilaginous, pubescent top culm leaf-sheaths, panicles ovate in outline, subequal glumes [(ratio lower glume length/upper glume length = (0.75–)0.85–0.92(–0.98)], palea almost or as long as the lemma (ratio palea length/lemma length = 0.8–1.05), and ovaries from sparsely to densely puberulous apically, rarely glabrous.

Font Quer and Muñoz Medina (Font Quer, 1946) described another species from Sierra Nevada, *T. antonii-josephii*. It was separated from *T. glaciale* by its narrower and 1-veined lower glumes, and its lanceolate lemmas, with longer awns. Paunero (1950) made a more detailed study, indicating the difference in the lemma apex (acute in *T. antonii-josephii*, and obtuse in *T. glaciale*), and noting that the leaf structure, which varies widely between the species of the genus, as well as the ovary indumentum, is identical in both species. Romero (2009) recognized both species and indicated that specimens with intermediate characters have been found, probably of hybrid origin. In the material studied, we determined that the number of nerves in the lower glumes depends on the stage of development of the specimen, and is, therefore, not a good taxonomical character state for discriminating these taxa. Awn length is also variable in specimens of the same population. Therefore, we consider *T. antoni-josephii* to be a synonym of *T. glaciale*.

Additional specimens examined—**SPAIN. Granada:** Sierra Nevada, ascensión al Veleta desde la parada del microbús, bordes del Corral del Veleta, 37º3'N, 3º22'W, 24 Jul. 2013, *Barberá et al. 937PB* (MA); ascensión al Veleta, trincheras junto a la parada del microbús, 37º3'N, 3º22'W, 24 Jul. 2013, *Barberá et al. 939PB* (MA); Caldera du Mulhacen, 37º3'N, 3º18'W, 25 Jul. 1851, *Bourgeau 1517* (G, GOET, K, P); Valle de Lanjarón, Peñón Elorrieta, 37º2'N, 3º23'W, 6 Jul. 1930, *Ceballos* & *Vicioso s.n.* (MA); Monachil, inter Laguna de Las Yeguas et Pico Veleta, 37º3'N, 3º22'W, 26 Jul. 1978, *Charpin et al. 15297* (G); autour des lagunas de Río Seco, 37º3'N, 3º20'W, 15 Jul. 1983, *Defferrard 4317* (G); Monte Pelado, 37º6'N, 3º15'W, 24 Aug. 1923, *Font Quer s.n.* (BC, BM, GDA, JE, K, MA, S, UPS); Laguna de la Caldera, 37º3'N, 3º19'W, 8 Aug. 1924, *Ginzberger s.n.* (W); Picacho de Veleta, 37º3'N, 3º22'W, 1 Aug. 1879, *Huter et al. 1172* (B, BM, G, GB, HBG, K, LE, M, MPU, P, PR, W, WU); Raspones de Río Seco, 37º3’N, 3º20’W, 4 Aug. 1997, *Martínez Lirola* & *Vargas s.n.* (GDA); entre 1ª y 2ª laguna del río Lanjarón, 37º2’N, 3º24’W, 28 Jul. 1997, *Martínez Lirola* & *Vargas s.n.* (GDA); Picacho de Veleta, 37º3’N, 3º22’W, 22 Aug. 1974, *Merxmüller* & *Lippert 29582* (M); Capileira, alrededores de la Laguna de Majano, 37º2’N, 3º19’W, 13 Aug. 1978, *Molero Mesa s.n.* (GDA); Pico del Veleta, 37º3’N, 3º22’W, 25 Jul. 1947, *Muñoz Medina* & *Serrano s.n.* (ARAN, BC, F, GDA, MA); Picacho de Veleta, 37º3’N, 3º22’W, Aug. 1891, *Porta* & *Rigo 630* (B, G, GB, JE, K, M, MA, NY, P, S, W, WU); subida al Pico Mulhacén, 37º3’N, 3º18’W, 18 Jun. 2014, *Quintanar et al. 5226* (MA); subida al Mojón Alto, entre la loma de Maitena y el Calvario, 37º7’N, 3º17’W, 21 Jun. 2014, *Quintanar et al. 5273* (MA); al pie del Collado de las Buitreras, 37º6’N, 3º16’W, 21 Jun. 2014, *Quintanar et al. 5275* (MA); bajada del Collado de las Buitreras en el camino hacia Cerro Pelao, 37º6’N, 3º15’W, 21 Jun. 2014, *Quintanar et al. 5277* (MA); Cerro Pelao, 37º6’N, 3º15’W, 21 Jun. 2014, *Quintanar et al. 5278* (MA); Barranco del Río Alhorí y Ventisquero de los Caballones, 37º6’N, 3º15’W, 21 Jun. 2014, *Quintanar et al. 5279* (MA); Laguna de la Caldera hasta la de Majano, 37º2’N, 3º19’W, 4 Aug. 1981, *Romero s.n.* (GDA); Barranco de San Juan, 37º4’N, 3º22’W, 18 Jul. 1981, *Romero s.n.* (GDA); alrededores de la Laguna de Aguas Verdes, 37º2’N, 3º22’W, 22 Jul. 1980, *Romero* & *Morales s.n.* (GDA); Refugio de Elorrieta, 37º2’N, 3º23’W, 24 Jul. 1981, *Romero* & *Sánchez s.n.* (GDA); Mulhacén, Laguna La Caldera, 37º3’N, 3º22’W, 28 Jul. 1967, *Segura Zubizarreta s.n.* (MA); Sierra Nevada, 4 Aug. 1845, *Willkomm 1281* (MPU, P); Picacho de Veleta, 37º3’N, 3º22’W, 31 Jul. 1876, *Winkler s.n.* (B, M, MPU, P, WU).

7. TRISETUM GRACILE (Moris) Boiss., Voy. Bot. Espagne 2: 654. 1844. *Avena gracilis* Moris, Stirp. Sard. Elench. 1: 50. 1827. *Trisetum morisii* Trin., Bull. Sc. Acad. Petersb. 1: 66. 1836, nom. illeg. superfl.—TYPE: ITALY. Sardinia, Nuoro prov., Gennargentu Mts, 40º01’N, 9º20’E, *G.G. Moris s.n.* (lectotype, designated here, LE!; possible isolectotypes, JE-00018855!, P-02222289!, P-02222295!).

Trisetum conradiae Gamisans, Candollea 26: 322. 1971. *Trisetaria conradiae* (Gamisans) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 382. 1996. *Trisetum gracile* subsp. *conradiae* (Gamisans) Gamisans, Fl. Corsica: 255. 2007.—TYPE: FRANCE. Corsica, Incudine Massif, 41º51’N, 9º12’E, 14 Jul. 1968, *J. Gamisans 68* (holotype, Gamisans private herbarium; isotype, G-00100183!).

Trisetum gracile var. *morisianum* Gamisans, Candollea 28: 54. 1973.—TYPE: ITALY. Sardinia, Ogliastra province, Punta La Marmora mountain, 39º59’N, 9º19’E, 24 Jun. 1970, *J. Gamisans & M. Reille S-2399* (holotype, G-00386420!).

Herb (4.5–)8.9–12.5(–18.2) cm high, cespitose to densely cespitose, shortly rhizomatous, culm (0.2–)0.4–0.6 mm diam., often bent at the nodes, glabrous, sometimes with hairs 0.2–0.4 mm below the basal node; nodes 2–3(–4), mostly concentrated in lower part of the culm, not included in the sheaths, rarely included, glabrous, blackish. Basal leaf-sheaths distinctly veined, somewhat inflated, glabrous to sparsely pubescent, with hairs up to 0.1 mm long, with a dense layer of the oldest ones decomposed into fibers, yellowish to brownish, rarely greenish; basal leaf-blades 1–2(–4) cm × (0.6–)1.3–1.7(–2.6) mm, rigid, flat to convolute or revolute, with the central nerve thickened, glabrous to sparsely puberulous adaxially, pubescent abaxially, also in the margins, with hairs (0.05–)0.1–1.2(–1.8) mm long, greenish to greyish; top culm leaf-sheaths (1.4–)2–3.2(–4) cm long, distinctly veined, somewhat inflated, glabrous, without cilia on the margins; top culm leaf-blades (0.2–)0.3–1(–1.8) cm × (0.6–)0.8–1.2 mm, conduplicate, rarely flat, parallel to the culm, glabrous to sparsely pubescent abaxially and adaxially, with hairs up to 0.2 mm long on the margins, brownish to yellowish, sometimes greyish; inner collar region glabrous, sometimes with few scattered hairs up to 0.3 mm long on the margins; ligules 0.5–0.9 mm long, laciniate to shortly irregularly toothed, with hairs 0.1–0.3 mm long on the upper part. Basal node of the panicle glabrous. Panicles (1.3–)1.6–2.5(–3.1) × (0.7–)1–1.5(–1.8) cm, ovate in outline, somewhat dense; rachis internodes glabrous to sparsely pubescent, with hairs 0.05–0.2 mm long; longest basal branches (0.2–)0.3–0.9(–1.1) cm long. Spikelets (4–)5.2–6.4(–6.7) × (1.7–)2.4–4(–5.2) mm, 2-3-flowered; pedicels (1.4–)1.8–3.2(–4.4) mm long, sparsely puberulous, with hairs up to 0.2 mm long. Glumes slightly subequal to almost equal [ratio lower glume length/upper glume length = (0.79–)0.82–0.89(–0.97)]; lower glume (3.6–)4–5.6(–6.5) × 1.2–1.6(–2.4) mm, elliptic to broadly lanceolate [ratio lower glume width/lower glume length = (0.28–)0.3–0.35(–0.4)], acuminate to long acuminate, 1(–2)-nerved, glabrous, greenish surrounded by purplish, margins hyaline; upper glume (4–)4.7–6.6(–6.8) × (1.8–)2–2.4 mm, elliptic to oblong, sometimes narrowly elliptic or narrowly lanceolate [ratio upper glume width/upper glume length = 0.33–0.43(–0.49)], acuminate, sometimes long acuminate, 3-nerved, glabrous, greenish surrounded by purplish, margins hyaline; rachilla segment between first and second floret 0.6–1.2 mm long, with hairs (1.6–)2–2.4(–3) mm long; rachilla segment to sterile floret (0.8–)1–1.3 mm long, with hairs (0.7–)1–1.5(–2) mm long. Lemma (3–)4–5(–5.6) × 1.2–1.6(–2.4) mm, narrowly elliptic to narrowly lanceolate, sometimes broadly lanceolate [ratio lemma width/lemma length = (0.26–)0.3–0.36(–0.47)], glabrous to pubescent, with hairs (0.05–)0.6–1.4(–2) mm long between the awn and the base, greenish, sometimes yellowish, surrounded by a purplish flush; apical teeth (0.1–)0.2–0.4 mm long, with aristules 0.3–0.6(–1) mm long; awn (4.5–)5–6.6(–9.1) mm long, inserted (1.3–)1.8–2.2(–2.8) mm from the base [ratio awn insertion from the base length/lemma length = (0.34–)0.41–0.49(–0.51)], geniculate and slightly twisted at the base, with very short adpressed hairs up to 0.05 mm; callus 0.1–0.4 mm long, elliptic to orbicular, with hairs (0.7–)1–1.3 mm long. Paleas (2.7–)3.7–4.2(–4.6) × 0.7–1.3 mm [ratio palea length/lemma length = (0.66–)0.76–0.84(–1.1)], elliptic or narrowly elliptic to slightly oblanceolate, margins glabrous; teeth (0.1–)0.2–0.4 mm long, glabrous or with short antrorse hairs. Lodicules (0.6–)0.9–1.2(–1.8) mm long, entire, sometimes with 2 lobules or irregularly dentate. Anthers (1.4–)1.8–2.3(–3) mm long. Ovary 0.5–1(–2) mm long, glabrous. Caryopsis 1.5–2.6 × 0.4–0.7 mm, oblong or narrowly elliptic. Figure 18.

Chromosome number—2*n* = 14 (Gamisans, 1973).

Additional illustrations—Fiori & Paoletii (1895: 27, 230); Chrtek & Jirásek (1963: 575, fig. 2, 1–3); Chrtek (1965: 214, Abb. 2, 4–5; 215, Abb. 3, 8; 217, Abb. 4, 6–7; 218, Abb. 5, 1–3); Gamisans (1971: 323, fig. 1, 1–5; 325, fig. 2, 1–3); Jeanmonod & Gamisans (2007: XXX, fig. 32, b).

Phenology—*Trisetum gracile* has been collected in flower and fruit from May to August.

Distribution and Habitat—This species is endemic to the mountains of southern Corsica and Sardinia. It grows in poor soils of granitique sands at 1300–2100 m. Figure 14.

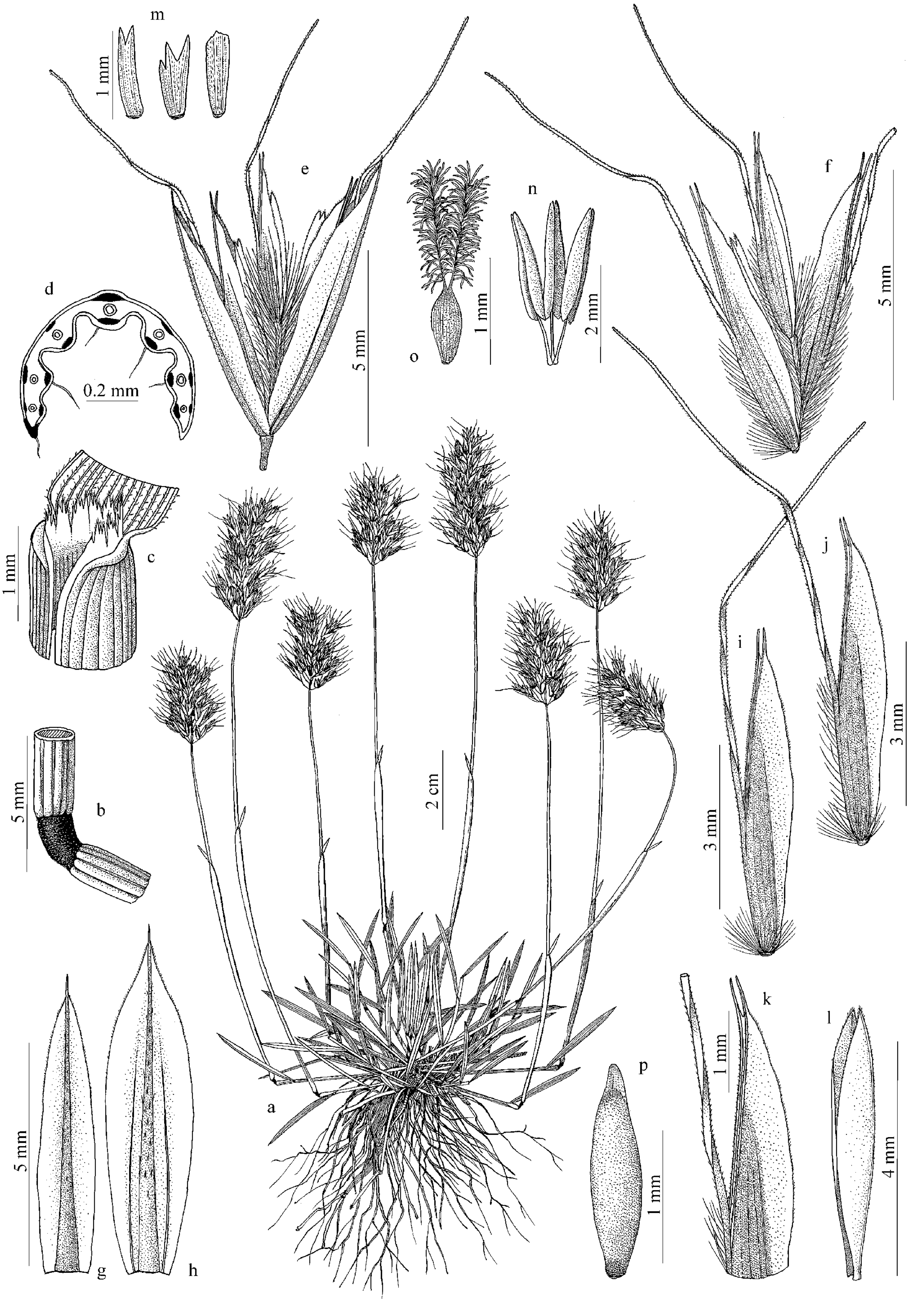

Figure 18. *Trisetum gracile*. a. Habit. b. Portion of the culm and node. c. Portion of sheath, ligule, and portion of the blade. d. Transverse section of leaf-blade. e. Spikelet. f. Florets. g. Lower glume, dorsal view. h. Upper glume, dorsal view. i. Floret. j. Floret. k. Lemma, upper part, lateral view. l. Palea, lateral view. m. Lodicules.n. Stamens. o. Pistil. p. Caryopsis. a based on *Gamisans 14148*, G-00220037; b-h, j-o based on *Reverchon 312* (S); i based on *Barberá & Quintanar 1441PB* (MA); p based on *Müller s.n.* (M-0223271).

Discussion—Moris´ herbarium is kept at TO, but Dr. Laura Guglielmone kindly informed us that the Moris´ collection was closed for security reasons. Fortunately, we have found original material at some herbaria. There is a specimen at LE with a label handwritten by Moris, and collected in the Gennargentu Mountains, one of the localities mentioned in the protologue, which has been selected as lectotype. P and JE specimens are potential isolectotypes, although their localities are less specific (the labels only read Sardinia).

Trisetum gracile and *T. glaciale* are two species of the section *Trisetum* with a similar habit, being densely tufted, having the shortest height [(4.5–)8.9–12.5(–18.2) cm, and (3–)8.8–14.4(–19.5) cm, respectively], rigid leaves with a thickened midrib, short upper leaf-blades [(0.2–)0.3–1(–1.8) cm, and (0.2–)0.5–1.5(–2.6) cm, respectively], panicles ovate in outline, and subequal glumes. Nevertheless, *T. gracile* is clearly differenciated from *T. glaciale* by its blackish nodes usually exerted from the sheaths, with culms often bent at the nodes and more or less glabrous, sheaths somewhat inflated, long rachilla hairs [(1.6–)2–2.4(–3) mm long, and (0.7–)1–1.4(–2) mm, respectively], lemmas usually hairy between its base and the awn insertion, awn inserted slightly below the middle of the lemma [ratio awn insertion from the base length/lemma length = (0.34–)0.41–0.49(–0.51)], long callus hairs [(0.7–)1–1.3 mm, and (0.2–)0.3–0.6(–0.9) mm, respectively], and glabrous ovaries.

Gamisans (1971) described a new species from Corsica very close to *T. gracile*, *T. conradiae*, based on its glabrous lemmas, among others characters. After collecting more material, Gamisans (1973) realized that this character was the only one that separated both species. Latter, Jeanmonod and Gamisans (2007) recognized *T. conradiae* at subspecific rank. In our own observations, specimens with and without hairy lemmas have been collected in the same populations, varying in the density and the length of the hairs [(0.05–)0.6–1.4(–2) mm]. In other species of the section, such as *T. flavescens* subsp. *griseovirens*, specimens with hairy lemmas have been found, hairs sometimes appearing only in the proximal lemma. Consequently, we agree with Tison & Foucault (2014) that this character does not have any taxonomical importance here, and *T. conradiae* is considered a synonym of *T. gracile*.

Additional specimens examined—**FRANCE. South Corsica:** Monte Incudine, Plateau de Cuscione, 41º50’N, 9º10’E, 5 Jul. 2014, *Barberá & Quintanar 1439PB* (MA); *Barberá & Quintanar 1440PB* (MA); *Barberá & Quintanar 1441PB* (MA); crête Monte Incudine, Tintennaga, 41º51’N, 9º13’E, 24 Jul. 1985, *Gamisans 11703* (G); Pianu di Cuscione, Fonda di Serra Longa, 41º50’N, 9º8’E, 1 Jul. 1989, *Gamisans 14148* (G); Monte Incudine, Foce Aperta, 41º52’N, 9º12’E, 6 Jul. 1989, *Gamisans 14203* (G); Massif de l´Incudine, Coscione, crête au S de la Punta Tozzarella, 41º51’N, 9º11’E, 1 Aug. 1972, *Gamisans 2242* (C); Massif de l´Incudine, crête à 100 m au SE de Bocca Chiralba, versant N, 41º50’N, 9º11’E, 1 Aug. 1972, *Gamisans 2247-I* (MPU); crête au S de la Punta Tozzarella, 41º51’N, 9º10’E, 25 Jul. 1974, *Gamisans 3591* (G); crête au S de Bocca Chiralba, 41º50’N, 9º11’E, 25 Jul. 1974, *Gamisans 3598* (G); Macizo del monte Incudine, meseta de Coscione, 41º50’N, 9º8’E, 6 Jul. 2014, *Quintanar & Barberá 5390AQ* (MA). **ITALY. Sardinia, Nuoro prov.:** Fonni, Gennargentu, Bronco Spina, 40º1’N, 9º18’E, 3 Jun. 2003, *Castroviejo et al. 17028* (MA); Gennargentu, Monte di Scudo, versant SW, 40º1’N, 9º19’E, 23 Jun. 1970, *Gamisans S-2394bis* (G); Monte Gennargentu, 40º1’N, 9º19’E, Jul. 1827, *Müller s.n.* (BM, H, HBG, JE, LE, M, PR, WU). **Sardinia, Sassari prov.:** Monte Limbara, lors d´un chemin près de l´extremité de la route, 40º51’N, 9º10’E, 30 May 1983, *Charpin et al. AC17871* (G); Tempio, Monte Limbardo [Limbara], 40º51’N, 9º10’E, 4 Jul. 1882, *Reverchon 312* (B, BM, G, JE, K, LE, M, MA, MO, MPU, NY, P, PR, UPS, WU); *Reverchon s.n.* (B, G, GB, GOET, H, HBG, JE, L, M, MPU, NY, P, PR, RO, S, UPS, US, WU).

8. TRISETUM LACONICUM Boiss. & Orph. in Boiss., Diagn. Pl. Orient., ser. 2, 4: 129. 1859. *Avena laconica* (Boiss. & Orph.) Nyman, Syll. Fl. Eur. Suppl.: 71. 1865. *Trisetaria laconica* (Boiss. & Orph.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135: 383. 1996.—TYPE: GREECE. Peloponnese: Malevós Mt., near Vrancopigadou, 37º37'N, 22º31'E, 19 Jul 1850, *T.G. Orphanides s.n.* [lectotype, designated by Tan & Iatrou (2001: 450), G-BOIS image!; isolectotypes, B-10_0508993!, JE-18853!, P-3365069!, W!]. Figures 9d, 10c, 15b.

Trisetum rechingeri Chrtek, Acta Univ. Carol., Biol. 1966: 92. 1967.—TYPE: GREECE. Central Greece: Euboea, Dirfi Mt., 38º37'N, 23º50'E, 7 Aug. 1858, *T.H.H. von Heldreich 3522* (holotype, P not seen; isotype, W!).

Herb 38.5–83.5 cm high, not cespitose, rhizomatous, culm 0.5–1.1 mm diam., straight, glabrous; nodes 4–6, separated along the culm, included or not in the sheaths, glabrous, yellowish or brownish. Basal leaf-sheaths pubescent, with hairs 0.5–1 mm long, decaying into fibers, brownish; basal leaf-blades 5–6 cm × 3.6–5 mm, flat, pubescent, with hairs 0.3–1 mm long, also on the margins, brownish to greyish; top culm leaf-sheaths 9.7–25 cm long, glabrous, with cilia; top culm leaf-blades 3.1–11.2 cm × 1.3–4 mm, flat, sometimes slightly inrolled and parallel to the culm, pubescent abaxially, glabrous adaxially, with hairs 0.2–0.6 mm long, also on the margins, greenish to greyish; inner collar region glabrous, sometimes with scattered hairs up to 0.1 mm long on the margins; ligules 2.5–3.2 mm long, irregularly dentate to laciniate, glabrous or with scattered hairs up to 0.2 mm long on the surface and upper part. Basal node of the panicle glabrous to sparsely pubescent with adpressed hairs up to 0.05 mm long. Panicles 8–19 × 1.5–6 cm, narrowly elliptic to oblong in outline, somewhat dense; rachis internodes glabrous to sparsely pubescent, with hairs up to 0.05 mm long; longest basal branches 1.3–2.4 cm long. Spikelets 8–9.2 × 2.3–4.8 mm, 3-4-flowered; pedicels 5–6.3 mm long, sparsely pubescent, with hairs up to 0.1 mm long. Glumes unequal (ratio lower glume length/upper glume length = 0.69–0.74); lower glume 4.3–5.4 × 0.8–1.1 mm, narrowly lanceolate (ratio lower glume width/lower glume length = 0.18–0.2), long acuminate, 1-nerved, glabrous, with hairs up to 0.05 mm long on the upper part and margins, yellowish to greenish; upper glume 6.2–7.3 × 1.4–2.1 mm, narrowly elliptic to lanceolate (ratio upper glume width/upper glume length = 0.22–0.29), acuminate, 3-nerved, glabrous, with scattered hairs up to 0.05 mm long on the upper part of the central nerve and margins, yellowish to greenish; rachilla segment between first and second floret 1.2–1.7 mm long, with hairs 1.5–2.5 mm long; rachilla segment to sterile floret 1.3–1.6 mm long, with hairs 0.7–1.1 mm long. Lemmas 6.5–6.6 × 0.8–1.1 mm, narrowly elliptic to narrowly lanceolate (ratio lemma width/lemma length = 0.21–0.23), scabridulous, with hairs up to 0.05 mm long, greenish to yellowish, sometimes with a purplish flush; apical teeth 0.2 mm long, with aristules 0.4–0.5 mm long; awn 6.3–7.2 mm long, inserted 4.1–4.5 mm from the base (ratio awn insertion from the base length/lemma length = 0.62–0.65), strongly bent near the base, more or less twisted at the base, with very short adpressed hairs up to 0.05 mm long; callus 0.3 mm long, elliptic to oblong, with hairs 0.6–0.9 mm long. Paleas 5.8–6 × 1.1–1.5 mm (ratio palea length/lemma length = 0.89–0.9), narrowly elliptic, ciliate on the upper part; teeth 0.3–0.4 mm long, with short antrorse hairs. Lodicules 0.6 mm long, with regular teeth or laciniate. Anthers 2.4–3.1 mm long. Ovary 0.8–0.9 mm long, glabrous. Caryopsis not seen.

Chromosome number—not known.

Phenology—Trisetum laconicum has been collected in flower from June to August.

Distribution and habitat—Trisetum laconicum is endemic to Greece, and is only known from two collections: a) Malevos Mountains in the south of the Peloponnese, and b) Dirfi Mountains in Euboea Island; on limestone rocks and cliffs. It has been found at elevations from 1220 to 1500 m. Figure 16.

Discussion—Boissier and Orphanides (Boissier, 1859) separated the Malevos Mountains species, *T. laconicum*, from *T. flavescens* mainly by its densely hairy leaves, bigger spikelets, and longer rachilla hairs. Apart from those characters, we have also discerned that *T. laconicum* has longer ligules (2.5–3.2 mm), pedicels (5–6.3 mm), lemmas (6.5–6.6 mm), callus indumentum (0.6–0.9 mm), and paleas (5.8–6 mm) than *T. flavescens*. Another distinguishing characteristic is the awn shape, which is strongly bent near the base in *T. laconicum* and geniculate to slightly geniculate in *T. flavescens*. We found no or only minor overlap with *T. flavescens* in any of the previously mentioned characters. For this reason, and considering that only the type material is available, *T. laconicum* is treated as a separated species.

Chrtek (1967a) described *T. rechingeri* from Euboae Island, based on a single sheet (*Heldreich 3522*, P). He indicated that *T. laconicum* was the closest species to *T. rechingeri*, separating them mainly by its smaller size, shorter rachilla hairs and spikelets. Chrtek (1967a) included both species in a serie within *T.* sect. *Rigida*, named *T.* ser. *Laconica,* and characterized by its general habit and shorter rachilla hairs. Jonsell (1980) decided to consider these species as conspecific until more material is available. Furthermore, Strid (2016) indicated that no more material have been collected on Mt. Dirfis, and considered that *T. rechingeri* represents individual variation within *T. laconicum*. We agree with these latter authors, and therefore we consider *T. rechingeri* to be a synonym of *T. laconicum*.

Miscellaneous doubtful, invalid, and excluded (from Trisetum) names

Avena alpestris DC.—The IPNI website attributed the name *Avena alpestris* to de Candolle. De Candolle (Lamarck, 1815), however, when recorded *Avena alpestris*, indicated "*A. Alpestris*. Host. gram. 3, p. 27", suggesting that he was not publishing a nom. nov. Consequently the isonym "*Avena alpestris* DC." should be disregarded (Art. 6, Note 2).

Avena flavescens var. *vulgaris* Alef., Landw. Fl.: 350. 1866, nom. inval. (Art. 24.3).—Alefeld (1866) divided *Avena flavescens* in three varieties, and he used the epithet “vulgaris” to the first, purporting to indicate the taxon containing the type of *Avena flavescens*.

Avena sesquitertia Host—The IPNI website attributed this to Host (1797) the name *Avena sesquitertia*. Host (1797), however, when recorded *Avena sesquitertia*, repeated the polynomial of Linné (1767) "A. paniculata, calycibus subtrifloris, flosculis omnibus aristatis, receptaculis barbatis. *Syst. veget.* p. 122” suggesting that he was not publishing a new taxon name. Consequently the isonym "*Avena sesquitertia* Host" should be disregarded (Art. 6, Note 2).

Avena tenuis Moench, Methodus: 195. 1794, nom. illeg. superfl. for *Avena dubia* Leers [= *Ventenata dubia* (Leers) Cosson].

Rebentischia flavescens Opiz, Lotos 4: 104. 1854, nom. inval., as syn. of *Trisetum flavescens*.

Trisetum alpestre var. *viviparum-macranthum* Schur, Oesterr. Bot. Z. 10: 74. 1860, nom. inval. (Art. 23.6).

Trisetum ciliare (Kit. ex Schult.) Domin, Preslia 13-15: 41. 1935, nom. inval.—The combination proposed by Domin (1935) is based in *Avena ciliaris* Kit. ex Schult., Oestr. Fl., ed. 2, 1: 268. 1814, nom. nud.

Trisetum debile Chrtek, Folia Geobot. Phytotax. 25: 334. 1990.—TYPE: CHINA. Yunnan prov., Dschungdien, 27º49'N 99º42'E, 22 Aug 1915, *H. R. E. Handel-Mazzetti 7739* (holotype, W!). The type is the only original material that could be located. It is a fragment that cannot be identified to species, but it may belong to one of the taxa allied to the genus *Trisetum*. Its slender habit may be due to the fact that the specimen was immature.

Trisetum flavescens var. *bulbosum* Holla ex Asch., Fl. Brandenburg 1: 830. 1864.—TYPE: GERMANY. Brandenburg, *Holla s.n.* (no original material found). Ascherson description seems to refer to *Arrhenatherum bulbosum* C. Presl.

Trisetum flavescens subsp. *copiosum* Printz, Veg. Siber.-Mongol. Front.: 124. 1921.—TYPE: RUSSIA. Krasnoyarsk Krai, Minusinsk distr., Jul. 1914, *K. Printz s.n.* (lectotype, designated here, C!); as syn. of *Trisetum sibiricum* Rupr. subsp. *sibiricum*. This name was not included in Barberá et al. (2017b).

Trisetum flavescens var. *dimorphantha* Maire & Weiller, Fl. Afrique N. 2: 248. 1953, nom. inval. (Art. 39.1).

Trisetum flavescens subsp. *fuscum* Domin, Preslia, 13–15: 41. 1935, nom. inval., as syn. of *Trisetum ciliare* (Kit.) Domin

Trisetum flavescens var. *latifolium-majus* Schur, Oesterr. Bot. Z. 10: 77. 1860, nom. inval. (Art. 23.6).

Trisetum flavescens var. *sibiricum* (Rupr.) Ostenf. ex B. Fedtsch., Izv. Imp. Bot. Sada Petra Velikago 14(2): 64. 1913, as syn. of *Trisetum sibiricum* Rupr. subsp. *sibiricum*.—This name was not included in Barberá et al. (2017b).

Trisetum flavescens var. *subtriflorum-transsilvanicum* Schur, Oesterr. Bot. Z. 10: 76. 1860, nom. inval. (Art. 23.6).

Trisetum miegevillii Duval-Jouve ex Miégev., Bull. Soc. Bot. France 21: 47. 1874, nom. nud., as syn. of *Trisetum baregense* Laffitte & Miégev.

Trisetum tenue Roem. & Schult., Syst. Veg., ed. 15 bis [Roemer & Schultes] 2: 657. 1817, nom. illeg.—According to Jonsell (1978: 320), *Trisetum tenue* Roem. & Schult. is a nomen superfluum for *Avena dubia* Leers [*Ventenata dubia* (Leers) Cosson].

Trisetum transsilvanicum Schur, Oesterr. Bot. Z. 10: 77. 1860, nom. inval., as syn. of *Trisetum flavescens* var. *subtriflorum-transsilvanicum* Schur, Oesterr. Bot. Z. 10: 76. 1860.

Trisetum varium Schur, Oesterr. Bot. Z. 10: 75. 1860, nom. illeg. superfl.—This forgotten name is based on *Avena varia* Schur, Sertum Flor. Transs.: 85. 1853, which is a superflous name for *Avena carpatica* Host, Icon. Descr. Gram. Austriac. 4: 18, tab. 31. 1809, *Trisetum carpaticum* (Host) Roem. & Schult., Syst. Veg. 2: 663. 1817, *Trisetum flavescens* var. *carpaticum* (Host) Zapal., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 4: 107. 1904. Host's illustration clearly represents *Avenula pubescens* (Huds.) Dumort.

Trisetum yunnanense Chrtek, Folia Geobot. Phytotax. 25: 335. 1990.—TYPE: CHINA. Yunnan prov., near Lidjiang, 26º52'N 100º14'E, 18 Jul 1914, *H. R. E. Handel-Mazzetti 4212* "(H-M Diar. Nr. 664)" (holotype, W!; isotype, WU!). Chrtek (1990) described this species as remarkable for its robust habit, relatively short, rigid leaves and big spikelets. Wu & Phillips (2006) included this species in the *Flora of China*, indicating that the hairy ovary is unusual in *Trisetum* and that they did not see the type. The type material has a thicker scarious palea, a densely hairy ovary with long hairs, and an inmature caryopsis with a long linear hilum. Those characters fit well with the genus *Helictotrichon*, suggesting that this species belongs to this genus.

ACKNOWLEDGEMENTS

This work was financed by *Flora iberica* CGL2014–52787–C3–1–P, CGL2012–32914 and CGL2015–66161–P, projects of the Spanish Government, supported by FEDER funds. We are indebted to the curators and staff of the herbaria mentioned in Material and Methods for kindly providing specimens. We thank the editor and anonymous reviewers for their critical reviews of the manuscript and for their helpful suggestions during the editing process. We thank Ramón Morales for translations of manuscripts in German. Toni Buira and Marta Fernandéz-Albert for their technical support. J. A. Alejandre, A. Quintanar, and R. Soreng for their helpful comments and suggestions during the development of this work. A. Managlia, L. Guglielmone, and T. Khmil helped in finding rare literature, type materials, and geographical localities. Roman Ufimov for Russian translations and helped in finding rare literature, and in many aspects. And for the rest of personal from the Komarov Institute, N. N. Tzvelev, Dmitry Geltman, Elena Glazkova, Denis Melnikov, for their help and their welcoming attitude during our stay.

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SUPPORTING INFORMATION

Appendix 1. Index of collectors.Collections are listed alphabetically by first collector´s last name. Numbers in parentheses refer to the corresponding species in the text.

Aedo, C. 20819 (4.1); 20920 (4.1); Aedo, C. et al. 4165 (4.1); 4381 (4.1); 8571 (4.1); 10141 (4.1); 10371 (4.1); 11722 (4.1); 13498 (4.1); 14173 (4.1); 14339 (4.1); 25040 (4.1); Aedo, C. & S. Gama CA3874 (4.1); Ahti, T. B426 (4.1); Alanko, P. et al. 53269 (2); Aldén, B. 2862 (4.1); Alpay, O. 112 (4.1); 414 (4.1); Alston, H.G. & N.Y. Sandwith 1994 (4.1); American-Iranian Botanical Delegation 34291 (4.1); Andrés Sánchez, S. et al. SA233 (4.1); Arsène, L. 2317 (4.1). Barberá, P. et al. 937PB (6); 938PB (6); 939PB (6); 951PB (1); 953PB (1); 954PB (1); 956PB (1); 957PB (1); 958PB (1); 1059PB (4.1); Barberá, P. & A. Quintanar 897PB (4.1); 1062PB (1); 1439PB (7); 1440PB (7); 1441PB (7); Beck, C. 270 (1); 271 (1); Bécker, J. 24 (4.1); Bergmeier, E. 95-263 (4.1); Birkmane, K. 28952 (4.1); Blom, L. & L. Thorán 4497 (4.1); Bogolyubov, S.N. 343 (2); Böhle 13551 (4.1); Boissier, P.E. 186 (6); Bor, N.L. 11A (4.1); Borisova, A. 184 (4.1); Bornmüller, J. 2202 (4.1); Borssum Waalkes, J.V. 5114 (4.1); Bourgeau, E. 1517 (6); Brummitt, R.K. 60394 (4.1); Bunge, A.A. 98 (4.1); Burtt, B.L. B145 (4.1). Cabezas, F.J. et al. FJC419 (4.2); 625 (4.1); Calvo, J. JC4997 (4.1); Calvo, J. & A. Quintanar JC2558 (4.1); Cannon, J.F. & M.J. Cannon 2735 (4.1); Castroviejo, S. et al. 11464SC (4.1); 15391SC (4.1); 17028 (7); 17057 (7); 17555 (4.1); 17687 (4.1); SC17882 (4.1); Charpin, A. et al. 15297 (6); AC17871 (7). Davis, P.H. 67647 (4.2); Davis, P.H. & O. Polunin 22187 (4.1); 24393 (4.1); de Vogel, E.F. 329 (4.1); de Wilde, J.J. et al. 2641 (4.1); Defferrard, C. 4317 (6); Degen, A. 120 (1); Dersch, G. 4487 (1); Dietrich, W. 4176 (1); Dobignard, A. 3861 (4.1). Egorova, T.V. et al. 1512 (4.1); Elias, T.S. et al. 4268 (2); Emanuelsson, E. 1319 (4.1). Franzén, R. & J. Akeroyd 169 (4.1); Franzén, R. & A. Andersson 640 (4.1); Fröhner, S. 3868 (4.1); 3911 (4.1). Gagnidze, R. et al. 2799 (4.1); 2936 (4.1); Galán Cela, P. & A. Martín 591 (4.1); Gamisans, J. 11701bis (7); 11703 (7); 11715bis (7); 14148 (7); 14149bis (7); 14203 (7); 14205 (7); 14681 (4.1); 2192 (7); 2242 (7); 2242-4 (7); 2242bis (7); 2242ter (7); 2245 (7); 2247-I (7); 2248bis (7); 2249ter (7); 2249ter (7); 2251bis (7); 2252 (7); 2253-3 (7); 3591 (7); 3594 (7); 3596 (7); 3598 (7); 3704bis (7); 615 (7); 68 (7); 9179 (7); S-2394bis (7); S-2397-1 (7); Gamisans, J. & Reille S-2399 (7); García, R. 5493RG (4.1); Geltman, D. et al. 2094I (1); Germain, R. 10598 (4.1); 10711 (4.1); Golubkova, V.F. & A.I. Pojarkova 1256 (4.1); Gonzalo, R. et al. RG789 (4.1); Green, P.S. 18 (4.1); Greuter, W. 14362 (4.1); Guinea, E. 963 (4.1). Hæggström, C.A. 5224 (4.1); Hæggström, C.A. 6966 (4.1); Halliday, G. 36/79 (4.1); 90/67 (4.1); Hämet-Ahti, L. 2440 (4.1); Heldreich, T.H. 3522 (8); Hepper, F.N. 9464 (4.1); Herrero, A. et al. 2985 (4.2); 2620 (4.1); 2841 (4.1); AH3383 (4.1); AH3636 (4.1); Holmberg, O.R. 1985 (4.1); Holtz, F. 03.892 (4.1); Huber-Morath, A. 17383 (4.1); Huter, R. et al. 1172 (6). Ib Olsen, G. 578 (4.1); Ikonnikov-Galitskiy, N.P. & V.A. Ikonnikov-Galitskiy 465 (2); 478 (2); 575 (2); 922 (2). Jakowleff, D. 40 (2); Jury, S.L. et al. 18170 (4.1); 8847 (4.2); 8876 (4.1). Karlsson, T. 87031 (4.1); Kejian Gua 2930 (2); Kesercioglu, T. 101 (4.1); Kislev, M.E. & Melamed 166 (4.1); Kleesadl 178 (4.1); Klein, J.C. 4832 (4.1); 4967 (4.1); 5525 (4.1); 879 (4.1); Korotkiy, M. et al. 849 (2); Krasnoborov, I. & V. Khanminchum 6812 (2); 749 (2); Kreisch, W. 92/0631 (4.2); Kukkonen, I. 11193 (4.1); Kusnezow, J.W. 29 (2); Kuvaev, V. 165-2 (2). Leavenworth, W.C. 17548 (4.1); Leenhouts, P.W. 1518 (4.1); 2037 (4.1); Leuschner, C. & M. Sigi 17397 (4.1); Lippert, W. 23598b (6); 24863 (4.2); 25525 (4.2); Lipskiy, V.I. 3411 (4.1); Lomosonova, L. 2590 (2); López, G. 2085GF (4.1); López, G. & F. Muñoz Garmendia 8979GL (4.1); 9033GL (4.1); Lyatifova, A. 24 (4.1). Malyshev, L. & V. Pezhemskiy 56 (2); Mateos, M.A. 64/2250 (4.1); Medina, L. et al. 2606 (4.1); Melderis, A. 19 (4.1); Merxmüller, H. & W. Lippert 29582 (6); Merxmüller, H. & W. Wiedmann 18/64 (3); 5532 (1); 5546 (1); 5548 (1); 5549 (1); 704/62 (6); Mikhelson et al. 4480 (4.1); Milne, J. 1 (4.1); Montserrat, P. 1339/65 (1); 3999/68 (4.1); 5222/70 (1); 5690/69

(1); 69/55 (4.1); 702/55 (4.1); 761/55 (1); Mouterde, P. 11697 (4.1); 9853 (4.1); Mrkvicka, A.C. 1109 (1); Myndel Pedersen, T. 2478 (4.1). Navarro, C. et al. 4234 (3); Nowak, B. It83/319 (4.1). Orsini, A. 863 (3); Ovchinnikov, B.N. & M.P. Usov 35 (2). Pabot, H. 7719 (4.1); Pobedimova, E.G. 649 (2); 706 (2); Podlech, D. 5892 (1); Podlech, D. & W. Lippert 15367 (1); Porta, P. & G. Rigo 630 (6). Quintanar, A. & P. Barberá 5390AQ (7); Quintanar, A. et al. 1408AQ (4.1); 2040AQ (4.1); 3630AQ (4.1); 5226 (6); 5231 (6); 5273 (6); 5275 (6); 5276 (6); 5277 (6); 5278 (6); 5279 (6). Rechinger, K.H. 1103 (6); 18583 (4.1); Reverchon, E. 312 (7); 607 (4.1); Rodin, L. 1108-A (2); Rothmaler, W. 16304 (6). Samuelsson, G. 180 (4.1); 2142 (4.1); Schuler, A. 1818 (4.1); 99/746 (4.1); Schwarz, O. 621 (1); Sell, P.D. 61/299 (4.1); Sennen, F. 3820 (4.1); Seregin, A. 4697 (4.1); Serogin, A. & I. Serogin S-443 (2); Sharif, G. 496 (4.1); Shaulo, D. & I. Belskaya 1520 (2); Shipchinskiy, N. 565 (4.1); Silva, P. & A.N. Teles 8348 (4.1); Smirnow, P. 10 (2); Smirnow, W 1433 (2); 615 (2); Soreng, R. 3818 (4.1); Soreng, R. et al. 7516a (4.1); 8024 (4.1); 8041 (4.1); Starcs, K. 3350 (4.1); Stebler, F.G. & C. Schröter 31 (4.1); Strid, A. et al. 18148 (4.1); 19163 (4.1); Strid, A. & Kjellsson 11406 (4.1); Strid, A. & K. Papanicolau 15238 (4.1); Studentenexcursie 11113 (4.1); Sukachev, V.N. et al. 1652 (2); Sukopp, U. et al. 1667 (2); Süme, U. 13790 (4.1); Summerhop, V.S. 3348 (4.1); Sundin, R. 57 (4.1); Suominen, J. 472 (4.1). Temnoev, N.I. 123 (2); Till, W. 100104 (4.1); Tomin, M.P. 313 (2); Tsvelev, N. 154 (4.1); 24 (4.1); Tsvelev, N. & S. Cherepanov 215 (4.1). Univ. Copenhagen Excurs. 775 (4.1); unknown 2052 (2). van Ooststroom, S.J. 22673 (4.1); van Soest, J.L. 15626 (4.1); Vitek, E. 03-0814 (4.1); Vitek, E. et al. 04-1074 (4.1); 04-1547 (4.1); 09-1870 (4.1); 09-1885 (4.1); Volkov, A.N. 397 (2); von Degen, A. 119 (4.1). Welch, B. 5200 (4.1); Willing, R. & E. Willing 13363 (4.1); 139.155 (4.1); Willkomm, H.M. 1281 (6). Zaballos, J.P. 36 (4.1).

CAPÍTULO V

A worldwide phylogenetic classification of the Poaceae (Gramineae) II: an update and a comparison of two 2015 classifications

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Published in *Journal of Systematics and Evolution* 55(4): 259-290 (2017)

Abstract**—**We present a new worldwide phylogenetic classification of 11 506 grass species in 768 genera, 12 subfamilies, seven supertribes, 52 tribes, five supersubtribes, and 90 subtribes; and compare two phylogenetic classifications of the grass family published in 2015 (Soreng et al. and Kellogg). The subfamilies (in descending order based on the number of species) are Pooideae with 3968 species in 202 genera, 15 tribes, and 30 subtribes; Panicoideae with 3241 species in 247 genera, 13 tribes, and 19 subtribes; Bambusoideae with 1670 species in 125 genera, three tribes, and 15 subtribes; Chloridoideae with 1602 species in 124 genera, five tribes, and 26 subtribes; Aristidoideae with 367 species in three genera, and one tribe; Danthonioideae with 292 species in 19 genera, and one tribe; Micrairoideae with 184 species in eight genera, and three tribes; Oryzoideae with 115 species in 19 genera, four tribes, and two subtribes; Arundinoideae with 40 species in 14 genera, two tribes, and two subtribes; Pharoideae with 12 species in three genera, and one tribe; Puelioideae with 11 species in two genera, and two tribes; and the Anomochlooideae with four species in two genera, and two tribes. We also include a radial tree illustrating the hierarchical relationships among the subtribes, tribes, and subfamilies. Newly described taxa include: supertribes Melicodae and Nardodae; supersubtribes Agrostidodinae, Boutelouodinae, Gouiniodinae, Loliodinae, and Poodinae; and subtribes Echinopogoninae and Ventenatinae.

Resumen**—**Presentamos una nueva clasificación filogenética mundial de 11506 especies de gramíneas en 768 géneros, 12 subfamilias, siete supertribus, 52 tribus, cinco supersubtribus y 90 subtribus; comparamos dos clasificaciones filogenéticas de la familia de las gramíneas publicadas en 2015 (Soreng et al. y Kellogg). Las subfamilias (en orden descendiente basado en el número de especies) son Pooideae con 3968 especies en 202 géneros, 15 tribus y 30 subtribus; Panicoideae con 3241 especies en 247 géneros, 13 tribus y 19 subtribus; Bambusoideae con 1670 especies en 125 géneros, tres tribus y 15 subtribus; Chloridoideae con 1602 especies en 124 géneros, cinco tribus y 26 subtribus; Aristidoideae con 367 especies en tres géneros y una tribu; Danthonioideae con 115 especies en 19 géneros, cuatro tribus y dos subtribus; Arundinoideae con 40 especies en 14 géneros, dos tribus y dos subtribus; Pharoideae con 12 especies en tres géneros y una tribu; Puelioideae con 11 especies en dos géneros y dos tribus; y Anomochlooideae con cuatro especies en dos géneros y dos tribus. Incluimos además un árbol radial ilustrando las relaciones jerárquicas entre las subtribus, tribus y subfamilias. Los táxones recientemente descritos incluyen: supertribus Melicodae y Nardodae; supertribus Agrostidodinae, Boutelouodinae, Gouiniodinae, Loliodinae y Poodinae; y las subtribus Echinopogoninae y Ventenatinae.

INTRODUCTION

Based on molecular DNA and morphological studies we presented a generic classification and hierarchical tree with detailed relationships of all subfamilies, tribes, and subtribes within the Poaceae (Soreng et al., 2015b). In the same year a comprehensive treatment of the Poaceae was completed by Kellogg (2015) that included, in addition to a generic classification outlining relationships among the subfamilies, tribes, and subtribes, chapters on overall morphology, phytochemistry, distribution, reproduction, and domestication, and keys to subdivisions and genera, along with diagnoses and comments.

The classifications of Soreng et al. (2015b) and Kellogg (2015) represent a synthesis of molecular studies that have greatly added to traditional classifications based entirely on morphology, anatomy, and cytology (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992). In our earlier publication we recognized 764 genera in 12 subfamilies, six supertribes, 51 tribes, and 79 subtribes encompassing ± 12 074 species (Soreng et al., 2015b) whereas Kellogg (2015) recognized 698 genera, and 13 isolated species, without formal generic names, in the same 12 subfamilies, no supertribes, 30 tribes, and 53 subtribes encompassing ca. 11 000 species. In order to reduce redundancy, i.e., the use of more than one hierarchical name to circumscribe a clade or group, Kellogg (2015) chose to use fewer ranks below subfamily, avoiding all supertribe names, and tribes in small or single tribe subfamilies, or subtribes in small tribes, whereas Soreng et al. (2015b) perpetuated tribal names since they are integral ranks in the botanical code and have traditionally been used in the classification of the grasses for 200 years. We feel that for equivalence across the family each genus ought to be aligned within a tribe, and if monophyletic and morphologically diagnosable, prefixes for additional suprageneric taxa, such as, sub- and super-, should be used to recognize larger or smaller clades within or above tribes.

In this paper we compare our earlier grass classification (Soreng et al., 2015b) with the classification in Kellogg (2015), and we present a new radial phylogenetic tree and updated classification incorporating new studies reported in the literature.

MATERIAL AND METHODS

Phylogenetic data

Starting with our radial phylogenetic tree derived from a large dataset of 448 grass species using matK and ndhF plastid DNA markers (Soreng et al., 2015b, Fig. 1), to assemble our new Figure 1we then inserted new tribal and subtribal names in the appropriate location based on publications supported by molecular analyses (Besnard et al., 2013; Hochbach et al., 2015; Kellogg, 2015; Soreng et al., 2015a; Peterson et al., 2016; Teisher, 2016; Teisher et al., in press; Wong et al., 2016). Joinvillea Gaudich. ex Brongn. & Gris and Ecdeiocolea F. Muell. were used as outgroups based on previous studies (Michelangeli et al., 2003). For our new classification we also used our unpublished DNA sequences that are not yet available to the public, particularly in the Pooideae and Chloridoideae. We base our generic limits and concepts on current phylogenetic studies, and when this is lacking, we generally take the conservative view using morphology, cytology, and anatomy as a guide. However, there are many occasions when a lineage is unresolved and requires additional study. The number of species per genus, leading to the total number per subtribe, tribe, and subfamily (Appendices 1 and 2) was calculated primarily by consulting GrassWorld (Simon, 2014), GrassBase (Clayton et al., 2016), and the entire taxonomic literature.

Nomenclature

All suprageneric taxa and genera are recorded in the Missouri Botanical Garden's taxonomic database, Tropicos (http://www.tropicos.org/Home.aspx), with their original place of publication and authorship. We used this database to generate all author names and we follow the suggested abbreviations in Brummitt & Powell (1992) and the International Plant Names Index (http://www.ipni.org/index.html). New updated classifications (Soreng et al., 2017) are also available at: http://www.tropicos.org/projectwebportal.aspx?pagename=ClassificationNWG&projectid=10.

Appendix 1 lists a comparison of the suprageneric classification of Kellogg (2015), Soreng et al. (2015b), and our current version. Appendix 2 arranges each genus in our current classification, and accounts for all legitimate (and some illegitimate and invalid) suprageneric names and synonyms we have documented along with authorship and date of publication. Each genus in Appendix 2 is color coded to indicate the predominant indigenous distribution of its species in the Americas (Western Hemisphere), Africa, Australasia, and Eurasia. Photosynthetic pathway is noted as C_3 or C_4 for each highest rank where it is internally constant. Generic names in italics indicate DNA has been studied for one or more of the species. Comments are liberally inserted after accepted names to indicate special issues such as reticulate origins (nothotaxa are not listed). Doc. S1 lists all the treated genera with their authors, their acceptance or synonymy, and an estimate of the number of species in each genus, and its subfamily classification.

RESULTS

Comparison of two classifications

The following is a list of 40 genera accepted by Soreng et al. (2015b) and in our new classification (except *Leptophyllochloa* which is now a synonym of *Cinnagrostis*); names in parentheses were treated as synonyms by Kellogg (2015), and 14 of these (marked with an asterisk*) we now place as synonyms in our new classification: *Aegilops* (syn. *Amblyopyrum*), *Agrostis* (syn. *Chaetopogon**), *Arthropogon* (syn. *Achlaena*, *Altoparadisium*), *Axonopus* (syn. *Baptorhachis*), *Bambusa* (syn. *Phuphanochloa*), *Chasmanthium* (syn. *Bromuniola**), *Chionachne* (syn. *Polytoca*, *Sclerachne*, *Trilobachne*), *Cleistochloa* (syn. *Ancistrachne*, *Calyptochloa*), *Desmazeria* (syn. *Catapodium*), *Deyeuxia* (syn. *Dichelachne*), *Diarrhena* (syn. *Neomolinia*), *Dupontia* (syn. *Arctophila*), *Ehrharta* (syn. *Microlaena*, *Tetrarrhena*, *Zotovia*), *Elymus* (syn. *Anthosachne*, *Connorochloa*, *Douglasdeweya*, *Kengyilia*, *Pascopyrum*), *Eragrostis* (syn. *Ectrosia**, *Harpachne**, *Pogonarthria**, *Psammagrostis**), *Eulalia* (syn. *Pseudopogonatherum*), *Homopholis* (syn. *Walwhalleya**), *Leptatherum* (syn. *Polliniopsis**), *Leucopoa* (syn. *Drymochloa*, *Leucopoa*), *Leymus* (syn. *Hordelymus*), *Melinis* (syn. *Mildbraediochloa**), *Microchloa* (syn. *Rendlia**), *Miscanthus* (syn. *Miscanthidium*, *Narenga*, *Miscanthus*, *Sclerostachya*), *Mnesithea* (syn. *Ratzeburgia*), *Munroa* (syn. *Dasyochloa*), *Neurachne* (syn. *Paraneurachne*), *Otachyrium* (syn. *Plagiantha*, *Steinchisma*), *Panicum* (syn. *Yakirra**), *Parabambusa* (syn. *Pinga*), *Paractaenum* (syn. *Plagiosetum*), *Paspalum* (syn. *Spheneria**), *Phleum* (syn. *Pseudophleum*), *Saccharum* (syn. *Erianthus*), *Schizostachyum* (syn. *Dendrochloa**), *Sorghum* (syn. *Hemisorghum*), *Trisetaria* (syn. *Avellinia*, *Gaudinia*, *Koeleria*, *Leptophyllochloa*, *Peyritschia*, *Rostraria*, *Trisetum*), *Tristachya* (syn. *Dilophotriche*, *Loudetiopsis*, *Zonotriche*), *Urochloa* (syn. *Megathyrsus*, *Scutachne*), *Ventenata* (syn. *Gaudinopsis*), *Zeugites* (syn. *Pohlidium**).

The following is a list of 16 genera accepted by Kellogg (2015) with names in parentheses treated as synonyms by Soreng et al. (2015b), four of which (marked with an asterisk*) we now accept in our new classification: *Andropogon* (syn. *Hypogynium*), *Aulonemia* (syn. *Colanthelia**), *Calamagrostis* (syn. *Deyeuxia*), *Cenchrus* (syn. *Snowdenia*), *Chloris* (syn. *Ochthochloa*), *Coelachyrum* (syn. *Coelachyriopsis*), *Deschampsia* (syn. *Scribneria*), *Dichanthium* (syn. *Eremopogon**), *Festuca* (syn. *Loliolum*), *Leptochloa* (syn. *Trichloris*), *Mnesithea* (syn. *Hackelochloa**), *Puccinellia* (syn. *Pseudosclerochloa*), *Reitzia* (syn. *Piresia*), *Sorghum* (syn. *Cleistachne**, *Sarga*), and *Sporobolus* (syn. *Calamovilfa*, *Crypsis*, *Spartina*, *Thellungia*).

The following 24 genera were accepted by Soreng et al. (2015b) but were not accounted for in Kellogg (2015), five of these (marked with an asterisk*) were recently published and could not have been addressed by Kellogg: *Aconisia*, *Adenochloa*, *Brizochloa*, *Chloachne*, *Dupontiopsis**, *Helictochloa*, *Kalinia**, *Lorenzochloa*, *Micrachne**, *Moliniopsis*, *Morronea**, *Parianella**, *Parvotrisetum*, *Patzkea*, *Sasaella*, *Schenckochloa*, *Semiarundinaria*, *Sesleriella*, *Taeniorhachis*, *Tricholemma*, *Tripidium*, *Veldkampia*, *Vietnamocalamus*, *Vietnamochloa*. In our new classification we place *Aconisia* as a synonym of *Hymenachne*, all others are still accepted by us. *Rendlia* was inadvertently accepted and synonymized (intended) by Soreng et al. (2015b).

New classification

A radial tree (Fig. 1) illustrating the hierarchical relationships among the subtribes, tribes, and subfamilies depicts Poaceae as monophyletic with 12 monophyletic subfamilies, in order of divergence: Anomochlooideae (four species in two genera), Pharoideae (12 species in three genera), and Puelioideae (11 species in two genera) forming the basal lineages; Oryzoideae (115 species in 19 genera), Bambusoideae (1670 species in 125 genera), and Pooideae (3968 species in 202 genera) forming the BOP clade (Clark et al., 1995); and Aristidoideae (367 species in three genera) + Panicoideae (3241 species in 247 genera) as sister to the remaining set of Arundinoideae (40 species in 14 genera) + Micrairoideae (184 species in eight genera), and Danthonioideae (292 species in 19 genera) + Chloridoideae (1602 species in 124 genera), forming the PACMAD clade (Sánchez-Ken & Clark, 2010) [Appendices I & II].

Figure 1. A phylogenetic classification of the Poaceae, includes 12 subfamilies, 53 tribes, and 90 subtribes evolving clockwise from *Joinvillea* and *Ecdeiocolea* (outgroups). BOP=Bambusoideae, Oryzoideae, and Pooideae; PACMAD=Panicoideae, Aristidoideae, Chloridoideae, Micrairoideae, Arundinoideae, and Danthonioideae. Thick branches represent subfamily splits; medium thick branches represent tribe splits; and thin branches represent subfamily splits.

In the above 12 subfamilies we recognize 52 tribes, 90 subtribes, and 768 genera in approximately 11 506 species (Appendices I & II, Doc. S1). The numbers of genera and species in each of the 52 tribes are as follows: Ampelodesmeae (1, 1),Andropogoneae (98, 1202), Anomochloeae (1, 1), Aristideae (3, 367), Arundinarieae (31, 581), Arundineae (4, 17), Arundinelleae (3, 86), Atractocarpeae (1, 5), Bambuseae (73, 966), Brachyelytreae (1, 3), Brachypodieae (1, 22), Bromeae (1, 165), Brylkinieae (1, 1), Centotheceae (2, 3), Centropodieae (2, 6), Chasmanthieae (1, 7), Cynodonteae (95, 859), Cyperochloeae (2, 2), Danthonieae (18, 291), Diarrheneae (2, 5), Duthieeae (8, 16), Eragrostideae (14, 489), Ehrharteae (4, 38), Eriachneae (1, 50), Guaduelleae (1, 6), Gynerieae (1, 1), Isachneae (6, 119), Lecomtelleae (1, 1), Littledaleeae (1, 4), Lygeeae (1, 1), Meliceae (7, 158), Micraireae (1, 15) Molinieae (14, 178), Nardeae

(1, 1), Olyreae (21, 123), Oryzoideae (11, 71), Paniceae (83, 1227), Paspaleae (39, 597), Phaenospermateae (1, 1), Phareae (3, 12), Phyllorachideae (2, 3), Poeae (121, 2562), Steyermarkochloeae (2, 2), Stipeae (28, 527), Streptochaeteae (1, 3), Streptogyneae (1, 2), Thysanolaeneae (1, 1), Triraphideae (3, 15), Tristachyideae (8, 87), Triticeae (27, 501), Zeugiteae (4, 17), and Zoysieae (4, 233) [Appendix 1]. We recognize 90 subtribes (number of genera, number of species): Aeluropodinae (2, 7), Agrostidinae (11, 409), Airinae (7, 43), Alopecurinae (3, 47), Ammochloinae (1, 3), Andropogoninae (25, 514), Anthephorinae (8, 291), Anthoxanthinae (1, 42), Aristaveninae (1, 51), Arthraxoninae (1, 27), Arthropogoninae (16, 71), Arthrostylidiinae (15, 185), Arundinariinae (31, 581), Aveninae (18, 343), Bambusinae (17, 324), Beckmanniinae (4, 6), Boivinellinae (18, 146), Boutelouinae (1, 60), Brizinae (2, 6), Buergersiochloinae (1,1), Calothecinae (1, 22), Cenchrinae (24, 287), Chinoachninae (5, 15), Chusqueinae (1, 175), Cinninae (5, 13), Coicinae (1, 4), Coleanthinae (10, 156), Cotteinae (4, 28), Crinipinae (4, 10), Cteniinae (1, 20), Cynosurinae (1, 10), Dactylidinae (2, 4), Dactylocteniinae (4, 20), Dichantheliinae (2, 76), Dinochloinae (7, 56), Echinopogoninae (5, 20), Eleusininae (27, 231), Eragrostidinae (5, 451), Farragininae (2, 4), Germainiinae (4, 31), Gouiniinae (6, 21), Greslaniinae (1, 2), Guaduinae (5, 53), Hickeliinae (9, 32), Hilariinae (1, 10), Holcinae (2, 11), Holttumochloinae (3, 6), Hubbardochloinae (8, 27), Ischaeminae (7, 151), Loliinae (9, 659), Melinidinae (13, 166), Melocanninae (9, 99),Miliinae (1, 5), Moliniinae (4, 7), Monanthochloinae (1, 11), Muhlenbergiinae (1, 182), Neurachninae (6, 21), Olyrinae (17, 88), Orcuttiinae (2, 9), Orininae (2, 20),Oryzinae (4, 44), Otachyriinae (5, 34), Panicinae (3, 157), Pappophorinae (3, 25), Parapholiinae (8, 26), Parianinae (3, 34), Paspalinae (17, 491), Perotidinae (3, 19), Phalaridinae (1, 17), Phleinae (1, 16), Poinae (1, 550), Racemobambosinae (3, 31), Rottbolliinae (16, 112), Saccharinae (26, 179), Scleropogoninae (6, 15), Scolochloinae (2, 3), Sesleriinae (5, 39), Sporobolinae (2, 221), Temburongiinae (1, 1), Torreyochloinae (2, 16), Traginae (6, 16), Trichoneurinae (1, 8), Triodiinae (1, 69), Tripogoninae (7, 66) Tripsacinae (7, 59), Uniolinae (5, 10), Ventenatinae (6, 21), Zaqiqahinae (1, 1), Zizaniinae (7, 27), and Zoysiinae (2, 12) [Appendices I & II, Doc. S1].

We tally 4783 species with known C_4 metabolism occurring in Aristidoideae, Chloridoideae, Micrairoideae, and Panicoideae or approximately 41.6% of the grasses.

Taxonomy

Based on our results we propose two new supertribes, five new supersubtribes, and two new subtribes below.

Agrostidodinae Soreng, **supersubtribe nov.**

Type: *Agrostis* L., Sp. Pl. 1: 61. 1753.

Description: Annuals or perennials; upper culm leaf sheaths open to the base; ligules membranous without a fringe of hairs; synflorescence paniculate, sometimes densely contracted; spikelets 1-flowered, or several-flowered (Brizinae and Calothecinae, rarely elsewhere); disarticulation above or below the glumes; multi-flowered spikelets often plump, and with broad paleas; glumes shorter or longer than the lowest floret; rachilla extension absent or minute, or well-developed and often pilulose or pilose; lemmas glabrous or with a short line of hairs along the margins, with or without awns, awns terminal subterminal or dorsal, lateral veins often excurrent as short teeth or setae or forming awns; callus glabrous, bearded, or with a crown of hairs (hairs rarely in several tufts); paleas coriaceous, chartaceous, scarious, or hyaline (and frequently rudimentary), keels well-spaced with narrow flanges, or approximate with flanges broader than the gap between the keels; lodicules lanceolate, unlobed or sometimes lobed, hyaline, obscurely veined; ovary glabrous or hairy; caryopsis hard or soft, with lipid (where known), hilum linear, elliptical, or round.

Included subtribes: Agrostidinae, Brizinae, Calothecinae, and Echinopogoninae.

Distribution: Echinopogoninae and Calothecinae are primarily southern hemisphere (excluding Africa), Brizinae are in Europe and southwest Asia, and Agrostidinae are worldwide.

Boutelouodinae P.M. Peterson & Romasch., **supersubtribe nov.**

Type: *Bouteloua* Lag., Varied. Ci. 2(4, 21): 134 . 1805.

Description: Perennials or annuals, sometimes stoloniferous or rhizomatous; ligules membranous or a fringe of hairs; synflorescence a panicle, occasionally a false spike with spicate branches; spikelets 1–10(–25)-flowered, bisexual, unisexual (monoecious or dioecious) or sterile, solitary, paired or in triplets; glumes 1–3(–11)-veined; lemmas usually 3(7–13)-veined, the apex entire, lobed or cleft, unawned, mucronate or awned.

Included subtribes and genera: Boutelouinae, Hilariinae, Monanthochloinae, Muhlenbergiinae, Scleropogoninae, and Traginae; included orphan genera: *Allolepis*, *Jouvea*, *Kalinia*, and *Sohnsia*.

Distribution: Boutelouinae, Hilariinae, Monanthochloinae, Muhlenbergiinae, Scleropogoninae, *Allolepis*, *Jouvea*, *Kalinia*, and *Sohnsia* are almost exclusively from the western hemisphere; Traginae is primarily African.

Echinopogoninae Soreng, **subtribe nov.**

Type: *Echinopogon*, P. Beauv., Ess. Agrostogr. 42, 148, 161.1812.

Description: Annuals and perennials; spikelets 1-flowered (1 or infrequently 2-flowered in *Relchela*); rachilla extension present, terete in cross section, 1/5–4/5 the lemma in length (minute in *Dichelachne*), glabrous or the longer ones short pilose to hispid along the length; callus blunt, rounded or oblique (rarely sharp), with a distinct crown of hairs around the base or along the sides, to 1/10–1/2 the lemma in length (rarely bearded along the sides in *Dichelachne crinata*); lemmas subcoriaceous to coriaceous, smooth or scabrous, awnless (*Relchela*) or awned, central awn stout, entered by intermediate veins (*Echinopogon* and *Ancistragrostis*), and straight or sinuous (uncinate in *Ancistragrostis*), or only the central vein, frequently scabrid; palea at least distally, coriaceous to chartaceous, and green in part, or scarious (*Dichelachne*), as long as the lemma, keels closely spaced and densely scabrous to ciliate distally (or smooth or minutely scabrous in *Dichelachne*), lateral margins more than (1–) 2–3 x broader than the gap between the keels; ovary apex with stiff hairs at least on the base of the styles or glabrous (some *Dichelachne*); caryopsis solid (*Relchela*, *Echinopogon*) or soft (*Dichelachne*), rounded, lanceoloid, narrowly sulcate; hilum 1/3–1/2 the grain in length, broadly to narrowly linear.

Included genera: *Ancistragrostis*, *Dichelachne*, *Echinopogon*, *Pentapogon*, and *Relchela*.

Distribution: The genera are confined to the southern hemisphere, mainly in Australasia, but *Relchela* is endemic to southern South America.

Gouiniodinae P.M. Peterson & Romasch., **supersubtribe nov.**

Type: Gouinia E. Fourn. ex Benth. & Hook. f., Gen. Pl. 3: 1178. 1883.

Description: Perennials or annuals; culms erect, often geniculate or decumbent; ligules membranous, sometimes a fringe of hairs; synflorescence of many racemes scattered along a central axis, sometimes subdigitally arranged; spikelets 1–14-flowered with bisexual (perfect) florets; glumes 1–7-veined; lemmas usually (0 or 1)3(5–9)-veined, unawned, mucronate or awned.

Included subtribes: Cteniinae, Farragininae, Gouiniinae, Hubbardochloinae, Perotidinae, Trichoneurinae, and Zaqiqahinae.

Distribution: Farragininae and Zaqiqah are African; Gouiniinae is western hemisphere; Ctenium, Hubbardochloinae, and Trichoneurinae are African and western hemisphere; Perotidinae is African and southeast Asian.

Loliodinae Soreng, **supersubtribe nov.**

Type: *Lolium* L., Sp. Pl. 1: 83. 1753.

Description: Annuals and perennials; upper culm leaf sheaths usually open to the base; ligules membranous without a fringe of hairs; synflorescence paniculate, racemose, or spicate; spikelets multiple-flowered spikelets (except *Hainardia*), disarticulation above or below the glumes, sometimes along branches or axes; glumes shorter than the first lemma, infrequently equaling the first lemma, the lower glume sometimes rudimentary; rachilla joints glabrous, often slightly flattened in cross section; lemmas with terminal, rarely subterminal, awned or without awns, glabrous, infrequently hispidulous; callus glabrous, rarely short hairy; lodicules 2, rarely absent, hyaline, usually lobed, obscurely veined; ovary with styles well separated; caryopses glabrous or hairy, hard without lipid or with lipid (soft in some Parapholiinae), hilum long linear (short linear in some Parapholiinae).

Included subtribes: Ammochloinae, Dactylidinae, Loliinae, Parapholiinae.

Distribution: *Festuca* is worldwide, but other than *Megalachne* and *Podophorus* of the Juan Fernandez Islands off the coast of Chile, the rest of the genera are confined to the eastern hemisphere, mostly around the Mediterranean; *Pseudobromus* is African.

Melicodae Soreng, **supertribe nov.**

Type: *Melica* L., Sp. Pl. 1: 66. 1753.

Description: Perennials; leaf sheath margins fused for much of their length; spikelets multiple-flowered (1-flowered in *Triniochloa*); lodicules 2, usually truncate fleshy, usually fused over part of their margins (*Brylkinia* and Koordersiochloa lodicules lanceolate, distally hyaline, and free or partly fused); ovary glabrous; styles 2, subapical, bases persistent, lanceoloid (*Brylkinia* and *Koordersiochloa*) or globose in outline; stigmatic branches rebranched often divaricate; caryopses hard without lipid and with compound starch grains, hilum long linear.

Included tribes: Brylkinieae, and Meliceae.

Distribution: *Melica* and *Glyceria* are widespread; *Koordersiochloa* is in continents surrounding the Indian Ocean in subtropical uplands; *Triniochloa* is western hemisphere; the other genera are relatively localized.

Nardodae Soreng, **supertribe nov.**

Type: *Nardus* L., Sp. Pl. 1: 53. 1753.

Description: Perennials; sheaths open to the base; leaf blades with bicellular microhairs with the terminal cell inflated (*Lygeum*); synflorescence a secund spike (*Nardus*) or reduced to a single spatheolate highly modified compound spikelet per flowering culm (*Lygeum*); spikelets 1-flowered (*Nardus*) or 2(3)-flowered (*Lygeum*); rachilla extension absent; glumes rudimentary or absent; lodicules absent; styles 1, linear, non-plumose and papilliate (*Lygeum*) or simple plumose (*Nardus*); caryopsis hilum long-linear.

Included tribes: Lygeeae, Nardeae.

Distribution and habitat: Europe and Mediterranean to southwestern Asia, *Nardus* occurs in alpine and moor lands, *Lygeum* in arid low hills and plains of subcoastal Mediterranean.

Poodinae L.J. Gillespie & Soreng, **supersubtribe nov.**

Type: *Poa* L., Sp. Pl. 1: 67. 1753.

Description: Annuals and perennials; upper culm leaf sheaths open to the base or closed for some length; synflorescence paniculate, rarely racemose (*Gaudinopsis*) or spicate (*Pholiurus*); spikelets 1- or several-flowered; disarticulation above or infrequently below the glumes; glumes well developed, the upper glume usually ¾ to slightly exceeding the proximal lemma in length (sometimes saccate in Beckmanniinae); rachilla joints in multiple flowered spikelets terete in cross section, glabrous, scabrous, or puberulent (with an apical crown of hairs in *Bellardiochloa*); lemmas laterally compressed, often distinctly keeled, frequently pubescent; awns terminal, subterminal or dorsal; callus in multiple-flowered spikelets commonly with a short crown or infrequently a beard of hairs (hairs commonly dorsal in *Poa*),sometimes glabrous; paleas usually chartaceous or membranous and green in part (hyaline or absent in Alopecurinae); lodicules 2 (rarely absent), hyaline, often lobed, obscurely veined; ovary with styles approximate or connate at base, plumose, compound or simple; caryopsis glabrous, hard or soft, lipid usually present, hilum (< ⅓ the grain in length, short, round to narrowly elliptical (not linear).

Included subtribes: Alopecurinae, Beckmanniinae, Cinninae, Miliinae, Phleinae, Poinae, and Ventenatinae; included orphan genera: *Arctagrostis*, *Arctophila*, *Brizochloa*, *Dupontia*, *Dupontiopsis*, *Hookerochloa*, *Nicoraepoa*, *Saxipoa*, *Sylvipoa*.

Distribution: Worldwide, *Hookerochloa*, *Nicoraepoa*, *Saxipoa*, *Simplicia*, and *Sylvipoa* are confined to the southern hemisphere, others to Eurasia and Mediterranean Africa, or more widespread, *Poa* occurs on all continents.

Ventenatinae Holub ex L.J. Gillespie, Cabi & Soreng, **subtribe nov.**

Ventenatinae Holub, Philip Maximilian Opiz und seine Bedeut. fur Pflanzentax. 104 (1958), nom. nud.

Type: *Ventenata* Koeler, Descr. Gram. 272. 1802.

Description: Annual (perennial in *Bellardiochloa*); tufted; upper leaf sheath fused for 1–4 mm at the base (1–4% the length); leaf blades involute, sometimes weakly so, infrequentlyflat, adaxially usually with pronounced ribs, scabrous or scabrous-hispidulous when involute; ligules (1–)2–7 mm long, membranous, apex often lacerate; synflorescence paniculate (racemose in *Gaudinopsis*), sometimes whorled; spikelets disarticulation above (rarely also below in *Ventenata*) the glumes and between the florets, with a rachilla extension; glumes shorter or longer than the lowest floret, 1–9-veined; spikelets 1- or (2)-flowered (*Apera*), or 2–5(–10)-flowered; callus with a beard or crown of hairs (hairs sometimes minute), or glabrous; lemmas 2–15 mm long, (1 or 3)5-veined, lanceoloid to oblanceoloid, abaxially rounded, glabrous or sometimes proximally with a short line of hairs on lateral veins and keel, awned, the awn dorsal and geniculate, or terminal (rarely absent in all florets), sometimes with awns from the lobes of a bifid apex; paleas chartaceous or membranous, green in part, 2-keeled, keels scabrous or pectinate ciliate in part; flowers bisexual; lodicules 2, free, distally hyaline, lanceolate, lobed or entire; anthers (1)3; styles terminal, adjacent and free or briefly connate at base, stigmatic branching plumose or simple plumose; caryopses glabrous, endosperm with lipid, soft, hilum less than $^{1}/_{10}$ – $^{1}/_{5}$ the grain in length. x = 7 (only diploids known).

Included genera: *Apera*, *Bellardiochloa*, *Gaudinopsis*, *Nephelochloa*, *Parvotrisetum*, and *Ventenata*.

Distribution: The species are found primarily in southwestern Asia and adjacent Europe.

DISCUSSION

Overall comparison

Kellogg (2015) accepted 698 genera along with 13 additional clades or grades for a total of 711 generic level entries whereas Soreng et al. (2015b) included 764; 675 genera were accepted in both accounts. Eighty-nine genera accepted by Soreng et al. (2015b) were not accepted by Kellogg (2015); 65 of these were placed in synonymy while 24 were unaccounted for. Twenty-four genera accepted by

Kellogg (2015) were not accepted by Soreng et al. (2015b). Nineteen of the 24 genera were placed in synonymy and five were unaccounted for. There were 87genera and synonyms that we were unaware of having molecular data to aid in a decision (Soreng et al., 2015b).Twelve of Kellogg's genera include a total of 40 generic names (as synonyms) accepted by Soreng et al. (2015b) while *Trisetaria*, *Elymus*, and *Eragrostis* sensu Kellogg account for 17genera accepted by Soreng et al.; another 27 accepted genera were placed as synonyms in Kellogg. More significant is consensus between these two classifications by using the criterion of monophyly, and the inherent importance of molecular synthesis in dictating the acceptance of the same 12subfamilies. Remarkably, only three genera (*Alloeochaete*, *Danthonidium*, and *Phaenanthoecium*) were placed in different subfamilies (Arundinoideae versus Danthonioideae), and only one genus (*Streptogyna*, in Kellogg, 2015) was left unplaced in a subfamily with the acknowledgment that it may be sister to the subfamily in which Soreng et al. (2015b) placed it (Oryzoideae). Kellogg (2015) explicitly united the following tribes accepted by Soreng et al. (2015b): Brylkinieae in Meliceae, Lygeeae in Nardeae, Ampelodesmeae in Stipeae, Zeugiteae in Chasmanthieae, Thysanolaeneae and Cyperochloeae in Centotheceae (all without subtribes); and Arundinelleae in Andropogoneae (as a subtribe). However, overall there were very few genera placed explicitly in different tribes. Each classification listed *incertae sedis* genera (i.e., of uncertain alignment) within the next lower accepted rank, and usually the difference here depended on availability of molecular data for assessing relationships, particularly for poorly known, small or monotypic genera with limited distribution.

Keeping up with recent changes and newly published taxa also contributed to divergent classifications. For instance, 179 genera have been published since Clayton & Renvoize (1986), 53 of these since 2009, and 14 since 2014. Needless to say, several recently described genera were absent from each of our classifications, or accepted without reciprocal evaluation. In Soreng et al. (2015b) we indicated (in Table 1 by *italics*) 783 genera (accepted and synonyms) that were known to have DNA sequence data and 87 genera that lack this information. In our current classification we indicate that 863 genera have DNA sequence data, including 700 of our currently accepted genera. Of course, not all of the DNA sequence markers are from the same region. In our current classification 667 of our 768 accepted genera are in common with Kellogg (2015). Of the 101 generic differences, Kellogg did not account for 48, including 15 new genera and 33 other genera not mentioned in synonymy. There are multiple reasons for the above differences: different molecular publications or data sets available to the authors (including unpublished data), different interpretations of the results, different circumscriptions of some genera, planned or ongoing research to resolve conflicts of non-monophyly, different taxonomic expertise, the timing of the writing (Kellogg's manuscript took many years to prepare and review, leading to some inflexibility in making updates), and sometimes a tendency to split or lump taxa.

Anomochlooideae, Pharoideae, and Puelioideae

The basal lineages Anomochlooideae and Puelioideae each have two tribes and Pharoideae has a single tribe in Soreng et al. (2015b) whereas Kellogg (2015) recognized the same genera only within subfamily rank. These three subfamilies are unchanged from Soreng et al. (2015b) in our new classification.

Oryzoideae

Kellogg (2015) placed *Streptogyna* as *incertae sedis* in the BOP clade whereas Soreng et al. (2015b) placed it in the tribe Streptogyneae at the base of the Oryzoideae. The Ehrharteae sensu Soreng et al. (2015b) comprised four genera, *Ehrharta*, *Microlaena*, *Tetrarrhena*, and *Zotovia* whereas Kellogg (2015) placed the last three within Ehrharta. Even though Verboom et al. (2003) found *Microlaena* polyphyletic and recognition of *Tetrarrhena* and *Zotovia* appears to render *Ehrharta* paraphyletic, better plastid DNA markers and taxa need to be surveyed to address the monophyly of these four genera. Soreng et al. (2015b) placed Maltebrunia and Prosphytochloa in Zizaniinae whereas Kellogg (2015) followed Tang et al. (2010) who indicated the pair are sister to *Leersia* and belong in the Oryzinae. In our new classification we still retain *Ehrharta*, *Microlaena*, *Tetrarrhena*, and *Zotovia* in the Ehrharteae, and we have aligned *Maltebrunia* and *Prosphytochloa* in the Oryzinae. Like *Oryza*, *Maltebrunia* and *Prosphytochloa* have spikelets with two basal sterile florets and 5-veined lemmas while most members of the Zizaniinae lack basal sterile florets and have3–10-veined lemmas (Terrell et al., 2001; Clayton et al., 2016).

Bambusoideae

The Bambusoideae represent the only major clade of grasses to diversify primarily in association with forests (Clark et al., 2015) and in our new treatment the subfamily includes 1670 species in 125 genera in 3 tribes: Arundinarieae (temperate woody bamboos), Bambuseae (tropical woody bamboos) and Olyreae (herbaceous bamboos (Kelchner et al., 2013; Clarket al., 2015; Wysocki et al., 2015; Dransfield, 2016; Zhang et al., 2016; Vorontsova et al., 2016). In addition to strong molecular support for their monophyly, the bamboos are distinguished by the presence of strongly asymmetrically invaginated arm cells in the leaf mesophyll as seen in transverse section, although this is modified to weakly invaginated arm cells or rosette cells in some taxa (Clark et al., 2015). Bamboos also possess relatively broad and pseudopetiolate leaf blades usually with fusoid cells flanking the vascular bundles, features considered plesiomorphic within the family. The woody bamboos (Arundinarieae and Bambuseae) share well developed rhizome systems, highly lignified culms, culm leaves well differentiated from the foliage leaves, well developed and often complex aerial branching, and foliage leaves with outer (contra) ligules (Clark et al., 2015). Culms develop in two phases: first, new, unbranched shoots bearing a culm leaf at each node emerge from the soil and elongate to their full height; second, the culms become lignified and aerial branches develop and produce foliage leaves. Woody bamboos all have bisexual spikelets and usually exhibit gregarious flowering followed by monocarpy after long vegetative cycles (Guerreiro, 2014; Clark et al., 2015). The two tribes differ, however, in their patterns of branch development and cytology and to a lesser extent, rhizome morphology. The Arundinarieae generally exhibit basipetal branch development and are uniformly tetraploid (2*n*=48, x=12). Most are strictly runners, with leptomorph, monopodial rhizomes, but some genera (e.g., *Bergbambos*, *Fargesia*, *Kuruna*) possess only pachymorph, sympodial rhizomes (Clark et al., 2015; Attigala et al., 2016). The Bambuseae, however, exhibit acropetal or bidirectional branch development and are either tetraploid or hexaploid [2*n* = 40, 44, 48 with x = 10, (11) or 12 or 2*n* = 72, with x = 12]. Most have strictly pachymorph, sympodial rhizomes, but amphimorph or leptomorph rhizomes are documented in *Chusquea* (Clark et al., 2015). The herbaceous bamboos (Olyreae), on the other hand, lack well differentiated culm leaves and outer ligules, and have relatively weakly lignified culms, restricted vegetative branching, and unisexual spikelets. Virtually all exhibit seasonal flowering, with a very few species apparently exhibiting gregarious monocarpy (Clark et al., 2015).

Molecular data have confirmed that the Bambusoideae, especially the two woody tribes, exhibit a complex history of hybridization and allopolyploidy (Fisher et al., 2009, 2014; Triplett et al., 2010, 2014; Goh et al., 2013; Yang et al., 2013; Attigala et al., 2014; Oliveira et al., 2014). Within Arundinarieae, the three traditionally recognized subtribes are polyphyletic and have been abandoned in favor of numbered lineages or clades (now twelve) based on molecular support (cited in Kellogg, 2015 but not in Soreng et al., 2015b), and a number of genera, including *Ampelocalamus*, *Indocalamus*, *Pleioblastus* and *Pseudosasa* among others, are demonstrably non monophyletic (Triplett & Clark, 2010; Zeng et al., 2010; Yang et al., 2013; Zhang et al., 2016). Although some generic realignments have been formalized in recent years, such as the recognition of *Bergbambos* and *Oldeania* (Stapleton, 2013) and *Kuruna* (Attigala et al., 2014), and a much narrower concept of *Arundinaria* (Triplett et al., 2010), much work remains to be done in this taxonomically challenging tribe. Two major clades based primarily on molecular support comprise the Bambuseae: the Neotropical woody bamboos (tetraploid) and the Paleotropical woody bamboos (hexaploid) (Clark et al., 2015). Within the Neotropical clade of the Bambuseae, the recognition of three subtribes has remained stable, with Chusqueinae well supported as sister to the Arthrostylidiinae + Guaduinae clade (Clark et al., 2015). For the most part the generic classification has remained stable as well; the classifications of Kellogg (2015) and Soreng et al. (2015b) for this clade are virtually identical, except for the placement of *Colanthelia* in synonymy with *Aulonemia* in Soreng et al. (2015b) and the annotation of some genera (e.g., *Aulonemia*, *Arthrostylidium*, *Rhipidocladum*) as non-monophyletic in Kellogg (2015). On-going molecular and morphological studies of the Neotropical woody bamboos will likely produce some additional changes at the generic level as more taxa are sampled.

Recent work by Goh et al. (2013), Chokthaweepanich (2014), Zhang et al. (2016), and Wong et al. (2016) has refined phylogenetic relationships within the Paleotropical clade of the Bambuseae and produced some changes in classification. The generic classifications of Kellogg (2015) and Soreng et al. (2015b) are very similar, again with the annotation of non-monophyletic genera in Kellogg (2015) but not in Soreng et al. (2015b). Wong et al. (2016) based on both molecular and morphological data recognize eight subtribes instead of the previous four (see Soreng et al., 2015b) and also highlight some generic realignments (e.g., resurrection of *Chloothamnus* for most of the Southeast and Australasian species of *Nastus* and the segregation of *Ruhooglandia* and *Widjajachloa* for aberrant species previously included in *Nastus*). Dransfield (2016) described *Sokinochloa* to accommodate three Madagascan species previously classified within the otherwise Eurasian *Cephalostachyum*. These changes resolved some of the obvious generic problems noted by Kellogg (2015), but generic circumscriptions within the Melocanninae deserve further scrutiny, as does the *Bambusa-Dendrocalamus-Gigantochloa* complex (Goh et al., 2013).

Kellogg (2015) and Soreng et al. (2015b) recognized more or less the same genera within the Olyreae (although *Parianella* was not mentioned in the Kellogg treatment), and the subtribal classification of the Olyreae, with three subtribes, (Soreng et al., 2015b) remains stable. Oliveira et al. (2014) demonstrated that *Olyra* and *Parodiolyra* as currently circumscribed are non-monophyletic, and on-going work by that group is expected to resolve the major generic issues that remain in the Olyrinae.

The classification here largely follows Clark et al. (2015) and Vorontsova et al. (2016). The Arundinarieae with only the subtribe Arundinariinae contains 581 species in 31 genera that are almost exclusively distributed in Eurasia; only the three species of *Arundinaria* are native to North America (Triplett & Clark, 2010; Triplett et al., 2010; Zhang et al., 2016). The species are principally temperate or subtemperate in distribution, associated primarily with forest vegetation but also in high elevation grasslands, with about 20 species occurring at high elevations in the Asian (India, Sri Lanka) or African (including Madagascar) tropics (Clark et al., 2015). Tribe Bambuseae includes 966 species in 73 genera placed in 11 subtribes. Subtribes Melocanninae (99 species in 9 genera), Hickeliinae (32 species in 9 genera), Bambusinae (324 species in 17 genera), Racemobambosinae (31 species in 3 genera), Dinochloinae (56 species in 7 genera), Greslaniinae (2 species in 1 genus), Holttumochloinae (6 species in 3 genera) and Temburongiinae (1 species in 1 genus) plus 2 monotypic genera (*Ruhooglandia* and *Temochloa*) currently considered *incertae sedis* form the Paleotropical woody bamboo clade distributed in Eurasia, Australasia or Africa (Kelchner et al., 2013; Clark et al., 2015; Wong et al., 2016). This clade shares a common ancestor with the Neotropical woody bamboo clade, formed by subtribes Arthrostylidiinae (185 species in 15 genera), Guaduinae (53 species in 5 genera), and Chusqueinae (175 species in 1 genus) distributed in the western hemisphere, in South and Central America, Mexico and the West Indies. Although many Bambuseae grow in association with lowland forests, or form extensive bamboo-dominated forests, a significant proportion of this tribe's diversity is found in tropical montane forests or high elevation grasslands (Clark et al., 2015). Tribe Olyreae includes 123 species in 21 genera, and these, with the exception of the monotypic *Buergersiochloa* from New Guinea and *Olyra latifolia* L. populations in Africa, occur in the western hemisphere, primarily in the understory of tropical forests in South and Central America (Clark et al., 2015).

Pooideae

The two 2015 classifications differed in combining three small tribes with their sister tribes by Kellogg (2015), for 10 total tribes, and the addition of one new tribe by Soreng et al. (2015b), for 14 total tribes. Placement of all genera within tribes was consistent between the two classifications except where the tribes were placed in synonymy or split. Kellogg (2015) included *Lygeum* in Nardeae (Schneider et al., 2009, 2011; Hochbach et al., 2015), and *Ampelodesmos* in Stipeae, rather than in their own monotypic tribes (Soreng et al., 2015b). *Brylkinia* and *Koordersiochloa* (Brylkinieae) of Soreng et al. (2015b) were merged into Meliceae by Kellogg (2015). In addition, the genus *Littledalea*, (Littledaleeae sensu Soreng) was included in Bromeae by Kellogg (2015), retaining Bromeae and Triticeae as sister tribes as done by Soreng et al. (2015b), rather than recognizing three subtribes within Triticeae as proposed by Schneider et al. (2009) and Hochbach et al.(2015). Kellogg (2015), without knowledge that Littledaleeae was published in 2015, favored making a new tribe for *Littledalea*. Soreng et al. (2015b) used the rank of supertribe Triticodae to unite Littledaleeae, Bromeae, and Triticeae tribes, and supertribe Poodae as sister to Triticodae. Kellogg (2015) did not use this rank.

In tribe Poeae Kellogg (2015) recognized 15 of 19 subtribes accepted by Soreng et al. (2015b). The tribe has two consistently resolved and well supported chloroplast DNA lineages (first resolved by Soreng et al., 1990) that were recognized in our 2015 classifications as Poeae chloroplast groups 1 and 2. Using DNA restriction site data within the tribe Poeae chloroplast clades 1 (Aveneae type) and 2 (Poeae type) were identified using six-base-pair restriction enzyme digests (Soreng et al., 1990; Soreng & Davis, 1998, 2000). Seven of the sites were unique to chloroplast group 1 (Aveneae type) and three were unique to chloroplast group 2 (Poaeae type). At least 65 species were surveyed using this restriction site protocol, and these two clades within the Poeae are still supported with new phylogenetic studies of chloroplast DNA sequences and whole plastids (Schneider et al., 2009; Hochbach et al., 2015; Saarela et al., 2015). Chloroplast group 1 contained genera of traditional Aveneae morphology (plus *Torreyochloa*, Brizinae, and Calothecinae), and Chloroplast group 2 contained genera with traditional Poeae morphology (plus Airinae, Alopecurinae, Holcinae, and Phleinae) sensu Clayton & Renvoize (1986) and older classifications. Recognition of the tribe Aveneae (sensu lato with Agrostideae included) usually was based on spikelets with one or multiple florets, one or both glumes longer than the lower florets, and lemmas with a dorsal, geniculate awn, and hyaline or scarious paleas, whereas Poeae spikelets usually have multiple florets, glumes shorter than the lowest floret, and lemmas with terminal awns or no awns, and chartaceous paleas that are green in part.

These characteristics are believed to have evolved multiple times in the two chloroplast groups (Soreng et al., 2007). When nrDNA was analyzed, the genera within chloroplast group 1 emerge as a clade nested within chloroplast group 2, with the Airinae, Aristaveninae, Holcinae, and Scolochloinae in a grade sister to the genera in chloroplast group 1. Moreover, genera of Sesleriinae (chloroplast group 2) nest within the set of *Arrhenatherum*, *Avena*, and *Helictotrichon* of subtribe Aveninae (Döring et al., 2007; Quintanar et al., 2007; Döring, 2009; Schneider et al., 2009). The evident mixing of morphologies and chloroplast types indicating hybridization and reticulation led to the abandonment of the two tribe (Aveneae and Poeae) system in favor of series of subtribes (Soreng & Davis, 2000; GPWG, 2001; Kellogg, 2015; Soreng et al., 2015b). The merging of Aveneae into Poeae was presaged prior to the availability of DNA phylogenetic data by Tzvelev (1987, 1989). Tzvelev also recognized a broad tribe Phleeae that encompassed several subtribes recognized by Kellogg (2015) and here in Poeae (corresponding to subtribes Alopecurinae, Ammochloinae, Beckmanniinae, Phalaridinae, Phleinae, and Sesleriinae sensu Soreng et al.), which he characterized as having basally connate, linear, simple plumose or merely papillate styles (versus styles separated, with more complex stigmatic branching in his Poeae).

In chloroplast group 1, Kellogg (2015) subsumed Brizinae s.l. (of our earlier on-line classifications, which included genera of Calothecinae) in Agrostideae. Brizinae (natives of Eurasia) and Calothecinae (of Latin America) have multiple-flowered spikelets with glumes shorter than the lower lemma, lemmas with flared margins and only vestiges of awns, and chartaceous paleas with well-spaced keels and narrow flanges, in contrast to the much of remainder of the Agrostidinae which have primarily single-flowered spikelets, lemmas without flared margins and often dorsally-awned, and hyaline paleas with keels that are often approximate and flanges often broader than the gap between the keels. In addition, within subtribe Aveninae, Kellogg (2015) lumped *Koeleria*, *Trisetum*, *Gaudinia*, *Rostraria*, *Avellinia*, *Peyritschia*, *Leptophyllochloa*, *Parafestuca* within *Trisetaria* based on interpretation of complex early DNA phylogenies (Quintanar et al., 2007; Saarela et al., 2007, 2010). Although the type species of *Trisetaria* had not yet been sampled in DNA studies until the work of Wölk & Röser (2017). Anticipating that further work on the subtribe might resolve these genera as monophyletic, Soreng et al. (2015b) retained all these genera (except *Parafestuca*). Both 2015 classifications overlooked *Trisetopsis* which is of complex reticulate origin within Aveninae (Wölk & Röser, 2013, 2014, 2017; Wölk et al., 2015).

In chloroplast group 2, Kellogg (2015) merged Holcinae sensu Soreng et al. (2015b) into Airinae, an option that seems reasonable on morphological grounds (all having been placed in the historical Aveneae), but this has not been supported on phylogenetic grounds (more study is needed here as the subtribes are closely related). Both 2015 classifications accepted Coleanthinae and a broad Poinae, with Miliinae accepted by Soreng et al. (2015b) and subsumed in Poinae by Kellogg (2015).

Within subtribe Loliinae, Kellogg (2015) treated the "broadleaf" clade of *Festuca* s.l. (Torrecilla & Catalán, 2002) as the "*Leucopoa* grade", rather than apportioning its species among five small genera (*Drymochloa*, *Leucopoa*, *Lolium*, *Patzkea*, *Pseudobromus*) as accepted by Soreng et al. (2015b). The wisdom of any approach here is expected to be tested soon by an in-depth study of phylogeny of *Festuca* s.l., worldwide (Minaya et al., 2017). A few other genera were aligned indifferent subtribes (e.g. *Cyathopus*, *Limnodea*) or were recognized by Soreng et al. (2015b) but not Kellogg (2015) [e.g., *Arctophila*, *Brizochloa*, *Catapodium*, *Dupontiopsis* (new in 2015, Soreng et al., 2015a), *Gaudinopsis*, *Pseudophleum*] or visaversa (e.g., *Deyeuxia*, *Loliolum*, *Pseudosclerochloa*).

In our new classification of Pooideae we have 3968 species in 202 genera in 15 tribes. Poeae is the largest tribe with 2562 species in 121 genera in 25 subtribes, 41 (39 tested) genera are placed among those with chloroplast group 1 type, 80 (78 tested) are placed among those with chloroplast group 2 type.

Currently we retain Nardeae and Lygeeae as separate tribes. Recognizing the strong support for the sister status of *Lygeum* and *Nardus* found in molecular studies (Catalán et al., 1997; Davis & Soreng, 2007; Schneider et al., 2009; Hochbachet al., 2015; Saarela et al., 2015) and morphological synapomorphies, we here describe supertribe Nardodae. Both genera have bicellular microhairs (otherwise absent in Pooideae) and single linear (non-plumose or simple plumose) styles, and lack lodicules. However, the spatheate, single compound "spikelet" synflorescences of *Lygeum* are so modified that the traditional grass spikelet structure is unrecognizable.

In our current classification we separate a monotypic Phaenospermateae from Duthieeae based on molecular results of Schneider et al. (2011) and Hochbach et al. (2015). Among the Duthieeae and other Pooideae, *Phaenosperma* is morphologically odd with globose spikelets that disarticulate below the glumes, pseudopetiolate and resupinate leaf blades (Schneider et al., 2011), and it is apparently widely reticulate in origin among tribes Duthieeae, Stipeae, and possibly Meliceae (Hochbach et al., 2015). We retain *Ampelodesmos* in the Ampelodesmeae separate from Stipeae based on evidence of a reticulate origin with Duthieeae (Romaschenko et al., 2012, 2014). We recognize the strong genetic influence of Stipeae parentage in *Ampelodesmos*, by uniting Ampelodesmeae and Stipeae in supertribe Stipodae. One could argue for placing Phaenospermateae and Duthieeae within the Stipodae since some members possess three styles and three lodicules, but the origins of *Phaenosperma* might be broader. Alternatively, Ampelodesmeae, Duthieeae, Phaenospermateae, and Stipeae tribes might one day be aligned within the Stipodae.

Although *Brylkinia* is well supported as sister to Meliceae, Meliceae sensu Soreng et al. (2015b) have several morphological synapomorphies (globose styles, short-truncate fleshy lodicules that are usually fused) that are not shared with Brylkinia or Koordersiochloa, so the latter two genera were placed in Brylkinieae. Although our unpublished DNA data support *Koordersiochloa* as sister to Meliceae, and *Brylkinia* assister to these, Schneider et al. (2011) and Hochbach et al. (2015) found support for placing *Koordersiochloa* within Meliceae. Here we place *Koordersiochloa* in Meliceae, and unite the tribes Brylkinieae and Meliceae in supertribe Melicodae.

In the Poeae, chloroplast group 1, we recognize *Ancistragrostis*, *Dichelachne*, *Echinopogon*, and *Relchela*, all primarily Australasian or South American, in a new subtribe, Echinopogoninae that have coriaceous to chartaceous lemmas and paleas (scarious to chartaceous in *Dichelachne*), lemmas with terminal or sub-terminal awns (absent in *Relchela*), hairy calluses, caryopses with a hairy apex and solid endosperm (soft in *Dichelachne*, and usually glabrous). *Ancistragrostis* is placed here based on morphological similarity to Echinopogon, the former has coriaceous lemmas a stout, central, hooked awn entered by lateral veins, and its caryopsis characters are unknown. *Echinopogon* and *Relchela* have been linked in plastid and nrDNA ITS studies (Döring, 2009; Barberá et al., unpublished data). *Dichelachne* is apparently reticulate and was resolved with *Echinopogon* (and *Relchela* where included) in plastid trees as sister to Agrostidinae + Calothecinae (Döring et al., 2007; Soreng et al., 2007; Döring, 2009; Barberá et al., unpublished data). However, in nrDNA-derived phylogenies *Dichelachne* was embedded in *Calamagrostis*. We here propose to unite subtribes Agrostideae, Brizinae, Calothecinae, and Echinopogoninae within supersubtribe Agrostidodinae. Within subtribe Agrostidinae our new data

(Barberá et al., unpublished data) indicate *Calamagrostis* (which also includes *Deyeuxia* p.p. typica, of the eastern hemisphere) ispolyphyletic with *Ammophila* embedded; *Chaetopogon* belongs in *Agrostis*, and *Chaetotropis* has a different origin from *Polypogon*. *Chaetotropis*, *Lachnagrostis* and *Polypogon* appear reticulate in origin.

Within subtribe Aveninae, at least three additional genera (*Graphephorum*, *Sphenopholis* and *Trisetopsis*) would need to be added to the expanded *Trisetaria* sensu Kellogg (2015) bringing the total to more than 260 species (Saarela et al., 2017; Barberá et al., unpublished data). Here we retain all genera, except *Leptophyllochloa* and *Parafestuca*, based on extensive new molecular studies in the Aveninae by Saarela et al. (2017), Barberá et al. (unpublished data), Wölk & Röser (2014, 2017), and Wölk et al. (2015). In order to salvage *Koeleria*, *Trisetum*, *Gaudinia*, *Rostraria*, *Avellinia*, *Peyritschia*, *Graphephorum*, *Sphenopholis*, *Trisetopsis* along with *Trisetaria* we propose to resurrect *Acrospelion* s.l. for 12 to 14 Eurasian species of *Trisetum* that generally have hairy ovaries, distichous leaves, and lax panicles (or combinations of these), and *Cinnagrostis* for the majority of the South American "*Calamagrostis/Deyeuxia*" species (ca. 80 to 90 spp.). Also we would move the *Trisetum spicatum* complex (ca. 25 species) to an expanded *Koeleria* (ca. 70 spp.), and expand *Graphephorum* (ca. 6 spp.) and *Peyritschia* (ca. 27 spp.). Reticulation is evident in the origin of several genera such as *Graphephorum*, and sporadic among *Koeleria* and miscellaneous species of other lineages.

In chloroplast group 2 we here correct for polyphyly in our Holcinae (Soreng et al., 2015b) by recognizing subtribe Aristaveninae with only *Deschampsia*, which is expanded to include species of *Calamagrostis* sect. *Stylagrostis* (Saarela et al., 2017; Barberá et al., unpublished data). We here describe supersubtribe Loliodinae to unite the consistently resolved clade that includes the Ammochloinae, Dactylidinae, Loliinae, and Parapholiinae. These subtribes have multiple-flowered spikelets, glumes shorter than the first lemma, lemmas with terminal awns when present, a glabrous callus, and caryopses with a linear hilum that is usually long.

For lack of a rank below subtribe, we erect supersubtribe Poodinae to unite the diverse, but internally homogeneous, subtribes Alopecurinae, Beckmanniinae, Cinninae, Miliinae, Phleinae, Poinae, and Ventenatinae (validated here). Some subsets of the genera placed here have sometimes been accepted in traditional classifications (Tzvelev, 1976, 1989; Davis, 1985), or implied by generic arrangements (Tutin, 1980; Clayton & Renvoize, 1986). However, these subtribes were not banded together until recent molecular studies verified their relationships (Döring et al., 2007; Gillespie et al., 2008, 2010, unpublished data; Döring, 2009; Schneider et al., 2011; Soreng et al., 2015a). They share glabrous caryopses, usually with lipid, and a short hilum (mostly less than ¼ the length), and a hairy callus in genera with more than one floret per spikelet. The large subtribe Poinae sensu Soreng et al. (2015b) and Kellogg (2015) is subdivided, Poinae is revised to include only *Poa*, and the new subtribe Ventenatinae is recognized here based on the above molecular studies.

Within the Pooideae *Agropyropsis*, *Agrostopoa*, *Ancistragrostis*, *Bromidium*, *Hypseochloa*, and *Duthiea* s.s. need molecular study. A GenBank DNA sequence for *Pentapogon* suggests placement in Arundinoideae, but this needs corroboration since its morphology agrees with Poeae.

Aristidoideae

Kellogg (2015) and Soreng et al. (2015b) both recognized *Aristida*, *Sartidia*, and *Stipagrostis* in the Aristidoideae and the latter authors retained the tribe Aristideae. *Sartidia* now includes six species with the description of the Madagascar endemic, *S. isaloensis* Voronts., Razanatsoa & Besnard, and *Aristida* includes 305 species with the addition of *A. helleriana* M. Marchi, J. Mujica & R. L. Barbieri from Rio Grande do Sul, Brazil (Marchi et al., 2015; Vorontsova et al., 2015). Morphologically, Aristidoideae can be distinguished from other grasses in having 3-awned lemmas, a line of hairs for a ligule,1-flowered spikelets, lemmas with overlapping margins(involute), and a sharp-pointed callus (GPWG, 2001; Cerros-Tlatilpa et al., 2011).

Panicoideae

In our new classification, subfamily Panicoideae consists of 3241 species in 247 genera and 13 tribes. Morphological trends within the Panicoideae include two-flowered, dorsally compressed spikelets with the lower floret staminate or sterile, although many of the basal tribes, such as the Centotheceae, Chasmanthieae, and Zeugiteae, have laterally compressed, multi-flowered spikelets. Kellogg (2015) accepted eight tribes and 217 genera whereas Soreng et al. (2015b) accepted 12 tribes and 241genera. Kellogg (2015) merged Zeugiteae into Chasmanthieae; Cyperochloeae and Thysanolaeneae into Centotheceae; and Arundinelleae into Andropogoneae as a subtribe. Soreng et al. (2015b) followed the classification of Sánchez-Ken & Clark (2010) in recognizing centothecoid tribes.

The genera placed in each of these tribes, or merged tribes, were the same with several exceptions. Kellogg (2015) placed *Arundoclaytonia* in Chasmanthieae whereas Soreng et al. (2015b) retained it in Steyermarkochloeae based on the similarity of the two genera in spikelet form and organization. DNA sequences obtained for *Arundoclaytonia* by Sánchez-Ken & Clark (2010) were incomplete and confusing for the regions sequenced. Therefore, Soreng et al. (2015b) were not prepared to accept the phylogenetic placement of *Arundoclaytonia* in Chasmanthieae. Kellogg (2015) placed *Chandrasekharania* and *Jansenella* in Tristachyideae whereas Soreng et al. (2015b) left these in *incertae sedis*. In Tristachyideae, Kellogg (2015) lumped *Dilophotriche*, *Loudetiopsis*, and *Zonotriche* in *Tristachya*, all historically accepted genera maintained by Soreng et al. (2015b). Kellogg merged *Bromuniola* in *Chasmanthium*, and *Pohlidium* in *Zeugites*, both accepted by Soreng et al. (2015b).

Kellogg (2015) recognized Panicoideae s.s. including Andropogoneae, Paniceae and Paspaleae tribes (and four *incertae sedis* genera) with Paniceae sister to Andropogoneae + Paspaleae, whereas Soreng et al. (2015b) grouped Paniceae and Paspaleae as supertribe Panicodae (a rank not used by Kellogg), and Arundinelleae + Andropogoneae as supertribe Andropogonodae. Each classification of

Paniceae and Paspaleae included the same subtribes, except subtribe Dichantheliinae (Zuloaga et al., 2014) was not mentioned by Kellogg (2015). Alignments of genera were much the same, but Kellogg submerged several genera that were accepted by Soreng et al. (2015b). In Paspaleae Kellogg lumped *Achlaena* and *Altoparadisium* in *Arthropogon*, *Steinchisma* and *Plagiantha* in *Otachyrium*, *Baptorhachis* in *Axonopus*, and *Spheneria* in *Paspalum*. In Paniceae Kellogg (2015) placed *Walwhalleya* in *Homopholis*, *Ancistrachne* and *Calyptochloa* in *Cleistochloa*, *Paraneurachne* in *Neurachne*, *Plagiosetum* in *Paractaenum*, *Scutachne* and *Megathyrsus* in *Urochloa*, *Mildbraediochloa* in *Melinis*, and *Yakirra* in *Panicum*. Also in Paniceae, *Adenochloa* (Zuloaga et al., 2014), accepted by Soreng et al. (2015b), was not accounted for by Kellogg (2015) except as African members of *Dichanthelium* s.l. Soreng et al. (2015b) placed *Snowdenia* in *Cenchrus* whereas Kellogg accepted it.

Whole plastid analyses align *Whiteochloa* within *Panicum*, rendering the latter genus paraphyletic, although they are not recommending reclassification until more species within *Whiteochloa* are analyzed (Burke et al., 2016). Soreng et al. (2015b), Kellogg (2015), and our current classification place *Whiteochloa* within the subtribe Cenchrinae. In an unpublished molecular analysis of plastid markers, all six species of *Whiteochloa* appear as a clade within the Cenchrinae (Zuloaga & Scataglini, unpublished data). Morphologically, *Whiteochloa* differs from *Panicum* in having laterally compressed spikelets, glumes with tubercle-based hairs forming rows along the veins, a deeply sulcate lemma, and cymbiform upper glumes with a hardened and constricted apex (Lazarides, 1978; Watson & Dallwitz, 1992; Kellogg, 2015).

Even though most members of subtribe Melinidinae appear monophyletic, the synflorescence structure of species and genera is highly diverse with different degrees of branching (Reinheimer & Vegetti, 2008; Reinheimer et al., 2009; Salariato et al., 2010). Preliminary molecular evidence supports a broad view for *Urochloa* and we follow this in our new classification while continuing to recognize *Megathyrsus* (two species) with open and lax panicles, and *Scutachne*, a Cuban monotypic genus with stipitate synflorescences and indurate upper glumes and lower lemmas (Clayton et al., 2016). In addition, we maintain a large *Eriochloa* with 24 species as opposed to Kellogg's (2015) view of restricting it to the type species. A detailed molecular study increasing the number of species sampled is needed before we can interpret the evolutionary history and realign the classification.

In Soreng et al. (2015b), the Andropogoneae included 12subtribes excluding Arundinelleae (treated as a sister tribe to Andropogoneae, the two united as supertribe Andropogonodae), whereas Kellogg (2015) had eight subtribes including the Arundinellinae. Soreng et al. (2015b) accepted Arthraxoninae, Chinonachninae, and Coicinae, while genera of these were placed *incertae sedis* by Kellogg (2015). Soreng et al. (2015b) accepted Dimeriinae but noted it was nested in Ischaeminae, which is where Kellogg placed it. Sorghinae and Anthistiriinae were accepted by Soreng et al. (2015b) while Kellogg (2015) placed these within Saccharinae and Andropogoninae, respectively.

Within the Andropogoneae the genera accepted in each account in each subtribe, or *incertae sedis*, differ in so many cases, we hesitate to list them all. Soreng et al. (2015b) accepted 90 genera while

Kellogg accepted 86 genera. Soreng et al. (2015b) accepted 11 genera that Kellogg treated as synonyms (*Erianthus*, *Hemisorghum*, *Miscanthidium*, *Narenga*, *Polytoca*, *Pseudopogonatherum*, *Ratzeburgia*, *Sclerachne*, *Sclerostachya*, *Trilobachne*), and two more she didnot account for (*Tripidium* and *Veldkampia*) whereas she accepted five genera we placed in synonymy (*Cleistachne*, *Eremopogon*, *Hackelochloa*, *Hypogynium*, and *Sarga*), and four we did not account for (*Jardinea*, *Lakshmia*, *Lasiorhachis*, and *Leptatherum*). Some of the differences result from Kellogglumping four genera in Chinonachne (which we placed in subtribe Chionachninae; she placed *Chionachne* in *incertae sedis*), and lumping three more genera in *Miscanthus* (*Miscanthidium*, *Narenga*, *Sclerostachya*). The classification of Soreng et al. (2015b) attempted to follow the subtribe and generic arrangements of Clayton & Renvoize (1986), in so far as molecular studies and GenBank DNA sequence data seemed to provide support. However, it was noted by Soreng et al. (2015b) that significant rearrangements were anticipated for which there was limited data available to us. Kellogg (2015) provided many rearrangements of genera and subtribes, and yet many more are anticipated based on a series of DNA studies she is currently pursuing. This is one of the most complex tribes of grasses, with many polyploidization and reticulation events blurring boundaries between traditional genera higher ranks.

Here we revise Panicodae to include only tribe Paniceae, and expand Andropogonodae to included Paspaleae. Trends within the supertribe Andropogonodae include a base chromosome number of x = 10 and the occurrence of paired spikelets, these commonly sessile and pedicelled. In supertribe Panicodae the base chromosome number is x = 9 and spikelets are mostly upaired. In our new classification we attempt to follow Kellogg (2015) for Andropogoneae, as far as we are comfortable in doing so while acknowledging Kellogg is far more knowledgeable of the tribe worldwide than any of our coauthors. Accordingly, Dimeriinae is placed in Ischaeminae, Sorghinae in Saccharinae, and Anthistiriinae in Andropogoninae. Gosavi et al. (2016) and Arthan et al. (2016) offer new insights in Rottboelliinae, and we now accept *Hackelochloa* (as did Kellogg). Kellogg (2015, p. 300) mentioned an unpublished DNA study where *Coelorachis* is placed in *Rottboellia* rather than *Mnesithea* as proposed by Veldkamp et al. (1986); and we now follow that here.

New DNA data allow placement of *Jansenella* in Arundinelleae in our new classification but we are not aware of any DNA data for *Chandrasekharania* (both of which Kellogg placed in Tristachyideae), so we leave the latter genus *incertae sedis*. We now have 98 accepted genera in the Andropogoneae and 247 genera for the subfamily. The following changes are accepted here. The monotypic tribe Lecomtelleae was resurrected by Besnard et al. (2013) as sister to Paniceae in various combinations with Paspaleae and Sacchareae (=Andropogoneae). The single species of *Lecomtella* occurs in Madagascar, occupying a phylogenetically and biogeographically interesting position. *Lecomtella madagascariensis* A. Camus has C_3 leaf anatomy, an external ligule, and a fertile upper lemma with wing-like rachilla appendages and a dense covering of trichomes on a papillate surface (Besnard et al., 2013). Silva et al. (2016) resurrected *Chasechloa* as another monotypic genus of Panicoideae from Madagascar, placing it in Boivinellinae of Paniceae, rather than in *Echinolaena* of Paspaleae as done by and Soreng et al. (2015b);

Chasechloa was not mentioned by Kellogg (2015). *Kellochloa*, *Hildaea*, and *Oedochloa* are new genera, and *Setiacis* is tentatively accepted as a segregate of *Acroceras* (Chen & Phillips, 2006). Newsynonyms are: *Walwhalleya* now placed in *Homopholis*, *Mildbraediochloa* in *Melinis*, *Arthragrostis* in *Panicum*, *Leptocoryphium* in *Anthaenantia*, and *Spheneria* in *Paspalum*.

Arundinoideae

Soreng et al. (2015b) treated the Arundinoideae as having 16 genera aligning in two tribes, Arundineae and Molinieae, with the Crinipes group (*Crinipes*, *Lepatgrostis*, *Nematopoa*, *Piptophyllum*, *Styppeiochloa*, and *Zenkeria*) sensu Linder et al. (1997) and Barker et al. (1998) placed in the Molinieae. Kellogg (2015) accepted 18 genera plus "*Eragrostis walteri* Pilg."[=*Pratochloa walteri* (Pilg.) Hardion] without subtribe affiliation (Hardion et al, in press). Soreng et al. (2015b) placed *Alloeochaete*, *Danthonidium*, and *Phaenanthoecium* in the Danthonioideae but also included *Moliniopsis* in the Arundineae and reported that "*Eragrostis walteri*" belonged in the Arundinoideae.

Recent whole chloroplast phylogenies (Cotton et al., 2015; Duvall et al., 2016, 2017) have corroborated generic relationships within Arundinoideae identified by previous analyses of chloroplast genes (GPWG II, 2011) and mixed morphological and molecular datasets (GPWG, 2001). Based on plastome analysis, Teisher et al. (in press) found that *Crinipes* and *Styppeiochloa* are sister and the remaining "crinipoid" grasses are polyphyletic, with *Nematopoa* aligning within the Chloridoideae, and Alloeochaete and *Dichaetaria* aligning within the Panicoideae. This latter placement is in contrast with Teisher'sprior preliminary analyses that placed *Dichaetaria* in the Arundinoideae in a position sister to *Dregeochloa* (Soreng et al., 2015b).

In our new classification we recognize two tribes and two subtribes in Arundinoideae. The Arundineae is characterized by glumes that are typically as long as or longer than the lowest floret and contain 17 species in four genera: *Amphipogon*, *Arundo*, *Dregeochloa*, and *Monachather*. The Molinieae generally have glumes that are shorter than thelowest floret and contain 24 species in 11 genera. The Moliniinae consists of *Hakonechloa*, *Molinia*, *Moliniopsis* and *Phragmites* while the Crinipinae consists of *Crinipes*, *Elytrophorus*, *Styppeiochloa*, and "*Eragrostis walteri*." Three genera in this group, *Leptagrostis*, *Piptophyllum*, and *Zenkeria* still lack molecular data, and given the polyphyletic nature of the former crinipoid group, it is likely one or more of these genera are misplaced in Arundinoideae (Hardion et al., in press).

Micrairoideae

Soreng et al. (2015b) divided the Micrairoideae into four tribes: Micraireae, Eriachneae, Isachneae, and Hubbardieae whereas Kellogg (2015) did not recognize any subtribes below the rank of subfamily but did suggest, "if they are to be recognized, then Micraireae include only *Micraira*, Eriachneae include *Eriachne* and *Pheidochloa*, and Isachneae include the rest." New plastome phylogenies align *Hubbardia* and *Limnopoa* within Isachneae (Teisher, 2016; Duvall et al., 2017; Teisher et al., in press) and

Pheidochloa considered a synonym of *Eriachne* (Teisher, 2016; Teisher et al., in press). Our current classification incorporates these changes, recognizing an unchanged Micraireae and Eriachneae, both monotypic, and an expanded Isachneae containing *Isachne*, *Coelachne*, *Heteranthoecia*, *Sphaerocaryum*, and *Hubbardia*. The Isachneae is by far the largest tribe in the subfamily (113 species) and is in need of a worldwide revision since *Isachne* is portrayed as paraphyletic (Teisher et al., in press). A salient morphological synapomorphy for this subfamily is lacking, although most species tend to have a line of hairs for a ligule, 2-flowered (1-flowered in *Sphaerocaryum* and one species of *Coelachne*), spikelets without a rachilla extension, both florets fertile in most, or the lower sterile (*Limnopoa*, *Hubbardia* and some *Isachne*), and caryopses with small embryos (Sánchez-Ken et al., 2007).

Danthonioideae

Soreng et al. (2015b) recognized the tribe Danthonieae with 17 genera whereas Kellogg (2015) included these same 17 genera within the Danthonioideae without a tribe. In addition, Soreng et al. (2015b) recognized *Alloeochaete*, *Danthonidium*, and *Phaenanthoecium* as *incertae sedis* in the subfamily. New molecular DNA results confirm that *Phaenanthoecium* is aligned within the Danthonieae and that, as previously mentioned, *Alloeochaete* aligns within the Panicoideae (Teisher et al., in press). *Phaenanthoecium koestlinii* (Hochst. ex A. Rich.) C.E. Hubb. has Danthonioideae-like characteristics with flattened awns inserted from the sinus of a bilobed lemma (Teisher et al., in press). In our new classification with the addition of *Phaenanthoecium* there are 18 genera in the Danthonieae and only *Danthonidium* remains as *incertae sedis* within the subfamily.

Chloridoideae

Kellogg's (2015) classification of the Chloridoideae is very similar to that of Soreng et al. (2015b), both recognize five tribes and about the same number of genera. However, Kellogg includes the Zoysiinae and Sporobolinae as synonyms in the Zoysieae, and within the Cynodonteae, the Aeluropodinae is omitted. As pointed out by Kellogg (2015), earlier studies render *Aeluropus* in an unresolved position (Peterson et al., 2010a); with additional data Peterson et al. (2016) found *Odyssea paucinervis* (Nees) Stapf to be a strongly supported sister [bootstrap (BS)=100, posterior probability (PP)=1.00] and therefore an additional member of the Aeluropodinae. In Kellogg, the Hilariinae, Monanthochloinae, Muhlenbergiinae, Scleropogoninae, and Traginae are placed as synonyms within Boutelouinae; and Cteniinae, Farraginінae, Gymnopogoninae, Perotidinae, and Trichoneurinae are synonymized within Gouniinae. It is clear how she arrived at this since Peterson et al. (2010a, 2010b, 2014a, 2016) had found strong support for clades of the expanded Boutelouinae sensu Kellogg (BS=93or 94, PP=1.00) and Gouiniinae sensu Kellogg (BS=100, PP=1.00). We describe two new supersubtribes for these clades in the taxonomy section.

In our new classification, subfamily Chloridoideae consists of 1602 species in 124 genera and five tribes. Most members of the Chloridoideae share two structural synapomorphies: C_4 leaf anatomy (except two species of *Ellisochloa*) and bicellular microhairs with a broad, short terminal cell the same thickness as the basal cell (Peterson et al., 2007). Morphological trends within the subfamily include a base chromosome number of x=10 (a pleisiomorphy), caryopses with a nonlinear hilum that are usually punctiform or small, embryos with elongated mesocotyl internodes, two non-membranous (fleshy) lodicules (Soreng & Davis, 1998; GPWG, 2001; Peterson et al., 2007).

The largest tribe, Cynodonteae includes 850 species in 94 genera, followed by the Eragrostideae with 489 species in 14genera, the Zoysieae with 233 species in four genera, the Triraphideae with 15 species in three genera, and the Centropodieae with six species in two genera. We recognize 21 subtribes within the Cynodonteae and this includes three new subtribes: Dactylocteniinae, Orininae, Zaqiqahinae (Peterson et al., 2016). Species in the Dactylocteniinae (includes *Acrachne*, *Brachychloa*, *Dactyloctenium*, and *Neobouteloua*) have synflorescences composed of digitately arranged racemes or racemes borne on a central axis, caryopses usually with a free pericarp (excluding *Neobouteloua*), 1–9-floweredlaterally compressed spikelets, glumes that are usually shorter than the spikelets (excluding a single species of *Dactyloctenium*), and (1–)3(–5)-veined lemmas (excluding a single species of *Dactyloctenium*) (Clayton et al., 2016). We have evidence of a possible hybridization event and subsequent genomic introgression between *Acrachne racemosa* (B. Heyneex Roem. & Schult.) Ohwi and an unknown member of the Eleusininae since our plastid and nuclear DNA markers are not congruent (Peterson et al., 2015, 2016; Peterson & Romaschenko, unpublished data).

Species in the Orininae (includes *Cleistogenes* and *Orinus*) have paniculate synflorescences with racemose branches borne along a central axis, (1)2–8-flowered spikelets, glumes that are shorter than the adjacent florets, and 3–7-veined lemmas (Peterson et al., 2016). The two genera are often difficult to separate morphologically, and have been linked historically since the basionym of *Orinus kokonorica* (K. S. Hao) Tzvelev was described as a *Cleistogenes* (Hao, 1938). However, *Cleistogenes* (13 or 14 species ranging from southern Europe to Turkey and eastward through central Asia and China) has hidden cleistogamous spikelets concealed within the upper sheaths (not found in *Orinus*), a cespitose habit or very short rhizomes (vs. elongated rhizomes in *Orinus*), and 3–7-veined lemmas (vs. 3-veined lemmas in *Orinus*) (Chen et al., 2006).

The Zaqiqahinae includes a single species, *Zaqiqah mucronata* (Forssk.) P. M. Peterson & Romasch. [*Odyssea mucronata* (Forssk.) Stapf], a suffrutescent perennial with stiff, hard, much-branched culms up to 2mtall, lemmas 4–5mmlong, and is found along the immediate coast bordering the Red Sea in sand dunes or plains (Peterson et al., 2016). Molecular analyses of the three species formerly placed in *Odyssea* confirmed that each one had a different evolutionary origin (Peterson et al., 2014b, 2016). *Odyssea paucinervis*, as previously mentioned, is sister to *Aeluropus*, and both genera have elongated rhizomes, stiff and pungent leaf blades, synflorescences composed of racemes born on a central axis, multiple-flowered spikelets, and mucronate lemmas (Clayton et al., 2016). In addition, we have evidence of a possible hybridization event and subsequent genomic introgression between *O. paucinervis* and an unknown member of Dactylocteniinae (Peterson et al., 2016). Morphologically, *Zaqiqah mucronata* and

Odyssea paucinervis are very similar in having short, rigid to pungent leaf blades; narrow and contracted panicles; several-flowered spikelets with 1-veinedglumes; lemmas that are 3-veined with silky villous veins, apices dentate and mucronate; and caryopses with free pericarps (Stapf, 1922; Phillips, 1951, 1995; Cope, 1999, 2007). The third species, *Odyssea jaegeri* (Pilg.) Robyns & Tournay, with smooth, glabrous, and unawned lemmas was placed in *Psilolemma* by Phillips (1974) and has recently been found to be sister to *Sporobolus*, a member of the tribe Zoysieae and Sporobolinae (Peterson et al., 2014b). Clearly, the morphological features of these three former species of *Odyssea* are a result of convergent evolution.

Since our last classification, new molecular DNA studies have aligned *Halopyrum* in the Tripogoninae, *Decaryella* (Vorontsova 1398 in GenBank) and *Hubbardochloa* in the Hubbardochloinae (older name for the Gymnopogoninae), and *Pogononeura* in the Traginae (Peterson et al., 2015, 2016). New genera include: *Orthacanthus* (monotypic) in the Traginae, *Triplasiella* (monotypic) in the Gouiniinae, and *Tripogonella* (3 species) in the Tripogoninae (Peterson et al., 2016). Within the Eleusininae, Chloris now includes *Lintonia* as a synonym, *Microchloa* (includes syn. *Rendlia*), *Tetrapogon* (includes syn. *Saugetia*), and *Neostapfiella* (Vorontsova 1486 in GenBank) is new to the subtribe (Peterson et al., 2015). Within the Orcuttiinae, *Orcuttia* now includes *Tuctoria* as a synonym, and within the Triodiinae, *Triodia* includes *Monodia* and *Symplectrodia* as synonyms (Crisp et al., 2015; Toon et al., 2015). *Nematopoa* (formerly placed in Molinieae of the Arundinoideae) is now a synonym of *Triraphis* in the Triraphideae (Teisher et al., in press). *Catalepis*, *Ectrosia*, *Harpachne*, *Nematopoa*, *Pogonarthria*, and *Psammagrostis*, are all synonyms of *Eragrostis* (Eragrostidinae). *Stiburus conrathii* Hack. [=*Eragrostis conrathii* (Hack.) S.M. Phillips] (formerly placed in Eragrostidinae) aligns with the Uniolinae (Peterson & Romaschenko, unpublished data) and requires further study. *Stiburus alopecuroides* (Hack.) Stapf (type) appears to be sister to *Eragrostis* (Peterson & Romaschenko, unpublished data).

ACKNOWLEDGEMENTS

We thank the National Geographic Society Committee for Research and Exploration (Grant Nos. 8848-10, 8087-06) for field and laboratory support, the Smithsonian Institution’s Restricted Endowments Fund, the Scholarly Studies Program, Research Opportunities, Atherton Seidell Foundation, Biodiversity Surveys and Inventories Program, Small Grants Program, the laboratory of Analytical Biology, the Missouri Botanical Garden for supporting Tropicos, and the United States Department of Agriculture, all for financial support. We thank Heather Stimmel for Tropicos database support. We would also like to acknowledge Maria S. Vorontsova and Jerrold I Davis for providing helpful comments on the manuscript, and Jeffery M. Saarela for discussions on the classification.

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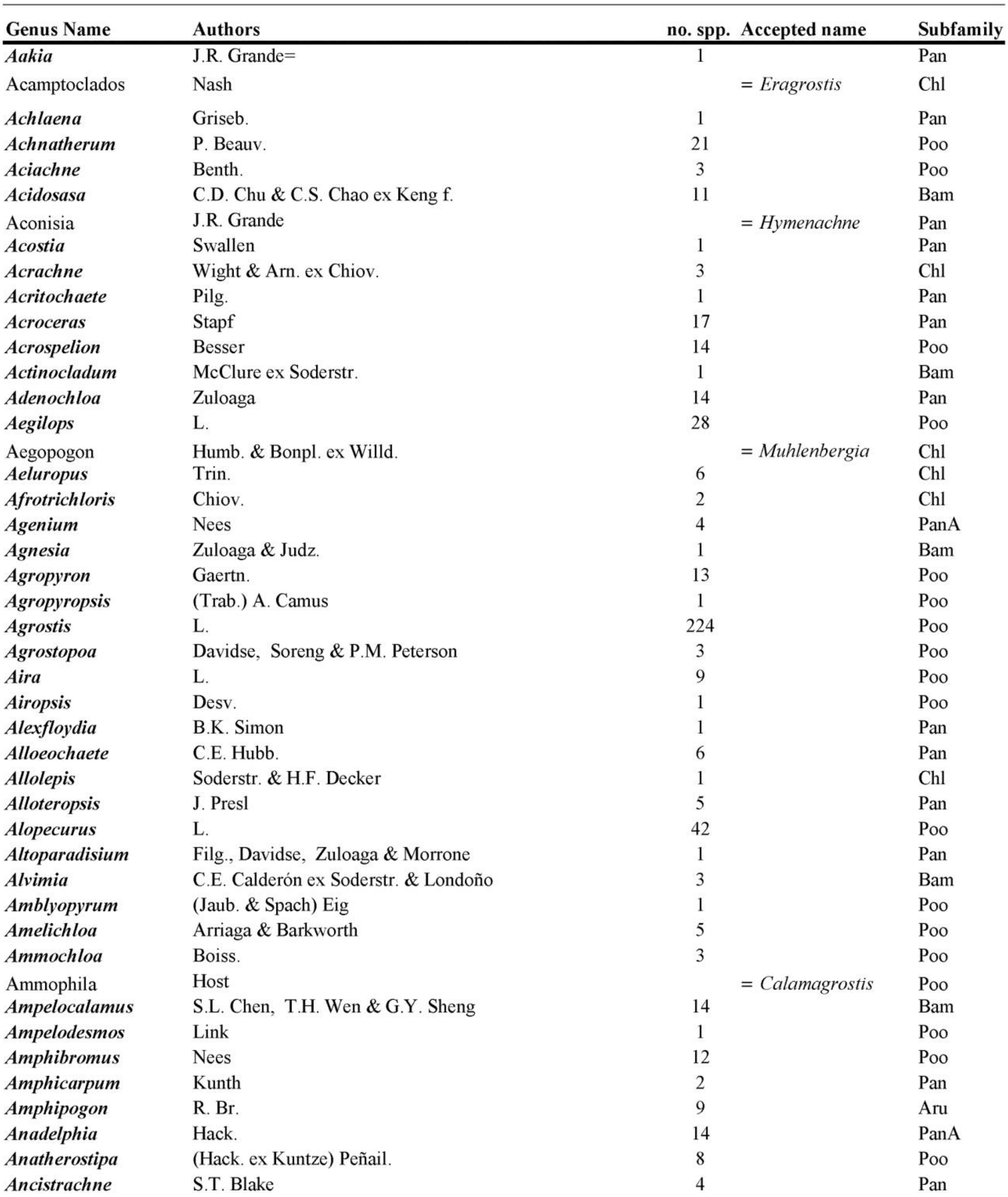
SUPPORTING INFORMATION

Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.



Genus Name	Authors	no. spp.	Accepted name	Subfamily
Aakia	J.R. Grande=	1		Pan
Acamptoclados	Nash		= *Eragrostis*	Chl
Achlaena	Griseb.	1		Pan
Achnatherum	P. Beauv.	21		Poo
Aciachne	Benth.	3		Poo
Acidosasa	C.D. Chu & C.S. Chao ex Keng f.	11		Bam
Aconisia	J.R. Grande		= *Hymenachne*	Pan
Acostia	Swallen	1		Pan
Acrachne	Wight & Arn. ex Chiov.	3		Chl
Acritochaete	Pilg.	1		Pan
Acroceras	Stapf	17		Pan
Acrospelion	Besser	14		Poo
Actinocladum	McClure ex Soderstr.	1		Bam
Adenochloa	Zuloaga	14		Pan
Aegilops	L.	28		Poo
Aegopogon	Humb. & Bonpl. ex Willd.		= *Muhlenbergia*	Chl
Aeluropus	Trin.	6		Chl
Afrotrichloris	Chiov.	2		Chl
Agenium	Nees	4		PanA
Agnesia	Zuloaga & Judz.	1		Bam
Agropyron	Gaertn.	13		Poo
Agropyropsis	(Trab.) A. Camus	1		Poo
Agrostis	L.	224		Poo
Agrostopoa	Davidse, Soreng & P.M. Peterson	3		Poo
Aira	L.	9		Poo
Airopsis	Desv.	1		Poo
Alexfloydia	B.K. Simon	1		Pan
Alloeochaete	C.E. Hubb.	6		Pan
Allolepis	Soderstr. & H.F. Decker	1		Chl
Alloteropsis	J. Presl	5		Pan
Alopecurus	L.	42		Poo
Altoparadisium	Filg., Davidse, Zuloaga & Morrone	1		Pan
Alvimia	C.E. Calderón ex Soderstr. & Londoño	3		Bam
Amblyopyrum	(Jaub. & Spach) Eig	1		Poo
Amelichloa	Arriaga & Barkworth	5		Poo
Ammochloa	Boiss.	3		Poo
Ammophila	Host		= *Calamagrostis*	Poo
Ampelocalamus	S.L. Chen, T.H. Wen & G.Y. Sheng	14		Bam
Ampelodesmos	Link	1		Poo
Amphibromus	Nees	12		Poo
Amphicarpum	Kunth	2		Pan
Amphipogon	R. Br.	9		Aru
Anadelphia	Hack.	14		PanA
Anatherostipa	(Hack. ex Kuntze) Peñail.	8		Poo
Ancistrachne	S.T. Blake	4		Pan

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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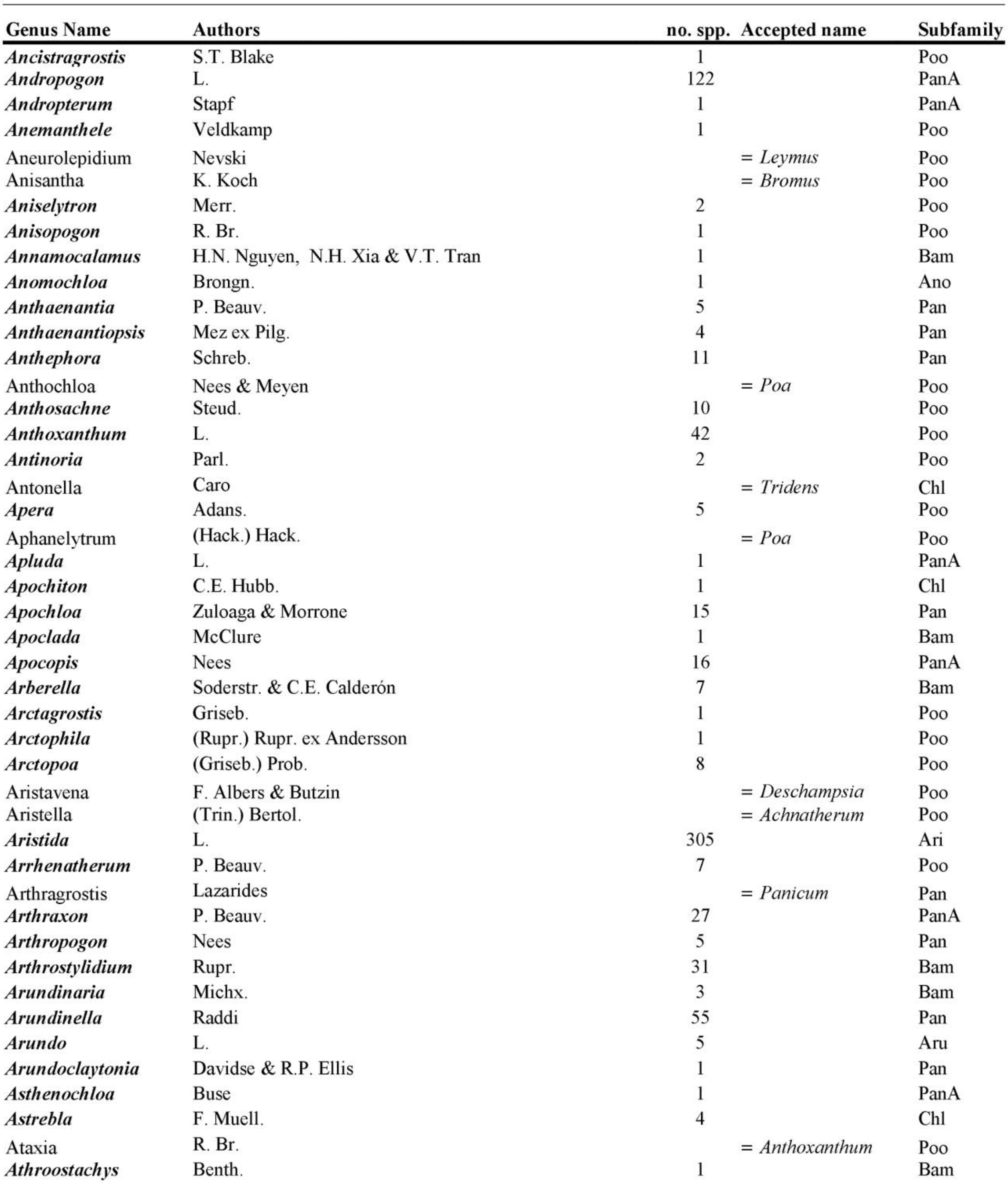

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Ancistragrostis	S.T. Blake	1		Poo
Andropogon	L.	122		PanA
Andropterum	Stapf	1		PanA
Anemanthele	Veldkamp	1		Poo
Aneurolepidium	Nevski		= *Leymus*	Poo
Anisantha	K. Koch		= *Bromus*	Poo
Aniselytron	Merr.	2		Poo
Anisopogon	R. Br.	1		Poo
Annamocalamus	H.N. Nguyen, N.H. Xia & V.T. Tran	1		Bam
Anomochloa	Brongn.	1		Ano
Anthaenantia	P. Beauv.	5		Pan
Anthaenantiopsis	Mez ex Pilg.	4		Pan
Anthephora	Schreb.	11		Pan
Anthochloa	Nees & Meyen		= *Poa*	Poo
Anthosachne	Steud.	10		Poo
Anthoxanthum	L.	42		Poo
Antinoria	Parl.	2		Poo
Antonella	Caro		= *Tridens*	Chl
Apera	Adans.	5		Poo
Aphanelytrum	(Hack.) Hack.		= *Poa*	Poo
Apluda	L.	1		PanA
Apochiton	C.E. Hubb.	1		Chl
Apochloa	Zuloaga & Morrone	15		Pan
Apoclada	McClure	1		Bam
Apocopis	Nees	16		PanA
Arberella	Soderstr. & C.E. Calderón	7		Bam
Arctagrostis	Griseb.	1		Poo
Arctophila	(Rupr.) Rupr. ex Andersson	1		Poo
Arctopoa	(Griseb.) Prob.	8		Poo
Aristavena	F. Albers & Butzin		= *Deschampsia*	Poo
Aristella	(Trin.) Bertol.		= *Achnatherum*	Poo
Aristida	L.	305		Ari
Arrhenatherum	P. Beauv.	7		Poo
Arthragrostis	Lazarides		= *Panicum*	Pan
Arthraxon	P. Beauv.	27		PanA
Arthropogon	Nees	5		Pan
Arthrostylidium	Rupr.	31		Bam
Arundinaria	Michx.	3		Bam
Arundinella	Raddi	55		Pan
Arundo	L.	5		Aru
Arundoclaytonia	Davidse & R.P. Ellis	1		Pan
Asthenochloa	Buse	1		PanA
Astrebla	F. Muell.	4		Chl
Ataxia	R. Br.		= *Anthoxanthum*	Poo
Athroostachys	Benth.	1		Bam

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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Genus Name	Authors	no. spp.	Accepted name	Subfamily
Atractantha	McClure	6		Bam
Atractocarpa	Franch.		= *Puelia*	Pue
Aulonemia	Goudot	47		Bam
Australopyrum	(Tzvelev) Á. Löve	5		Poo
Austrochloris	Lazarides	1		Chl
Austroderia	N.P. Barker & H.P. Linder	5		Dan
Austrofestuca	(Tzvelev) E.B. Alexeev		= *Poa*	Poo
Austrostipa	S.W.L. Jacobs & J. Everett	63		Poo
Avellinia	Parl.	1		Poo
Avena	L.	24		Poo
Avenella	Drejer	2		Poo
Avenula	(Dumort.) Dumort.	1		Poo
Axonopus	P. Beauv.	105		Pan
Baldingera	G. Gaertn., B. Mey. & Scherb.		= *Phalaris*	Poo
Bambusa	Schreb.	153		Bam
Baptorhachis	Clayton & Renvoize	1		Pan
Bashania	Keng f. & T.P. Yi	7		Bam
Bealia	Scribn.		= *Muhlenbergia*	Chl
Beckmannia	Host	2		Poo
Bellardiochloa	Chiov.	5		Poo
Bergbambos	Stapleton	1		Bam
Bewsia	Gooss.	1		Chl
Bhidea	Stapf ex Bor	3		PanA
Blepharidachne	Hack.	4		Chl
Blepharoneuron	Nash		= *Muhlenbergia*	Chl
Boissiera	Hochst. ex Steud.		= *Bromus*	Poo
Bonia	Balansa	5		Bam
Borinda	Stapleton		= *Fargesia*	Bam
Bothriochloa	Kuntze	37		PanA
Bouteloua	Lag.	60		Chl
Brachiaria	(Trin.) Griseb.		= *Urochloa*	Pan
Brachyachne	(Benth. & Hook. f.) Stapf		= *Cynodon*	Chl
Brachychloa	S.M. Phillips	2		Chl
Brachyelytrum	P. Beauv.	3		Poo
Brachypodium	P. Beauv.	22		Poo
Brachystachyum	Keng		= *Semiarundinaria*	Bam
Briza	L.	5		Poo
Brizochloa	V. Jirásek & Chrtek	1		Poo
Bromidium	Nees & Meyen	5		Poo
Bromopsis	(Dumort.) Fourr.		= *Bromus*	Poo
Bromuniola	Stapf & C.E. Hubb.		= *Chasmanthium*	Pan
Bromus	L.	165		Poo
Brylkinia	F. Schmidt	1		Poo
Buchloe	Engelm.		= *Bouteloua*	Chl
Buchlomimus	Reeder, C. Reeder & Rzed.		= *Bouteloua*	Chl

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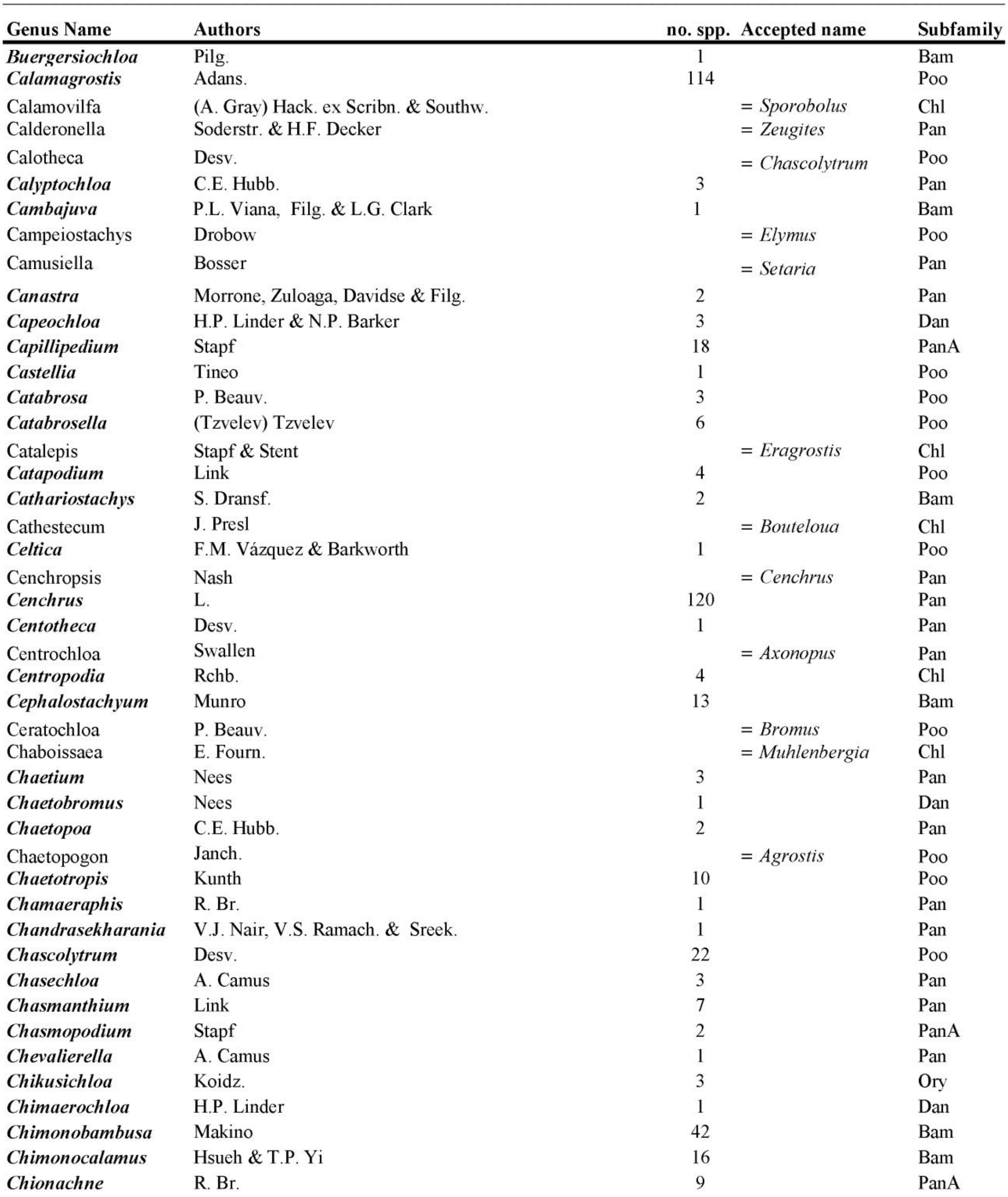

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Buergersiochloa	Pilg.	1		Bam
Calamagrostis	Adans.	114		Poo
Calamovilfa	(A. Gray) Hack. ex Scribn. & Southw.		= *Sporobolus*	Chl
Calderonella	Soderstr. & H.F. Decker		= *Zeugites*	Pan
Calotheca	Desv.		= *Chascolytrum*	Poo
Calyptochloa	C.E. Hubb.	3		Pan
Cambajuva	P.L. Viana, Filg. & L.G. Clark	1		Bam
Campeiostachys	Drobow		= *Elymus*	Poo
Camusiella	Bosser		= *Setaria*	Pan
Canastra	Morrone, Zuloaga, Davidse & Filg.	2		Pan
Capeochloa	H.P. Linder & N.P. Barker	3		Dan
Capillipedium	Stapf	18		PanA
Castellia	Tineo	1		Poo
Catabrosa	P. Beauv.	3		Poo
Catabrosella	(Tzvelev) Tzvelev	6		Poo
Catalepis	Stapf & Stent		= *Eragrostis*	Chl
Catapodium	Link	4		Poo
Cathariostachys	S. Dransf.	2		Bam
Cathestecum	J. Presl		= *Bouteloua*	Chl
Celtica	F.M. Vázquez & Barkworth	1		Poo
Cenchropsis	Nash		= *Cenchrus*	Pan
Cenchrus	L.	120		Pan
Centotheca	Desv.	1		Pan
Centrochloa	Swallen		= *Axonopus*	Pan
Centropodia	Rchb.	4		Chl
Cephalostachyum	Munro	13		Bam
Ceratochloa	P. Beauv.		= *Bromus*	Poo
Chaboissaea	E. Fourn.		= *Muhlenbergia*	Chl
Chaetium	Nees	3		Pan
Chaetobromus	Nees	1		Dan
Chaetopoa	C.E. Hubb.	2		Pan
Chaetopogon	Janch.		= *Agrostis*	Poo
Chaetotropis	Kunth	10		Poo
Chamaeraphis	R. Br.	1		Pan
Chandrasekharania	V.J. Nair, V.S. Ramach. & Sreek.	1		Pan
Chascolytrum	Desv.	22		Poo
Chasechloa	A. Camus	3		Pan
Chasmanthium	Link	7		Pan
Chasmopodium	Stapf	2		PanA
Chevalierella	A. Camus	1		Pan
Chikusichloa	Koidz.	3		Ory
Chimaerochloa	H.P. Linder	1		Dan
Chimonobambusa	Makino	42		Bam
Chimonocalamus	Hsueh & T.P. Yi	16		Bam
Chionachne	R. Br.	9		PanA

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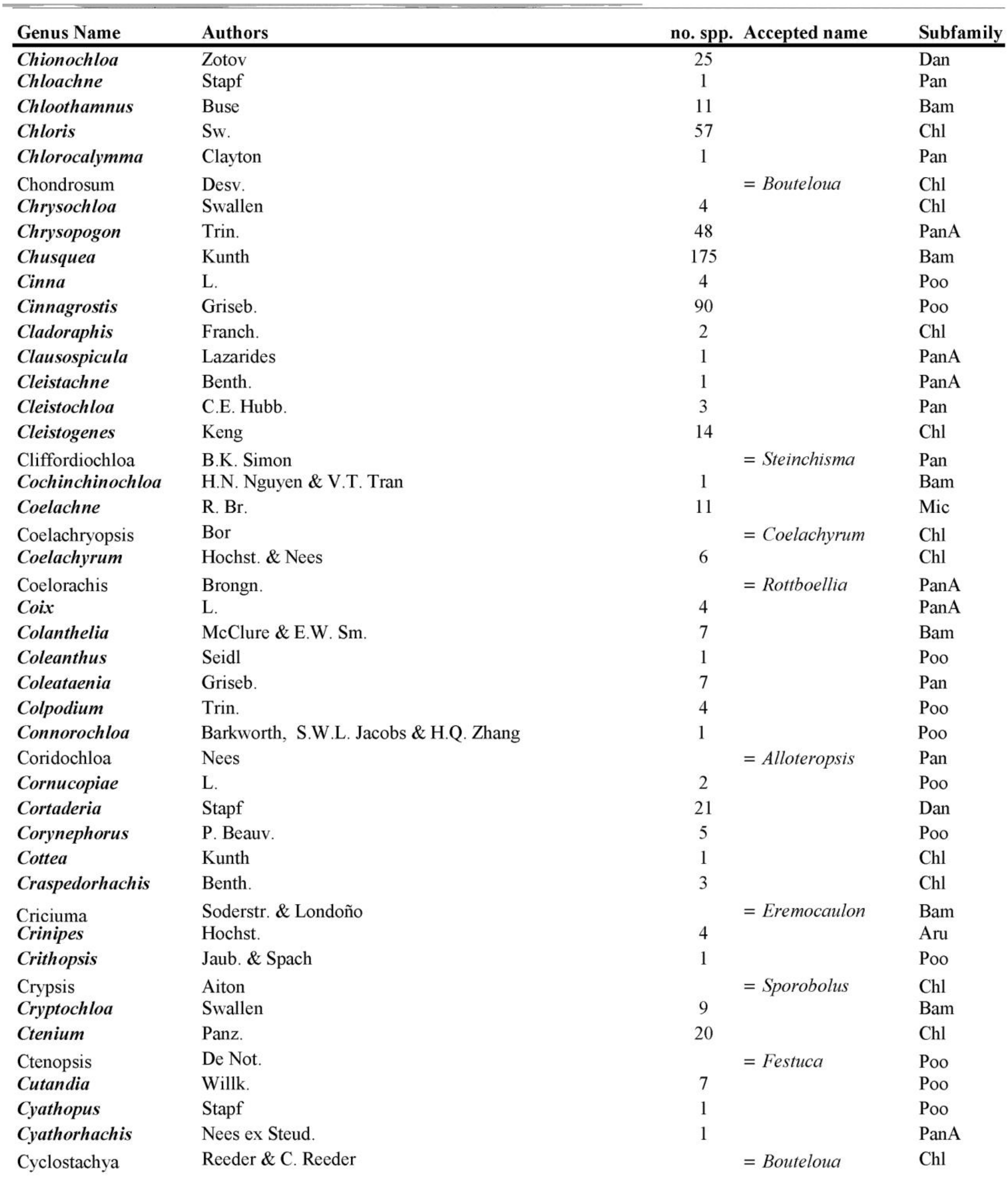

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Chionochloa	Zotov	25		Dan
Chloachne	Stapf	1		Pan
Chloothamnus	Buse	11		Bam
Chloris	Sw.	57		Chl
Chlorocalymma	Clayton	1		Pan
Chondrosum	Desv.		= *Bouteloua*	Chl
Chrysochloa	Swallen	4		Chl
Chrysopogon	Trin.	48		PanA
Chusquea	Kunth	175		Bam
Cinna	L.	4		Poo
Cinnagrostis	Griseb.	90		Poo
Cladoraphis	Franch.	2		Chl
Clausospicula	Lazarides	1		PanA
Cleistachne	Benth.	1		PanA
Cleistochloa	C.E. Hubb.	3		Pan
Cleistogenes	Keng	14		Chl
Cliffordiochloa	B.K. Simon		= *Steinchisma*	Pan
Cochinchinochloa	H.N. Nguyen & V.T. Tran	1		Bam
Coelachne	R. Br.	11		Mic
Coelachryopsis	Bor		= *Coelachyrum*	Chl
Coelachyrum	Hochst. & Nees	6		Chl
Coelorachis	Brongn.		= *Rottboellia*	PanA
Coix	L.	4		PanA
Colanthelia	McClure & E.W. Sm.	7		Bam
Coleanthus	Seidl	1		Poo
Coleataenia	Griseb.	7		Pan
Colpodium	Trin.	4		Poo
Connorochloa	Barkworth, S.W.L. Jacobs & H.Q. Zhang	1		Poo
Coridochloa	Nees		= *Alloteropsis*	Pan
Cornucopiae	L.	2		Poo
Cortaderia	Stapf	21		Dan
Corynephorus	P. Beauv.	5		Poo
Cottea	Kunth	1		Chl
Craspedorhachis	Benth.	3		Chl
Criciuma	Soderstr. & Londoño		= *Eremocaulon*	Bam
Crinipes	Hochst.	4		Aru
Crithopsis	Jaub. & Spach	1		Poo
Crypsis	Aiton		= *Sporobolus*	Chl
Cryptochloa	Swallen	9		Bam
Ctenium	Panz.	20		Chl
Ctenopsis	De Not.		= *Festuca*	Poo
Cutandia	Willk.	7		Poo
Cyathopus	Stapf	1		Poo
Cyathorhachis	Nees ex Steud.	1		PanA
Cyclostachya	Reeder & C. Reeder		= *Bouteloua*	Chl

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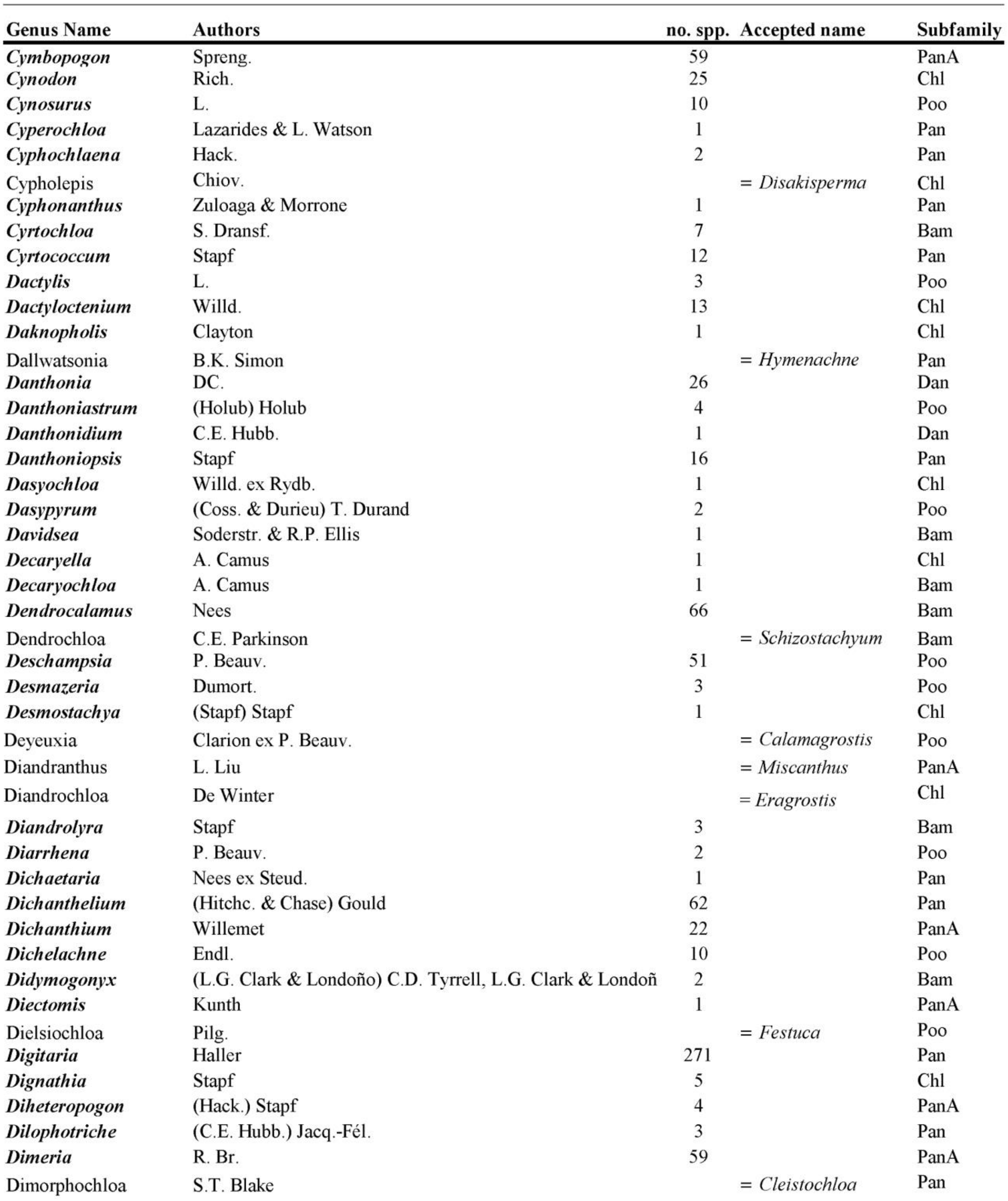

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Cymbopogon	Spreng.	59		PanA
Cynodon	Rich.	25		Chl
Cynosurus	L.	10		Poo
Cyperochloa	Lazarides & L. Watson	1		Pan
Cyphochlaena	Hack.	2		Pan
Cypholepis	Chiov.		= *Disakisperma*	Chl
Cyphonanthus	Zuloaga & Morrone	1		Pan
Cyrtochloa	S. Dransf.	7		Bam
Cyrtococcum	Stapf	12		Pan
Dactylis	L.	3		Poo
Dactyloctenium	Willd.	13		Chl
Daknopholis	Clayton	1		Chl
Dallwatsonia	B.K. Simon		= *Hymenachne*	Pan
Danthonia	DC.	26		Dan
Danthoniastrum	(Holub) Holub	4		Poo
Danthonidium	C.E. Hubb.	1		Dan
Danthoniopsis	Stapf	16		Pan
Dasyochloa	Willd. ex Rydb.	1		Chl
Dasypyrum	(Coss. & Durieu) T. Durand	2		Poo
Davidsea	Soderstr. & R.P. Ellis	1		Bam
Decaryella	A. Camus	1		Chl
Decaryochloa	A. Camus	1		Bam
Dendrocalamus	Nees	66		Bam
Dendrochloa	C.E. Parkinson		= *Schizostachyum*	Bam
Deschampsia	P. Beauv.	51		Poo
Desmazeria	Dumort.	3		Poo
Desmostachya	(Stapf) Stapf	1		Chl
Deyeuxia	Clarion ex P. Beauv.		= *Calamagrostis*	Poo
Diandranthus	L. Liu		= *Miscanthus*	PanA
Diandrochloa	De Winter		= *Eragrostis*	Chl
Diandrolyra	Stapf	3		Bam
Diarrhena	P. Beauv.	2		Poo
Dichaetaria	Nees ex Steud.	1		Pan
Dichanthelium	(Hitchc. & Chase) Gould	62		Pan
Dichanthium	Willemet	22		PanA
Dichelachne	Endl.	10		Poo
Didymogonyx	(L.G. Clark & Londoño) C.D. Tyrrell, L.G. Clark & Londoñ	2		Bam
Diectomis	Kunth	1		PanA
Dielsiochloa	Pilg.		= *Festuca*	Poo
Digitaria	Haller	271		Pan
Dignathia	Stapf	5		Chl
Diheteropogon	(Hack.) Stapf	4		PanA
Dilophotriche	(C.E. Hubb.) Jacq.-Fél.	3		Pan
Dimeria	R. Br.	59		PanA
Dimorphochloa	S.T. Blake		= *Cleistochloa*	Pan

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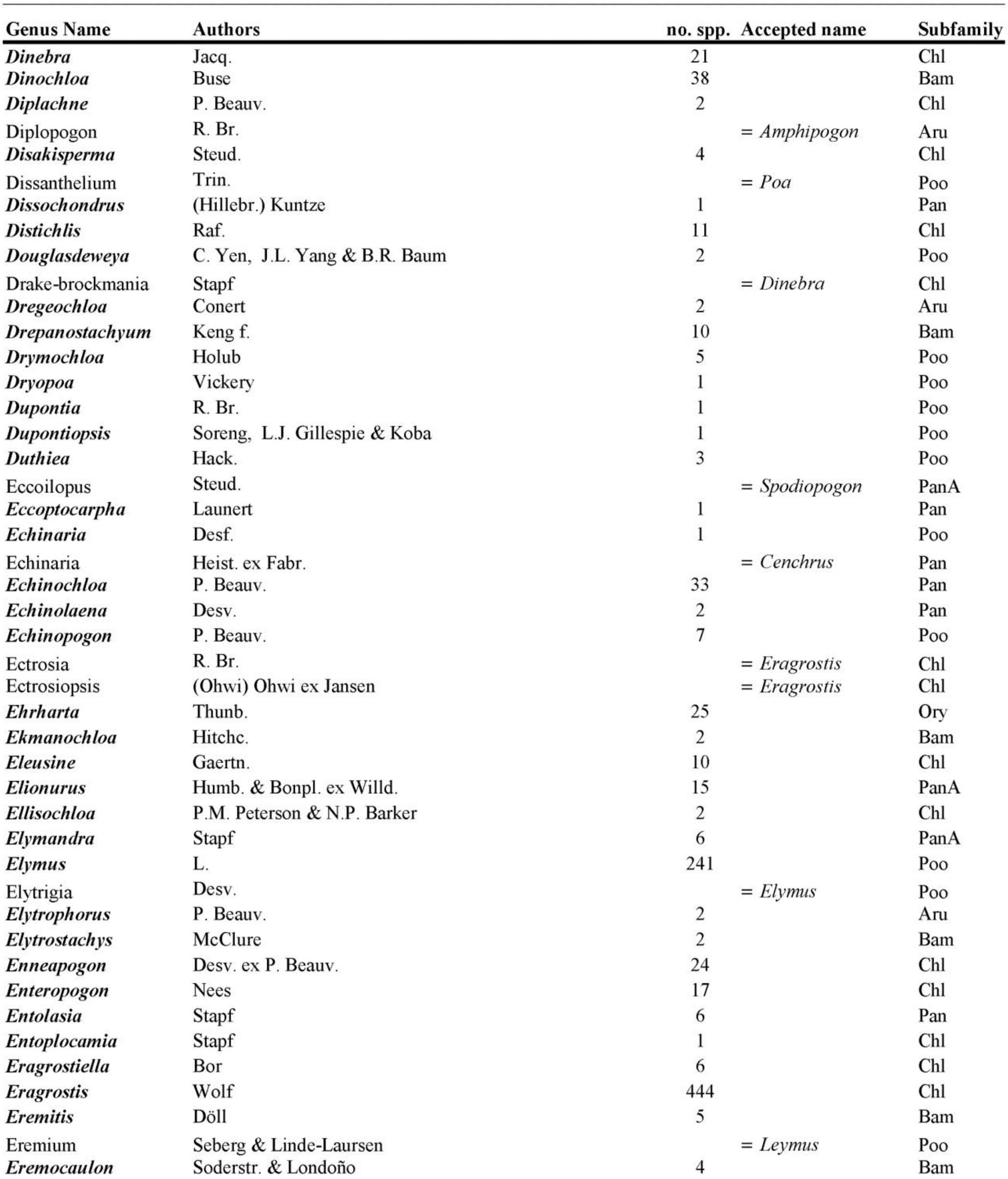

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Dinebra	Jacq.	21		Chl
Dinochloa	Buse	38		Bam
Diplachne	P. Beauv.	2		Chl
Diplopogon	R. Br.		= *Amphipogon*	Aru
Disakisperma	Steud.	4		Chl
Dissanthelium	Trin.		= *Poa*	Poo
Dissochondrus	(Hillebr.) Kuntze	1		Pan
Distichlis	Raf.	11		Chl
Douglasdeweya	C. Yen, J.L. Yang & B.R. Baum	2		Poo
Drake-brockmania	Stapf		= *Dinebra*	Chl
Dregeochloa	Conert	2		Aru
Drepanostachyum	Keng f.	10		Bam
Drymochloa	Holub	5		Poo
Dryopoa	Vickery	1		Poo
Dupontia	R. Br.	1		Poo
Dupontiopsis	Soreng, L.J. Gillespie & Koba	1		Poo
Duthiea	Hack.	3		Poo
Eccoilopus	Steud.		= *Spodiopogon*	PanA
Eccoptocarpha	Launert	1		Pan
Echinaria	Desf.	1		Poo
Echinaria	Heist. ex Fabr.		= *Cenchrus*	Pan
Echinochloa	P. Beauv.	33		Pan
Echinolaena	Desv.	2		Pan
Echinopogon	P. Beauv.	7		Poo
Ectrosia	R. Br.		= *Eragrostis*	Chl
Ectrosiopsis	(Ohwi) Ohwi ex Jansen		= *Eragrostis*	Chl
Ehrharta	Thunb.	25		Ory
Ekmanochloa	Hitchc.	2		Bam
Eleusine	Gaertn.	10		Chl
Elionurus	Humb. & Bonpl. ex Willd.	15		PanA
Ellisochloa	P.M. Peterson & N.P. Barker	2		Chl
Elymandra	Stapf	6		PanA
Elymus	L.	241		Poo
Elytrigia	Desv.		= *Elymus*	Poo
Elytrophorus	P. Beauv.	2		Aru
Elytrostachys	McClure	2		Bam
Enneapogon	Desv. ex P. Beauv.	24		Chl
Enteropogon	Nees	17		Chl
Entolasia	Stapf	6		Pan
Entoplocamia	Stapf	1		Chl
Eragrostiella	Bor	6		Chl
Eragrostis	Wolf	444		Chl
Eremitis	Döll	5		Bam
Eremium	Seberg & Linde-Laursen		= *Leymus*	Poo
Eremocaulon	Soderstr. & Londoño	4		Bam

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Genus Name	Authors	no. spp.	Accepted name	Subfamily
Eremochloa	Buse	12		PanA
Eremopoa	Roshev.		= *Poa*	Poo
Eremopogon	Stapf	4		PanA
Eremopyrum	(Ledeb.) Jaub. & Spach	4		Poo
Eriachne	R. Br.	50		Mic
Erianthecium	Parodi		= *Chascolytrum*	Poo
Erianthus	Michx.	8		PanA
Eriochloa	Kunth	24		Pan
Eriochrysis	P. Beauv.	12		PanA
Eriocoma	Nutt.	29		Poo
Erioneuron	Nash	3		Chl
Euchlaena	Schrad.		= *Zea*	PanA
Euclasta	Franch.	2		PanA
Eulalia	Kunth	34		PanA
Eulaliopsis	Honda	2		PanA
Eustachys	Desv.	16		Chl
Euthryptochloa	Cope		= *Phaenosperma*	Poo
Exotheca	Andersson	1		PanA
Fargesia	Franch.	86		Bam
Farrago	Clayton	1		Chl
Fasciculochloa	B.K. Simon & C.M. Weiller		= *Steinchisma*	Pan
Ferrocalamus	Hsueh & Keng f.	3		Bam
Festuca	L.	610		Poo
Festucella	E.B. Alexeev		= *Hookerochloa*	Poo
Festucopsis	(C.E. Hubb.) Melderis	1		Poo
Filgueirasia	Guala	2		Bam
Fimbribambusa	Widjaja	2		Bam
Fingerhuthia	Nees ex Lehm.	2		Chl
Froesiochloa	G.A. Black	1		Bam
Gaoligongshania	D.Z. Li. Hsueh & N.H. Xia	1		Bam
Garnotia	Brongn.	30		Pan
Gastridium	P. Beauv.	2		Poo
Gaudinia	P. Beauv.	8		Poo
Gaudinopsis	(Boiss.) Eig	6		Poo
Gelidocalamus	T.H. Wen	11		Bam
Geochloa	H.P. Linder & N.P. Barker	3		Dan
Germainia	Balansa & Poitr.	10		PanA
Gerritea	Zuloaga, Morrone & T. Killeen	1		Pan
Gigantochloa	Kurz ex Munro	63		Bam
Gilgiochloa	Pilg.	1		PanA
Glaziophyton	Franch.	1		Bam
Glyceria	R. Br.	48		Poo
Glyphochloa	Clayton	10		PanA
Gossweilerochloa	Renvoize	1		Chl
Gouinia	E. Fourn. ex Benth. & Hook. f.	14		Chl

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Genus Name	Authors	no. spp.	Accepted name	Subfamily
Gouldochloa	Valdés-Reyna, Morden & S.L. Hatch		= *Chasmanthium*	Pan
Graphephorum	Desv.	7		Poo
Greslania	Balansa	2		Bam
Griffithsochloa	G.J. Pierce		= *Bouteloua*	Chl
Guadua	Kunth	33		Bam
Guaduella	Franch.	6		Pue
Gymnachne	Parodi		= *Chascolytrum*	Poo
Gymnopogon	P. Beauv.	14		Chl
Gynerium	Willd. ex P. Beauv.	1		Pan
Habrochloa	C.E. Hubb.	1		Chl
Hackelochloa	Kuntze	2		PanA
Hainardia	Greuter	1		Poo
Hakonechloa	Makino ex Honda	1		Aru
Halopyrum	Stapf	1		Chl
Harpachne	A. Rich.		= *Eragrostis*	Chl
Harpochloa	Kunth	2		Chl
Heleochloa	Rauschert		= *Sporobolus*	Chl
Helictochloa	Romero Zarco	22		Poo
Helictotrichon	Besser	38		Poo
Helleria	Host ex Roem.		= *Festuca*	Poo
Hellerochloa	E. Fourn		= *Festuca*	Poo
Hemarthria	R. Br.	14		PanA
Hemisorghum	C.E. Hubb. ex Bor	2		PanA
Henrardia	C.E. Hubb.	2		Poo
Hesperostipa	(M.K. Elias) Barkworth	5		Poo
Heterachne	Benth.		= *Eragrostis*	Chl
Heteranthelium	Hochst.	1		Poo
Heteranthoecia	Stapf	1		Mic
Heterocarpha	Stapf & C.E. Hubb.		= *Dinebra*	Chl
Heteropholis	C.E. Hubb.	6		PanA
Heteropogon	Pers.	6		PanA
Hickelia	A. Camus	4		Bam
Hierochloe	R. Br.		= *Anthoxanthum*	Poo
Hilaria	Kunth	10		Chl
Hildaea	C. Silva & R.P. Oliveira	5		Pan
Himalayacalamus	Keng f.	9		Bam
Hitchcockella	A. Camus	1		Bam
Holcolemma	Stapf & C.E. Hubb.	3		Pan
Holcus	L.	9		Poo
Holttumochloa	K.M. Wong	3		Bam
Homalotrichon	Banfi, Galasso & Bracchi		= *Avenula*	Poo
Homolepis	Chase	5		Pan
Homopholis	C.E. Hubb.	4		Pan
Homozeugos	Stapf	6		PanA
Hookerochloa	E.B. Alexeev	2		Poo

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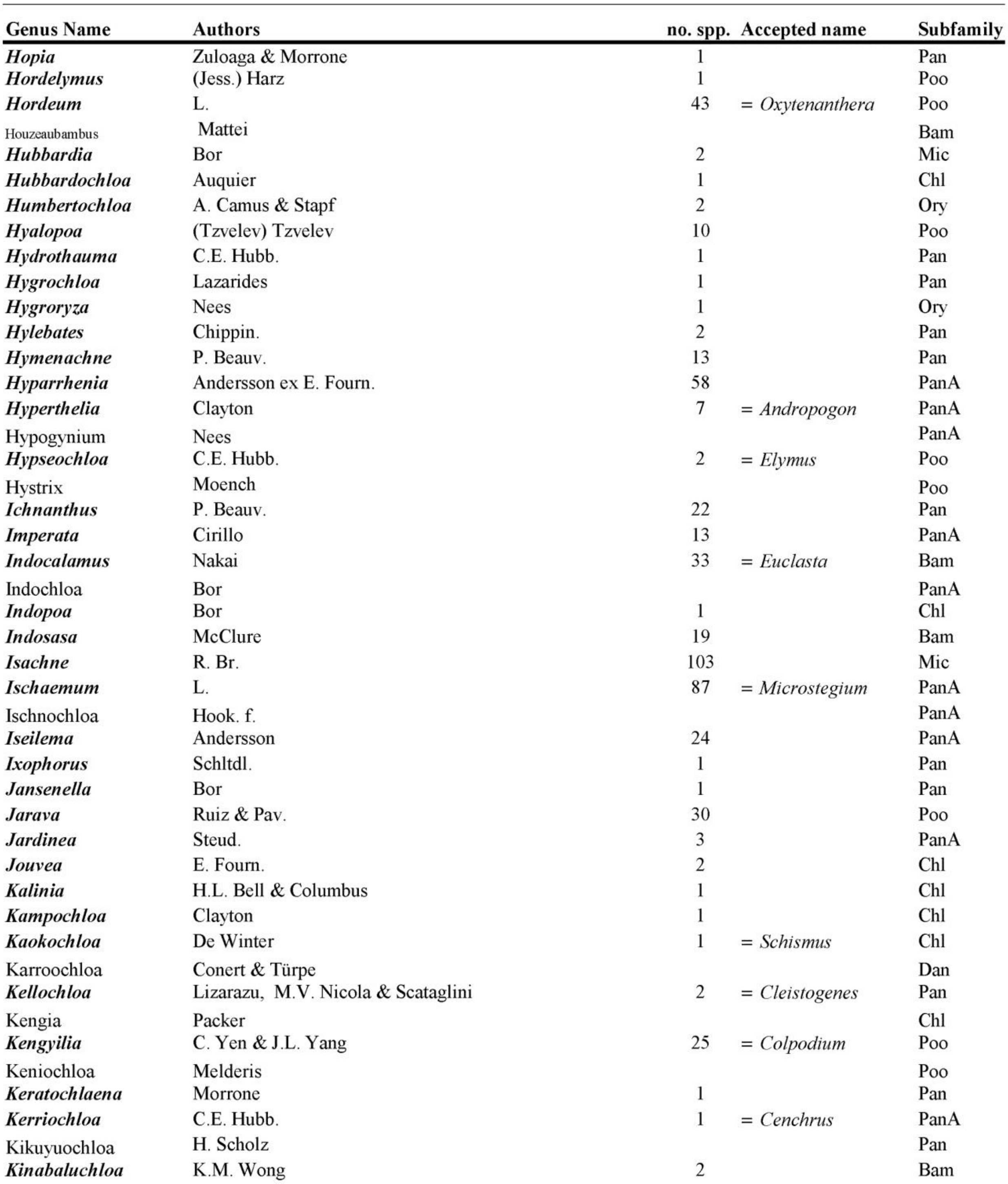

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Hopia	Zuloaga & Morrone	1		Pan
Hordelymus	(Jess.) Harz	1		Poo
Hordeum	L.	43	= *Oxytenanthera*	Poo
Houzeaubambus	Mattei			Bam
Hubbardia	Bor	2		Mic
Hubbardochloa	Auquier	1		Chl
Humbertochloa	A. Camus & Stapf	2		Ory
Hyalopoa	(Tzvelev) Tzvelev	10		Poo
Hydrothauma	C.E. Hubb.	1		Pan
Hygrochloa	Lazarides	1		Pan
Hygroryza	Nees	1		Ory
Hylebates	Chippin.	2		Pan
Hymenachne	P. Beauv.	13		Pan
Hyparrhenia	Andersson ex E. Fourn.	58		PanA
Hyperthelia	Clayton	7	= *Andropogon*	PanA
Hypogynium	Nees			PanA
Hypseochloa	C.E. Hubb.	2	= *Elymus*	Poo
Hystrix	Moench			Poo
Ichnanthus	P. Beauv.	22		Pan
Imperata	Cirillo	13		PanA
Indocalamus	Nakai	33	= *Euclasta*	Bam
Indochloa	Bor			PanA
Indopoa	Bor	1		Chl
Indosasa	McClure	19		Bam
Isachne	R. Br.	103		Mic
Ischaemum	L.	87	= *Microstegium*	PanA
Ischnochloa	Hook. f.			PanA
Iseilema	Andersson	24		PanA
Ixophorus	Schltdl.	1		Pan
Jansenella	Bor	1		Pan
Jarava	Ruiz & Pav.	30		Poo
Jardinea	Steud.	3		PanA
Jouvea	E. Fourn.	2		Chl
Kalinia	H.L. Bell & Columbus	1		Chl
Kampochloa	Clayton	1		Chl
Kaokochloa	De Winter	1	= *Schismus*	Chl
Karroochloa	Conert & Türpe			Dan
Kellochloa	Lizarazu, M.V. Nicola & Scataglini	2	= *Cleistogenes*	Pan
Kengia	Packer			Chl
Kengyilia	C. Yen & J.L. Yang	25	= *Colpodium*	Poo
Keniochloa	Melderis			Poo
Keratochlaena	Morrone	1		Pan
Kerriochloa	C.E. Hubb.	1	= *Cenchrus*	PanA
Kikuyuochloa	H. Scholz			Pan
Kinabaluchloa	K.M. Wong	2		Bam

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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Genus Name	Authors	no. spp.	Accepted name	Subfamily
Klemachloa	R. Parker		= *Dendrocalamus*	Bam
Koeleria	Pers.	70		Poo
Koordersiochloa	Merr.	3		Poo
Kuruna	Attigala, Kathriar. & L.G. Clark	7		Bam
Lachnagrostis	Trin.	32		Poo
Lagurus	L.	1		Poo
Lakshmia	Veldkamp	1		PanA
Lamarckia	Moench	1		Poo
Lamprothrysus	Pilg.		= *Cortaderia*	Dan
Lasiacis	(Griseb.) Hitchc.	15		Pan
Lasiorhachis	(Hack.) Stapf	3		PanA
Lasiurus	Boiss.	1		PanA
Latipes	Kunth		= *Leptothrium*	Chl
Lecomtella	A. Camus	1		Pan
Leersia	Sw.	18		Ory
Leptagrostis	C.E. Hubb.	1		Aru
Leptaspis	R. Br.	3		Pha
Leptatherum	Nees	3		PanA
Leptocanna	L.C. Chia & H.L. Fung		= *Cephalostachyum*	Bam
Leptocarydion	Hochst. ex Stapf	1		Chl
Leptochloa	P. Beauv.	7		Chl
Leptochloopsis	Yates		= *Uniola*	Chl
Leptocoryphium	Nees		= *Anthaenantia*	Pan
Leptophyllochloa	C.E. Calderón		= *Cinnagrostis*	Poo
Leptosaccharum	(Hack.) A. Camus		= *Eriochrysis*	PanA
Leptothrium	Kunth	2		Chl
Lepturidium	Hitchc. & Ekman	1		Chl
Lepturopetium	Morat	2		Chl
Lepturus	R. Br.	16		Chl
Leucophrys	Rendle	1		Pan
Leucopoa	Griseb.	12		Poo
Leymus	Hochst.	55		Poo
Libyella	Pamp.		= *Poa*	Poo
Limnas	Trin.	3		Poo
Limnodea	L.H. Dewey	1		Poo
Limnopoa	C.E. Hubb.	1		Mic
Lindbergella	Bor		= *Poa*	Poo
Lintonia	Stapf		= *Chloris*	Chl
Lithachne	P. Beauv.	4		Bam
Littledalea	Hemsl.	4		Poo
Loliolum	V.I. Krecz. & Bobrov		= *Festuca*	Poo
Lolium	L.	21		Poo
Lombardochloa	Roseng. & B.R. Arrill.		= *Chascolytrum*	Poo
Lophacme	Stapf	2		Chl
Lophatherum	Brongn.	2		Pan

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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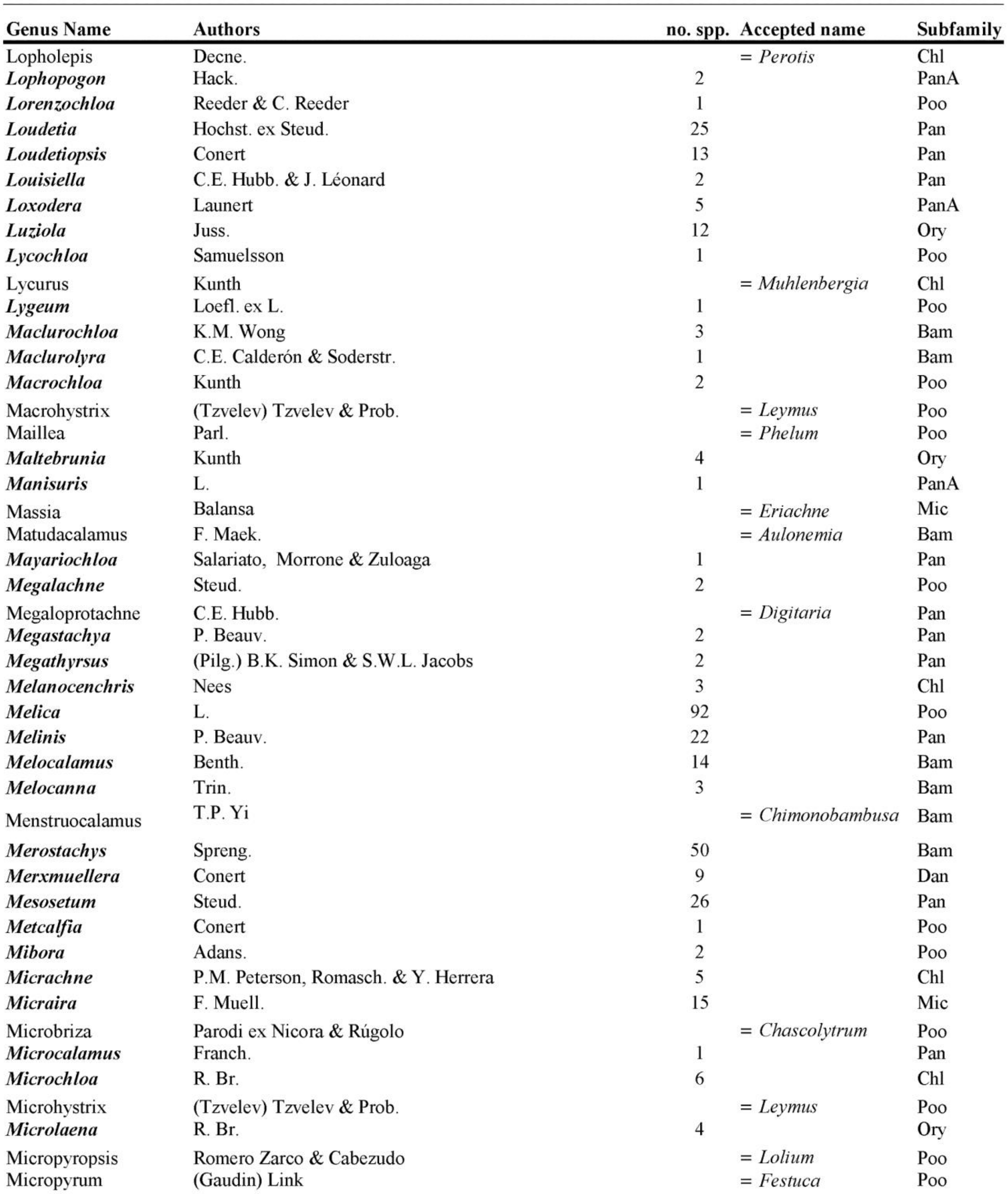

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Lopholepis	Decne.		= *Perotis*	Chl
Lophopogon	Hack.	2		PanA
Lorenzochloa	Reeder & C. Reeder	1		Poo
Loudetia	Hochst. ex Steud.	25		Pan
Loudetiopsis	Conert	13		Pan
Louisiella	C.E. Hubb. & J. Léonard	2		Pan
Loxodera	Launert	5		PanA
Luziola	Juss.	12		Ory
Lycochloa	Samuelsson	1		Poo
Lycurus	Kunth		= *Muhlenbergia*	Chl
Lygeum	Loefl. ex L.	1		Poo
Maclurochloa	K.M. Wong	3		Bam
Maclurolyra	C.E. Calderón & Soderstr.	1		Bam
Macrochloa	Kunth	2		Poo
Macrohystrix	(Tzvelev) Tzvelev & Prob.		= *Leymus*	Poo
Maillea	Parl.		= *Phelum*	Poo
Maltebrunia	Kunth	4		Ory
Manisuris	L.	1		PanA
Massia	Balansa		= *Eriachne*	Mic
Matudacalamus	F. Maek.		= *Aulonemia*	Bam
Mayariochloa	Salariato, Morrone & Zuloaga	1		Pan
Megalachne	Steud.	2		Poo
Megaloprotachne	C.E. Hubb.		= *Digitaria*	Pan
Megastachya	P. Beauv.	2		Pan
Megathyrsus	(Pilg.) B.K. Simon & S.W.L. Jacobs	2		Pan
Melanocenchris	Nees	3		Chl
Melica	L.	92		Poo
Melinis	P. Beauv.	22		Pan
Melocalamus	Benth.	14		Bam
Melocanna	Trin.	3		Bam
Menstruocalamus	T.P. Yi		= *Chimonobambusa*	Bam
Merostachys	Spreng.	50		Bam
Merxmuellera	Conert	9		Dan
Mesosetum	Steud.	26		Pan
Metcalfia	Conert	1		Poo
Mibora	Adans.	2		Poo
Micrachne	P.M. Peterson, Romasch. & Y. Herrera	5		Chl
Micraira	F. Muell.	15		Mic
Microbriza	Parodi ex Nicora & Rúgolo		= *Chascolytrum*	Poo
Microcalamus	Franch.	1		Pan
Microchloa	R. Br.	6		Chl
Microhystrix	(Tzvelev) Tzvelev & Prob.		= *Leymus*	Poo
Microlaena	R. Br.	4		Ory
Micropyropsis	Romero Zarco & Cabezudo		= *Lolium*	Poo
Micropyrum	(Gaudin) Link		= *Festuca*	Poo

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Genus Name	Authors	no. spp.	Accepted name	Subfamily
Microstegium	Nees	27		PanA
Mildbraediochloa	Butzin		= *Melinis*	Pan
Milium	L.	5		Poo
Miscanthidium	Stapf	6		PanA
Miscanthus	Andersson	20		PanA
Mnesithea	Kunth	3		PanA
Mniochloa	Chase	1		Bam
Molineriella	Rouy	2		Poo
Molinia	Schrank	1		Aru
Moliniopsis	Hayata	1		Aru
Monachather	Steud.	1		Aru
Monanthochloe	Engelm.		= *Distichlis*	Chl
Monelytrum	Hack.	1		Chl
Monocymbium	Stapf	3		PanA
Monodia	S.W.L. Jacobs		= *Triodia*	Chl
Monostachya	Merr.		= *Rytidosperma*	Dan
Moorochloa	Veldkamp	3		Pan
Morronea	Zuloaga & Scataglini	6		Pan
Mosdenia	Stent	1		Chl
Muhlenbergia	Schreb.	182		Chl
Mullerochloa	K.M. Wong	1		Bam
Munroa	Torr.	5		Chl
Myriocladus	Swallen	12		Bam
Myriostachya	(Benth.) Hook. f.	1		Chl
Nanooravia	Kiran Raj & Sivad.	1		PanA
Narduroides	Rouy		= *Festuca*	Poo
Nardus	L.	1		Poo
Narenga	Bor	1		PanA
Nassella	(Trin.) E. Desv.	117		Poo
Nastus	Juss.	12		Bam
Nastus	Lunell		= *Cenchrus*	Pan
Neeragrostis	Bush		= *Eragrostis*	Chl
Neesiochloa	Pilg.	1		Chl
Nematopoa	C.E. Hubb.		= *Trirhaphis*	Chl
Neobouteloua	Gould	2		Chl
Neoholubia	Tzvelev		= *Avenula*	Poo
Neohouzeaua	A. Camus	6		Bam
Neololeba	Widjaja	5		Bam
Neomicrocalamus	Keng f.	3		Bam
Neomolinia	Honda	3		Poo
Neosasamorpha	Tatew.		= *Sasa*	Bam
Neoschischkinia	Tzvelev		= *Agrostis*	Poo
Neostapfia	Burtt Davy	1		Chl
Neostapfiella	A. Camus	3		Chl
Nephelochloa	Boiss.	1		Poo

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Genus Name	Authors	no. spp.	Accepted name	Subfamily
Neurachne	R. Br.	7		Pan
Neurolepis	Meisn.		= *Chusquea*	Bam
Neuropoa	Clayton		= *Poa*	Poo
Nevskiella	V.I. Krecz. & Vved.		= *Bromus*	Poo
Neyraudia	Hook. f.	5		Chl
Nianhochloa	H.N. Nguyen & V.T. Tran	1		Bam
Nicoraella	Torres		= *Anatherostipa*	Poo
Nicoraepoa	Soreng & L.J. Gillespie	6		Poo
Nipponocalamus	Nakai		= *Pleioblastus*	Bam
Notochloe	Domin	1		Dan
Notodanthonia	Zotov		= *Rytidosperma*	Dan
Notonema	Raf.		= *Agrostis*	Poo
Ocellochloa	Zuloaga & Morrone	12		Pan
Ochlandra	Thwaites	10		Bam
Ochlopoa	(Asch. & Graebn.) H. Scholz		= *Poa*	Poo
Ochthochloa	Edgew.		= *Chloris*	Chl
Odontelytrum	Hack.		= *Cenchrus*	Pan
Odyssea	Stapf	1		Chl
Oedochloa	C. Silva & R.P. Oliveira	9		Pan
Oldeania	Stapleton	1		Bam
Oligostachyum	Z.P. Wang & G.H. Ye	17		Bam
Olmeca	Soderstr.	5		Bam
Oloptum	Röser & H. R. Hamasha	1		Poo
Olyra	L.	25		Bam
Oncorachis	Morrone & Zuloaga	2		Pan
Ophiochloa	Filg., Davidse & Zuloaga		= *Axonopus*	Pan
Ophiuros	C.F. Gaertn.	4		PanA
Opizia	J. Presl		= *Bouteloua*	Chl
Oplismenopsis	Parodi	1		Pan
Oplismenus	P. Beauv.	8		Pan
Orcuttia	Vasey	8		Chl
Oreiostachys	H. Scholz & Parolly		= *Nastus*	Bam
Oreobambos	K. Schum.	1		Bam
Oreocalamus	Keng		= *Chimonobambusa*	Bam
Oreochloa	Link	4		Poo
Oreopoa	Gamble		= *Poa*	Poo
Orinus	Hitchc.	6		Chl
Oropetium	Trin.	6		Chl
Ortachne	Nees ex Steud.	2		Poo
Orthacanthus	P.M. Peterson & Romasch.	1		Chl
Orthoclada	P. Beauv.	2		Pan
Orthoraphium	Nees	1		Poo
Oryza	L.	21		Ory
Oryzidium	C.E. Hubb. & Schweick.	1		Pan
Oryzopsis	Michx.	1		Poo

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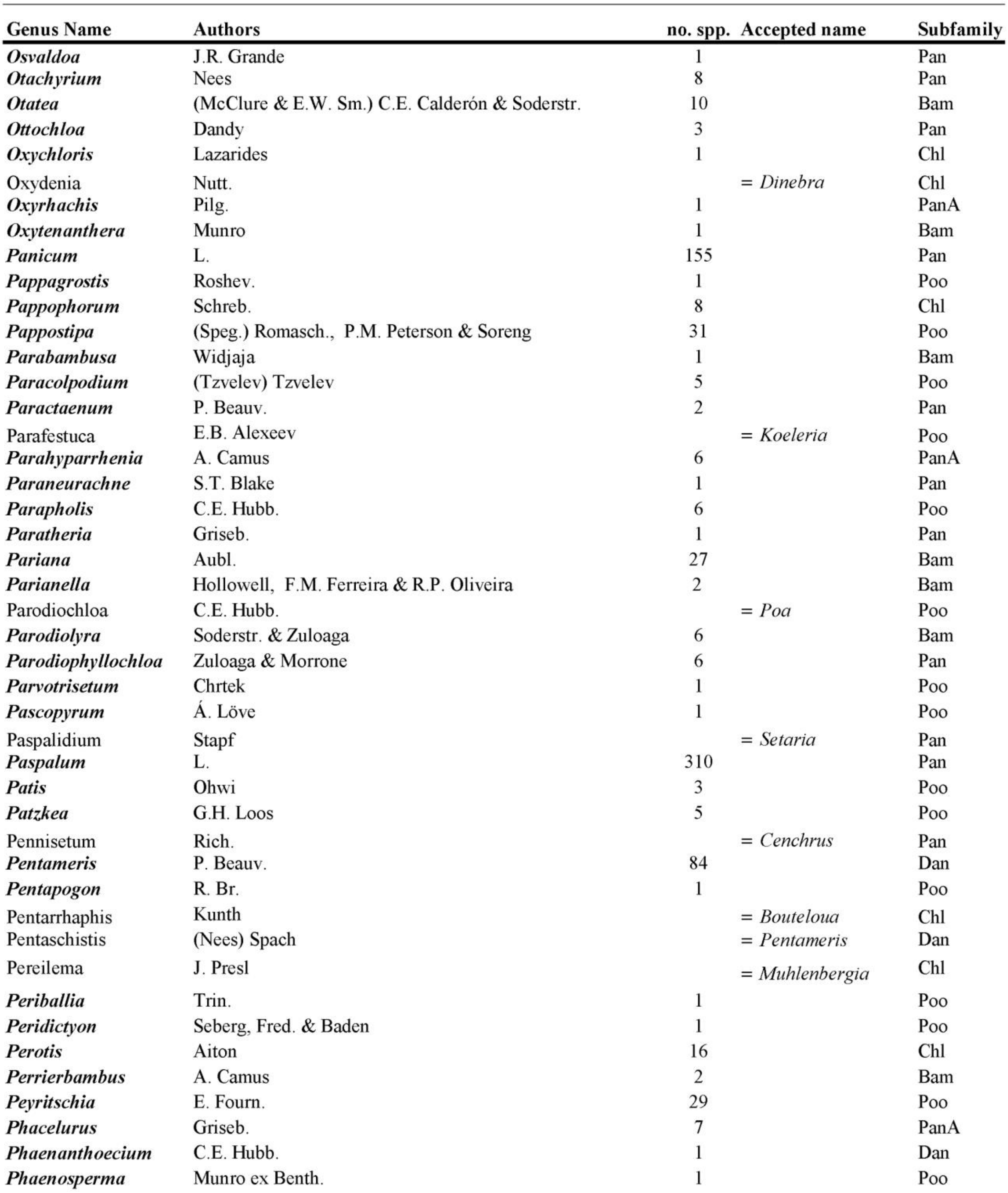

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Osvaldoa	J.R. Grande	1		Pan
Otachyrium	Nees	8		Pan
Otatea	(McClure & E.W. Sm.) C.E. Calderón & Soderstr.	10		Bam
Ottochloa	Dandy	3		Pan
Oxychloris	Lazarides	1		Chl
Oxydenia	Nutt.		= *Dinebra*	Chl
Oxyrhachis	Pilg.	1		PanA
Oxytenanthera	Munro	1		Bam
Panicum	L.	155		Pan
Pappagrostis	Roshev.	1		Poo
Pappophorum	Schreb.	8		Chl
Pappostipa	(Speg.) Romasch., P.M. Peterson & Soreng	31		Poo
Parabambusa	Widjaja	1		Bam
Paracolpodium	(Tzvelev) Tzvelev	5		Poo
Paractaenum	P. Beauv.	2		Pan
Parafestuca	E.B. Alexeev		= *Koeleria*	Poo
Parahyparrhenia	A. Camus	6		PanA
Paraneurachne	S.T. Blake	1		Pan
Parapholis	C.E. Hubb.	6		Poo
Paratheria	Griseb.	1		Pan
Pariana	Aubl.	27		Bam
Parianella	Hollowell, F.M. Ferreira & R.P. Oliveira	2		Bam
Parodiochloa	C.E. Hubb.		= *Poa*	Poo
Parodiolyra	Soderstr. & Zuloaga	6		Bam
Parodiophyllochloa	Zuloaga & Morrone	6		Pan
Parvotrisetum	Chrtek	1		Poo
Pascopyrum	Á. Löve	1		Poo
Paspalidium	Stapf		= *Setaria*	Pan
Paspalum	L.	310		Pan
Patis	Ohwi	3		Poo
Patzkea	G.H. Loos	5		Poo
Pennisetum	Rich.		= *Cenchrus*	Pan
Pentameris	P. Beauv.	84		Dan
Pentapogon	R. Br.	1		Poo
Pentarrhaphis	Kunth		= *Bouteloua*	Chl
Pentaschistis	(Nees) Spach		= *Pentameris*	Dan
Pereilema	J. Presl		= *Muhlenbergia*	Chl
Periballia	Trin.	1		Poo
Peridictyon	Seberg, Fred. & Baden	1		Poo
Perotis	Aiton	16		Chl
Perrierbambus	A. Camus	2		Bam
Peyritschia	E. Fourn.	29		Poo
Phacelurus	Griseb.	7		PanA
Phaenanthoecium	C.E. Hubb.	1		Dan
Phaenosperma	Munro ex Benth.	1		Poo

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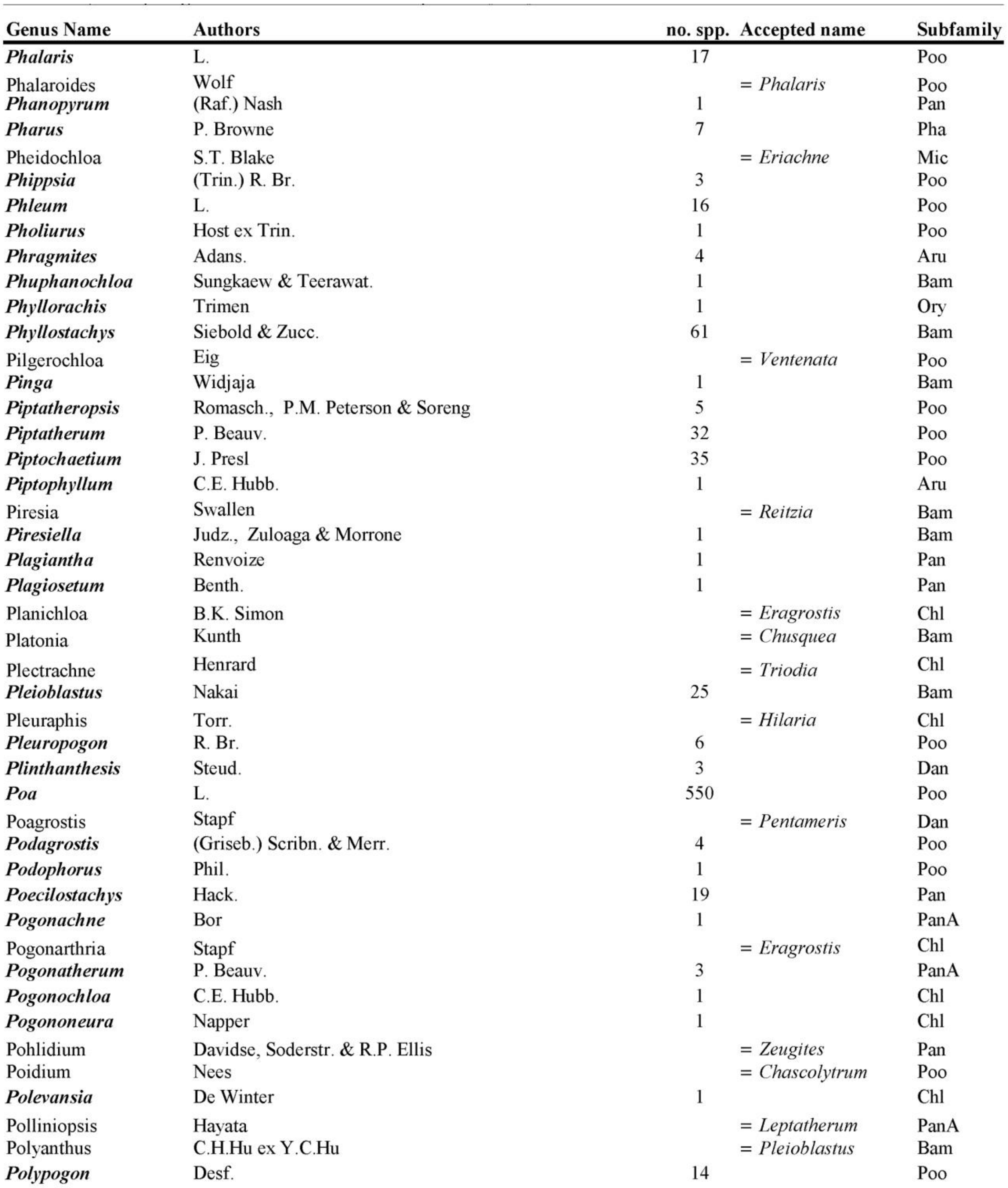

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Phalaris	L.	17		Poo
Phalaroides	Wolf		= *Phalaris*	Poo
Phanopyrum	(Raf.) Nash	1		Pan
Pharus	P. Browne	7		Pha
Pheidochloa	S.T. Blake		= *Eriachne*	Mic
Phippsia	(Trin.) R. Br.	3		Poo
Phleum	L.	16		Poo
Pholiurus	Host ex Trin.	1		Poo
Phragmites	Adans.	4		Aru
Phuphanochloa	Sungkaew & Teerawat.	1		Bam
Phyllorachis	Trimen	1		Ory
Phyllostachys	Siebold & Zucc.	61		Bam
Pilgerochloa	Eig		= *Ventenata*	Poo
Pinga	Widjaja	1		Bam
Piptatheropsis	Romasch., P.M. Peterson & Soreng	5		Poo
Piptatherum	P. Beauv.	32		Poo
Piptochaetium	J. Presl	35		Poo
Piptophyllum	C.E. Hubb.	1		Aru
Piresia	Swallen		= *Reitzia*	Bam
Piresiella	Judz., Zuloaga & Morrone	1		Bam
Plagiantha	Renvoize	1		Pan
Plagiosetum	Benth.	1		Pan
Planichloa	B.K. Simon		= *Eragrostis*	Chl
Platonia	Kunth		= *Chusquea*	Bam
Plectrachne	Henrard		= *Triodia*	Chl
Pleioblastus	Nakai	25		Bam
Pleuraphis	Torr.		= *Hilaria*	Chl
Pleuropogon	R. Br.	6		Poo
Plinthanthesis	Steud.	3		Dan
Poa	L.	550		Poo
Poagrostis	Stapf		= *Pentameris*	Dan
Podagrostis	(Griseb.) Scribn. & Merr.	4		Poo
Podophorus	Phil.	1		Poo
Poecilostachys	Hack.	19		Pan
Pogonachne	Bor	1		PanA
Pogonarthria	Stapf		= *Eragrostis*	Chl
Pogonatherum	P. Beauv.	3		PanA
Pogonochloa	C.E. Hubb.	1		Chl
Pogononeura	Napper	1		Chl
Pohlidium	Davidse, Soderstr. & R.P. Ellis		= *Zeugites*	Pan
Poidium	Nees		= *Chascolytrum*	Poo
Polevansia	De Winter	1		Chl
Polliniopsis	Hayata		= *Leptatherum*	PanA
Polyanthus	C.H.Hu ex Y.C.Hu		= *Pleioblastus*	Bam
Polypogon	Desf.	14		Poo

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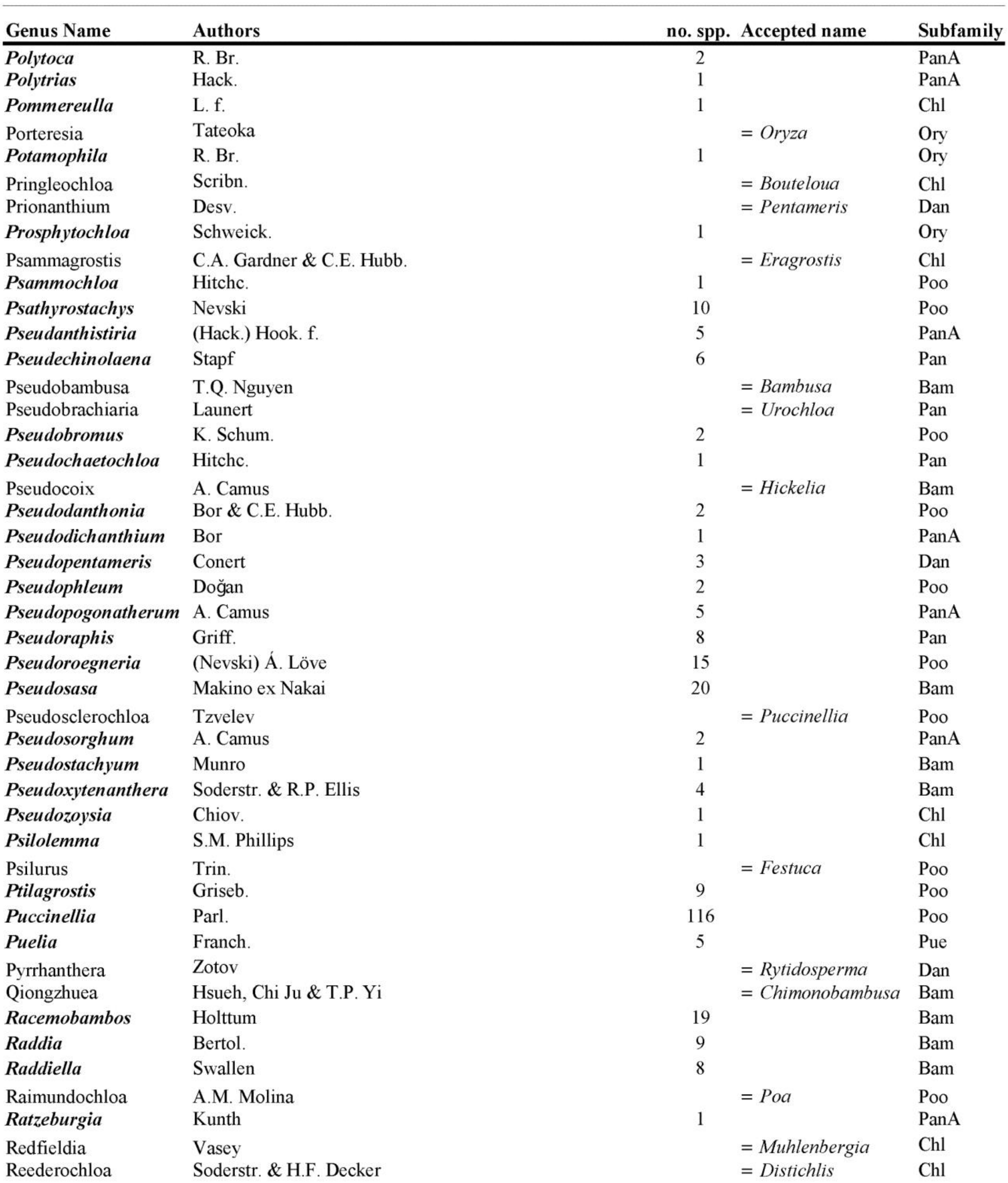

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Polytoca	R. Br.	2		PanA
Polytrias	Hack.	1		PanA
Pommereulla	L. f.	1		Chl
Porteresia	Tateoka		= *Oryza*	Ory
Potamophila	R. Br.	1		Ory
Pringleochloa	Scribn.		= *Bouteloua*	Chl
Prionanthium	Desv.		= *Pentameris*	Dan
Prosphytochloa	Schweick.	1		Ory
Psammagrostis	C.A. Gardner & C.E. Hubb.		= *Eragrostis*	Chl
Psammochloa	Hitchc.	1		Poo
Psathyrostachys	Nevski	10		Poo
Pseudanthistiria	(Hack.) Hook. f.	5		PanA
Pseudechinolaena	Stapf	6		Pan
Pseudobambusa	T.Q. Nguyen		= *Bambusa*	Bam
Pseudobrachiaria	Launert		= *Urochloa*	Pan
Pseudobromus	K. Schum.	2		Poo
Pseudochaetochloa	Hitchc.	1		Pan
Pseudocoix	A. Camus		= *Hickelia*	Bam
Pseudodanthonia	Bor & C.E. Hubb.	2		Poo
Pseudodichanthium	Bor	1		PanA
Pseudopentameris	Conert	3		Dan
Pseudophleum	Doğan	2		Poo
Pseudopogonatherum	A. Camus	5		PanA
Pseudoraphis	Griff.	8		Pan
Pseudoroegneria	(Nevski) Á. Löve	15		Poo
Pseudosasa	Makino ex Nakai	20		Bam
Pseudosclerochloa	Tzvelev		= *Puccinellia*	Poo
Pseudosorghum	A. Camus	2		PanA
Pseudostachyum	Munro	1		Bam
Pseudoxytenanthera	Soderstr. & R.P. Ellis	4		Bam
Pseudozoysia	Chiov.	1		Chl
Psilolemma	S.M. Phillips	1		Chl
Psilurus	Trin.		= *Festuca*	Poo
Ptilagrostis	Griseb.	9		Poo
Puccinellia	Parl.	116		Poo
Puelia	Franch.	5		Pue
Pyrrhanthera	Zotov		= *Rytidosperma*	Dan
Qiongzhuea	Hsueh, Chi Ju & T.P. Yi		= *Chimonobambusa*	Bam
Racemobambos	Holttum	19		Bam
Raddia	Bertol.	9		Bam
Raddiella	Swallen	8		Bam
Raimundochloa	A.M. Molina		= *Poa*	Poo
Ratzeburgia	Kunth	1		PanA
Redfieldia	Vasey		= *Muhlenbergia*	Chl
Reederochloa	Soderstr. & H.F. Decker		= *Distichlis*	Chl

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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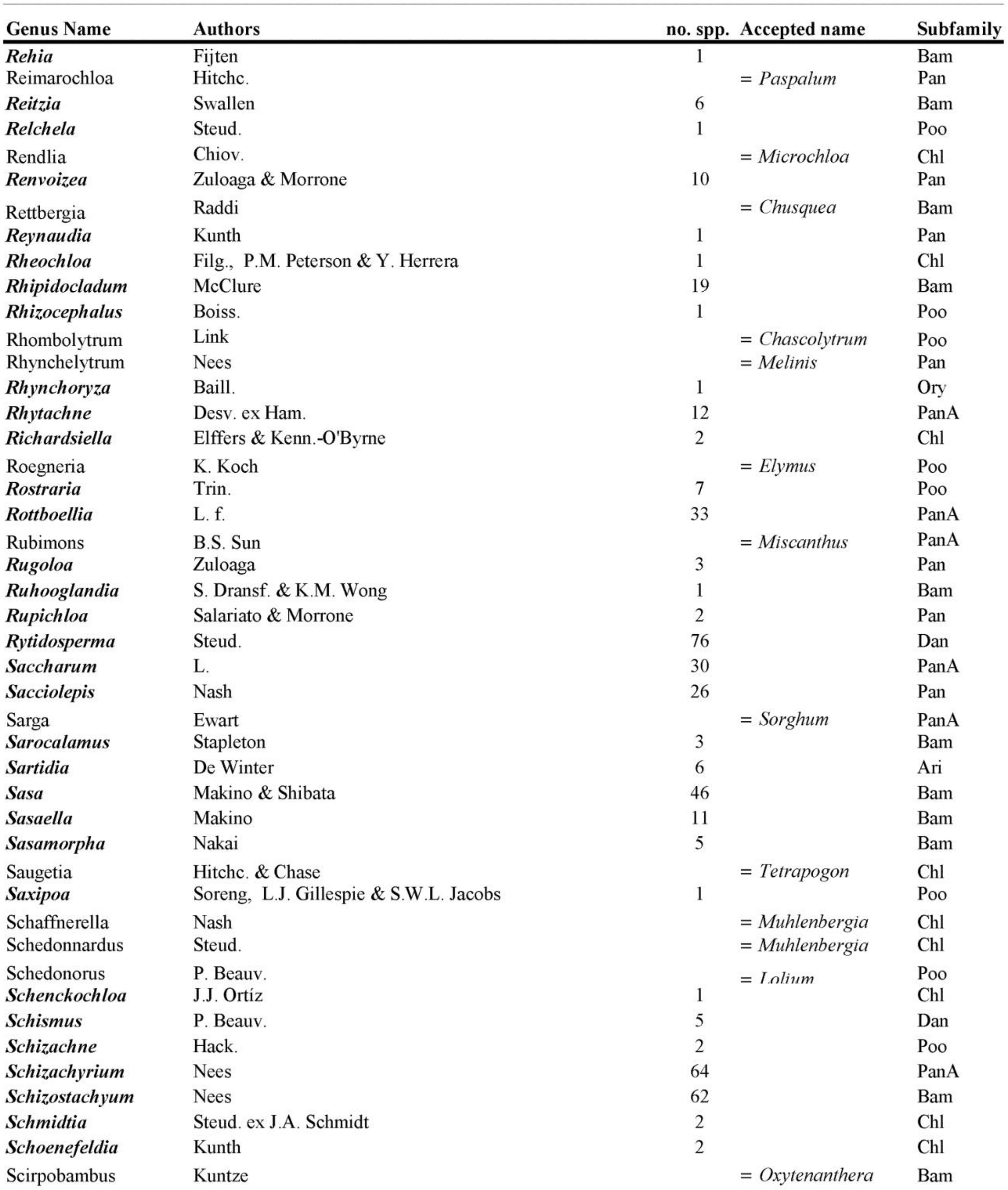

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Rehia	Fijten	1		Bam
Reimarochloa	Hitchc.		= *Paspalum*	Pan
Reitzia	Swallen	6		Bam
Relchela	Steud.	1		Poo
Rendlia	Chiov.		= *Microchloa*	Chl
Renvoizea	Zuloaga & Morrone	10		Pan
Rettbergia	Raddi		= *Chusquea*	Bam
Reynaudia	Kunth	1		Pan
Rheochloa	Filg., P.M. Peterson & Y. Herrera	1		Chl
Rhipidocladum	McClure	19		Bam
Rhizocephalus	Boiss.	1		Poo
Rhombolytrum	Link		= *Chascolytrum*	Poo
Rhynchelytrum	Nees		= *Melinis*	Pan
Rhynchoryza	Baill.	1		Ory
Rhytachne	Desv. ex Ham.	12		PanA
Richardsiella	Elffers & Kenn.-O'Byrne	2		Chl
Roegneria	K. Koch		= *Elymus*	Poo
Rostraria	Trin.	7		Poo
Rottboellia	L. f.	33		PanA
Rubimons	B.S. Sun		= *Miscanthus*	PanA
Rugoloa	Zuloaga	3		Pan
Ruhooglandia	S. Dransf. & K.M. Wong	1		Bam
Rupichloa	Salariato & Morrone	2		Pan
Rytidosperma	Steud.	76		Dan
Saccharum	L.	30		PanA
Sacciolepis	Nash	26		Pan
Sarga	Ewart		= *Sorghum*	PanA
Sarocalamus	Stapleton	3		Bam
Sartidia	De Winter	6		Ari
Sasa	Makino & Shibata	46		Bam
Sasaella	Makino	11		Bam
Sasamorpha	Nakai	5		Bam
Saugetia	Hitchc. & Chase		= *Tetrapogon*	Chl
Saxipoa	Soreng, L.J. Gillespie & S.W.L. Jacobs	1		Poo
Schaffnerella	Nash		= *Muhlenbergia*	Chl
Schedonnardus	Steud.		= *Muhlenbergia*	Chl
Schedonorus	P. Beauv.		= *Lolium*	Poo
Schenckochloa	J.J. Ortíz	1		Chl
Schismus	P. Beauv.	5		Dan
Schizachne	Hack.	2		Poo
Schizachyrium	Nees	64		PanA
Schizostachyum	Nees	62		Bam
Schmidtia	Steud. ex J.A. Schmidt	2		Chl
Schoenefeldia	Kunth	2		Chl
Scirpobambus	Kuntze		= *Oxytenanthera*	Bam

Continued

Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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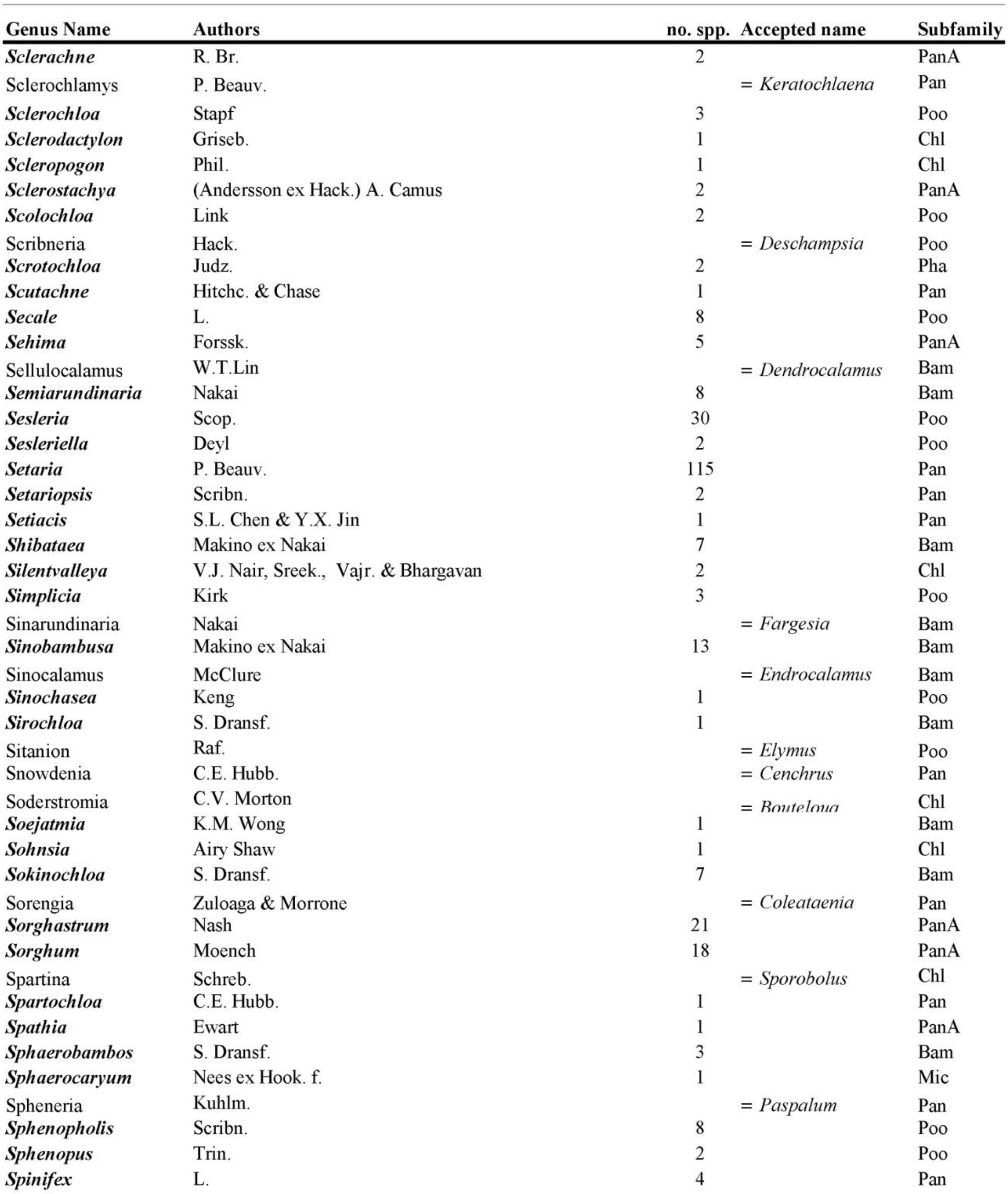

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Sclerachne	R. Br.	2		PanA
Sclerochlamys	P. Beauv.		= *Keratochlaena*	Pan
Sclerochloa	Stapf	3		Poo
Sclerodactylon	Griseb.	1		Chl
Scleropogon	Phil.	1		Chl
Sclerostachya	(Andersson ex Hack.) A. Camus	2		PanA
Scolochloa	Link	2		Poo
Scribneria	Hack.		= *Deschampsia*	Poo
Scrotochloa	Judz.	2		Pha
Scutachne	Hitchc. & Chase	1		Pan
Secale	L.	8		Poo
Sehima	Forssk.	5		PanA
Sellulocalamus	W.T.Lin		= *Dendrocalamus*	Bam
Semiarundinaria	Nakai	8		Bam
Sesleria	Scop.	30		Poo
Sesleriella	Deyl	2		Poo
Setaria	P. Beauv.	115		Pan
Setariopsis	Scribn.	2		Pan
Setiacis	S.L. Chen & Y.X. Jin	1		Pan
Shibataea	Makino ex Nakai	7		Bam
Silentvalleya	V.J. Nair, Sreek., Vajr. & Bhargavan	2		Chl
Simplicia	Kirk	3		Poo
Sinarundinaria	Nakai		= *Fargesia*	Bam
Sinobambusa	Makino ex Nakai	13		Bam
Sinocalamus	McClure		= *Endrocalamus*	Bam
Sinochasea	Keng	1		Poo
Sirochloa	S. Dransf.	1		Bam
Sitanion	Raf.		= *Elymus*	Poo
Snowdenia	C.E. Hubb.		= *Cenchrus*	Pan
Soderstromia	C.V. Morton		= *Bouteloua*	Chl
Soejatmia	K.M. Wong	1		Bam
Sohnsia	Airy Shaw	1		Chl
Sokinochloa	S. Dransf.	7		Bam
Sorengia	Zuloaga & Morrone		= *Coleataenia*	Pan
Sorghastrum	Nash	21		PanA
Sorghum	Moench	18		PanA
Spartina	Schreb.		= *Sporobolus*	Chl
Spartochloa	C.E. Hubb.	1		Pan
Spathia	Ewart	1		PanA
Sphaerobambos	S. Dransf.	3		Bam
Sphaerocaryum	Nees ex Hook. f.	1		Mic
Spheneria	Kuhlm.		= *Paspalum*	Pan
Sphenopholis	Scribn.	8		Poo
Sphenopus	Trin.	2		Poo
Spinifex	L.	4		Pan

Continued

Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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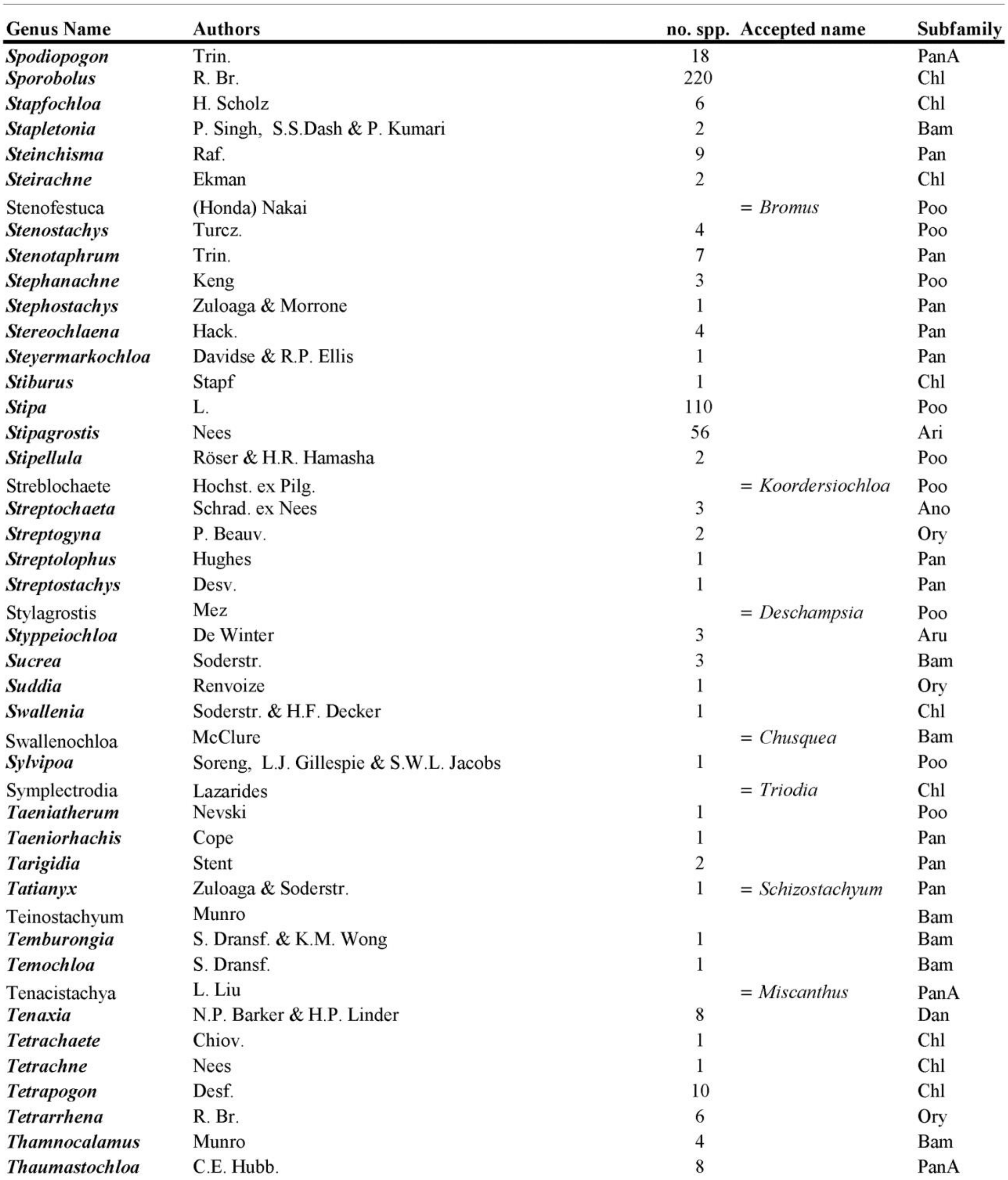

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Spodiopogon	Trin.	18		PanA
Sporobolus	R. Br.	220		Chl
Stapfochloa	H. Scholz	6		Chl
Stapletonia	P. Singh, S.S.Dash & P. Kumari	2		Bam
Steinchisma	Raf.	9		Pan
Steirachne	Ekman	2		Chl
Stenofestuca	(Honda) Nakai		= *Bromus*	Poo
Stenostachys	Turcz.	4		Poo
Stenotaphrum	Trin.	7		Pan
Stephanachne	Keng	3		Poo
Stephostachys	Zuloaga & Morrone	1		Pan
Stereochlaena	Hack.	4		Pan
Steyermarkochloa	Davidse & R.P. Ellis	1		Pan
Stiburus	Stapf	1		Chl
Stipa	L.	110		Poo
Stipagrostis	Nees	56		Ari
Stipellula	Röser & H.R. Hamasha	2		Poo
Streblochaete	Hochst. ex Pilg.		= *Koordersiochloa*	Poo
Streptochaeta	Schrad. ex Nees	3		Ano
Streptogyna	P. Beauv.	2		Ory
Streptolophus	Hughes	1		Pan
Streptostachys	Desv.	1		Pan
Stylagrostis	Mez		= *Deschampsia*	Poo
Styppeiochloa	De Winter	3		Aru
Sucrea	Soderstr.	3		Bam
Suddia	Renvoize	1		Ory
Swallenia	Soderstr. & H.F. Decker	1		Chl
Swallenochloa	McClure		= *Chusquea*	Bam
Sylvipoa	Soreng, L.J. Gillespie & S.W.L. Jacobs	1		Poo
Symplectrodia	Lazarides		= *Triodia*	Chl
Taeniatherum	Nevski	1		Poo
Taeniorhachis	Cope	1		Pan
Tarigidia	Stent	2		Pan
Tatianyx	Zuloaga & Soderstr.	1	= *Schizostachyum*	Pan
Teinostachyum	Munro			Bam
Temburongia	S. Dransf. & K.M. Wong	1		Bam
Temochloa	S. Dransf.	1		Bam
Tenacistachya	L. Liu		= *Miscanthus*	PanA
Tenaxia	N.P. Barker & H.P. Linder	8		Dan
Tetrachaete	Chiov.	1		Chl
Tetrachne	Nees	1		Chl
Tetrapogon	Desf.	10		Chl
Tetrarrhena	R. Br.	6		Ory
Thamnocalamus	Munro	4		Bam
Thaumastochloa	C.E. Hubb.	8		PanA

Continued

Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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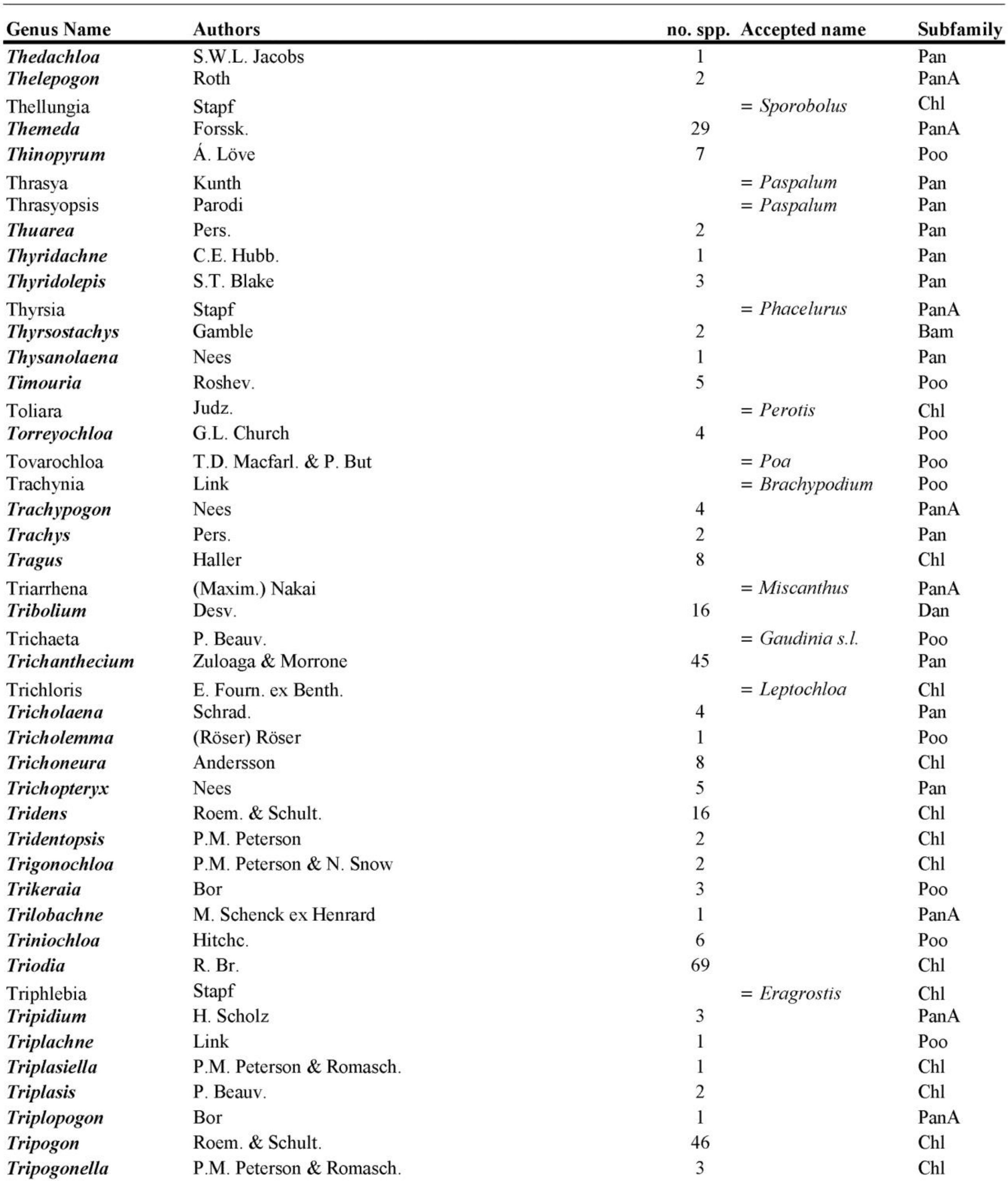

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Thedachloa	S.W.L. Jacobs	1		Pan
Thelepogon	Roth	2		PanA
Thellungia	Stapf		= *Sporobolus*	Chl
Themeda	Forssk.	29		PanA
Thinopyrum	Á. Löve	7		Poo
Thrasya	Kunth		= *Paspalum*	Pan
Thrasyopsis	Parodi		= *Paspalum*	Pan
Thuarea	Pers.	2		Pan
Thyridachne	C.E. Hubb.	1		Pan
Thyridolepis	S.T. Blake	3		Pan
Thyrsia	Stapf		= *Phacelurus*	PanA
Thyrsostachys	Gamble	2		Bam
Thysanolaena	Nees	1		Pan
Timouria	Roshev.	5		Poo
Toliara	Judz.		= *Perotis*	Chl
Torreyochloa	G.L. Church	4		Poo
Tovarochloa	T.D. Macfarl. & P. But		= *Poa*	Poo
Trachynia	Link		= *Brachypodium*	Poo
Trachypogon	Nees	4		PanA
Trachys	Pers.	2		Pan
Tragus	Haller	8		Chl
Triarrhena	(Maxim.) Nakai		= *Miscanthus*	PanA
Tribolium	Desv.	16		Dan
Trichaeta	P. Beauv.		= *Gaudinia s.l.*	Poo
Trichanthecium	Zuloaga & Morrone	45		Pan
Trichloris	E. Fourn. ex Benth.		= *Leptochloa*	Chl
Tricholaena	Schrad.	4		Pan
Tricholemma	(Röser) Röser	1		Poo
Trichoneura	Andersson	8		Chl
Trichopteryx	Nees	5		Pan
Tridens	Roem. & Schult.	16		Chl
Tridentopsis	P.M. Peterson	2		Chl
Trigonochloa	P.M. Peterson & N. Snow	2		Chl
Trikeraia	Bor	3		Poo
Trilobachne	M. Schenck ex Henrard	1		PanA
Triniochloa	Hitchc.	6		Poo
Triodia	R. Br.	69		Chl
Triphlebia	Stapf		= *Eragrostis*	Chl
Tripidium	H. Scholz	3		PanA
Triplachne	Link	1		Poo
Triplasiella	P.M. Peterson & Romasch.	1		Chl
Triplasis	P. Beauv.	2		Chl
Triplopogon	Bor	1		PanA
Tripogon	Roem. & Schult.	46		Chl
Tripogonella	P.M. Peterson & Romasch.	3		Chl

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

Continued

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Tripsacum	L.	16		PanA
Triraphis	R. Br.	9		Chl
Triscenia	Griseb.	1		Pan
Trisetaria	Forssk.	3		Poo
Trisetobromus	Nevski		= *Bromus*	Poo
Trisetopsis	Röser & A. Wölk	28		Poo
Trisetum	Pers.	4		Poo
Tristachya	Nees	21		Pan
Triticum	L.	18		Poo
Tuctoria	Reeder		= *Orcuttia*	Chl
Typhoides	Moench		= *Phalaris*	Poo
Tzvelevia	E.B. Alexeev		= *Poa*	Poo
Tzveleviochloa	Röser & A. Wölk	3		Poo
Uniola	L.	5		Chl
Uranthoecium	Stapf	1		Pan
Urelytrum	Hack.	7		PanA
Urochlaena	Nees		= *Tribolium*	Dan
Urochloa	P. Beauv.	100		Pan
Urochondra	C.E. Hubb.	1		Chl
Vacoparis	Spangler		= *Sorghum*	PanA
Vahlodea	Fr.	2		Poo
Valiha	S. Dransf.	2		Bam
Vaseyochloa	Hitchc.	1		Chl
Veldkampia	Y. Ibaragi & Shiro Kobay.	1		PanA
Ventenata	Koeler	3		Poo
Vetiveria	Bory		= *Chrysopogon*	PanA
Vietnamocalamus	T.Q. Nguyen	1		Bam
Vietnamochloa	Veldkamp & Nowack	1		Chl
Vietnamosasa	T.Q. Nguyen	3		Bam
Viguierella	A. Camus		= *Eragrostis*	Chl
Vossia	Wall. & Griff.	1		PanA
Vulpia	C.C. Gmel.		= *Festuca*	Poo
Vulpiella	(Batt. & Trab.) Burollet	2		Poo
Walwhalleya	Wills & J.J. Bruhl		= *Homopholis*	Pan
Wangenheimia	Moench		= *Festuca*	Poo
Whiteochloa	C.E. Hubb.	6		Pan
Widjajachloa	K.M. Wong & S. Dransf.	1		Bam
Willbleibia	Herter		= *Willcommia*	Chl
Willkommia	Hack.	4		Chl
Xanthochloa	(Krivot.) Tzvelev		= *Leucopoa*	Poo
Xerochloa	R. Br.	3		Pan
Yadakeya	Makino		= *Pseudosasa*	Bam
Yakirra	Lazarides & R.D. Webster		= *Panicum*	Pan
Yersinochloa	H.N. Nguyen & V.T. Tran	1		Bam
Yushania	Keng f.	86		Bam

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Doc. S1. Genera of Poaceae with authors, numbers of species, and subfamily codes (Ano=Anomochlooideae; Ari=Aristidoideae; Aru=Arundinoideae; Bam=Bambusoideae; Chl=Chloridoideae; Dan=Danthonioideae; Mic=Micrairoideae; Ory=Oryzoideae; Pan=Panicoideae, except PanA=tribe Andropogoneae; Pha=Pharoideae; Poo=Pooideae; Pue=Puelioideae). Accepted genera are in ***bold italic*** and important synonyms are listed.

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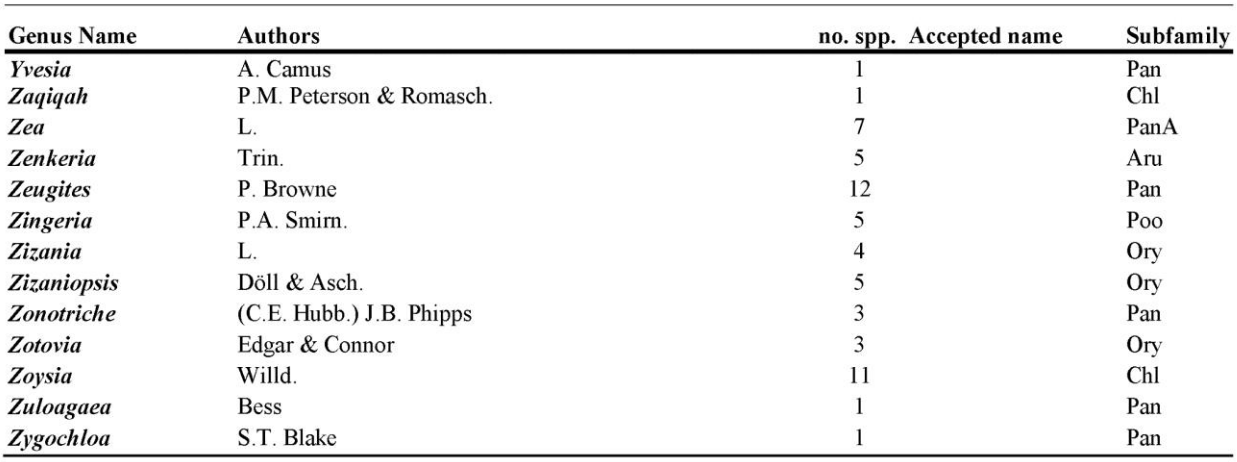

Genus Name	Authors	no. spp.	Accepted name	Subfamily
Yvesia	A. Camus	1		Pan
Zaqiqah	P.M. Peterson & Romasch.	1		Chl
Zea	L.	7		PanA
Zenkeria	Trin.	5		Aru
Zeugites	P. Browne	12		Pan
Zingeria	P.A. Smirn.	5		Poo
Zizania	L.	4		Ory
Zizaniopsis	Döll & Asch.	5		Ory
Zonotriche	(C.E. Hubb.) J.B. Phipps	3		Pan
Zotovia	Edgar & Connor	3		Ory
Zoysia	Willd.	11		Chl
Zuloagaea	Bess	1		Pan
Zygochloa	S.T. Blake	1		Pan

Appendix 1. Comparison of the Poaceae suprageneric classifications of Kellogg (2015) and Soreng et al. (2015b); new treatment numbers of genera and species; NA = not applied by Kellogg, considered superfluous, although used by Soreng et al.; a dash (–) = not accepted or not available.

Subfamily	Supertribe	Tribe	Supersubtribe	Subtribe	Kellogg 2015 no. genera	Soreng et al. 2015 no. genera	New treatment no. genera	New treatment no. species
Totals					698		768	11506
Anomochlooideae					2		2	4
"		Anomochloeae			NA		1	2
"		Streptochaeteae			NA		1	3
Pharoideae					3		3	12
"		Phareae			NA		3	12
"					2		2	11
"		Atractocarpeae			NA		1	5
"		Guaduelleae			NA		1	6
Oryzoideae					16		19	115
"		Streptogyneae			1, no subfamily		1	2
"		*incertae sedis*			1		1	1
"		Ehrharteae			1		4	38
"		Oryzeae			11		11	71
"		"	–	Oryzinae	4		4	44
"		"	–	Zizaniinae	7		7	27
"					2		2	3
Bambusoideae					114		125	1670
"	Arundinariodae				NA		–	–
"	"	Arundinarieae			28		31	581
"	"	"		Arundinariinae	NA		31	581
"	Olyrodae				NA		–	–
"	"	Olyreae			21		21	123
"	"	"	–	Buergersiochloinae	1		1	1
"	"	"	–	Olyrinae	18		17	88
"	"	"	–	Parianinae	2		3	34
"	Bambusodae				NA		–	–
"	"	Bambuseae			65		73	966
"	"	"	–	*incertae sedis*	–	–	2	2
"	"	"	–	Melocanninae	9	10	9	99
"	"	"	–	Hickeliinae	8	8	9	32
"	"	"	–	Bambusinae	26	29	17	324
"	"	"	–	Racemobambosinae	1	1	3	31
"	"	"	–	Dinochloinae	–	–	7	56
"	"	"	–	Greslaniinae	–	–	1	2
"	"	"	–	Holttumochloinae	–	–	3	6

Continued

Appendix 1. Comparison of the Poaceae suprageneric classifications of Kellogg (2015) and Soreng et al. (2015b); new treatment numbers of genera and species; NA = not applied by Kellogg, considered superfluous, although used by Soreng et al.; a dash (–) = not accepted or not available.

Continued

Subfamily	Supertribe	Tribe	Supersubtribe	Subtribe	Kellogg 2015 no. genera	Soreng et al. 2015 no. genera	New treatment no. genera	New treatment no. species
Bambusoideae	Bambusodae	Bambuseae	–	Temburongiinae	–	–	1	1
"	"	"	–	Chusqueinae	1	1	1	175
"	"	"	–	Guaduinae	5	5	5	53
"	"	"	–	Arthrostylidiinae	1	14	15	185
Pooideae					1	198	202	3968
"	–	Brachyelytreae			1	1	1	3
"	Nardodae				–	2	2	2
"	"	Nardeae			2	1	1	1
"	"	Lygeeae			in Nardeae	1	1	1
"	–	Duthieeae			in Phaenospermatideae	in Phaenospermatideae	8	16
"	–	Phaenospermateae			8	8	1	1
"	Melicodae				–	–	8	159
"	"	Brylkinieae			in Meliceae	2	1	1
"	"	Meliceae			8	6	7	158
"	Stipodae				NA	–	27	528
"	"	Ampelodesmeae			in Stipeae	1	1	1
"	"	Stipeae			28	28	28	527
"	–	Diarrheneae			1	2	2	5
"	–	Brachypodieae			1	1	1	22
"	Poodae				28	118	121	2562
"	"	Poeae			1	118	121	2562
"	"	"	–	*incertae sedis*	2	–	–	–
"	"	"	–	Torreyochloinae	2	2	2	16
"	"	"	–	Aveninae	7	15	18	343
"	"	"	–	Phalaridinae	1	1	1	17
"	"	"	–	Anthoxanthinae	1	1	1	42
"	"	"	Agrostidodinae		–	–	19	457
"	"	"	"	Brizinae	in Agrostideae	2	2	6
"	"	"	"	Calothecinae	in Agrostideae	2	1	22
"	"	"	"	Echinopogoninae	–	–	5	20
"	"	"	"	Agrostidinae	20	16	11	409
"	"	"	–	Scolochloinae	1	2	2	3
"	"	"	–	Sesleriinae	4	5	5	39
"	"	"	–	Holcinae	in Airinae	3	2	11
"	"	"	–	Airinae	10	7	7	43
"	"	"	–	Aristaveninae	in Airinae	in Airinae	1	51
"	"	"	Loliodinae		–	–	21	692

Continued

Appendix 1. Comparison of the Poaceae suprageneric classifications of Kellogg (2015) and Soreng et al. (2015b); new treatment numbers of genera and species; NA = not applied by Kellogg, considered superfluous, although used by Soreng et al.; a dash (–) = not accepted or not available.

Continued

Subfamily	Supertribe	Tribe	Supersubtribe	Subtribe	Kellogg 2015 no. genera	Soreng et al. 2015 no. genera	New treatment no. genera	New treatment no. species
Pooideae	Poodae	Poeae	Loliodinae	Loliinae	6	9	9	659
"	"	"	"	Dactylidinae	2	2	2	4
"	"	"	"	Cynosurinae	1	1	1	10
"	"	"	"	Ammochloinae	1	1	1	3
"	"	"	"	Parapholiinae	7	8	8	26
"	"	"	"	*incertae sedis*	–	–	1	1
"	"	"	"	Coleanthinae	11	10	10	156
"	"	"	Poodinae		–	–	31	681
"	"	"		*incertae sedis*	–	1	10	15
"	"	"	Poodinae	Poinae	25	30	1	550
"	"	"	"	Miliinae	in Poinae	1	1	5
"	"	"	"	Phleinae	in Poinae	in Poinae	1	16
"	"	"	"	Beckmanninae	in Poinae	in Poinae	4	6
"	"	"	"	Cinninae	in Poinae	in Poinae	5	13
"	"	"	"	Alopecurinae	in Poinae	in Poinae	3	47
"	"	"	"	Ventenatinae	in Poinae	in Poinae	6	21
"	Triticodae				NA	29	29	29
"	"	Littledaleeae	–	–	–	1	1	4
"	"	Bromeae	–	–	2	1	1	165
"	"	Triticeae	–	–	20	27	27	501
"	"	"	–	Hordeinae	in Triticeae	22	in Triticeae	–
"	"	"	–	Triticinae	in Triticeae	5	in Triticeae	–
Aristidoideae					3	3	3	367
"		Aristideae			NA	3	3	367
Panicoideae					216	243	247	3241
"		*incertae sedis*			4	2	3	8
"		Thysanolaeneae			in Centotheceae	1	1	1
"		Cyperochloeae			in Centotheceae	2	2	2
"		Centhoteceae			5	2	2	3
"		Chasmanthieae			6	2	1	7
"		Zeugiteae			in Chasmanthieae	5	4	17
"		Steyermarkochloeae			1	2	2	2
Panicoideae		Tristachyideae			7	8	8	87
"		Gynerieae			1	1	1	1
"		Lecomtelleae			–	–	1	1
"	Panicodae		–		71	84	82	1227
"	"	Paniceae			71	84	82	1227
"	"	"	–	*incertae sedis*	11	10	10	83

Continued

Appendix 1. Comparison of the Poaceae suprageneric classifications of Kellogg (2015) and Soreng et al. (2015b); new treatment numbers of genera and species; NA = not applied by Kellogg, considered superfluous, although used by Soreng et al.; a dash (–) = not accepted or not available.

Continued

Subfamily	Supertribe	Tribe	Supersubtribe	Subtribe	Kellogg 2015 no. genera	Soreng et al. 2015 no. genera	New treatment no. genera	New treatment no. species
Panicoideae	Panicodae	Paniceae	–	Anthephorinae	7	9	8	291
"	"	"	–	Dichantheliinae	–	2	2	76
"	"	"	–	Boivinellinae	14	15	18	146
"	"	"	–	Neurachninae	3	6	6	21
"	"	"	–	Melinidinae	11	14	13	166
"	"	"	–	Panicinae	3	4	2	157
"	"	"	–	Cenchrinae	22	24	24	287
"	Andropogonodae		–		NA	132	140	1885
"	"	Paspaleae			32	39	39	597
"	"	"	–	*incertae sedis*	–	1	1	1
"	"	"	–	Paspalinae	13	16	17	491
"	"	"	–	Otachyriinae	4	6	5	34
"	"	"	–	Arthropogoninae	14	16	16	71
"	"	Arundinellieae			in Andropogoneae	2	3	86
"	"	"	–	Arundinelliinae	2	–	–	–
"	"	Andropogoneae			87	91	98	1202
"	"	"	–	*incertae sedis*	21	10	6	85
"	"	"	–	Arthraxoninae	NA	1	1	27
"	"	"	–	Tripsacinae	6	2	7	59
"	"	"	–	Chinonachninae	NA	4	5	15
"	"	"	–	Coicinae	NA	1	1	4
"	"	"	–	Rottboelliinae	13	18	16	112
"	"	"	–	Ischaeminae	2	6	7	151
"	"	"	–	Dimeriinae	in Ischaeminae	1	in Ischaeminae	–
"	"	"	–	Germainiinae	4	3	4	31
"	"	"	–	Sorghinae	in Saccharinae	7	in Saccharinae	–
"	"	"	–	Sacchariinae	14	16	26	179
"	"	"	–	Andropogoninae	25	6	25	514
"	"	"	–	Anthistiriinae	in Andropogoninae	16	in Andropogoninae	–
Arundinoideae			–		18	16	14	40
"		Arundineae			NA	3	4	17
"		Molinieae			NA	13	11	24
"		"	–	*incertae sedis*	–	–	3	7
"		"	–	Moliniinae	in Poinae	in Molinieae	4	7
"		"	–	Crinipinae	in Arundinoideae	in Molinieae	4	10
Micrairoideae					9	9	8	184
"		Micraireae			NA	1	1	15
"		Eriachneae			NA	2	1	50

Continued

Appendix 1. Comparison of the Poaceae suprageneric classifications of Kellogg (2015) and Soreng et al. (2015b); new treatment numbers of genera and species; NA = not applied by Kellogg, considered superfluous, although used by Soreng et al.; a dash (–) = not accepted or not available.

Continued

Subfamily	Supertribe	Tribe	Supersubtribe	Subtribe	Kellogg 2015 no. genera	Soreng et al. 2015 no. genera	New treatment no. genera	New treatment no. species
Micrairoideae		Isachneae			NA	5	6	119
"		Hubbardieae			NA	1	in Isachneae	–
Danthonioideae					17	20	19	292
"		*incertae sedis*			–	3	1	1
"		Danthonieae			NA	17	18	291
Chloridoideae					121	131	124	1602
"		*incertae sedis*			12	9	7	9
"		Centropodieae			2	2	2	6
"		Triraphideae			3	3	3	15
"		Eragrostideae			16	9	14	489
"		"	–	*incertae sedis*	2	–	–	–
"		"	–	Cotteinae	4	4	4	28
"		"	–	Eragrostidinae	5	11	5	451
"		Eragrostideae	–	Uniolinae	5	5	5	10
"		Zoysieae			8	4	4	233
"		"		Sporobolinae	NA	2	2	221
"		Zoysieae		Zoysiinae	NA	2	2	12
"		Cynodonteae			82	94	94	850
"		"	–	*incertae sedis*	11	15	4	4
"		"	–	Aeluropodinae	–	2	2	7
"		"	–	Dactylocteniinae	–	–	4	20
"		"	–	Eleusininae	24	31	27	231
"		"		Orcuttinae	3	3	2	9
"		"		Orininae	–	–	2	20
"		"		Pappophorinae	3	3	3	25
"		″	–	Triodiinae	3	3	1	69
"		"	–	Tripogoninae	5	5	7	66
"		"	Boutelouodinae		–	–	20	299
"		"	–	*incertae sedis*	–	–	4	5
"		"	"	Boutelouinae	16	1	1	60
"		"	"	Hilariinae	in Boutelouinae	1	1	10
"		"	"	Monanthochloinae	in Boutelouinae	1	1	11
"		"	"	Muhlenbergiinae	in Boutelouinae	1	1	182
"		"	"	Scleropogoninae	in Boutelouinae	6	6	15
"		"	"	Traginae	in Boutelouinae	4	6	16
"		"	Gouiniodinae		–	–	21	100
"		"	"	Cteniinae	in Gouiniinae	1	1	20
"		"	"	Farragininae	in Gouiniinae	2	2	4

Continued

Appendix 1. Comparison of the Poaceae suprageneric classifications of Kellogg (2015) and Soreng et al. (2015b); new treatment numbers of genera and species; NA = not applied by Kellogg, considered superfluous, although used by Soreng et al.; a dash (–) = not accepted or not available.

Continued

Subfamily	**Supertribe**	**Tribe**	**Supersubtribe**	**Subtribe**	**Kellogg 2015 no. genera**	**Soreng et al. 2015 no. genera**	**New treatment no. genera**	**New treatment no. species**
Chloridoideae		Cynodonteae	Gouiniodinae	Gouiniinae	17	5	6	21
"		"	"	Gymopogoninae	in Gouiniinae	6	in Hubbardochloinae	–
"		"	"	Hubbardochloinae	–	*incertae sedis*	8	27
"		″	"	Perotidinae	in Gouiniinae	3	3	19
"		"	"	Trichoneurinae	in Gouiniinae	1	1	8
"		"	"	Zaqiqahinae	–	–	1	1

Appendix 2. A world-wide phylogenetic classification of Poaceae (Gramineae) II.: căo (草), capim, çayır, çimen, darbha, ghaas, ghas, gish, gramas, graminius, gräser, grasses, gyokh, he-ben-ke, hullu, kasa, kusa, nyasi, pastos, pillu, pullu, zlaki, etc. Accepted suprageneric names appear in **bold** type. The indigenous range of each genus is colored as follows: Western Hemisphere, Eurasia (including genera that in Africa are exclusively Mediterranean, but not exclusively African), Australasia, and Africa. Genera with bimodal distributions are bicolored, those with broader distributions tricolored, or are red if more widely distributed. Genera in synonymy (syn. – …..) are colored if the accepted genus is more widely distributed, i.e., in more than one area. *Genera in italics have been sampled in DNA studies*. Comments and C_3 and C_4 photosynthetic pathways are in brackets { }. Publication dates for suprageneric taxa appear in square brackets [ ].

superorder **Lilianae** Takht. order **Poales** Small
family **Poaceae** Barnhart [1895] (nom. alt.: Gramineae Juss. [1789])

subfamily **Anomochlooideae** Pilg. ex Potztal [1957] (syn. – Streptochaetoideae Butzin [1965]) {all C_3}:

tribe **Anomochloeae** C.E. Hubb. [1934]: *Anomochloa*.

tribe **Streptochaeteae** C.E. Hubb. [1934]: *Streptochaeta*.

subfamily **Pharoideae** L.G. Clark & Judz. [1996] (syn. – subfamily Leptaspidoideae C.O. Morales [1998], supertribe Pharodae L. Liu [1980]) {all C_3}:

tribe **Phareae** Stapf [1898] (syn. – Leptaspideae Tzvelev [1987]): *Leptaspis*, *Pharus*, Scrotochloa.

subfamily **Puelioideae** L.G. Clark, M. Kobay, S. Mathews, Spangler & E.A. Kellogg [2000] {all C_3}:

tribe **Atractocarpeae** Jacq.-Fél. ex Tzvelev [1987] (syn. – tribe Atractocarpeae Jacq.-Fél. [1962, nom. inval.], Puelieae Soderstr. & R.P. Ellis [1988], subtribe Atractocarpinae E.G. Camus [1913], Pueliinae Stapf [1917]): *Puelia* (syn. – *Atractocarpa*).

tribe **Guaduelleae** Soderstr. & R.P. Ellis [1988]: *Guaduella*.

"BOP" clade {Clark et al., 1995; Clark et al., 2000, as **BEP**} {all C_3}

subfamily **Oryzoideae** Kunth ex Beilschm. [1833] (syn. – Ehrhartoideae Caro [1982], Oryzoideae Caro [1982, isonym]; Ehrhartinae Link [1827, invalid], Oryzeae Burmeist. [1837, unranked]) {all C_3}:

incertae sedis: *Suddia* {probably Phyllorachideae}.

tribe **Streptogyneae** C. E. Hubb. ex C. E. Calderón & Soderstr. [1980] (syn. – tribe Streptogyneae C.E. Hubb. [1956, nom. inval.]; subtribe Streptogyninae Pilg. ex Potztal [1969]): *Streptogyna*.

tribe **Ehrharteae** Nevski [1937]: *Ehrharta*, *Microlaena*, *Tetrarrhena*, *Zotovia* {genera okay in Verboom et al., 2003, except for placement of one species of *Microlaena*; more study is needed}.

tribe **Oryzeae** Dumort. [1824] (syn. – Zizanieae Hitchc. [1920]):

subtribe **Oryzinae** Griseb. [1853] (syn. – Oryzeae Horan. [1847 {rank tribe or subtribe?}]): *Leersia*, *Maltebrunia*, *Oryza* (syn. – *Porteresia*), *Prosphytochloa*.

subtribe **Zizaniinae** Benth. [1881] (syn. – Luziolinae Terrell & H. Rob. [1974]): *Chikusichloa*, *Hygroryza*, *Luziola*, *Potamophila*, *Rhynchoryza*, *Zizania*, *Zizaniopsis*.

tribe **Phyllorachideae** C.E. Hubb. [1939] {may be better in Oryzeae as a subtribe}: *Humbertochloa*, Phyllorachis.

subfamily **Bambusoideae** Luerss. [1893] (syn. – Olyroideae Pilg. [1956], Parianoideae Butzin [1965]) {all C$_3$}:

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

tribe **Arundinarieae** Asch. & Graebn. [1902] (syn. – supertribe Arundinariodae L. Liu [1980]; tribes Chimonocalameae Keng f. [1982, nom. inval.], Shibataeeae Nakai [1933]):

subtribe **Arundinariinae** Nees ex Lindl. [1836] (syn. – Aruninariinae Benth. [1881, isonym], Hack. [1887, isonym], Phyllostachydinae Keng f. [1992], Pleioblastinae Keng & Keng f. [1959], Sasinae Keng. f. [1992], Shibataeinae Soderstr. & R.P. Ellis [1988], Sinobambusinae Z.B. Wang [1987], Thamnocalaminae Keng. f. [1992]): *Acidosasa*, *Ampelocalamus* (s.s.), *Arundinaria*, *Bashania*, *Bergbambos*, *Chimonobambusa* (syn. – *Menstruocalamus*, *Oreocalamus*, *Qiongzhuea*), *Chimonocalamus*, *Drepanostachyum*, *Fargesia* (syn. – *Borinda*, *Sinarundinaria*), *Ferrocalamus*, *Gaoligongshania*, *Gelidocalamus*, *Himalayacalamus*, *Indocalamus* (s.s.), *Indosasa*, *Kuruna*, *Oldeania*, *Oligostachyum*, *Phyllostachys* (s.s.), *Pleioblastus* (syn. – Nipponocalamus, Polyanthus), *Pseudosasa* (syn. – Yadakeya), *Sarocalamus*, *Sasa* (syn. – *Neosasamorpha*), *Sasaella*, *Sasamorpha*, *Semiarundinaria* (syn. – *Brachystachyum*), *Shibataea*, *Sinobambusa*, *Thamnocalamus* s.s, Vietnamocalamus, *Yushania*.

tribe **Olyreae** Kunth ex Spenn. [1825] (syn. – supertribe Olyrodae Soderstr. & R.P. Ellis [1987 {1988}]; tribes Buergersiochloeae S.T. Blake [1946], Parianeae C.E. Hubb. [1934]).

subtribe **Buergersiochloinae** L.G. Clark & Judz. [2007]: *Buergersiochloa*.

subtribe **Olyrinae** Kromb. [1875] (syn. – Olyreae Horan. [1847 {rank tribe or subtribe?}]: Agnesia, *Arberella*, *Cryptochloa*, *Diandrolyra*, Ekmanochloa, Froesiochloa, *Lithachne*, Maclurolyra, Mniochloa, *Olyra*, *Parodiolyra*, Piresiella, *Raddia*, *Raddiella*, Rehia, *Reitzia* (syn. – *Piresia*), *Sucrea*.

subtribe **Parianinae** Hack. [1887]: *Eremitis*, *Pariana*, *Parianella*.

tribe **Bambuseae** Kunth ex Dumort. [1829] (syn. – supertribe Bambusodae L. Liu [1980]; tribes Arthrostylidieae E.G. Camus [1913], Baccifereae E.G. Camus [1913, nom. inval.], Chusqueae E.G. Camus [1913], Hickelieae A. Camus [1935, nom. inval.], Oxytenanthereae Tzvelev [1987]):

subtribe **Melocanninae** Benth. [1881] (syn. – Schizostachydinae Soderstr. & R.P. Ellis [1988]): Annamocalamus, *Cephalostachyum* (syn. – *Leptocanna*), *Davidsea*, *Melocanna*, *Neohouzeaua*, *Ochlandra*, *Pseudostachyum*, *Schizostachyum* (syn. – *Dendrochloa*, *Teinostachyum*), Stapletonia.

subtribe **Hickeliinae** A. Camus [1924] (syn. – Nastinae Soderstr. & R.P. Ellis [1988]): *Cathariostachys*, *Decaryochloa*, *Hickelia* (syn. – Pseudocoix), *Hitchcockella*, *Nastus* (syn. – *Oreiostachys*), *Perrierbambus*, *Sirochloa*, *Sokinochloa*, *Valiha*.

subtribe **Bambusinae** J. Presl [1830] (syn. – Dendrocalaminae Benth. [1881]): *Bambusa* (syn. – *Dendrocalamopsis*, *Neosinocalamus*, Pseudobambusa), *Bonia*, Cochinchinochloa, *Dendrocalamus* (syn. – Klemachloa, Sellulocalamus, *Sinocalamus*), Fimbribambusa, *Gigantochloa*, *Maclurochloa*, *Melocalamus*, *Neomicrocalamus*, *Oreobambos*, *Oxytenanthera* (syn. – Houzeaubambus, Scirpobambus), *Phuphanochloa*, *Pseudoxytenanthera*, *Soejatmia*, *Thyrsostachys*, *Vietnamosasa*, *Yersinochloa*.

subtribe **Racemobambosinae** Stapleton [1984]: Chloothamnus (syn. – Oreiostachys), *Racemobambos* s.s., Widjajachloa.

subtribe **Dinochloinae** K.M. Wong & W.L. Goh [2016]: *Cyrtochloa*, *Dinochloa*, *Mullerochloa*, *Neololeba*, Pinga, Parabambusa, Sphaerobambos.

subtribe **Greslaninae** K.M. Wong & W.L. Goh [2016]: *Greslania*.

subtribe **Holttumochloinae** K.M. Wong & W.L. Goh [2016]: *Holttumochloa*, *Kinabaluchloa*, Nianhochloa.

subtribe **Temburongiinae** K.M. Wong [2016]: *Temburongia*.

incertae sedis: Ruhooglandia, *Temochloa*.

subtribe **Chusqueinae** Soderstr. & R.P. Ellis [1988] (syn. – Neurolepidinae Soderstr. & R.P. Ellis [1988]): *Chusquea* (syn. – *Neurolepis*, *Platonia*, *Rettbergia*, *Swallenochloa*).

subtribe **Guaduinae** Soderstr. & R.P. Ellis [1988]: *Apoclada*, *Eremocaulon* (syn. – Criciuma), *Guadua*, *Olmeca*, *Otatea*.

subtribe **Arthrostylidiinae** Soderstr. & R.P. Ellis [1988]: *Actinocladum*, *Alvimia*, *Arthrostylidium*, Athroostachys, *Atractantha*, *Aulonemia* (syn. – *Matudacalamus*), *Cambajuva*, *Colanthelia*, *Didymogonyx*, *Elytrostachys*, *Filgueirasia*, *Glaziophyton*, *Merostachys*, *Myriocladus*, *Rhipidocladum*.

subfamily **Pooideae** Benth. [1861] (syn. – Secaloideae Rouy [1913]; Agrostidoideae Kunth ex Beilschm. [1833]; Hordeaceae Burmeist. [1837, unranked], Phalarideae Burmeist. [1837, unranked], Stipaceae Burmeist. [1837, unranked]) {all C_3}:

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

tribe **Brachyelytreae** Ohwi [1941] (syn. – subtribe Brachyelytrinae Ohwi [1942]): *Brachyelytrum*.

supertribe **Nardodae** Soreng [2017] **supertribe nov.** {Nardeae + Lygeeae}:

tribe **Nardeae** W.D.J. Koch. [1837] (syn. – subtribe Nardinae Kromb. [1875]): *Nardus*.

tribe **Lygeeae** J. Presl [1846] (syn. – subtribe Lygeinae Röser [2009], Spartineae Trin. [1824, nom. inval., based on *Lygeum*]): *Lygeum*.

tribe **Duthieeae** Röser & Jul.Schneider [2011], subtribe Duthieinae Pilg. ex Potztal [1969]): *Anisopogon*, *Danthoniastrum*, Duthiea s.s. (s.l., syn. – *Triavenopsis*), *Metcalfia*, *Pappagrostis*, *Pseudodanthonia*, *Sinochasea*, *Stephanachne*.

tribe **Phaenospermateae** Renvoize & Clayton [1985]: *Phaenosperma* {reticulate; see Hochbach et al., 2015}.

supertribe **Melicodae** Soreng [2017] **supertribe nov.** {Brylkineae + Meliceae}:

tribe **Brylkinieae** Tateoka [1960] {sister to Meliceae} (syn. – subtribe Brylkiniinae Ohwi [1941]): *Brylkinia*.

tribe **Meliceae** Link ex Endl. [1830] (syn. – Glycerieae Link ex Endl. [1830] {sister to Brylkinieae}; subtribe Glyceriinae Dumort. [1869], Melicinae Fr. [1835]): *Glyceria*, *Koordersiochloa* (syn. – *Streblochaete*), *Lycochloa*, *Melica*, *Pleuropogon*, *Schizachne*, *Triniochloa*.

supertribe **Stipodae** L. Liu [1980] {Stipeae + Amplelodesmeae}:

tribe **Ampelodesmeae** Tutin [1978] (syn. – Ampelodesminae Conert [1961]): *Ampelodesmos* {reticulate, apparently an ancient hybrid between parents from Stipeae and Duthieeae; see Romaschenko et al., 2012; Hochbach et al. 2015}.

tribe **Stipeae** Dumort. [1824] (syn. – subtribe Stipinae Griseb. [1846]; Aciachninae Caro [1982], Ortachninae Caro [1982]): *Achnatherum* (syn. – *Aristella*) {Eurasian/African only, Western Hemisphere species are in limbo, none belong in *Achnatherum* s.s., most are *Eriocoma* but not yet transferred}, *Aciachne*, *Amelichloa* {nested within *Nassella*, but an intergeneric hybrid origin has not been ruled out}, *Anatherostipa* (syn. – *Nicoraella*), *Anemanthele*, *Austrostipa*, *Celtica*, *Eriocoma* {incl. most American spp. of *Achnatherum*}, *Hesperostipa*, *Jarava*, *Lorenzochloa*, *Macrochloa*, *Nassella*, *Oloptum*, *Ortachne*, *Orthoraphium*, *Oryzopsis*, *Pappostipa*, *Patis*, *Piptochaetium*, *Piptatheropsis*, *Piptatherum*, *Psammochloa*, *Ptilagrostis*, *Stipa*, *Stipellula* (*Stipella* nom. illeg. hom.), *Timouria*, *Trikeraia*.

tribe **Diarrheneae** C.S. Campb. [1985] (syn. – subtribe Diarrheninae Ohwi [1941]): *Diarrhena*, *Neomolinia*.

tribe **Brachypodieae** Harz [1880] (syn. – subtribe Brachypodiinae Hack. [1887]; Brachypodieae Hayek [1925, isonym]): *Brachypodium* (syn. – *Trachynia*).

supertribe **Poodae** L. Liu [1980] (syn. – Poodae T.D. Macfarl. & L. Watson [1982], isonym {tribe Poeae only}):

tribe **Poeae** R.Br. [1814] (syn. – Agrostideae Martinov [1820] {as Koleno = tribe, indirect ref. to Kunth}, Agrostideae Dumort. [1824], Airopsideae Gren. & Godr. [1855], Alopecureae W.D.J. Koch[1837], Anthoxantheae Link ex Endl. [1830], Aveneae Dumort. [1824], Beckmannieae Nevski [1937], Calamagrostideae Trin. [1824], Cinneae Ohwi [1941], Coleantheae Husn. [1896], Cynosureae Dumort. [1824], Dupontieae A. Löve & D. Löve, [1961, nom. nud.], Festuceae Dumort. [1824], Gaudinieae Rouy [1913], Graphephoreae Hyl. [1953], Hainardieae Greuter [1967], Holceae J. Presl [1846], Lolieae Link ex Endl. [1830], Koelerieae Schur [1866, nom. nud.], Milieae Link ex Endl. [1830], Phalarideae Kunth [1829], Phleeae Dumort. [1824], Scolochloeae Tzvelev [1968], Seslerieae W.D.J. Koch [1837], Triseteae Gren. & Godr. [1855], Vilfeae Trin. [1824]):

Poeae CHLOROPLAST GROUP 1 (Aveneae type) {Soreng et al., 2007}:

subtribe **Torreyochloinae** Soreng & J.I Davis [2003]: *Amphibromus*, *Torreyochloa*.

subtribe **Aveninae** J. Presl [1830] (syn. – Gaudiniinae Holub ex Tzvelev [1976, nom. nud.], Graphephorinae Asch. & Graebn. [1900], Koeleriinae Asch. & Graebn. [1900]): *Acrospelion*, *Arrhenatherum*, *Avellinia*, *Avena*, *Cinnagrostis* (syn. – *Leptophyllochloa*) {“Deyeuxia” of Western Hemisphere p.p.}, *Gaudinia* (syn. – *Trichaeta*), *Graphephorum* {reticulate}, *Helictotrichon* s.s. (syn. – *Pseudarrhenathrum*; excl. *Avenula* and *Helictochloa*), *Koeleria* (syn. – *Parafestuca*), *Lagurus*, *Peyritschia*, *Rostraria* s.s. {reticulate in type spp. only}, *Sphenopholis*, *Tricholemma*, *Trisetaria* s.s., *Trisetum* s.s., *Trisetopsis* {reticulate}, *Tzveleviochloa* {reticulate}.

subtribe **Phalaridinae** Fr. [1835]: *Phalaris* (syn. – *Baldingera*, *Phalaroides*, *Typhoides*).

subtribe **Anthoxanthinae** A. Gray [1856] (syn. – Foenodorinae Krause [1909, nom. inval.]): *Anthoxanthum* (syn. – *Ataxia*, *Hierochloe*).

supersubtribe: **Agrostidodinae** Soreng **supersubtribe nov.** [2017]: {Brizinae + Calothecinae + Dichelachninae + Agrostidinae}:

subtribe **Brizinae** Tzvelev s.s. [1968]: *Airopsis*, *Briza* (syn. – *Macrobriza*; excl. *Brizochloa*).

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

subtribe **Echinopogoninae** Soreng [2017] **subtribe nov.**: Ancistragrostis {tentatively placed here}, *Dichelachne* {apparently reticulate with *Calamagrostis* s.s.}, *Echinopogon*, *Pentapogon* {GenBank DNA data for placement among Danthonioid or Arundinoid needs verification}, *Relchela*.

subtribe **Calothecinae** Soreng [2015]: *Chascolytrum* (syn. – *Calotheca*, *Erianthecium*, *Gymnachne*, *Lombardochloa*, *Microbriza*, *Poidium*, *Rhombolytrum*).

subtribe **Agrostidinae** Fr. [1835] (syn. – Calamagrostidinae Lindl. [1836, nom. nud.], Vilfinae Steud. [1854]; Chaeturaceae Link [1827, unranked]): *Agrostis* (syn. – *Chaetopogon*, *Neoschischkinia*, *Notonema*), Bromidium {may be related to *Dichelachne*}, *Calamagrostis* p.p. (syn. – *Ammophila*, *Deyeuxia*) {polyphyletic in Western Hemisphere, see *Cinnagrostis*, *Deschampsia*}, *Chaetotropis* {reticulate}, Hypseochloa {odd here}, *Gastridium*, *Lachnagrostis* {reticulate}, *Limnodea*, *Podagrostis* {reticulate}, *Polypogon* {reticulate}, *Triplachne*.

Poeae CHLOROPLAST GROUP 2 (Poeae type) {Soreng et al., 2007}:

subtribe **Scolochloinae** Tzvelev [1987] {this subtribe seems to share plastids with the classical Poeae and nrDNA with early GROUP 1 Aveninae}: *Dryopoa*, *Scolochloa*.

subtribe **Sesleriinae** Parl. [1845] (syn. – Miborinae Asch. & Graebn. [1899]) {this subtribe seems to share plastids with the old Poeae and nrDNA with early Aveninae GROUP 1 above}: *Mibora*, *Echinaria*, *Oreochloa*, *Sesleria*, Sesleriella.

subtribe **Airinae** Fr. [1835] (syn. – Corynephorinae V. Jirásek & Chrtek [1962]) {a heterogenous subtribe with no satisfactory resolution}: *Aira*, *Antinoria*, *Avenella*, *Corynephorus*, *Helictochloa* {incl. *Avenula* p.p. non-typica, *A.* subg. *Pratavenastrum*}, *Molineriella*, *Periballia*.

subtribe **Holcinae** Dumort. [1868]: *Holcus*, *Vahlodea*.

subtribe **Aristaveninae** F. Albers & Butzin [1977] (syn. – Deschampsinae Holub [1958, nom. nud.], Scribneriinae Soreng & J.I. Davis [2003]): *Deschampsia* s.s. (syn. – *Aristavena*, *Scribneria*, *Stylagrostis*) {excl. *Avenella*}.

supersubtribe **Loliodinae** Soreng [2017] **supersubtribe nov.** {Loliinae + Dactylidinae + Cynosurinae + Ammochloinae + Parapholiinae}:

subtribe **Loliinae** Dumort. [1829] (syn. – Festucinae J. Presl [1830], Psilurinae Pilg. ex Potztal [1969]): *Castellia*, *Drymochloa*, *Festuca* (syn. – *Ctenopsis*, *Dielsiochloa*, *Helleria* E.

Fourn., *Hellerochloa*, *Loliolum*, *Micropyrum*, *Narduroides*, *Psilurus*, *Vulpia*, *Wangenheimia*), *Leucopoa* (syn. – *Xanthochloa*), *Lolium* (syn. – *Micropyropsis*, *Schedonorus*), *Megalachne*, *Patzkea*, *Podophorus*, *Pseudobromus* {the latter seems odd here. DNA data show a long branch, but outgroup selection has not clarified its placement}.

subtribe **Dactylidinae** Stapf [1898]: *Dactylis*, *Lamarckia*.

subtribe **Cynosurinae** Fr. [1835]: *Cynosurus*.

subtribe **Ammochloinae** Tzvelev [1976]: *Ammochloa*.

subtribe **Parapholiinae** Caro [1982] (syn. – Monerminae Tzvelev [1987, nom. inval.]): *Agropyropsis*, *Catapodium*, *Cutandia*, *Desmazeria*, *Hainardia*, *Parapholis*, *Sphenopus*, *Vulpiella*.

PPAM clade {Gillespie et al. 2008, 2010; Soreng et al. 2015b} {Coleanthinae + Poodinae + *Avenula*}:

incertae sedis: *Avenula* (syn. – *Homalotrichon*, *Neoholubia*) {s.s., p.p. typica – *A. pubescens*; excl. *Helictochloa*. *Avenula* s.s. is a floater, apparently allied to the set of Coleanthinae and Poodinae}.

subtribe **Coleanthinae** Rouy [1913] (syn. – Puccinelliinae Soreng & Davis [2003]): *Catabrosa*, *Catabrosella*, *Coleanthus*, *Colpodium* (syn. – *Keniochloa*), *Hyalopoa* {apparently heterogenous}, *Paracolpodium* {apparently heterogenous}, *Phippsia*, *Puccinellia* (syn. – *Pseudosclerochloa*), *Sclerochloa*, *Zingeria* {probably best united with *Colpodium* s.s.}.

supersubtribe **Poodinae** Soreng & L.J. Gillespie [2017] **supersubtribe nov.** {Poinae + Miliinae + Phleinae + Beckmanniinae + Cinninae + Alopecurinae + Ventenatinae + DAD & HSAQN clades + *Arctopoa* + *Brizochloa*}:

-incertae sedis: *Arctopoa* {an ancient hybrid genus with a *Poa* plastid and nrDNA from something related to *Cinna*}, *Brizochloa* {usually placed in *Briza*}; DAD clade {hybrid between an ancient taxon allied to Alopecurinae and an ancient Poodinae taxon sensu Soreng et al. 2015b}**:** *Arctophila*, *Dupontia*, *Dupontiopsis*; HSAQN clade {Gillespie et al. 2010, Kellogg 2015}**:** *Arctagrostis*, *Hookerochloa* (syn. – *Festucella*), *Nicoraepoa* {one known hybrid with *Poa*}, *Saxipoa*, *Sylvipoa*.

subtribe **Poinae** Dumort**.** **s.s.** [1829]: *Poa* (syn. – *Anthochloa*, *Aphanelytrum*, *Austrofestuca*, *Dissanthelium*, *Eremopoa*, *Libyella*, *Lindbergella*, *Neuropoa*, *Ochlopoa*, *Oreopoa*, *Parodiochloa*, *Raimundochloa*, *Tovarochloa*, *Tzvelevia*).

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

subtribe **Miliinae** Dumort. [1829] {sister to *Poa* or *Phleum* in plastid analyses; nrDNA analyses are equivocal for placing it within Poodinae versus sister to Coleanthinae}: *Milium*.

subtribe **Phleinae** Dumort. [1868]: *Phleum* (syn. – *Maillea*).

subtribe **Beckmanniinae** Nevski [1937]: *Beckmannia*, *Pholiurus*, *Pseudophleum*, *Rhizocephalus*.

subtribe **Cinninae** Caruel. [1892]: *Agrostopoa* {tentatively placed here}, *Aniselytron* {ancient hybrid, with *Cinna* like plastids and different copies of nrDNA aligning near *Cinna* and early *Poa*}, *Cinna*, *Cyathopus*, *Simplicia*.

subtribe **Alopecurinae** Dumort. [1829]: *Alopecurus*, *Cornucopiae*, *Limnas*.

subtribe **Ventenatinae** Holub ex L.J. Gillespie, Cabi & Soreng **subtribe nov**.: *Apera*, *Bellardiochloa*, *Gaudiniopsis*, *Nephelochloa*, *Parvotrisetum*, *Ventenata* (syn. – *Pilgerochloa*).

supertribe **Triticodae** T.D. Macfarl. & L. Watson [1982] {Littledaleeae + Bromeae + Triticeae}:

tribe **Littledaleeae** Soreng & J.I. Davis [2015] (syn. – subtribe Littledaleinae Röser [2009]: *Littledalea* {this isolated genus appears to be the sister to Bromeae plus Triticeae}. {reticulate}

tribe **Bromeae** Dumort. [1824] (syn. – subtribe Brominae Dumort. [1829]): *Bromus* (syn. – *Anisantha*, *Boissiera*, *Bromopsis*, *Ceratochloa*, *Nevskiella*, *Stenofestuca*, *Trisetobromus*).

tribe **Triticeae** Dumort. [1824] (syn. – tribes Aegilopineae Orb. [1841], Hordeeae Kunth ex Spenn. [1825], Frumenteae E.H.L. Krause [1903, nom. illeg.], Secaleinae Rchb. [1828, unranked]; – subtribesAegilopinae Nevski [1933]), Agropyrinae Nevski [1933], Clinelyminae Nevski [1933, nom. illeg.], Elyminae Benth. [1881], Henrardiinae C.E. Hubb. [1948], Hordeinae Dumort. [1829], Roegneriinae Nevski [1933], Triticinae Fr. [1835]) {many of the genera are reticulate in origin}: *Agropyron*, *Anthosachne* {reticulate}, *Australopyrum*, *Connorochloa* {reticulate}, *Crithopsis*, *Douglasdewya* {reticulate}, *Elymus* (syn. – *Campeiostachys*, *Elytrigia*, *Hystrix*, *Roegneria*, *Sitanion*) {reticulate}, *Eremopyrum*, *Festucopsis*, *Henrardia*, *Heteranthelium*, *Hordelymus* {reticulate}, *Hordeum* (syn. – *Critesion*), *Kengyilia* {reticulate}, *Leymus* (syn. – *Aneurolepidium*, *Eremium*, *Macrohystrix*, *Microhystrix*) {reticulate}, *Pascopyrum* {reticulate}, *Peridictyon*, *Psathyrostachys*, *Pseudoroegneria*, *Secale*, *Stenostachys* {reticulate}, *Taeniatherum*; (*Triticum* subclade): *Aegilops*, *Amblyopyrum*, *Dasypyrum*, *Thinopyrum* {reticulate}, *Triticum* {reticulate}.

"PACMAD" clade {Sánchez-Ken & Clark, 2010; also known as PACC (Davis & Soreng, 1993), PACCAD (GPWG, 2001), or PACCMAD (Sánchez-Ken et al. 2007)} {Cotton et al. 2015 resolve Panicoideae at the base of PACMAD and Aristidoideae as sister to sister to CMAD but a basal position for Aristidoideae was resolved by Teisher (2016, 2017) and others, see also Burke et al. 2016}

subfamily **Aristidoideae** Caro [1982]:

tribe **Aristideae** C.E. Hubb. [1960]: *Aristida* {C$_4$, one C$_3$}, *Sartidia* {C$_3$}, *Stipagrostis* {C$_4$}.

subfam. **Panicoideae** A. Braun [1864] (syn. − Andropogonoideae Rouy [1913], Centothecoideae Soderst. [1981]; Andropogineae Burmeist. [1837, unranked], Paniceae Burmeist. [1837, unranked], Paniceae Link [1827, unranked], Rottboelliaceae Burmeist. [1837, unranked], Panicinae Horan. [1847 {rank tribe or subfam.?}]):

incertae sedis {clade at base of Panicoideae; fide Teisher 2017}: *Alloeochaete*, *Dichaetaria*.

incertae sedis: Chandrasekharania {C$_3$} {treated in Arundinellae by Clayton & Renvoize, 1986}.

tribe **Thysanolaeneae** C.E. Hubb. [1934] {possibly better as subtribe within Centotheceae} {C$_3$}: *Thysanolaena*.

tribe **Cyperochloeae** L. Watson & Dallwitz ex Sánchez-Ken & L.G. Clark [2010] (syn. – Cyperochloeae L. Watson & Dallwitz [1992, nom. nud.]) {possibly better as subtribe within Centotheceae} {C$_3$}: *Cyperochloa*, *Spartochloa*.

tribe **Centotheceae** Ridl. [1907] (subtribe Centothecinae Benth. [1881]) {C$_3$}: *Centotheca*, *Megastachya*.

tribe **Chasmanthieae** W.V. Br. & B.N. Smith ex Sánchez-Ken & L.G. Clark [2010] {C$_3$}: *Chasmanthium* (syn. – *Gouldochloa*, *Bromuniola*).

tribe **Zeugiteae** Sánchez-Ken & L.G. Clark [2010] (syn. – subtribe Zeugitinae Caro [1982]) {sister to Chasmanthieae} {C_3}: Chevalierella, *Lophatherum*, *Orthoclada*, *Zeugites* (syn. – Calderonella, *Pohlidium*).

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

tribe **Steyermarkochloeae** Davidse & R.P. Ellis [1984] {DNA places with Chasmanthieae s.l. or Tristachyideae, the placement remains tentative} {C_3}: *Arundoclaytonia*, *Steyermarkochloa*.

tribe **Tristachyideae** Sánchez-Ken & L.G. Clark [2010] (syn. – subtribe Trichopteryginae Jacq.-Fél. [1962, nom. inval.]) {C_4}: *Danthoniopsis*, Dilophotriche, *Gilgiochloa*, *Loudetia*, *Loudetiopsis*, *Trichopteryx*, *Tristachya*, *Zonotriche*.

tribe **Gynerieae** Sánchez-Ken & L.G. Clark [2001] {C_3}: *Gynerium*.

tribe **Lecomtelleae** Pilg. ex Potztal [1957] (syn. – subtribe Lecomtellinae Pilg. [1940]): *Lecomtella* {possibly sister to Panicodae + Andropogonodae} {C_3}.

supertribe **Panicodae** L. Liu [1980]:

tribe **Paniceae** R.Br. [1814] (syn. – Cenchreae Rchb. [1828, unranked], Digitarieae J.J. Schmitz & Regel [1841], Paniceae Horan. [1847{rank tribe or subtribe?}], Spinificeae Dumort. [1829], Melinideae Hitchc. [1920], Boivinelleae A. Camus [1925], Anthephoreae Pilg. ex Potztal [1957], Trachideae Pilg. Ex Potztal [1957], Cyphochlaeneae Bosser [1965], Neurachneae S.T. Blake [1972]):

incertae sedis: Chloachne {C_3}, Hydrothauma {C_3}, *Hylebates* {C_4}, *Kellochloa* {C_3}, Oryzidium {C_4}, *Sacciolepis* {C_3}, Thedachloa, *Trichanthecium* {C_3}.

subtribe **Anthephorinae** Benth. [1881] (syn. – Digitariinae Butzin [1972]; Trachidinae Pilg. [1940, nom. inval.], Trachydastrae Stapf [1917]): *Anthephora* {C_4}, *Chaetopoa* {C_4}, *Chlorocalymma* {C_4}, *Digitaria* (syn. – *Megaloprotachne*) {C_4}, Taeniorhachis {C_4?}, *Tarigidia* {C_4}, Thyridachne {C_3}, *Trachys* {C_4}.

subtribe **Dichantheliinae** Zuloaga [2014] {C3}: *Adenochloa*, *Dichanthelium*.

subtribe **Boivinellinae** Pilg. [1940]: *Acroceras* {C_3}, *Alloteropsis* (syn. – Coridochloa) {mixed C_3 C_4}. *Amphicarpum* {C_3}, *Chasechloa*, *Cyphochlaena* {C_3}, *Cyrtococcum* {C_3}, *Echinochloa* {C_4}, *Entolasia* {C_3}, *Lasiacis* {C_3}, *Mayariochloa* {C_4}, *Morronea* {C_3}, *Microcalamus* {C_3}, *Oplismenus* {C_3}, *Ottochloa* {C_3}, *Parodiophyllochloa* {C_3}, *Poecilostachys* {*p.p*} {C_3}, *Pseudechinolaena* {C_3}, *Setiacis* {segregate of *Acroceras*, GenBank DNA odd}.

subtribe **Neurachninae** Clayton & Renvoize [1986]: *Ancistrachne* {C_3}, *Calyptochloa* {C_3}, *Cleistochloa* {C_3}, *Neurachne* {C_4 and mixed C_3 C_4}, *Paraneurachne* {C_4}, *Thyridolepis* {C_3}.

incertae sedis {clade of ambiguous placement among latter set of subtribes}: *Homopholis* (syn. – *Walwhalleya* {C_4}) {C_3 and C_4}.

subtribe **Melinidinae** Stapf [1917, as Melinidastrae] (syn. – Brachiariinae Butzin [1970], Thuarinae Ohwi [1942], Tristegininae Harv. [1869, nom. illeg.]; Melinidinae Pilg. [1940]) {C_4}: *Chaetium*, *Eccoptocarpha*, *Eriochloa*, Leucophrys, *Megathyrsus* (syn. – , *Pseudobrachiaria*?), *Melinis* (syn. – *Mildbraediochloa*, *Rhynchelytrum*), *Moorochloa*, *Rupichloa*, *Scutachne*, *Thuarea*, *Tricholaena*, *Urochloa* (syn. – *Brachiaria* s.s), *Yvesia*.

subtribe **Panicinae** Fr. [1835]: *Louisiella* {C$_4$}, *Panicum* (syn. – *Arthragrostis* {C$_4$}, *Yakirra* {C$_4$}) {all C$_4$, some C$_3$ & C$_4$?}.

subtribe **Cenchrinae** Dumort. [1829] (syn. – Pennisetinae Rchb. [1828, unranked], Setariinae Dumort. [1829]; Pseudoraphidinae Keng & Keng f. [1990], Snowdeniinae Butzin [1972], Spinificinae Owhi [1942], Uranthoeciinae Butzin [1970], Xerochloinae Butzin [1970]): *Acritochaete* {C$_3$}, *Alexfloydia* {C$_4$}, *Cenchrus* (syn. – Cenchropsis, *Echinaria* Heist. ex Fabr., *Kikuyuochloa*, *Nastus* Lunell, *Odontelytrum*, *Pennisetum*, *Snowdenia*) {C$_4$}, *Chamaeraphis* {C$_4$}, *Dissochondrus* {Hawaii} {C$_4$}, *Holcolemma* {C$_3$}, *Hygrochloa* {C$_4$}, *Ixophorus* {C$_4$}, *Paractaenum*, {C$_4$} *Paratheria* {C$_4$}, *Plagiosetum* {C$_4$}, *Pseudochaetochloa* {C$_4$}, *Pseudoraphis* {C$_4$}, *Setaria* (syn. – Camusiella, *Paspalidium*) {C$_4$}, *Setariopsis* {C$_4$}, *Spinifex* {C$_4$}, *Stenotaphrum* {C$_4$}, *Stereochlaena* {C$_4$}, *Streptolophus* {C$_4$}, *Uranthoecium* {C$_4$}, *Whiteochloa* {C$_4$}, *Xerochloa* {C$_4$}, *Zuloagaea* {C$_4$}, *Zygochloa* {C$_4$}.

supertribe **Andropogonodae** L. Liu [1980] {Paspaleae + Arundinelleae + Andropogoneae}:

tribe **Paspaleae** J. Presl [1830] (syn. – Arthropogoneae Pilg. ex Butzin [1972]):

incertae sedis: *Reynaudia* {basal to the other subtribes} {C$_4$}.

subtribe **Paspalinae** Griseb. [1846] (syn. – Paspalinae Griseb.[1853], Paspalidinae Keng & Keng f, ex S.L. Chen & Y.X. Jin [1984], Reimarochloinae Caro [1982]): *Aakia* {C$_4$}, *Acostia* {C$_4$}, *Anthaenantia* (syn. –*Leptocoryphium*) {C$_4$}, *Anthaenantiopsis* {C$_4$}, *Axonopus* (syn. – *Centrochloa*, *Ophiochloa*) {C$_4$}, *Baptorhachis* {C$_4$}, *Echinolaena* {C$_3$}, *Gerritea* {C$_3$}, *Hildaea* {C$_3$}, *Hopia* {C$_4$}, *Ichnanthus* {C$_3$}, *Ocellochloa* {C$_3$}, *Oedochloa* {C$_3$}, *Osvaldoa* {C$_4$}, *Paspalum* (syn. – *Thrasya*, *Thrasyopsis*, *Reimarochloa*, *Spheneria*) {C$_4$}, *Renvoizea* {C$_3$}, *Streptostachys* {C$_3$}.

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

subtribe **Otachyriinae** Butzin [1970]: *Hymenachne* (syn. – *Aconisia*, *Dallwatsonia*) {C$_3$}, *Otachyrium* {C$_3$}, *Plagiantha* {C$_3$}, *Rugoloa* {C$_3$}, *Steinchisma* (syn. – Cliffordiochloa, Fasciculochloa) {C$_3$ and mixed C$_3$ C$_4$}.

subtribe **Arthropogoninae** Butzin [1972]: *Achlaena* {C$_4$}, *Altoparadisium* {C$_4$}, *Apochloa* {C$_3$}, *Arthropogon* {C$_4$}, *Canastra* {C$_3$}, *Coleataenia* (syn. – *Sorengia*) {C$_4$}, *Cyphonanthus* {C$_4$}, *Homolepis* {C$_3$ and mixed C$_3$ C$_4$?}, *Keratochlaena* (syn. – *Sclerochlamys*) {C$_4$}, *Mesosetum* {C$_4$}, *Oncorachis* {C$_4$}, *Oplismenopsis* {C$_3$}, *Phanopyrum* {C$_3$}, *Stephostachys* {C$_3$}, *Tatianyx* {C$_4$}, *Triscenia* {C$_3$}.

tribe **Arundinelleae** Stapf [1898] (syn. – tribe Garnotieae Tateoka [1957]; subtribe Arundinellinae Honda [1930], Garnotiinae Pilg. [1956]): *Arundinella* {C$_4$}, *Garnotia* {C$_4$}, *Jansenella* {C$_3$}.

tribe **Andropogoneae** Dumort. [1824] (syn. – Sacchareae Dumort. [1824], Coiceae Nakai [1943], Euchlaeneae Nakai [1943], Imperateae Godr. & Gren. [1855], Maydeae Dumort. [1824, nom. illeg.], Ophiureae Dumort. [1824], Rottboellieae Kunth [1829], Saccharinae Rchb. ex Horan. [1847{rank tribe or subfam.?}], Tripsaceae C.E. Hubb. ex Nakai [1943], Zeeae Rchb. [1828, unranked], Zeeae Nakai

[1943]) {Papers by Hodkinson et al., 2002, Skendzic et al., 2007, and Estep, et al. 2014, portend lots of problems for classification within this tribe} {all C_4}:

incertae sedis: *Apluda* {subtribe Apludinae Hook.f. [1896]) entangled with Saccharinae}, *Chrysopogon* (syn. – *Vetiveria*) {*Chrysopogon* and *Thelepogon* appear to be sisters and isolated from other tribes}, *Eulaliopsis*, *Microstegium* (syn. – Ischnochloa), *Sehima*, *Thelepogon*.

subtribe **Arthraxoninae** Benth. [1881]: *Arthraxon*.

subtribe **Tripsacinae** Dumort. [1829] (syn. – Maydinae Harv. [1868, nom. illeg.], Vossiastae Stapf [1917], Zeinae Tzvelev [1968]): *Elionurus* {orth. var. *Elyonurus*}, *Oxyrhachis*, *Rhytachne*, *Tripsacum*, *Vossia*, *Urelytrum*, *Zea* (syn. – *Euchlaena*).

subtribe **Chionachninae** Clayton [1981]: *Chionachne*, *Cyathorhachis*, *Polytoca*, *Sclerachne*, Trilobachne.

subtribe **Coicinae Rchb. ex** Clayton & Renvoize [1986] (syn. – Coicinae Rchb. [1828, unranked]) {Apparently sister to Rottboelliinae}: *Coix*.

subtribe **Rottboelliinae** J. Presl [1830] {probably polyphyletic}: *Chasmopodium*, *Eremochloa*, *Glyphochloa*, *Hackelochloa*, *Hemarthria*, *Heteropholis*, Jardinea {a segregate of *Phacelurus*}, Lasiurus, Loxodera, *Manisuris*, *Mnesithea*, *Ophiuros*, *Phacelurus* (syn. – Thyrsia) {apparently polyphyletic}, Ratzeburgia, *Rottboellia* (syn. – *Coelorachis*), *Thaumastochloa*.

subtribe **Ischaeminae** J. Presl [1830] (syn. – Dimeriinae Hack ex C.E. Hubb. [1934], Dimeriinae Hack [1887, nom. nud.]): *Andropterum*, *Dimeria*, *Ischaemum*, *Kerriochloa*, Nanooravia {possibly = *Dimeria*}, Pogonachne, Triplopogon.

subtribe **Germainiinae** Clayton [1972] (syn. – Apocopidinae Keng [1939, nom. inval.]): *Apocopis*, *Germainia*, Lophopogon, *Pogonatherum*.

subtribe **Saccharinae** Griseb. [1846] (syn. – Amphilophiastrae Stapf [1917], Erianthinae Hack. [1883]; Polliniastrae Stapf [1917], Sorghinae Stapf [1917] as Sorghastrae; Sorgha Bluff, Nees & Schauer [1836, unranked]): Agenium, Asthenochloa, *Cleistachne*, *Erianthus*, *Eriochrysis* (syn. – Leptosaccharum), *Euclasta* (syn. – Indochloa), *Eulalia* s.s. {s.l. is apparently polyphyletic}, Hemisorghum { = *Sorghum*?}, Homozeugos, *Imperata*, *Lasiorhachis*, *Leptatherum* (syn. – *Polliniopsis*), *Miscanthidium*, *Miscanthus* (syn. – Diandranthus, Rubimons, Triarrhena, Tenacistachya), *Narenga*, *Polytrias*, Pseudodichanthium, *Pseudopogonatherum*, *Pseudosorghum* {= *Eulalia*?}, *Saccharum* s.s., *Sclerostachya*, Veldkampia, *Sorghastrum*, *Sorghum* (syn. – *Sarga*, *Vacoparis*), *Tripidium* {seems related to *Imperata* and *Erianthus* s.s., probably reticulate}, *Trachypogon*.

subtribe **Andropogoninae** J. Presl [1830] (syn. – Anadelphiastrae Stapf [1917], Anthistiriinae J. Presl [1830], Bothriochloinae Keng [1939, nom. inval.], Heteropogonastrae Stapf [1917], Hyparrheniastrae Stapf [1917], Hypogyniastrae Stapf [1917], Schizachyriastrae Stapf [1917], Themedastrae Stapf [1917]): Anadelphia, *Andropogon* (syn. – Hypogynium), *Bhidea*, *Bothriochloa*, *Capillipedium*, Clausospicula, *Cymbopogon*, *Dichanthium*, *Diectomis*, *Diheteropogon*, Elymandra, *Eremopogon*, *Exotheca*, *Heteropogon*, *Hyparrhenia*, *Hyperthelia*, *Iseilema*, *Lakshimia*, *Monocymbium*, Parahyparrhenia, Pseudanthistiria, *Schizachyrium*, Spathia, *Spodiopogon* (syn. – Eccoilopus), *Themeda*.

subfamily **Arundinoideae** Kunth ex Beilschm. [1833] (syn. – tribe Arundinoideae Tateoka [1957, isonym], Phragmitoideae Parodi [1958, nom. inval.], Phragmitoideae Parodi ex Caro [1982]; Arundinaceae Burmeist. [1837, unranked], {sister to Micrairoideae} {C_3}:

tribe **Arundineae** Dumort. [1824] (syn. – tribe Amphipogoneae L. Watson & T.D. Macfarl. [2002]; subtribe Arundininae Miq. [1857]): *Amphipogon* (syn. – *Diplopogon*), *Arundo*, *Dregeochloa* {fide Teisher 2017}, *Monachather*.

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

tribe **Molinieae** Jirásek [1966]:

incertae sedis: Leptagrostis, Piptophyllum, *Zenkeria*. {Hardion et al. in press, indicate this is near *Micraira*}

subtribe **Crinipinae** Conert, [1961] {emend Linder et al. (1997) on the Crinipoid group; emend Teisher here}: *Crinipes*, *Elytrophorus*, *Styppeiochloa*, and *Pratochloa* (syn. – *Eragrostis walteri*).

subtribe **Molininae** Ohwi [1941] (syn. – Phragmiteae Horan. [1847 {rank tribe or subtribe?}] {emend Teisher here}: *Hakonechloa*, *Molinia*, *Moliniopsis*, *Phragmites*.

subfamily **Micrairoideae** Pilg. [1956] {sister to Arundinoideae}:

tribe **Micraireae** Pilg. [1956] {C_3}: *Micraira*.

tribe **Eriachneae** Eck-Borsboom [1980]: *Eriachne* (syn. – Massia, *Pheidochloa* {fide Teisher 2016}) {C_4}.

tribe **Isachneae** Benth. [1881] (syn. – tribe Hubbardieae C.E. Hubb. [1960]; subtribe Isachninae Stapf [1898]) {C_3}: *Coelachne*, *Heteranthoecia*, *Hubbardia*, *Isachne*, *Limnopoa*, *Sphaerocaryum*.

subfamily **Danthonioideae** H.P. Linder & N.P. Baker [2001] {sister to Chloridoideae} {C_3}:

incertae sedis: Danthonidium.

tribe **Danthonieae** Zotov. [1963] (syn. – Cortaderieae Zotov. [1963]; subtribe Cortaderinae Conert [1961], Danthoniinae Fr. [1835]): *Austroderia*, *Capeochloa*, *Chaetobromus*, *Chimaerochloa*, *Chionochloa*, *Cortaderia* (syn. – *Lamprothyrsus*), *Danthonia*, *Geochloa*, *Merxmuellera*, *Notochloe*, *Pentameris* (syn. – *Pentaschistis*, *Poagrostis*, *Prionanthium*), *Phaenanthoecium* {fide Teisher 2017}, *Plinthanthesis*, *Pseudopentameris*, *Rytidosperma* (syn. – *Monostachya*, *Notodanthonia*, *Pyrrhanthera*), *Schismus* (syn. – *Karroochloa*), *Tenaxia*, *Tribolium*.

subfamily **Chloridoideae** Kunth ex Beilschm. [1833] (syn. – tribe Eragrostoideae Pilg. [1956]; Chlorideae Burmeist [1837, unranked], Pappophorae Burmeist. [1837, unranked]) {sister to Danthonioideae}:

incertae sedis: Gossweilerochloa, Indopoa, Lepturopetium, Myriostachya, Pogonochloa, Pseudozoysia, Silentvalleya.

tribe **Centropodieae** P.M. Peterson, N.P. Barker & H.P. Linder [2011]: *Centropodia* {C_4}, *Ellisochloa* {C_3}.

tribe **Triraphideae** P.M. Peterson [2010] (syn. – subtribe Triraphidinae Stapf [1917]) {C_4}: *Habrochloa*, *Neyraudia*, *Triraphis* (syn. – *Nematopoa*).

tribe **Eragrostideae** Stapf [1898] (syn. – supertribe Eragrostodae L. Liu [1980]; tribe Unioleae Roshev. ex C.S. Campb. [1985]) {C_4}:

subtribe **Cotteinae** Reeder [1965]: *Cottea*, *Enneapogon*, *Kaokochloa*, *Schmidtia*.

subtribe **Eragrostidinae** J. Presl [1830]: *Cladoraphis*, *Eragrostis* (syn. – *Acamptoclados*, *Catalepis*, *Diandrochloa*, *Ectrosia*, *Ectrosiopsis*, *Harpachne*, *Heterachne*, *Neeragrostis*, *Planichloa*, *Pogonarthria*, *Psammagrostis*, *Viguierella*), Richardsiella, Steirachne, *Stiburus* (syn. – *Triphlebia* Stapf).

subtribe **Unioliinae** Clayton [1982]: *Entoplocamia*, *Fingerhuthia*, *Tetrachaete*, *Tetrachne*, Uniola (syn. – Leptochloopsis).

tribe **Zoysieae** Benth. [1881] (syn. – Spartineae Steele [1847], Sporoboleae Stapf [1898]) {C_4}:

subtribe **Sporobolinae** Benth. [1881] (syn. – Crypsidinae Maire & Weiler [1953, nom. inval.], Spartininae Maire & Weiler [1953, nom. inval.]): *Psilolemma*, *Sporobolus* (nom. cons.; syn. – *Calamovilfa*, *Crypsis*, *Heleochloa*, *Spartina*, *Thellungia*).

subtribe **Zoysiinae** Benth. [1878]: *Urochondra*, *Zoysia*.

tribe **Cynodonteae** Dumort. [1824] (syn. – Aeluropodieae Nevski ex Bor [1965], Chlorideae Rchb. [1828, unranked], Chlorideae Trin. [1824, nom. illeg. superfl, later than Dumort., and included *Cynodon*], Jouveae Pilg. [1956], Leptureae Dumort. [1824, as Lepiureae], Monermeae C.E. Hubb. [1948, nom. inval.], Nazieae Hitchc. [1920, nom. illeg.], Pappophoreae Kunth [1829], Perotideae C.E. Hubb. [1960], Pommereulleae Bor [1960], Trageae Hitchc. [1927], Triodieae S.W.L. Jacobs [2004] {C4}:

incertae sedis: Kampochloa, *Lepturidium*, *Sclerodactylon*, Vietnamochloa.

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

subtribe **Aeluropodinae** P.M. Peterson [2010] (syn. – Aeluropodinae Jacq.-Fél. [1962, nom. inval.]): *Aeluropus*, *Odyssea* s.s. {reticulate}.

subtribe **Dactylocteniinae** P.M. Peterson, Romasch. & Y. Herrera [2016]: *Acrachne* {reticulate}, *Brachychloa*, *Dactyloctenium*, *Neobouteloua*.

subtribe **Eleusininae** Dumort. [1829] (syn. – Astreblinae Clayton [1982], Chloridinae J. Presl [1830], Cynodontinae Tzvelev [1968], Diplachninae Rouy [1913], Lepturinae Benth. [1881], Monerminae Janch. [1953, nom. nud.], Pommereullinae Potztal [1969]): *Afrotrichloris*, *Apochiton*, *Astrebla*, *Austrochloris*, *Chloris* (syn. – *Lintonia*, *Ochthochloa*), *Chrysochloa*, *Coelachyrum* (syn. – *Coelachyropsis*), *Cynodon*, (syn. – *Brachyachne*) *Daknopholis*, *Dinebra* {reticulate} (syn. – *Drake-Brockmania*, *Heterocarpha*, *Oxydenia*), *Diplachne*, *Disakisperma* (syn. – *Cypholepis*), *Eleusine*, *Enteropogon*, *Eustachys*, *Harpochloa*, *Leptochloa* (syn. – *Trichloris*), *Lepturus*, *Micrachne*, *Microchloa* (syn. – *Rendlia*), *Neostapfiella*, *Oxychloris*, *Pommereulla*, *Rheochloa*, *Schoenefeldia*, *Stapfochloa*, *Tetrapogon* (syn. – *Saugetia*).

subtribe **Orcuttiinae** P.M. Peterson & Columbus [2007]: *Neostapfia*, *Orcuttia* (syn. – *Tuctoria*).

subtribe **Orininae** P.M. Peterson, Romasch. & Y. Herrera [2016]: *Cleistogenes* (syn. – *Kengia*), *Orinus*.

subtribe **Pappophorinae** Dumort. [1829] (syn. – Tridentinae Keng & Keng f. [1960]): *Neesiochloa*, *Pappophorum*, *Tridens* s.s. (syn. – *Antonella*).

subtribe **Triodiinae** Benth. [1881]: *Triodia* (syn. – *Monodia*, *Plectrachne*, *Symplectrodia*).

subtribe **Tripogoninae** Stapf [1917]: *Desmostachya*, *Eragrostiella*, *Halopyrum*, *Melanocenchris*, *Oropetium*, *Tripogon*, *Tripogonella*.

supersubtribe **Boutelouodinae** P.M. Peterson & Romasch. **supersubtribe nov.** [2017] {Boutelouinae + Hilariinae + Monanthochloinae + Muhlenbergiinae + Scleropogoninae + Traginae}:

incertae sedis: *Allolepis*, *Jouvea*, *Kalinia*, *Sohnsia*.

subtribe **Boutelouinae** Stapf [1917]: *Bouteloua* (syn. – *Buchloe*, *Buchlomimus*, *Cathestecum*, *Chondrosum*, *Cyclostachya*, *Griffithsochloa*, *Opizia*, *Pentarrhaphis*, *Pringleochloa*, *Soderstromia*).

subtribe **Hilariinae** P.M. Peterson & Columbus [2007]: *Hilaria* (syn. – *Pleuraphis*).

subtribe **Monanthochloinae** Pilg. ex Potztal [1969] (syn. – Distichlinae Parodi [1946, nom. nud.]): *Distichlis* (syn. – *Monanthochloe*, *Reederochloa*).

subtribe **Muhlenbergiinae** Pilg. [1956] (syn. – Lycurinae Pilg. [1956]): *Muhlenbergia* (syn. – *Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Pereilema*, *Redfieldia*, *Schaffnerella*, *Schedonnardus*).

subtribe **Scleropogoninae** Pilg. [1956] (syn. – Munroinae Parodi ex P.M. Peterson [1995]): *Blepharidachne*, *Dasyochloa*, *Erioneuron*, *Munroa*, *Scleropogon*, *Swallenia*.

subtribe **Traginae** P.M. Peterson & Columbus [2007] (syn. – Lappagininеae Link ex Endl. [1830, nom. illeg.], Tragineae Rchb. [1845, unranked]): *Monelytrum*, *Orthacanthus*, *Pogononeura*, *Polevansia*, *Tragus*, *Willkommia* (syn. – *Willbleibia*).

supersubtribe **Gouiniodinae** P.M. Peterson & Romasch. **supersubtribe nov.** [2017] {Cteniinae + Farragininae + Gouiniinae + Hubbardochlinae + Perotidinae + Trichoneurinae + Zaqiqahinae}:

subtribe **Cteniinae** P.M. Peterson, Romasch. & Y. Herrera [2014]: *Ctenium*.

subtribe **Farragininae** P. M. Peterson, Romasch. & Y. Herrera [2014]: *Craspedorhachis*, *Farrago*.

subtribe **Gouiniinae** P.M. Peterson & Columbus [2007]): *Gouinia*, *Schenckochloa*, *Tridentopsis*, *Triplasiella*, *Triplasis*, *Vaseyochloa*.

subtribe **Hubbardochloinae** Auquire [1980] (syn. – Gymnopogoninae P. M. Peterson, Romasch. & Y. Herrera [2014]): *Bewsia*, *Decaryella*, *Dignathia*, *Gymnopogon*, *Hubbardochloa*, *Leptocarydion*, *Leptothrium* (syn. – *Latipes*), *Lophacme*.

subtribe **Perotidinae** P.M. Peterson, Romasch. & Y. Herrera [2014]: *Mosdenia*, *Perotis* (syn. – *Lopholepis*, *Toliara*), *Trigonochloa*.

subtribe **Trichoneurinae** P.M. Peterson, Romasch. & Y. Herrera [2014]: *Trichoneura*.

subtribe **Zaqiqahinae** P.M. Peterson, Romasch. & Y. Herrera [2016]: *Zaqiqah*.

Indigenous Ranges: Africa, Australasia, Eurasia, Western Hemisphere, Widespread.

CAPÍTULO VI

A molecular phylogeny and classification of the subtribe Koeleriinae and allied lineages (Poaceae: Pooideae: Poeae)

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Manuscript in preparation

***Abstract*—**A new phylogenetic analysis of the subtribe Koeleriinae and related lineages is presented, including 2044 new DNA sequences corresponding to 275 species, from one nuclear ribosomal region (ITS) and three plastid regions (*rpl32-trnL*, *rps16-trnK* spacer, and *rps16* intron sequences) to assess their systematic relationships as well as the role of past reticulation events in the origin of several close groups such as the Sesleriinae. Our results confirm a solid statistical support for the large lineage within Poeae called in the most recent works "Poeae chloroplast group 1", which includes the subtribes Aveninae s.s., Agrostidinae, Anthoxanthinae, Brizinae, Echinopogoninae, Koeleriinae, Lagurinae, Phalaridinae, and Torreyochloinae. A moderate to weakly supported clade also includes the subtribe Sesleriinae as sister to the *Avena* clade in the ITS topology (within Aveninae s.s.), whereas it is part of the "Poeae chloroplast group 2" in the plastid tree. Aveninae s.s. and Koeleriinae form sister and well-supported lineages; both, in turn, are sisters of the other members of the "Poeae chloroplast group 1", internally the subtribe Lagurinae is sister to the Koeleriinae. The Asiatic species *Trisetopsis junghunii* fall in Aveninae s.s. in the ITS tree and in the Koeleriinae in the plastid one. All species of *Trisetum* and *Koeleria* are part of the Koeleriinae, but both genera are polyphyletic. The Koeleriinae are divided into two major sublineages consisting of the following taxa: subclade 1) *Avellinia, Gaudinia, Helictotrichon* p.min.p., *Koeleria, Rostraria, Trisetaria, Trisetum* sect. *Acrospelion*, *T.* sect. *Trisetum* p.p., *T.* sect. *Trisetaera,* and *Tzveleviochloa*; subclade 2) *Calamagrostis*/*Deyeuxia* complex p.p. (Mexican to South American species), *Leptophyllochloa*, *Limnodea*, *Peyritschia*, *Sphenopholis*, *Trisetopsis*, *Trisetum* subg. *Deschampsioidea*, *T.* sect. *Trisetum* p.p., and *T.* sect. *Sibirica*. The placement of *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, *T. longiglume,* and *T. ortochaetum* is incongruent in both plastid and ITS topologies, falling in the different clades of the Koeleriinae, and probably of reticulate origin. The Eurasian species of *Trisetum* sect. *Acrospelion* are resolved in a clade without internal structure, together with some Eurasian species of *Trisetum* sect. *Trisetum*, *Helictotrichon delavayei*, *H. sumatrense*, and *Tzveleviochloa parviflora,* in addition to a group of New World taxa in the nuclear topology. *Koeleria* clade includes the species of the *Trisetum spicatum* complex (*T.* sect. *Trisetaera)*, characterized by its compact and dense panicles. *Trisetum* sect. *Sibirica* is resolved as sister to the "Koeleriinae subclade II" and is morphologically well characterized, thus supporting the possibility of recognizing it as a separate genus.

Resumen—Se presenta un nuevo análisis filogenético de la subtribu Koeleriinae y grupos afines, incluyendo 2044 nuevas secuencias de ADN que se corresponden con 275 especies, obtenidas con una región ribosómica nuclear (ITS) y tres plastidiales (*rpl32-trnL*, el espaciador *rps16-trnK* y el intrón *rps16*) para evaluar sus relaciones sistemáticas así como el papel de los procesos de hibridación en el origen de varios grupos cercanos como Sesleriinae. Nuestros resultados confirman un sólido apoyo estadístico para el gran clado de Poeae denominado en los recientes trabajos "Poeae chloroplast group 1", que incluye las subtribus Aveninae s.s., Agrostidinae, Anthoxanthinae, Brizinae, Echinopogoninae, Koeleriinae, Lagurinae, Phalaridinae y Torreyochloinae. Un clado de moderada a débilmente apoyado también incluye la subtribu Sesleriinae como hermano del clado *Avena* en la topología de ITS (incluido en Aveninae s.s.), mientras que forma parte de "Poeae chloroplast group 2" en el árbol de cloroplastos. Aveninae s.s. y Koeleriinae forma un clados hermanos y bien apoyados; ambos, a su vez, son hermanos de los otros miembros de "Poeae chloroplast group 1" e internamente la subtribu Lagurinae es grupo hermano de Koeleriinae. Las especies asiáticas *Trisetopsis junghunii* se resuelve en Aveninae s.s. en el árbol de ITS y en Koeleriinae en el cloroplástico. Todas las especies de *Trisetum* y *Koeleria* son parte de Koeleriinae, siendo ambos géneros polifiléticos. Koeleriinae se divide en dos grandes grupos formados por los táxones siguientes: subclado 1) *Avellinia*, *Gaudinia*, *Helictotrichon* p.min.p., *Koeleria*, *Rostraria*, *Trisetaria*, *Trisetum* sect.

Acrospelion, *T.* sect. *Trisetum* p.p., *T.* sect. *Trisetaera* y *Tzveleviochloa*; subclado 2) *Calamagrostis*/*Deyeuxia* complex p.p. (Mexican to South American species), *Leptophyllochloa*, *Limnodea*, *Peyritschia*, *Sphenopholis*, *Trisetopsis*, *Trisetum* subg. *Deschampsioidea*, *T.* sect. *Trisetum* p.p. y *T.* sect. *Sibirica*. La posición de *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, *T. longiglume* y *T. ortochaetum* es incongruente en la topología nuclear y plastidial, localizándose en diferentes clados de Koeleriinae, probablemente debido a reticulación ancestral. Las especies de *Trisetum* sect. *Acrospelion* conforman un clado sin estructura interna, junto a especies eurasiáticas de Trisetum sect. *Trisetum*, *Helictotrichon delavayei*, *H. sumatrense* y *Tzveleviochloa parviflora*, además de un grupo de táxones del Nuevo Mundo en la topología nuclear. El clado *Koeleria* incluye a las especies del complejo de *Trisetum spicatum* (*T.* sect. *Trisetaera)*, caracterizadas por sus panículas densas y compactas. *Trisetum* sect. *Sibirica* se agrupan en un clado hermano a “Koeleriinae subclado II” y está morfológicamente bien caracterizado, lo que apoya la posibilidad de su reconocimiento como un género separado.

INTRODUCTION

The subtribe Aveninae J. Presl. is classified in the tribe Poeae R. Br. (incl. Aveneae Dumort.), the largest and most polymorphic grass tribe in subfamily Pooideae Benth., one of the main groups of the family Poaceae (R. Br.) Barnhart (Tzvelev, 1989; Soreng et al., 2007). It includes the oats, *Avena* L., one of the most ancient food supplies for humankind, and also many temperate forage and lawn grasses (Soreng et al., 2015, 2017). Aveninae are "festucoid grasses" with simple panicles with laterally compressed spikelets habitually disarticulating above the glumes, shorter or longer glumes than the adjacent lemmas (a character often with diagnostic value), an indeterminate number of florets, lemmas either unawned or with dorsal, terminal or nearly terminal awns, and compound starch grains (Tzvelev, 1989; Soreng et al., 2007). This subtribe comprises 18 genera and ca. 343 species (Soreng et al., 2017), although several genera remain problematic (Saarela et al., 2017; Soreng et al., 2017). Soreng et al., (2017) classification was based in the most recent studies on this group and allied lineages of the tribe Poeae (Grebenstein et al., 1998; Röser et al., 2001, 2009; Rodionov et al., 2005; Quintanar et al., 2007; Nikoloudakis & Katsiotis, 2008; Wölk et al., 2015; Saarela et al., 2010, 2015, 2017; Wölk & Röser, 2014, 2017), including our unpublished data, and recognized the following genera: *Acrospelion* Besser, *Arrhenatherum* P. Beauv., *Avellinia* Parl., *Avena* L., *Cinnagrostis* Griseb., *Gaudinia* P. Beauv., *Graphephorum* Desv., *Helictotrichon* Besser, *Koeleria* Pers., *Lagurus* L., *Peyristchia* E. Fourn., *Rostraria* Trin., *Sphenopholis* Scribn., *Tricholemma* (Röser) Röser, *Trisetaria* Forssk., *Trisetum* Pers., *Trisetopsis* Röser & A. Wölk, and *Tzveleviochloa* Röser & A. Wölk. Recently, Saarela et al. (2017) described a new subtribe, Lagurinae, separating the genus *Lagurus* from subtribe Aveninae, and characterized by having glumes covered with woolly hairs and acuminate apices, and with hairy awns.

The systematics of the taxa classified in the tribe Poeae, including Aveninae, have been recently restructured thanks to the previous published works on their phylogeny using molecular markers. Soreng et al. (1990, 2000) firstly identified two consistently resolved and well supported chloroplast major clades in Poeae, which have been explored by the previous most current molecular phylogenetic studies (Grass Phylogeny Working Group II, 2012; Döring et al., 2007; Quintanar et al., 2007; Schneider et al., 2009; Saarela et al., 2015, 2017). These clades have been named in many ways on each study. We here follow Soreng et al., (2015, 2017) in naming these two clades as "Poeae chloroplast group 1" and "Poeae chloroplast group 2", which indeed roughly contain the ancient members of this tribe (including Aveneae). The Aveninae have consistently taken part of "Poeae chloroplast group 1", together with seven allied subtribes, namely Agrostidinae Fr., Anthoxanthinae A. Gray, Brizinae Tzvelev, Calothecinae Soreng, Echinopogoninae Soreng, Phalaridinae Fr., and Torreyochloinae Soreng & J.I. Davis (Soreng et al., 2017). Moreover, those studies using nuclear ribosomal DNA have shown that the Sesleriinae, part of "Poeae chloroplast group 2" according with plastid DNA data, are however closely related to "Poeae chloroplast group 1" (Quintanar et al., 2007; Gillespie et al., 2008; Saarela et al., 2010, 2017; Soreng et al., 2015), suggesting their hybrid origin and deep reticulation processes in the tribe.

Some of these abovementioned phylogenetic surveys identified two main clades within the Aveninae: one corresponded to Aveninae s.s. and comprised the genera *Arrhenatherum*, *Avena*, *Helictotrichon*, and *Tricholemma* (Quintanar et al., 2007; Schneider et al., 2009; Saarela et al., 2017); the other comprised the rest of the genera of the subtribe, separated by some authors as a separate subtribe Koeleriinae Asch. & Graebn. (Tzvelev, 1976; Quintanar et al., 2007, 2010; Saarela et al., 2017), which has been commonly subsumed within the Aveninae (Maire, 1953; Clayton & Renvoize, 1986; Soreng et al., 2003) or ignored due to the absence of any subtribal treatment (e.g. Watson & Dallwitz, 1992). The clade corresponding with the Koeleriinae include the two large perennial genera *Trisetum,* and *Koeleria,* and the annual *Trisetaria,* and *Rostraria*, traditionally considered part of this subtribe (Tzvelev, 1976; Clayton & Renvoize 1986), as well as other ones, such as *Avellinia*, *Gaudinia*, the American perennial *Graphephorum*, *Leptophyllochloa*, *Peyritschia*, and *Sphenopholis*, the American annual *Limnodea,* a Central and South American species complex of the genera *Calamagrostis*/*Deyeuxia* p.p., and the recently described *Trisetopsis* and *Tzveleviochloa*. The most familiar genera of the subtribe are the close related worldwide perennial *Trisetum* and *Koeleria*, not resolved as monophyletic. *Trisetum* have been traditionally characterized by its bifid, awned lemma and mostly glabrous ovary, comprising around 70 species mainly distributed in the northern hemisphere, but also found in South America, Australia, and New Zealand (Barberá et al., 2017a, 2017b). The current infrageneric classification of *Trisetum* recognizes four sections [*T.* sect. *Acrospelion* (Besser) Pfeiff., *T.* sect. *Sibirica* (Chrtek) Barberá, *T.* sect. *Trisetaera* Asch. & Graebn., and *T.* sect. *Trisetum*]. Beside of these ones, the Mexican and Central American *T.* subg. *Deschampsioidea* (Louis-Marie) Finot remains being the only infrageneric taxa of *Trisetum* not adapted to this sectional system (Barberá et al., 2017a, 2017b; Finot et al., 2004, 2005a, b). In the other hand, *Koeleria* has muticous, mucronate, or apically or subapically awned lemmas with a characteristically inconspicuous awnlet, comprising approximately 47 species distributed through Africa, America, Eurasia, and New Zealand (Clayton & Renvoize, 2006 onwards; Quintanar et al., 2010).

One of the most problematic taxonomic aspects arising in the light of these works with molecular markers is related to the systematics of the large genera *Trisetum* and *Koeleria*. Soreng et al. (2017) advanced some preliminary results for these lineages: the resurrection of *Acrospelion* for 12 to 14 Eurasian species of *Trisetum* characterized generally by having hairy ovaries, distichous leaves, and lax panicles (or combination of these), and the expansion of *Koeleria* including the species of the *Trisetum spicatum* complex (characterized by its compact and dense panicles). Another very striking and recently discovered aspect has been the polyphyly of the genus *Calamagrostis*, traditionally classified as a member of the sister subtribe Agrostidinae. A very recent study by Saarela et al. (2017) has showed this scenario of polyphyly for the generic complex *Calamagrostis/Deyeuxia*, resolving the species from north temperate regions in Agrostidinae, whereas those from Mexico, Central and South America in subtribe Aveninae. Additionally, Soreng et al. (2017) have already proposed the classification of the majority of the South American *Calamagrostis/Deyeuxia* species in the genus *Cinnagrostis*.

Here we present a new phylogenetic survey on the subtribe Aveninae which includes a broad sampling of the members of all the subtribes of “Poeae chloroplast group 1”, as well as a representative sampling of those of “Poeae chloroplast group 2”. We have placed special emphasis on the number of representatives of the genera *Trisetum* and *Koeleria* and all their related and smaller genera, since their phylogenetic relationships are the most poorly studied up to now, as well as those other lineages whose phylogenetic relationships have resulted incongruent in previous phylogenetic studies, many of them precisely related to the abovementioned genera *Trisetum* and *Koeleria*. The aim of our work is thus to discern the evolutionary relationships within Aveninae, clarifying as far as possible the taxa boundaries of this complex subtribe in order to contribute to a new classification congruent with our current morphological and molecular evidences. For this purpose, we have estimated its phylogeny by means of the analysis of four molecular markers: nuclear ITS and plastid *rpl32-trnL*, *rps16-trnK* spacer, and *rps16* intron sequences. The number of species sampled has been noticeable expanded compared to earlier studies. Finally, we have also focused on contrasting the available morphological and anatomical information about the involved taxa with that which has resulted from our molecular study, in order to assess the strength of the systematic relationships obtained through it and, therefore, the viability of the taxonomic decisions to be taken in a future publication.

MATERIAL AND METHODS

Taxon sampling

Our sampling consists of 658 samples, which corresponds with 275 species and subspecies of the studied lineages. It represents a broad taxonomic and geographic coverage of the taxa of the “Poeae chloroplast group 1”, though it is focused on the subtribe Koeleriinae [included in the Aveninae s.l. by Soreng et al., 2017], with 197 species, a part of a higher number of representatives of other close subtribes [Aveninae s.s. (27 species), Phalaridinae (1 species), Torreyochloinae (2 species), Anthoxanthinae (1 species), Brizinae (2 species), Echinopogoninae (3 species), and Agrostidinae (9 species)]. Additionally, those taxa corresponding with the major lineages of the "Poeae chloroplast group 2" have been generously represented in our analysis: Airinae (4 species), Aristaveninae (4 species), *Avenula* s.s. (1 species), Cinninae (1 species), Coleanthinae (5 species), Cynosurinae (1 species), Holcinae (2 species), Loliinae (1 species), Parapholiinae (4 species), Poinae (2 species), Scolochloinae (1 species), Sesleriinae (3 species), and Ventenatinae (1 species) (see Appendix 1 and 2). Our ingroup sampling was primarily focused on 16 genera of Koeleriinae and Aveninae s.s.: *Arrhenatherum*, *Avellinia*, *Avena*, *Gaudinia*, *Graphephorum*, *Helictotrichon*, *Koeleria*, *Lagurus*, *Peyritschia*, *Rostraria*, *Sphenopholis*, *Trisetaria*, *Tricholemma*, *Trisetopsis*, *Trisetum*, and *Tzveleviochloa* (see Appendix 1 and 2). We included 56 Central and South American species of the large species complex *Calamagrostis/Deyeuxia* (Agrostidinae), which has unclear taxonomical limits and unresolved and poorly supported relationships among its species (Saarela et al., 2010, 2017). The South American species of this complex are designated by their names in *Deyeuxia*, following the criteria by Rúgolo de Agrasar (2006) and Saarela et al. (2017) (except when there is no available combination in this genus) in order to make easier the comparison with the latter study. Some species of the Triticeae (*Agropyron cristatum*, *Elymus caninus*), and the Bromeae (*Bromus densus*) were chosen as outgroup.

The samples were either collected in silica or obtained from herbarium material, mainly from existing collections housed in the United States National Herbarium (US) and the herbarium of the Royal

Botanic Garden of Madrid (MA), also some from FI (1 sample), GOET (1 sample), H (2 samples), JE (1 sample), K (1 sample), LE (18 samples), M (2 samples), MEXU (1 samples), MO (1 sample), NY (2 sample), TEX (1 sample), and WU (1 sample) [herbarium acronyms follow Thiers (2017)]. A complete list of taxa and voucher information newly sequenced can be found in Appendix 1. Sources of previously published sequences are given in Appendix 2.

DNA extraction, amplification, and sequencing

Most of the procedures were performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution, and some in the Laboratory of Molecular Systematic (LSM) at the Royal Botanic Garden of Madrid. DNA isolation, amplification, and sequencing of *rpl32-trnL* spacer (small single-copy region), *rps16-trnK* spacer and *rps16* intron (large single-copy region), and ITS was accomplished following procedures outlined in Peterson et al. (2010a, b). We specifically targeted three of the plastid regions that proved to give good information in previous studies on chloridoid grasses (Peterson et al., 2010a, b, 2011, 2012, 2014a, b, c, 2015a, b).

Phylogenetic analyses

We used Geneious v.5.3.4 (Drummond et al., 2011) for contig assembly of bidirectional sequences of *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS regions, and to align consensus sequences, and then adjust the final alignment manually. We identified models of molecular evolution for the cpDNA and nrDNA regions using jModelTest (Posada, 2008) and applied maximum likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined datasets were partitioned in accordance with the number of the markers used.

Analyses were conducted on the CIPRES science Gateway (Miller et al., 2010). Nucleotide substitution models selected by Akaike´s information criterion, as implemented in jModelTest v.0.1.1 (Posada, 2008). The best fit models for the data partitions were SYM+G for each marker and the combined plastid and nuclear dataset, incorporating a gamma distribution for the combined plastid and ITS. ML analyses were performed using RAxML-HPC2 on XSEDE (Stamatakis, 2014), assuming a GTR model (default model), using the rapid bootstrap algorithm option, and 1000 replicates for assessing branch support (BS). In all analyses, gaps were treated as missing data. The output file containing trees of ML found for each bootstrap dataset was then read into PAUP v.4.b10 where the majority-rule consensus tree was constructed. Bootstrap (BS) values of 90%–100% were interpreted as strong support, 70%–89% as moderate, and 50%–69% as weak.

Bayesian analyses (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) were performed using Mr. Bayes v.3.2.6 (Ronquist et al., 2012), with default prior settings. Two runs were executed each with eight Markov chain Monte Carlo (MCMC) chains for two million generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences dropped below 0.01 and the potential scale reduction factor was close to or equal to 1.0. The fraction of the sampled values discarded as burn-in was set at 0.25. Posterior probabilities of 0.95-1.00 were considered to be strong support. Trees were visualized in FigTree v.1.4.3.

In the phylogram (Fig. 5-12) the place of origin of each studied Aveninae s.l. species is indicated by different colors, as indicated in the legend. We present the details of the combined plastid and ITS tree in multiple figures.

Assessment of incongruence and data combining strategy

The resulting plastid and ITS topologies were inspected for conflicting nodes with BS ≥ 80%. If no conflict was found, plastid and ITS sequences were combined. Where conflicting topologies were found, the datasets for inconsistently placed taxa were duplicated in the matrix. One set of the taxon was represented by the corresponding plastid sequences only, the other taxon set by only ITS sequences. The remaining positions for the truncated datasets were then coded as missing data. We use this "taxon duplication" approach (Pirie et al., 2008; Pelser et al., 2010; Peterson et al., 2015a) to resolve our phylogenetic tree minimizing the diffusing effects of taxa with strongly supported incongruence between the plastid and ITS data, and to represent their alternative placements in relation to the remaining phylogenetic groups among which relationships are congruent (Fig. 5–12). The combination of data has an obvious advantage since it can provide better backbone support for nodes and improve resolution for terminal nodes within the main phylogenetic groups. In our study, we justify combining the plastid and nuclear alignments (except for the incongruences discussed above) based on the high degree of congruence of plastid and nuclear trees.

RESULTS

Phylogenetic analyses

97% (2044/2106) of the sequences used in our study are newly reported here, 2.9% (62/2106) are from previous studies, and 15.6% (320) are missing or failed (Appendix 1 and 2). Total aligned characters for individual regions are noted in Table 1. All of the sequences of *rpl32-trnL* (563), *rps16 intron* (436), and *rps16-trnK* (516) are newly reported, followed by 529 sequences of ITS (89.5%).

DNA region	No. of sequences in matrix	No. of new sequences in matrix	No. of published sequences in matrix	Alignment length
ITS	591	529	62	769 bp
rpl32-trnL	563	563	—	1589 bp
rps16 intron	436	436	—	1075 bp
rps16-trnK	516	516	—	1044 bp

Table 1. Summary statistics for nuclear ribosomal and plastid sequence data.

Incongruences between the ITS and combined plastid phylograms

The ITS and combined plastid phylogenies rendered a high number of compatible characters between the two datasets, having similar patters overall. However, the ITS phylogeny differed from the plastid phylogeny (results not shown) in seven ways: **Incongruence 1:** Sesleriinae is sister to the clade A in ITS (PP = 0.78) while in the plastid tree were included with other subtribes of Poeae chloroplast group 2 (Holcinae, Scolochloinae, Airinae p.p., Loliinae, Parapholiinae, Cynosurinae, and Aristaveninae). **Incongruence 2:** *Trisetopsis junghuhnii* has a strongly supported (BS = 85, PP = 1.00) sister relationship with the clades B and C in ITS but it was included within the clade T in the plastid tree though with scarce support. **Incongruence 3:** *Tzveleviochloa*, *Helictotrichon sumatrense*, *Trisetum ambiguum*, *T. longiglume* subsp. *glabratum*, *T. cernuum* subsp. *cernuum*, *T. cernuum* subsp. *canescens*, *T. orthochaetum*, *Graphephorum*, and *Koeleria mendocinensis* are placed in the clade E in the ITS topology, while *Graphephorum melicoides* and two specimens of *T. cernuum* were included in the clade O (PP = 0.76), and the rest of the lineages in the clade P, all collapsing into a polytomy with few moderately to strongly supported clades. **Incongruence 4:** In the ITS topology, the representatives of *Rostraria cristata* were separated in two sister clades, one moderately to strongly supported (BS = 85; PP = 0.93) of *Rostraria cristata*, and the other weakly supported (BS = 64; PP = 0.76) with *R. cristata* and *R. obtusiflora*, all together forming a moderately supported (PP = 0.86) subclade in the clade K, which included also the ITS incongruence 5 (*R. hispida*) though with scarce support, all together sister of a weakly to a strongly supported clade with *Trisetaria* p.p. and *Gaudinia* p.p., also in a poorly supported relationship. In the plastid topology, *R. cristata*, *R. obtusiflora* and *R. smyrnacea* were included in the clade H, where resulted to be sister to *R. balansae* (PP = 0.64), and both clades sister to *R. pumila* (PP = 0.94). **Incongruence 5:** In the ITS topology, *Rostraria hispida* is sister to the ITS incongruence 4 but with scarce support, and both together sister to a moderately to strongly supported clade (BS = 62, PP = 1), which contained *Trisetaria loeflingiana*, *Gaudinia hispanica*, and *T. dufourei*, all included in the clade K; *Trisetaria panicea* resulted to be sister to *T. ovata*, *T. scabriuscula*, *Gaudinia fragilis, Gaudinia hispanica, Trisetaria dufourei*, *T. loeflingiana*, *Rostraria cristata,* and *R. obtusiflora*, though this relationship was scarcely supported. In the plastid topology, *R. hispida* was sister to *Trisetaria panicea* and formed a strongly supported clade (clade J; BS = 99, PP = 1). **Incongruence 6:** one representative of *Trisetum irazuense* and *T. foliosum* were placed in the clade L, which was included in the same clade of *Trisetum rosei* (BS = 58; PP = 0.89), while in the plastid topology they were included in the clade P, more specifically into a polytomy with Central and South American representatives of the complex *Calamagrostis/Deyeuxia* and the genus *Trisetum*, with moderate support (PP = 0.80). **Incongruence 7:** one representative of *Deyeuxia rupestris* f. *pilosa* was sister to *Sphenopholis pensylvanica* (PP = 0.64) in the clade O, while was placed with the rest of representatives of *Deyeuxia* sect. *Viridiflavescens* (clade T) in the plastid topology with scarce support.

Phylogenetic tree of Aveninae s.s. and Koeleriinae, and representatives of the rest of subtribes of Poeae chloroplast group 1 and Poeae chloroplast group 2

As simple look at the ML topology retrieved from the analysis of the combined plastid (*rpl32-trnL*, *rps16* intron, *rps16-trnK*) and ITS regions, allows us to recognize two strongly supported subclades within the tribe Poeae (BS = 100, PP = 1), corresponding to the abovementioned “Poeae chloroplast group 2” (BS = 99, PP = 1) and “Poeae chloroplast group 1” (BS = 100, PP = 1) (Fig.1) (see introduction).

In “Poeae chloroplast group 2” clade, a basal and strongly supported (BS = 100, PP = 1) clade of Airinae p.p. (*Aira caryophyllea* + *Avenella flexuosa*) is sister to the rest of its representatives, which are weakly grouped in another clade (PP = 0.51). This is separated in two sister clades, one of them strongly supported (BS = 93, PP = 1) and containing subtribes including Poinae (Poa), *Avenula* s.s. (*Avenula pubescens*), Ventenatinae (*Apera*), Cinninae (*Cinna*), and Coleanthinae (*Colpodium* + *Phippsia* + *Catabrosa* + *Schlerochloa* + *Puccinellia*). Poinae, *Avenula* s.s., Ventenatinae, and Cinninae are all together placed in a strongly supported clade (BS = 100, PP = 1) sister to Coleanthinae (BS = 100, PP = 1). Cinninae and Ventenatinae are resolved as sister in a strongly supported clade (BS = 99, PP = 1), being both subtribes sister to *Avenula* s.s. without strong support. Cinninae + Ventenatinae + *Avenula* s.s. are resolved as sister to subtribe Poinae, which form a strongly supported clade (BS = 99, PP = 1) (Fig. 2).

The second big clade of “Poeae chloroplast group 2” is moderate to weakly supported (BS = 54, PP = 0.99) and contains the here so-called “plastid incongruence 1” (corresponding to Sesleriinae), Holcinae (*Holcus* + *Vahlodea*; BS = 100, PP = 1), Scolochloinae (*Scolochloa*), Airinae p.p. (*Aira* + *Helictochloa*), Loliinae (*Psilurus*), Parapholiinae (*Cutandia* + *Catapodium* + *Desmazeria* + *Hainardia*; BS = 100, PP = 1), Cynosurinae (*Cynosurus*), and Aristaveninae (*Deschampsia* + *Calamagrostis gayana*). Aristaveninae form a strongly supported clade (BS = 100, PP = 1), including *Calamagrostis gayana* weakly grouped (BS = 77) as a sister group of *Deschampsia*. Aristaveninae is also sister to Cynosurinae with scarce support, and both subtribes resolved as sister ones with a higher but moderate support (PP = 0.87) to Loliinae and Parapholiinae. Parapholiinae is sister with a moderate support (BS = 75, PP = 0.91) to Loliinae, and both subtribes appear together in a larger clade resolved as sister with a weak to moderate support (BS = 62, PP = 0.85) to *Aira uniaristata*. *Helictochloa* and Scolochloinae are resolved as sister to Aristaveninae + Cynosurinae + Parapholiinae + Loliinae + *Aira uniaristata* but with scarce support, and all them are sister to Holcinae but with variable support (BS = 53, PP = 0.92). In the plastid topology (results not shown), the Sesleriinae form a strongly supported clade (BS = 99, PP = 1) at the base of the rest of the subtribes of the “Poeae chloroplast group 2” clade with a weak to strong support (BS = 54, PP = 0.99), being the genera *Oreochloa* and *Mibora* grouped into a strongly supported clade (BS = 98, PP = 1), sister to *Sesleria* (Fig. 2).

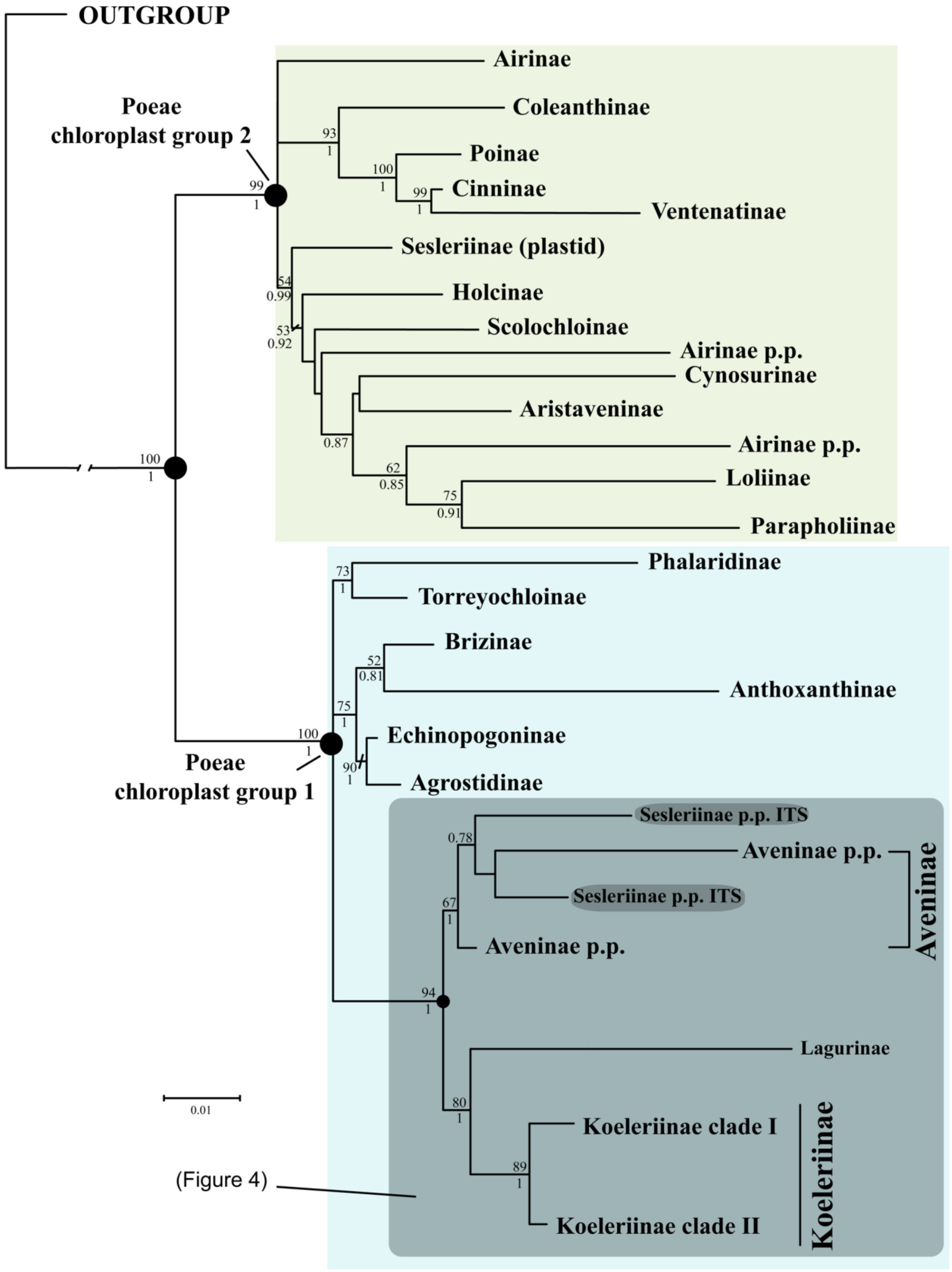

Figure 1. Overview of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data; major clades in the complete tree are collapsed; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.01 substitutions/site.

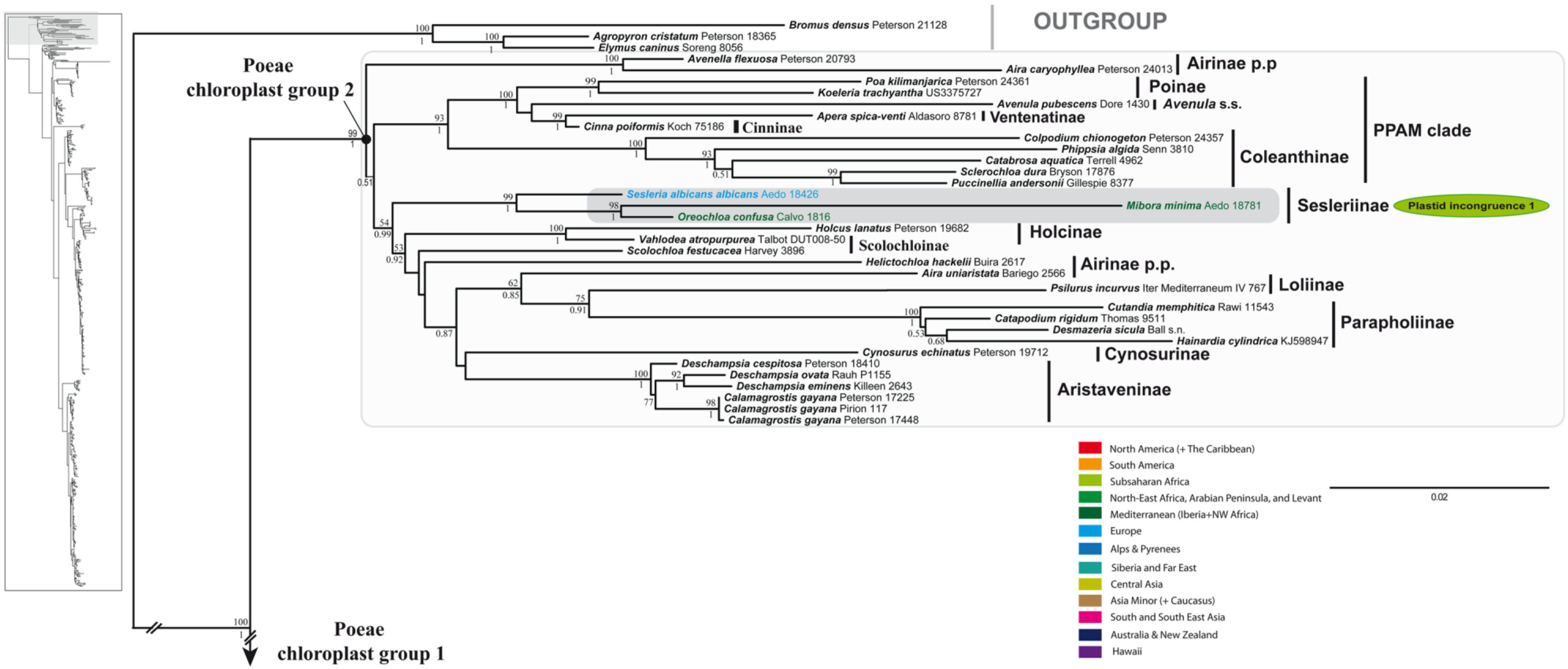

Figure 2. A portion (Poeae chloroplast group 2) of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

"Poeae chloroplast group 1" is divided into two main clades: one of the clades includes the subtribes Phalaridinae (*Phalaris*), Torreyochloinae (*Torreyochloa* + *Amphibromus*; BS = 100, PP = 1), Anthoxanthinae (*Anthoxanthum*), Brizinae (*Briza* + *Airopsis*; BS = 93, PP = 1), Echinopogoninae (*Relchela* + *Dichelachne* + *Calamagrostis coarctata*; BS = 92, PP = 1), and Agrostidinae (*Triplachne* + *Agrostis* + *Calamagrostis* s.s. + *Deyeuxia* p.p.; BS = 99, PP = 1) (Fig. 3). Phalaridinae and Torreyochloinae are sister groups to Anthoxanthinae, Brizinae, Echinopogoninae, and Agrostidinae, but this relationship is weakly supported (PP = 0.52). Phalaridinae is sister to Torreyochloinae with a moderate to strong support (BS = 73, PP = 1). A similar support was retrieved for the sister relationship of Brizinae and Anthoxanthinae (BS = 75, PP = 1) to Echinopogoninae + Agrostidinae, and much lower for the sister relationship of Brizinae and Anthoxanthinae. In their turn, Echinopogoninae is sister with a strong support (BS = 90, PP = 1) to Agrostidinae. The other large clade in "Poeae chloroplast group 1" is also strongly supported (BS = 94, PP = 1) and already includes the taxonomic groups which are the objective of the present work (Fig. 4). This clade, which we here examine more closely, includes: the "ITS incongruence 1" (corresponding to Sesleriinae), Aveninae, the "ITS incongruence 2" (*Trisetopsis junghuhnii*), Lagurinae, and Koeleriinae. At a glance, we detect a moderately to strongly supported relationship for Aveninae, the ITS incongruence 1, and the ITS incongruence 2 (BS = 67, PP = 1), all of them sister to another clade including Lagurinae (*Lagurus ovatus*) and Koeleriinae (BS = 80, PP = 1). From this point, we name with letters each of the subclades forming the main groups of Aveninae and Koeleriinae here studied to facilitate the follow-up of the explanation to the readers.

Aveninae and allies clade comprises the following monophyletic subclades: clade A (*Avena*; BS = 100, PP = 1), clade B (*Tricholemma*; BS = 100, PP = 1), clade C (*Arrhenatherum*; BS = 99, PP = 1), and clade D (*Helictotrichon* p.max.p.; BS = 70, PP = 0.99) (Fig. 5). The combined plastid topology is resolved as monophyletic, while the nuclear one includes the ITS incongruence 1 (subtribe Sesleriinae) and the ITS incongruence 2 (*Trisetopsis junghuhnii*). In the combined topology Sesleriinae and clade A form a moderately supported clade (PP = 0.78). Within the clade A, a group of species of *Avena* (*A. fatua*, *A. nuda*, *A. sativa* and *A. sterilis*) is separated with strong support (BS = 94, PP = 1) from the rest of its representatives. Clade B is sister with moderate support (PP = 0.55) to Clade C (BS = 99, PP = 1), and clades B and C are sister to the ITS incongruence 2 (*Trisetopsis junghuhnii*) (BS = 85, PP = 1). Within the clade C, a small group of species of *Arrhenatherum* (*A. calderae*, and *A. nebrodense*) is separated with strong support (BS = 94, PP = 1) from the rest of its representatives. Finally, clade D is sister with a weak to strong support (BS = 63, PP = 1) to the arrangement formed by the ITS incongruence 2 and the clades B and C. Not many strongly supported interspecific relationships are observed in the clade D, having the alliance among *H. desertorum*, *H. tianschanicum*, *H. hissaricum*, *H. fedtschenkoi*, *H. mongolicum* and *H. tibeticum* a weak support (PP = 0.59).

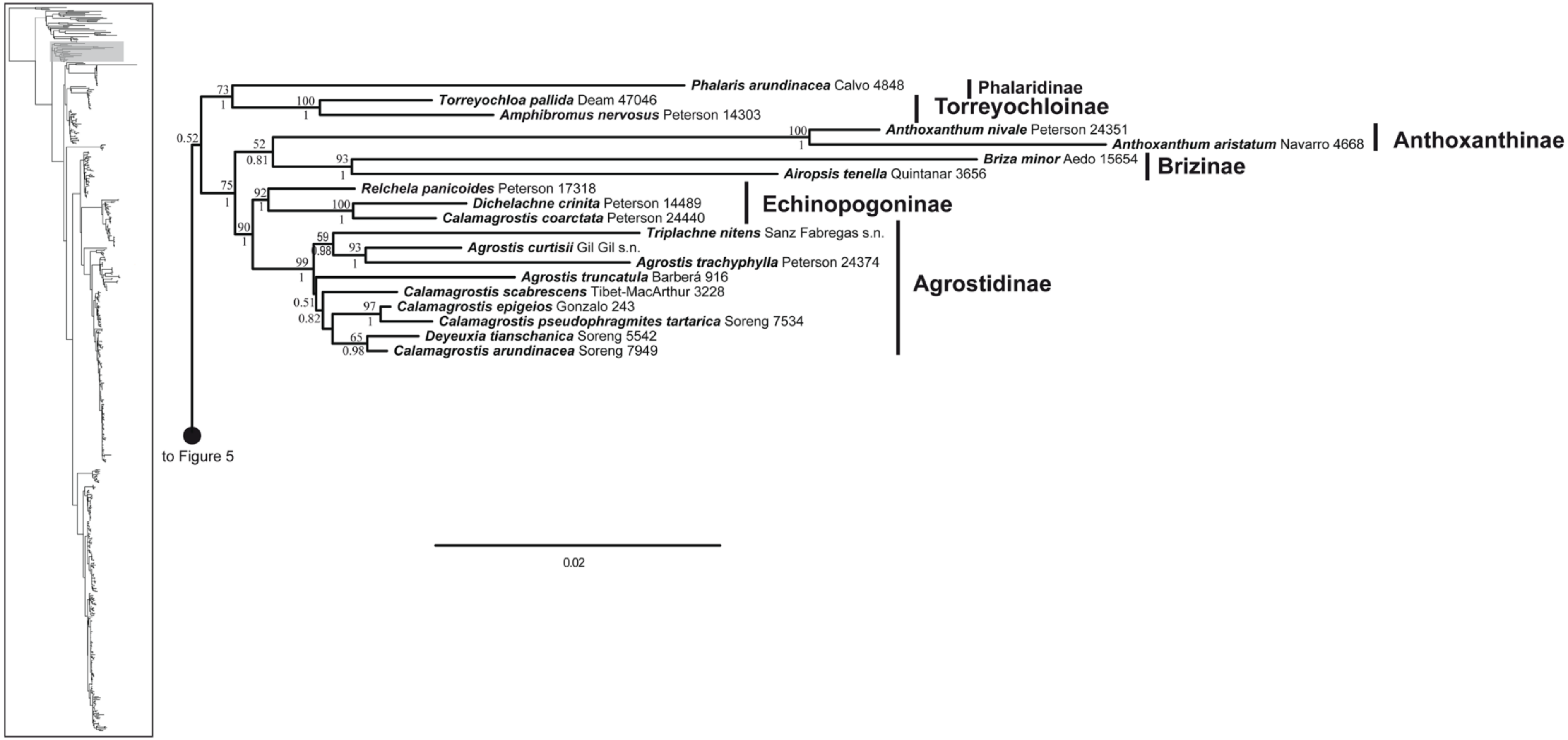

Figure 3. A portion (Agrostidinae, Anthoxanthinae, Brizinae, Echinopogoninae, Phalaridinae, and Torreyochloinae) of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

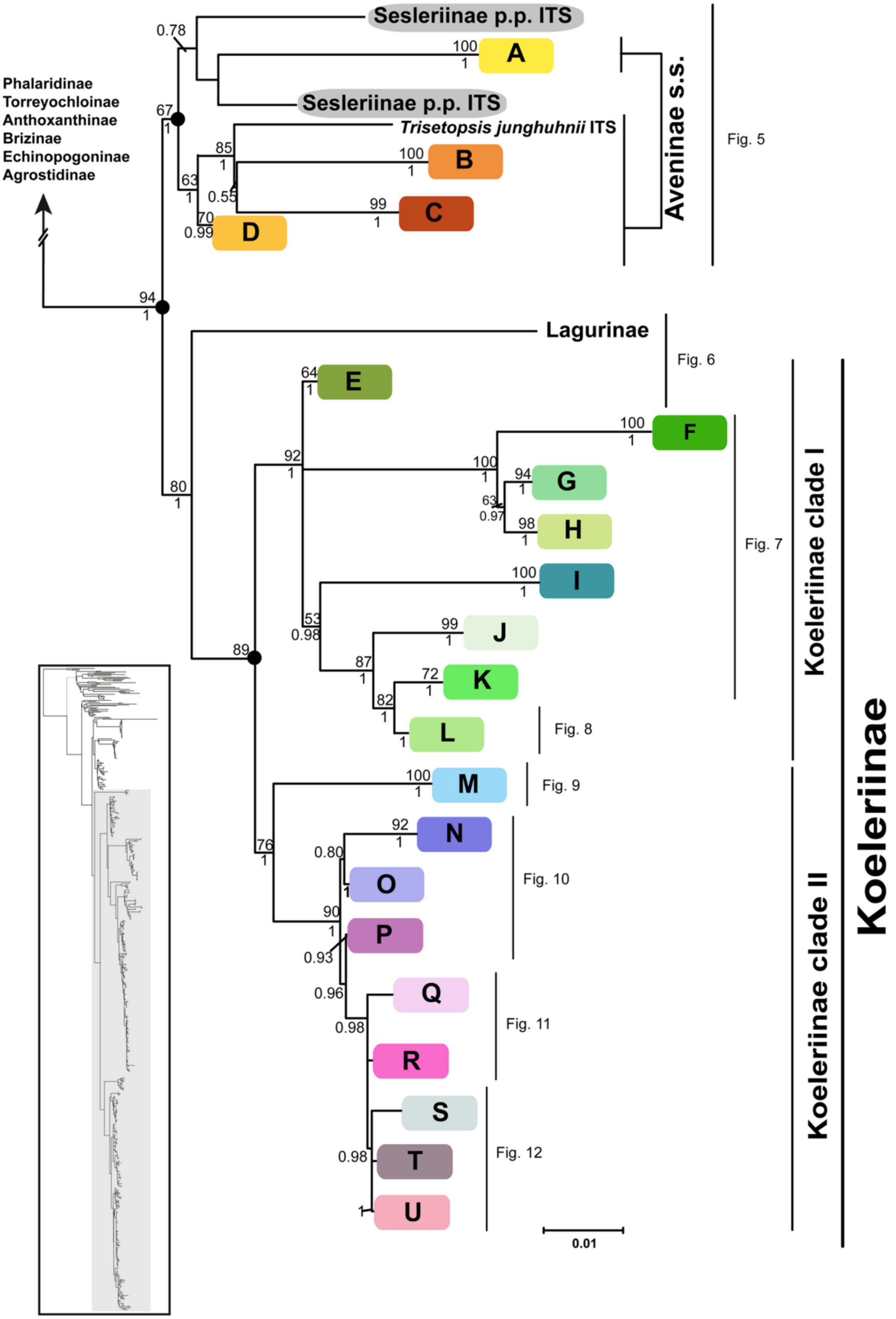

Figure 4. A portion (Aveninae s.l.) of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.01 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

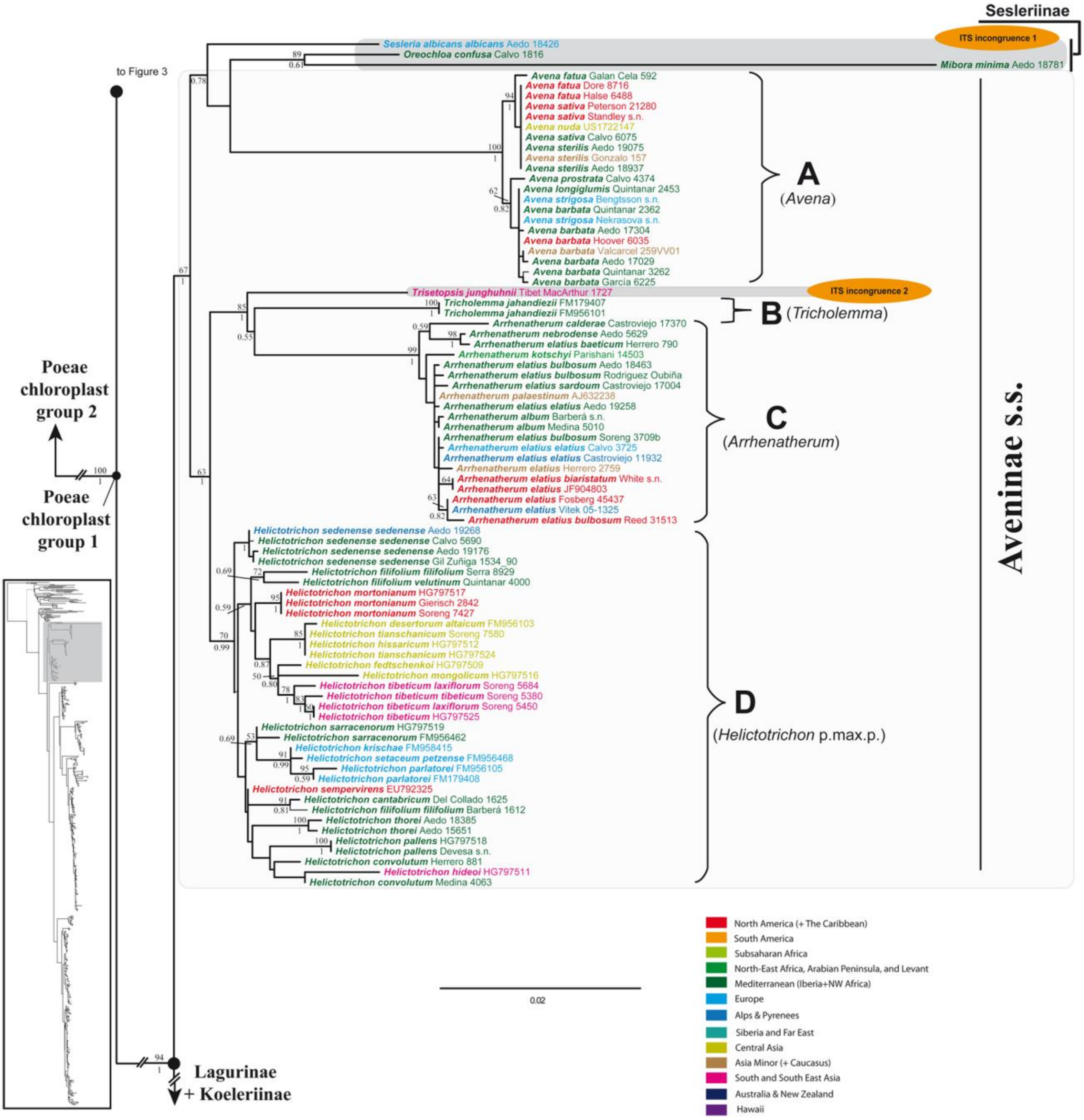

Figure 5. A portion (Aveninae s.s.) of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

The representatives of the Koeleriinae are divided into two moderate to strongly supported subclades here named Koeleriinae clade I (BS = 92, PP = 1) and Koeleriinae clade II (BS = 76, PP = 1). The Koeleriinae clade I is organized into eight subclades, here named clades E, F, G, H, I, J, K, and L. The clade E is sister to the rest of the clades, whose grouping is weakly supported (PP = 0.63). In turn, these clades are also organized into two larger and sister subclades, one strongly supported (BS = 100, PP =1) including clades F, G, and H, and the other weakly to strongly supported (BS = 53, PP = 0.98), including I, J, K, and L clades (Fig. 4).

The clade E is moderately to strongly supported (BS = 64, PP =1) and it is at the base of the rest of clades of Koeleriinae clade I and includes the genera *Trisetum* p.p., *Tzveleviochloa*, *Helictotrichon* p.min.p., and the ITS incongruence 3 (Fig. 6). *Trisetum bertolonii* (BS = 100, PP =1) is resolved at the base of this clade, being sister to the rest of lineages. *Trisetum glaciale* (BS = 96, PP = 1) form a polytomy with a weakly to strongly supported clade (BS = 59, PP = 0.97) formed by *T. macrotrichum*, *T. velutinum*, *T. distichophyllum*, and *T. argenteum*, and another scarcely supported group including the rest of the representatives of clade E. *Trisetum macrotrichum* is sister (PP = 0.91) to *T. velutinum* (BS = 93, PP =1), and both sister to a strongly supported clade (PP = 0.97) that includes *T. distichophyllum* (BS = 87, PP =1) and *T. argenteum* (BS = 64, PP =1). These clades are sister to a polytomy formed by several groups: 1) *T. alpestre* + *T. baregense* clade (BS = 67, PP =1); 2) *T. rigidum* subsp. *rigidum* (BS = 89, PP =1) as sister to a more strongly supported group (BS = 97, PP =1) of *T. rigidum* subsp. *teberdense*, *T. buschinaum* subsp. *buschianum*, and *T. buschinaum* subsp. *transcaucasicum*; 3) *T. altaicum* (BS = 89, PP = 1) sister with scarce support to a weakly supported clade (PP = 0.51) which includes two sister subclades: one is strongly supported (PP = 0.99) and includes *Helictotrichon delavayei*, *Tzveleviochloa parviflora* and *Helictotrichon sumatrense*; the second and scarcely supported clade consists of a part of the ITS incongruence 3, which includes *Trisetum longiglume* var. *glabratum*, *T. ambiguum*, a moderately to strongly supported clade of *Graphephorum melicoides* (BS = 88, PP = 0.94), and *Koeleria mendocinensis* (BS = 86, PP = 0.95); 4) the rest of species of the ITS incongruence 3, with scarce support, *Trisetum cernuum*, and a weakly supported inner clade (BS = 59, PP = 0.79) including *Trisetum orthochaetum* and *Graphephorum wolfii*.

The clade F (*Trisetaria linearis*; BS = 59, PP = 0.79) is basal to a larger clade (BS = 63, PP = 0.97) which includes the clades G and H (Fig. 7). The clade G (BS = 94, PP = 1) includes *Trisetum gracile* subsp. *gracile* and *Trisetum gracile* subsp. *conradiae* in a sister and poorly supported subclade to a consisting of several representatives of *T. flavescens* and its subspecies (*T. flavescens* subsp. *africanum*, *T. flavescens* subsp. *corsicum*, *T. flavescens* subsp. *flavescens*, *T. flavescens* subsp. *griseovirens*, *T. flavescens* subsp. *parvispiculatum*, *T. flavescens* subsp. *purpurascens*, and *T. flavescens* subsp. *tenue*), as well as *Trisetaria bungei*. The clade H (BS = 98, PP =1) includes two diverging lineages, one strongly supported (BS = 96, PP = 1) which includes *Rostraria litorea* and *R. salzmanni*, and other weakly to strongly supported (BS = 64, PP = 0.98) which includes *Trisetaria lapalmae*, *Rostraria pumila*, and the plastid incongruence 4. *Trisetaria lapalmae* is resolved as sister to *Rostraria pumila* and the plastid incongruence 4, and both resulted to be sister groups with a weak support (PP = 0.94). In the plastid incongruence 4, *Rostraria balansae* appears to be sister with a weak support to a moderately to strongly supported subclade (BS = 87, PP =1) which includes *R. cristata*, *R. obtusiflora,* and *R. smyrnacea* collapsing into a polytomy.

The clade I (*Avellinia festucoides*; BS = 100, PP = 1) is basal to a larger clade (BS = 87, PP = 1) which includes the clade J (plastid incongruence 5: *Rostraria hispida* and *Trisetaria panicea*; BS = 99, PP = 1) sister to the clades K and L clades (both grouped with moderate support: BS = 87, PP = 1) (Fig. 7).

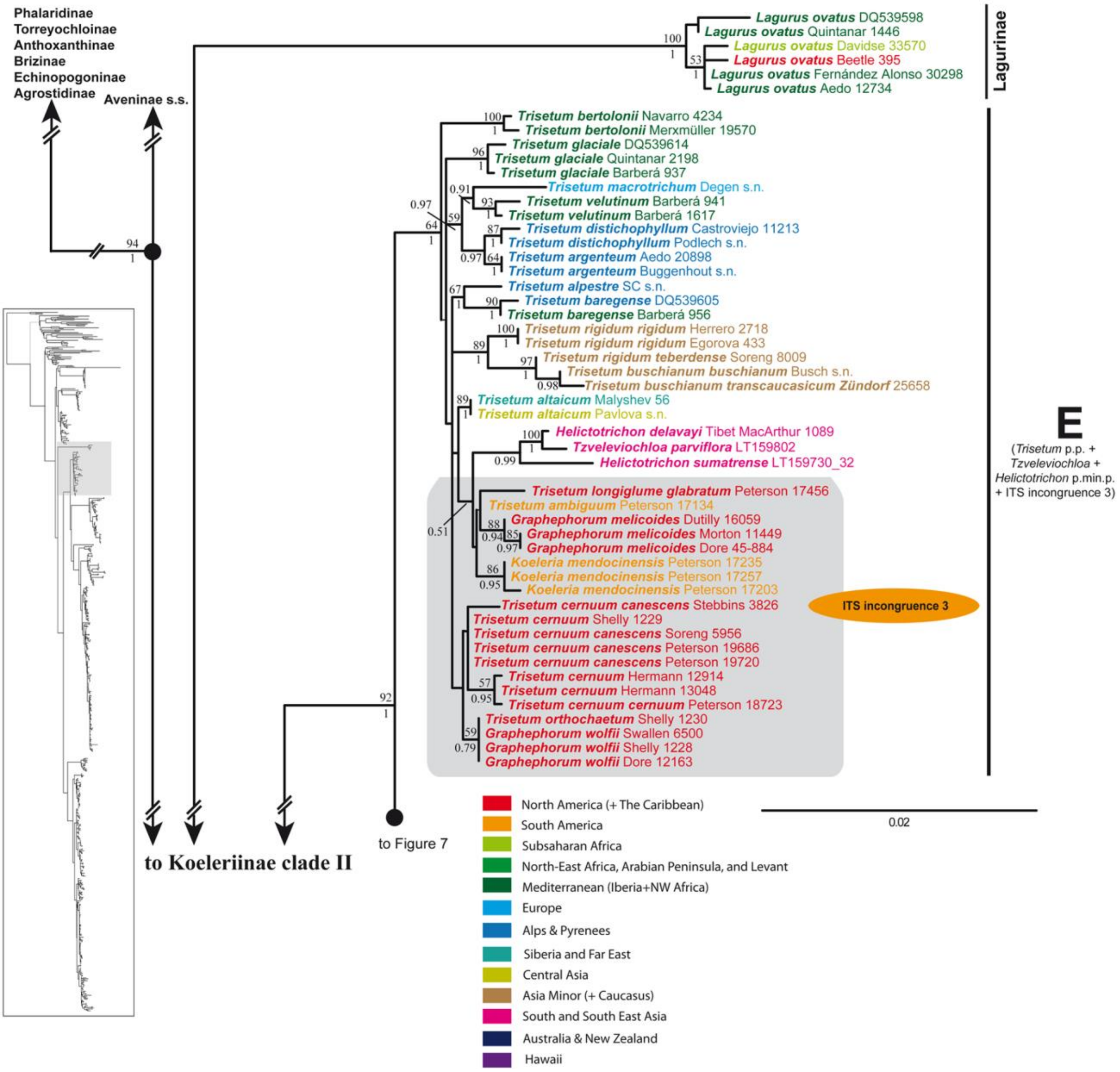

Figure 6. A portion (Lagurinae and clade E of "Koeleriinae clade I") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

In the plastid topology, the clade J is strongly supported (BS = 99, PP = 1) and sister to K + L clades (BS = 82, PP = 1). The clade K (BS = 72, PP = 1) includes a basal subclade of *Trisetaria* p.p. (*Trisetaria ovata* and *T. scabriuscula*; PP = 0.60), the plastid incongruence 5 (very scarcely supported), a subclade of *Gaudinia fragilis* (BS = 100, PP = 1), sister to two additional and weakly grouped subclades: 1) *Gaudinia hispanica* + *Trisetaria dufourei* (BS = 100, PP = 1), as sister (BS = 62, PP = 1) to *Trisetaria loeflingiana* (BS = 100, PP = 1); 2) the ITS incongruence 4 (*Rostraria cristata* + *R. obtusifolia*; PP = 0.86)+ the ITS incongruence 5 p.p. (*Rostraria hispida*; BS = 100, PP = 0.97). In the ITS topology, *Trisetaria panicea* (the ITS incongruence 5 p.p.) is weakly resolved as sister to *Gaudinia*, *Trisetaria dufourei*, *Trisetaria loeflingiana*, and *Rostraria hispida* which are also included in this clade, as sister to the ITS incongruence

4 (PP = 0.86), including *R. cristata* and *R. obtusiflora*.

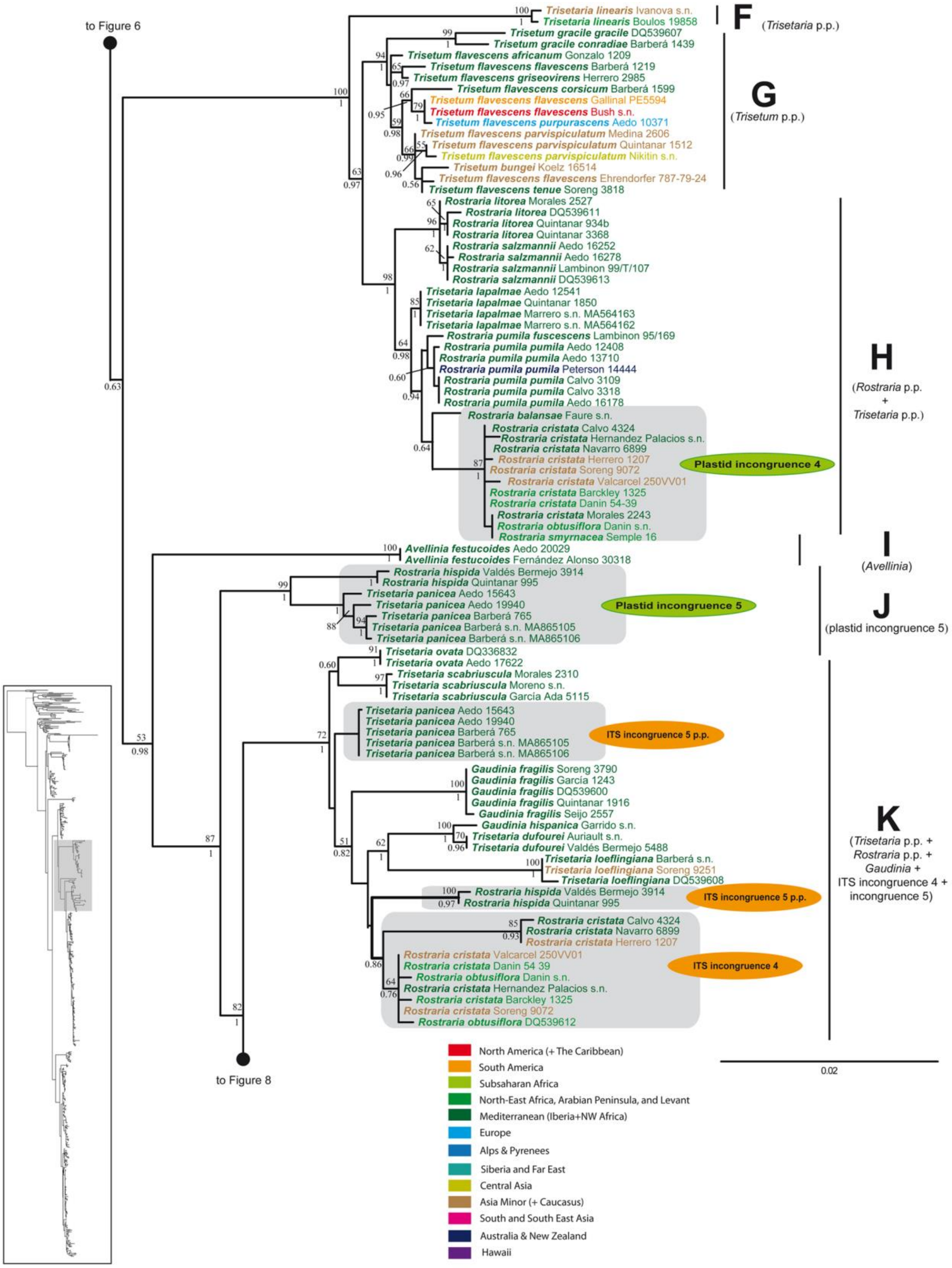

Figure 7. A portion (clades F-K of "Koeleriinae clade I") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

The clade L (PP = 1) comprises the genera *Koeleria* p.max.p. and *Trisetum* p.p. and is organized in several subclades that we identify from now adding a number to the letter L (Fig. 8). The clade L1 (PP = 0.78) is basal and sister to the rest of subclades, whose grouping is poorly supported. It includes the lineages of *Koeleria capensis* (BS = 68, PP = 1) and *K. caucasica*, *K. glauca*, *K. altaica*, and *K. transiliensis* (PP = 0.71) as sister groups (PP = 0.77). The other subclade (PP = 1) includes *Koeleria caucasica*, *K. eriostachya*, *K. brevis*, *K. splendens*, *K. pyramidata* p.p., *K. glaucovirens*, *K. nitidula*, and *K. kurdica,* collapsing into a polytomy. A second unsupported large group contains different unsupported to weakly supported clades (L2, L3, and L4) and polytomies. The clade L2 is paraphyletic with respect to the rest of the groups that are going to be commented on below. *Koeleria loweana* is basal to the rest of lineages of the clade L2. *Trisetum hispidum* (BS = 93, PP = 1) is grouped (PP = 0.84) with three representatives of *Koeleria pyramidata* (PP = 0.98). The rest of the representatives that complete the clade L2 (*Koeleria rodriguez-graciae*, *K. crassipes*, *K. vallesiana*, *K dasyphylla*, *K. castellana*, and *K. pyramidata*, plus *Trisetum spicatum* subsp. *molle* and *Trisetum spicatum* subsp. *pilosiglume*) is grouped more or less solidly with L3 and L4 (PP = 1), but there is little support for the inner relationships and situations of polyphilia or paraphilia for some of the species involved. The level of support obtained for the paraphyletic clade L3 has not been satisfactory either. Its representatives are grouped (PP = 0.99) with those of the monophyletic clade L4, and consist of the taxa *Koeleria hirsuta*, *Trisetum clarkei*, *T. spicatum*, *T. glomeratum*, *T. caudulatum*, *T. barbinode*, *T. preslii*, *K. vurilochensis*, *K. fueguina*, plus *T. rosei* and *K. pyramidata* weakly grouped with the ITS incongruence 6 (*T. foliosum*, and *T. irazuense*) (BS = 58, PP = 0.89), besides of *T. ligulatum*, *T. projectum*, and finally *T. tenellum*, *T. drucei*, and *T. youngii* (PP = 0.71). Many of these groupings are very poorly supported and polytomies are frequent. We find the same scenario in the monophyletic clade L4 (PP = 1), which groups the representatives of *Trisetum subalpestre*, *T. spicatum*, *Trisetokoeleria taymirica* and *T. gorodkowii*, *Koeleria litvinowii*, *Trisetum antarcticum*, *T. inaequale*, *T. glomeratum*, *K. pyramidata*, *K. asiatica*, *T. projectum*, *T. montanum*, *T. oreophilum*, *T. caudulatum*, *T. andinum*, *K. kurtzii*, and *K. boliviensis*.

The Koeleriinae clade II is organized into nine subclades, here named clades M, N, O, P, Q, R, S, T, and U. The clade M is strongly supported (BS = 100, PP = 1) and basal to the rest of the lineages of Koeleriinae clade II, whose grouping is strongly supported (BS = 90, PP = 1). It includes two subclades, one strongly supported (BS = 98, PP = 1) containing *T. aeneum* (BS = 91, PP = 1) as sister to *T. bifidum* and *T. scitulum* (BS = 88, PP = 1), and other poorly supported subclade that includes *T. sibiricum* subsp. *sibiricum* and *T. sibiricum* subsp. *litorale* (Fig. 9).

The clades N and O (PP = 0.80) are sister to the rest of the clades (O, P, Q, R, S, T, and U; PP = 0.96) (Fig. 10). The clade N (BS = 92, PP = 1) includes *Limnodea arkansana*. The clade O (PP = 1) includes several species of *Sphenopholis*, the ITS incongruence 7 (*Deyeuxia rupestris* f. *pilosa*), and part of the plastid incongruence 3 (*Graphephorum melicoides* and *Trisetum cernuum* p.p.). *Sphenopholis filiformis* (PP = 0.74) is poorly resolved at the base of the clade, followed by the *S. longiflora* (BS = 92, PP = 1), and the ITS incongruence 7, which is placed together with *S. pensylvanica* (PP = 0.64), whose union is resolved as sister with scarce support to *S. interrupta*. In their turn, these subclades are sister to a

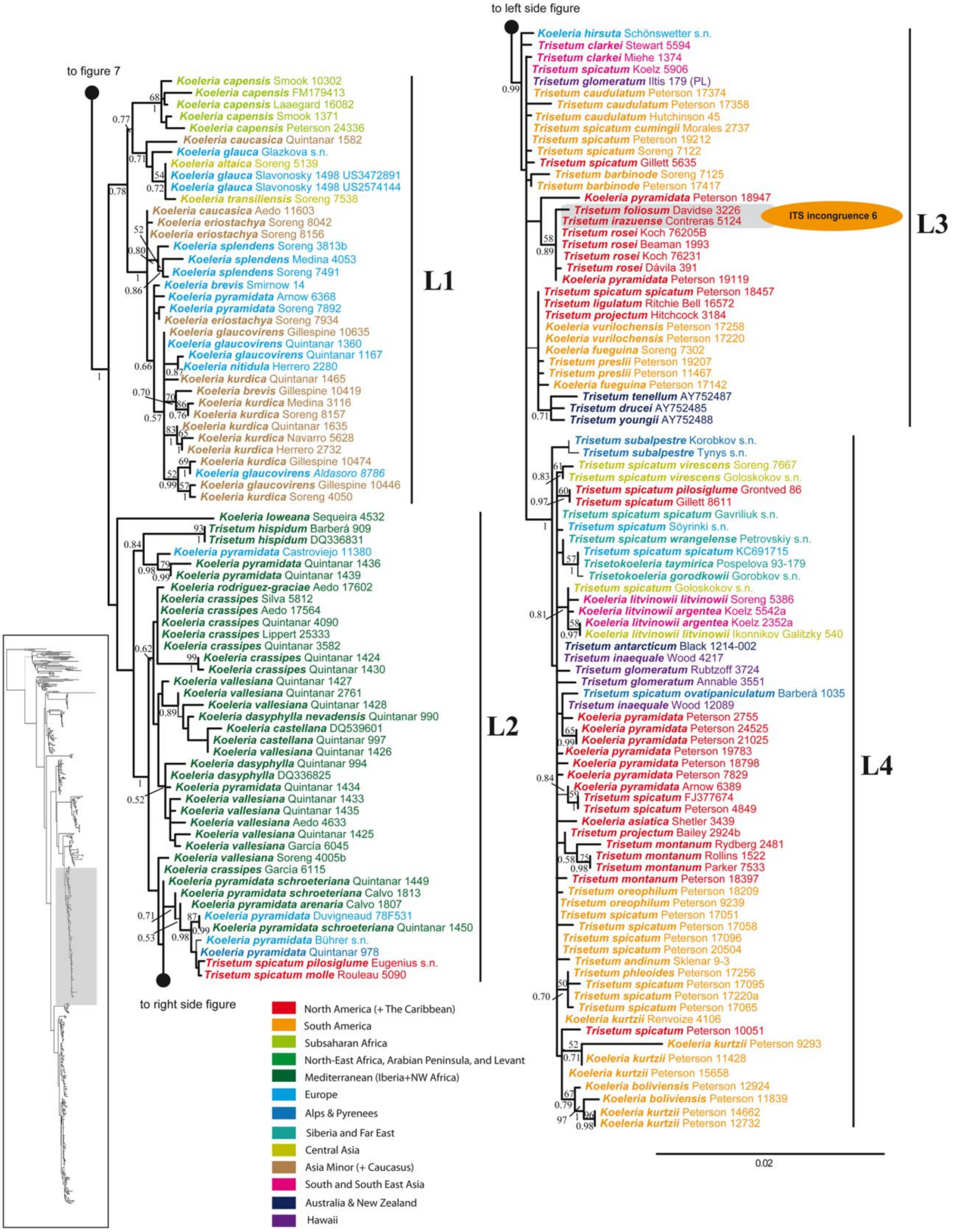

Figure 8. A portion (clades L of "Koeleriinae clade I") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

subclade (PP = 1) containing *S. nitida*, *S. obtusata*, *S. intermedia*, and the plastid incongruence 3 p.p. In this last subclade, *S. nitida* and *S. obtusata* p.min.p. and *S. intermedia* p.min.p. are a sister and moderately supported (PP = 1) group to the another collapsing into a polytomy, which consists of *S. intermedia* p.max.p., *S. obtusata* p.max.p., and the plastid incongruence 3 p.p.

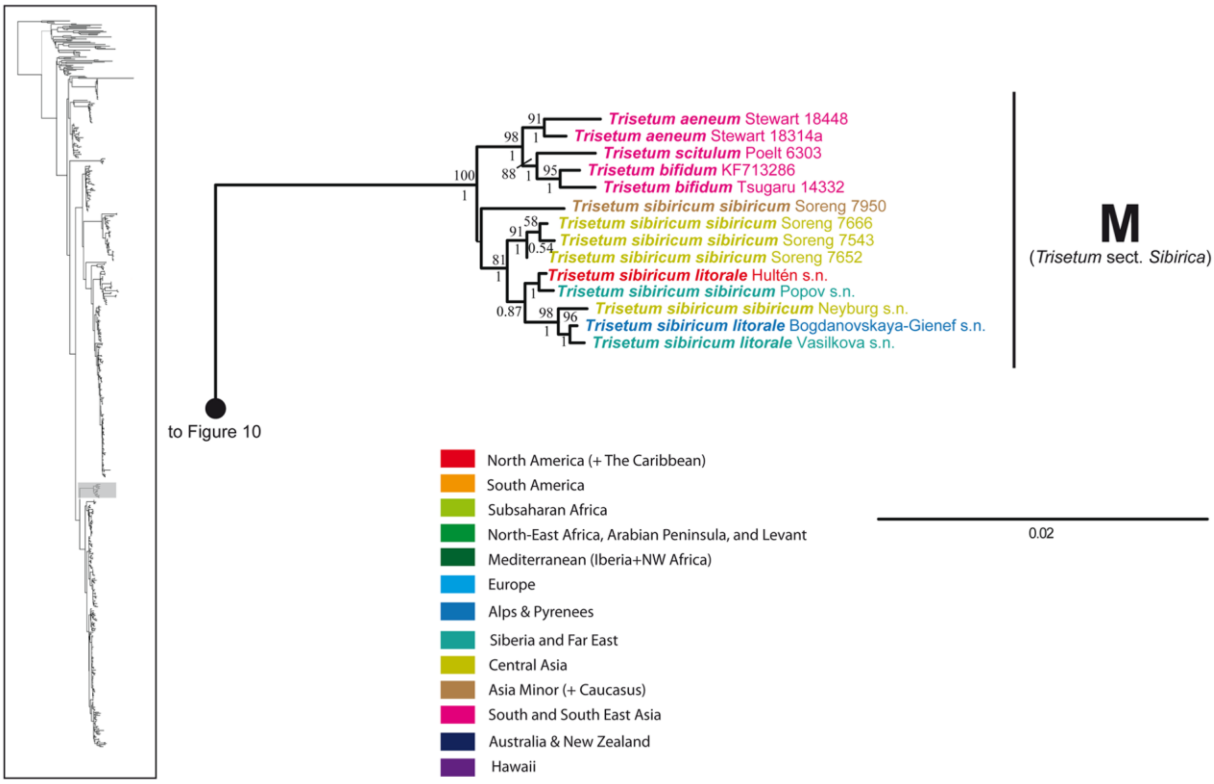

Figure 9. A portion (clade M of "Koeleriinae clade II") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

The clade P is moderately supported (PP = 0.93) and sister to the clades Q, R, S, T, and U (PP = 0.98). It includes many lineages frequently collapsing into polytomies: *Peyritschia*, the plastid incongruence 3 p.p, *Trisetum* p.p., *Calamagrostis*/*Deyeuxia* p.p., and the plastid incongruence 6. The following groups collapse into a general polytomy but are recognizable: *Trisetum cernuum* p.p. + *T. ortochaetum* (BS = 83, PP = 0.95), *Graphephorum wolfii* (BS = 61, PP = 0.71), *Trisetum ambiguum* + *T. longiglume* var. *glabratum* + *Koeleria mendocinensis* (BS = 84, PP = 0.79), *Trisetum cernuum* subsp. *canescens* + *T. pringlei* + *Calamagrostis coahuilensis* (PP = 0.81), *Calamagrostis pittieri* + *C. killipii* + *C. planifolia* (BS = 88, PP = 1), *C. vulcanica* + *C. mcvaughii* (BS = 57, PP = 1), and *C. tolucensis* + *C. eriantha* (PP = 0.94). The rest of the lineages are grouped with moderate support (PP = 0.95) and are distributed into two sister subclades: 1) *Peyritschia pringlei*, *P. deyeuxioides*, and *P. koelerioides* (PP = 0.78); 2) a weakly supported group with *Trisetum durangense*, *T. spellenbergii*, and *Calamagrostis pringlei* (PP = 0.60), sister to several lineages collapsing into a polytomy, corresponding to the plastid

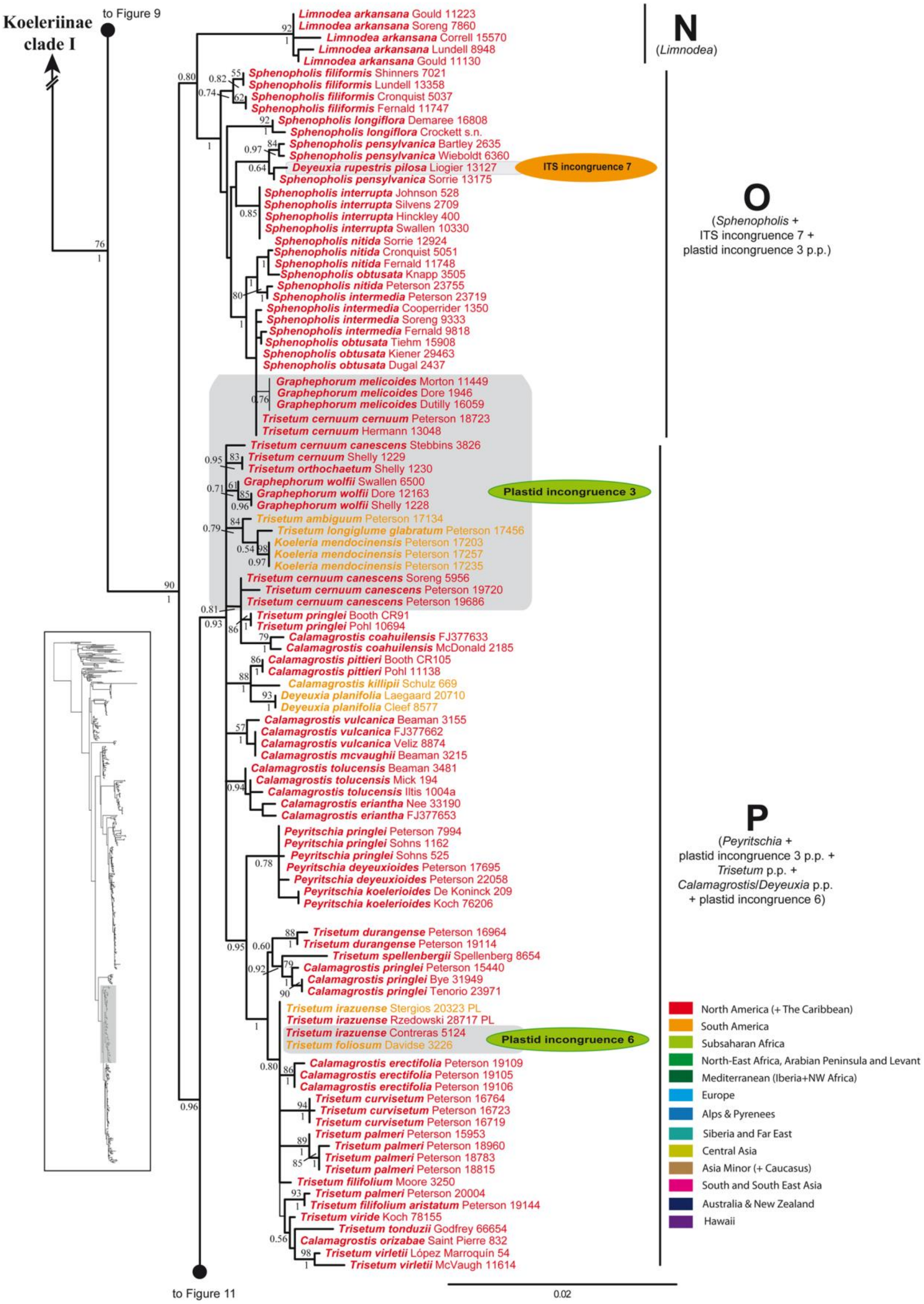

Figure 10. A portion (clade N, O, and P of "Koeleriinae clade II") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

incongruence 6 (*Trisetum irazuense* + *T. foliosum*), *Calamagrostis erectifolia*, *Trisetum curvisetum*, *T. palmeri*, *T. filifolium*, *T. viride*, *T. tonduzii*, *Calamagrostis orizabae*, and *T. virletii*.

The clade Q has scarce support and is basal to the clades R, S, T, and U clades, whose grouping has also very few support. Similarly, the clade R is also poorly supported and basal to the clades S, T, and U clades, whose grouping has a higher though moderate support (PP = 0.98). The clades Q and R contain species of the complex *Deyeuxia*/*Calamagrostis*. In the clade Q, *Deyeuxia fuscata* and *D. heterophylla* p.p. are basal to many lineages whose relationships are poorly supported, namely *Deyeuxia nana* as sister to *D. heterophylla* p.p. + *D. setiflora* + *D. vicunarum* p.p + *D. fibrovaginata* p.p. + *D. minima* (PP = 0.59), plus other group with *D. vicunarum* p.p. + *D. rigescens* + *D. fibrovaginata* p.p. + *D. macrophylla* + *Calamagrostis rauhii* + *D. heterophylla* p.p. Practically all the lineages of the larger clade R collapse into a polytomy and are grouped with moderate support (PP = 0.80), except for the basal *Deyeuxia boliviensis* and *D. jamesonii* (Fig. 11).

The clade S contain *Leptophyllochloa micrathera* and the plastid incongruence 2 (*Trisetopsis junghuhnii*), both collapsing into a polytomy with the clades T and U (PP = 0.53). The clade T includes *Deyeuxia rupestris*, *D. viridiflavescens*, *D. viridis*, and the plastid incongruence 7 (*Deyeuxia rupestris* f. *pilosa*) forming a scarcely supported group sister to the clade U. And finally, the clade U (PP = 1) contains a large polytomy of representatives of *Trisetopsis*: *T. natalensis*, *T. galpinii* + *T. friesiorum* (PP = 0.54), *T. umbrosa* p.p. + *T. elongata* p.p. (BS = 59, PP = 0.78), *T. mannii* + *T. umbrosa* p.p. + *T. milanjiana* p.p. (PP = 0.95), *T. elongata* p.p. (BS = 64, PP = 1), *T. longifolia* (BS = 77, PP = 0.82), *T. angusta* + *T. natalensis* + *T. capensis* p.p. + *T. dodii* + *T. imberbis* + *T. hirtula* (PP = 1), *T. milanjiana* p.p., *T. lachnantha* (BS = 97, PP = 0.98), *T. imberbis* (PP = 0.62), *T. leonina* + *T. longa* + *T. capensis* p.p. (PP = 0.62), and *T. barbata* + *T. roggeveldensis* + *T. namaquensis* (BS = 89, PP = 0.85) (Fig. 12).

DISCUSSION

The resulting phylogenetic topologies generated by our present analyses of nuclear and plastid DNA data of the "Poeae chloroplast group 1" are overall congruent with those presented in previous surveys: the clade formed by Aveninae (including Sesleriinae in nuclear topologies), Koeleriinae and the genus *Lagurus* have resulted to be sister group of other lineages of closely related grasses, such as Phalaridiinae + Torreyochloinae, Brizinae + Anthoxanthinae, and Agrostidiinae + Echinopogoninae (Quintanar et al., 2007; Saarela et al., 2017; Wölk & Röser, 2017), in which these groups also resulted to be basal and sister to Aveninae, including Koeleriinae). Several molecular studies based on plastid and nuclear data have treated the boundaries of the subtribe Aveninae (Grebenstein et al., 1998; Röser et al., 2001; Döring et al., 2007; Quintanar et al., 2007; Soreng et al., 2007; Döring, 2009; Schneider et al., 2009; Winterfeld et al., 2009, 2016; Wölk & Röser, 2014, 2017; Wölk et al., 2015). The Aveninae subtribe has resulted to be a monophyletic group, which includes three inner monophyletic lineages: Aveninae s.s. (including *Avena*, *Helictotrichon*, and allied genera, plus Sesleriinae in ITS topology), Koeleriinae (including *Trisetum*, *Koeleria* and allied genera), and *Lagurus*. These two broad groups of Aveninae are thus associated with the monospecific genus *Lagurus*, whose particular status in the group

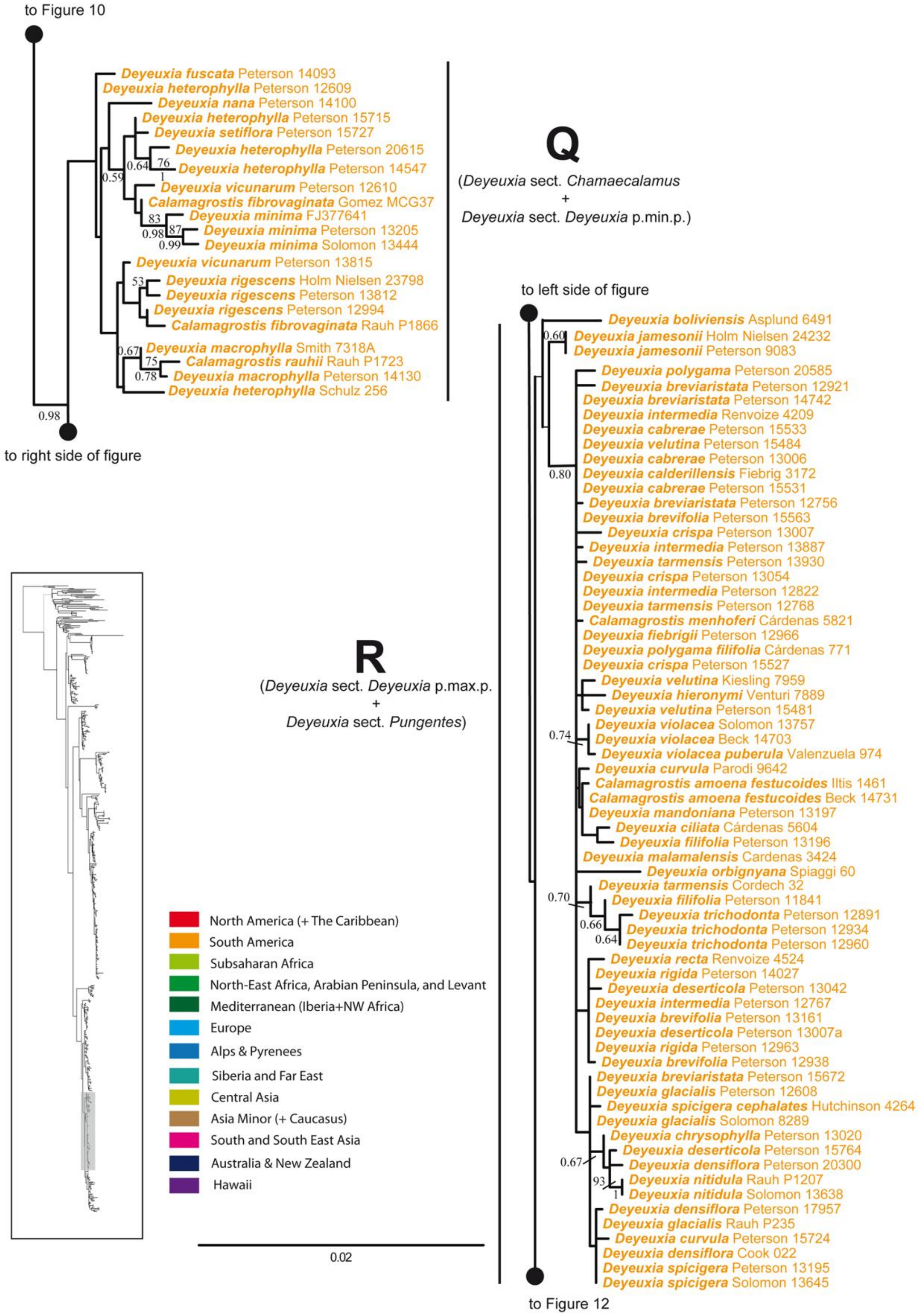

Figure 11. A portion (clade Q and R of "Koeleriinae clade II") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

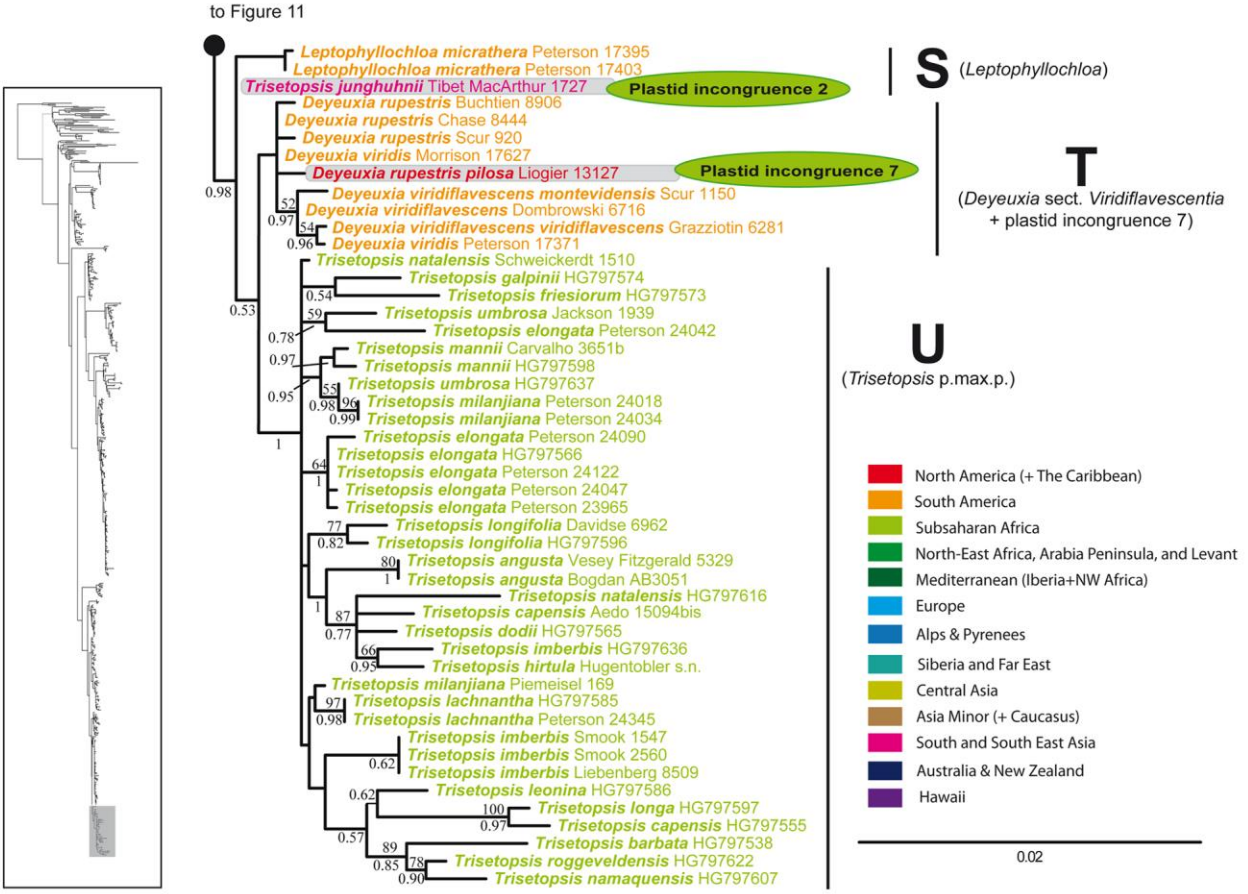

Figure 12. A portion (clade S, T and U of "Koeleriinae clade II") of the maximum likelihood phylogram inferred from combined plastid (*rpl32-trnL*, *rps16-trnK*, and *rps16 intron*), and ITS data. Letters indicate the clades discussed in the text; numbers above branches are bootstrap values and numbers below branches are posterior probabilities; no support is shown for branches with bootstrap support <50% and posterior probability <0.5; scale bar = 0.02 substitutions/site. The shaded area of the smaller tree on the left indicates the location in the overall of the portion shown.

has given it the rights to head its own subtribe, Lagurinae (Saarela et al., 2017). The relationship of *Lagurus* with and within Aveninae s.l. has been problematic and it changes in the different studies. *Lagurus* has varied from being included in the Aveninae s.l. in some plastid topologies (Soreng & Davis, 2000; Quintanar et al., 2007; Wölk & Röser, 2017) or in a phylogeny based on the 5S nrDNA spacer (Röser et al., 2001), or its sister group in the plastid topologies (Grass Phylogeny Working Group II, 2012; Saarela et al., 2017) to being only the sister group of Koeleriinae in the nuclear topologies with ITS and *topo6* (Quintanar et al., 2007; Saarela et al., 2017; Wölk & Röser, 2014, 2017), situation, this latter, corroborated in this study and that is more consistent with the greater number of common characters between Koeleriinae and *Lagurus*, such as generally glabrous ovaries, short hilum, and liquid endosperm (Quintanar et al., 2007, 2010).

Thus, the subtribe Koeleriinae, a group that includes as typical genera *Trisetum*, *Trisetaria*, *Koeleria*, and *Rostraria* (Tzvelev, 1976; Clayton & Renvoize, 1986), has been little used throughout the taxonomic history of its associated genera, sometime due to its inclusion within an enlarged subtribe Aveninae s.l. (Grebenstein et al., 1998; Soreng & Davis, 2000; Döring et al., 2007; Soreng et al., 2007, 2015, 2017; Schneider et al., 2009; Saarela et al., 2010; Wölk & Röser, 2014, 2017). The morpho-anatomical singularity of the genera of the Koeleriinae has been recognized by previous wide treatments on grasses: the lineages included in the “Trisetum group” of Clayton & Renvoize (1986) were characterized by having keeled lemmas and gaping paleas, with the genus *Trisetum* as the ancestral lineage of the group. Latter, Quintanar et al. (2010) characterized the subtribe Koeleriinae giving a list of morphological characters in contraposition to those of Aveninae.

Our current results show that Aveninae s.l. can be splitted into two monophyletic subtribes, Aveninae s.s. and Koeleriinae, two closely related but not intermingled groups. This result is in agreement with those previously obtained by some authors who have recently advocated the resurrection of this subtribe, to classify precisely the genera in which this work is especially focused (Quintanar et al., 2007, 2010; Saarela et al., 2017). Our results support that *Trisetum* is paraphyletic (Quintanar et al., 2007; Wölk & Röser, 2014, 2017; Saarela et al., 2010, 2017), and that it is situated at the base of the Koeleriinae in both clades, Koeleriinae clade I and Koeleriinae clade II. The combination of characters of *Trisetum* is the most plesiomorphic comparing with the other genera of the subtribe, having the less reduced structure of its lemmas, supporting the hypothesis that *Trisetum* is the original group of the rest of the generic variability of the Koeleriinae (Quintanar et al., 2007).

Aveninae s.s.

The subtribe Aveninae s.s. (excl. Koeleriinae) is thus restricted to the genera *Arrhenatherum*, *Avena*, *Helictotrichon*, and *Tricholemma*. In the nuclear topologies of those previous studies in which this subtribe was well sampled (Soreng & Davis, 2000; Quintanar et al., 2007; Saarela et al., 2017), the Aveninae included the subtribe Sesleriinae as a sister lineage to the genus *Avena*, as well as both *Arrhenatherum* and *Tricholemma* sister to *Helictotrichon*, while, in the plastid topologies (Winterfeld et al., 2009; Saarela et al., 2017), *Arrhenatherum* resulted to be sister to *Avena*. Wölk & Röser (2013, 2014) segregated the African genus *Trisetopsis* from *Helictotrichon*, which resulted to be a polyphyletic genus. *Trisetopsis* was indeed resolved with ITS and plastid markers within Koeleriinae clade, together with New World species of the genera *Calamagrostis*, *Graphephorum*, *Peyritschia*, and *Sphenopholis* (Wölk & Röser, 2014, 2017). As indicated below (see clade U), the analyses of *topo6* showed that *Trisetopsis* contained two different copy types (A and B). *Trisetopsis junghuhnii* and *T. virescens* are two Southeastern Asian species which have a second copy type of ITS not present in the African ones, which can be lost due to processes of gene conversion or unequal crossing over (Wölk & Röser, 2017), resolving in Aveneae clade. Wölk & Röser (2017) described the genus *Tzveleviochloa* (see clade E), which has some clones of the nuclear gene *topo6* included in *Helictotrichon* clade; moreover, they described a hybrid genus between *Helictotrichon* and *Trisetopsis* not included in our study, x*Trisetopsotrichon*, with its plastid and ITS topologies resolved in Aveninae clade, and in nuclear *topo6* topology with African *Trisetopsis*.

In major agreement with previous studies (Quintanar et al., 2007; Wölk & Röser, 2014, 2017; Saarela et al., 2017), in our plastid topology the Aveninae result to be a monophyletic lineage, enlarged in the nuclear topology with the Sesleriinae (here named ITS incongruence 1), and with a single species of

Trisetopsis from Southeastern Asia, *Trisetopsis junghuhnii* (ITS incongruence 2). In sum, the Aveninae is divided into two main subclades, the latter including three subgroups: 1) the clade A: *Avena* (plus the Sesleriinae in the nuclear topology, which are included in the "Poeae chloroplast group 2" in the plastid one); 2a) the clade B: *Tricholemma* (plus *Trisetopsis junghuhnii* in the nuclear topology, which is placed with *Deyeuxia* sect. *Viridiflavescentia*, *Leptophyllochloa* and the African species of *Trisetopsis* in the plastid one); 2b) the clade C: *Arrhenatherum*; 2c) the clade D: *Helictotrichon* p.max.p. The four genera considered to be classified in Aveninae s.s. have been resolved as monophyletic ones in our combined nuclear and plastid trees. The mostly annual genus *Avena* (clade A; except for one species, *A. macrostachya*, not sampled) is sister lineage to other formed by the perennial genera of the Aveninae (clades B, C, and D), as well as the pan-Mediterranean perennials *Tricholemma* and *Arrhenatherum* are both sister to the large perennial genus *Helictotrichon*. These results do not allow us to state the type the life cycle of the ancestors of this subtribe could have been. The inclusion of the only perennial representative of the genus *Avena* could enlighten this regard. The subtribe Aveninae s.s., conformed by the genera here mentioned and excluding the incongruences mainly due to the inclusion of the Sesleriinae, is morphologically well-characterized by their large spikelets and by having 1-7 florets per spikelet, hairy ovaries, long-linear hila, grooved embryos, and mostly solid endosperms (Clayton & Renvoice, 1986; Watson & Dallwitz, 1992; Quintanar et al., 2010).

Sesleriinae

The close relationship between the subtribe Sesleriinae and Aveninae s.l., as well as their incongruent placement in nuclear and plastid topologies, are a constant result in all previous phylogenetic studies which have included this group (Soreng & Davis, 2000; Döring et al., 2007; Döring 2009; Quintanar et al., 2007; Soreng et al., 2007; Gillespie et al., 2008; Schneider et al., 2009; Saarela et al., 2010, 2017). According to Soreng et al. (2015, 2017), the Sesleriinae include the genera *Sesleria, Oreochloa, Echinaria, Sesleriella,* and *Mibora*. The differences found in the relationships of this subtribe highly depend on the number of sampled representatives. Quintanar et al. (2007) included four genera (*Echinaria*, *Sesleria*, *Mibora*, and *Oreochloa*), being resolved with the Aveninae in the ITS tree and in the "Poeae chloroplast group 2" in the plastid tree. Minaya et al. (2013, 2015), using the nuclear gene *beta amylase*, presented a combined plastid and nuclear tree but did not point out any incongruence; in this study, the only representative of the Sesleriinae, the genus *Echinaria*, was placed into a clade with *Corynephorus*, *Deschampsia* and *Holcus*. Hochbach et al. (2015) combined nuclear markers (*Topo6*, *PhyB*, *Acc1*) and showed a polyphyletic Sesleriinae with *Mibora* included within Poeae chloroplast group 2 and *Echinaria* and *Sesleria* within Poeae chloroplast group 1. The nuclear topology of Saarela et al. (2017), with a much larger sampling, showed the genera *Echinaria* and *Sesleria* placed into a clade sister to another including *Mibora* and *Oreochloa*, being all together the sister group of the genus *Avena*, though this relationship was weakly supported. The plastid *trnL–trnF* topologies of Saarela et al. (2017) showed the Sesleriinae genera *Sesleria*, *Mibora* and *Oreochloa* to be sister to the Holcinae; however, the *matK* topology do not include the Holcinae, and the genus *Echinaria* was not placed in the same clade than those other three genera being sister to *Helictochloa*, *Dactylis* and *Lamarckia*, while in the *matK* topology presented by Hochbach et al. (2015) *Mibora*, *Sesleria* and *Echinaria* formed a moderate supported clade included in Poeae chloroplast group 1.

In our study we have included three of the five genera classified in the subtribe Sesleriinae: *Sesleria*, *Oreochloa* and *Mibora*. The nuclear topology (ITS incongruence 1) shows a polyphyletic scenario for the Sesleriinae. Both *Mibora* and *Oreochloa* were grouped in a weakly supported clade, which is resolved as sister to the genus *Avena* (clade A). All together (*Mibora* + *Oreochloa* + *Avena*) are shown as sister to *Sesleria* with a relationship not strongly supported but constant. Conversely, our combined plastid topology, all the genera of the Sesleriinae are resolved as a monophyletic and in a strongly supported clade, being part of the Poeae chloroplast group 2 (plastid incongruence 1) and sister to the subtribes Holcinae, Airinae p.p., Loliinae, Parapholiinae, Cynosurinae, and Aristaveninae, with which they form a weakly supported clade.

It is not easy to find diagnostic morpho-anatomical characters able to link the Sesleriinae with the groups to which they are associated in the different topologies, not even among the genera traditionally classified in this subtribe, such as *Sesleria*, *Oreochloa* and *Echinaria*. Sesleriinae is characterized by having leaf-sheaths of fused margins and dense, one-sided or capitate inflorescences (Kellogg, 2015). However, the western Mediterranean-Atlantic annual genus *Mibora* presents a higher number of morphological differences within the other genera of the subtribe, being characterized by having inflorescences with imbricate spikelets, borne on short pedicels on one side of the rachis, without rachilla extension, glumes longer than the floret, palea pubescent and no lodicules (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992; Kellogg, 2015). Kellogg (2015) affirmed that the low chromosome numbers of three of the genera of the subtribe ($2n = 14$, sometimes 18 in *Echinaria*) indicate that polyploidization may not be involved in explaining their problematic systematic affinities; however, considerable polyploidy have been found in *Sesleria*, sometimes attributed to autopolyploidy (Kuzmanović et al., 2013). Further studies with nuclear low copy genes will surely help to explain the conflicting gene trees and to determine if they really constitute a true natural group together with *Mibora*. Following Soreng et al. (2017), those evidences of the mixture of morphologies and chloroplast types indicating reticulation and hybridization support the classification in favor of series of subtribes, instead of the two tribes Aveneae and Poeae.

Koeleriinae

Our topologies show two moderate to strongly support monophyletic clades for Koeleriinae, here named Koeleriinae clade I and Koeleriinae clade II. The Koeleriinae clade I includes a wide sampling of the large perennial genera *Trisetum* p.p. and *Koeleria*, as well as many other small annual circum-Mediterranean lineages such as *Trisetaria*, *Rostraria*, *Avellinia*, and *Gaudinia*, the Central Asian x*Trisetokoeleria*, and the Asiatic recently described *Tzveleviochloa*. The Koeleriinae clade II also includes *Trisetum* p.p., as well as the American annual monospecific genus *Limnodea*, the perennial American genera *Sphenopholis*, *Graphephorum*, *Peyritschia*, and *Leptophyllochloa*, the Mexican Central and South American complex *Calamagrostis*/*Deyeuxia*, and the recently described *Trisetopsis*. In our combined plastid and ITS topology, there are two incongruent clades (incongruences 3 and 6) within the Koeleriinae clades I and II [clades A and B in Saarela et al., 2017].

Koeleriinae clade I

The clade E

In our results, the clade E of the combined plastid and ITS tree has an unsupported to weakly supported internal structure. This clade contains all of the sampled species of *T.* sect. *Acrospelion*, a part of the Eurasian species of *T.* sect. *Trisetum*, the Asiatic *Helictotrichon delavayei*, and a group of New World taxa including *Graphephorum* and *T. cernuum* corresponding with the ITS incongruence 3. Besides we also included in the ITS topology *Tzveleviochloa parviflora* and *Helictotrichon sumatrense*. The Eurasian *Trisetum* sect. *Acrospelion* comprises nine taxa: *T. argenteum*, *T. buschianum* subsp. *buschianum*, *T. buschianum* subsp. *transcaucasicum*, *T. distichophyllum*, *T. macrotrichum*, *T. rigidum* subsp. *rigidum*, *T. rigidum* subsp. *teberdense*, *T. tamonanteae*, and *T. velutinum*. This section is characterized mainly by the distichous-pectinated disposition of the leaf-blades in the young shoots, and the long hairs of both rachilla and callus (Barberá et al., 2017b). Except the Canarian *T. tamonanteae*, the rest of species of the section has been included in our study, being most of them sampled for the first time (the only previously sampled species have been *T. distichophyllum* and *T. argenteum*). Among the closely related species of *Trisetum* sect. *Trisetum* [*T. alpestre*, *T. altaicum*, *T. baregense* (now reduced to synonym of *T. alpestre* (Barberá et al., in review)), *T. bertolonii*, and *T. glaciale*], only *T. altaicum*, *T. glaciale*, and *T. baregense* had been included in previous studies (Quintanar et al., 2007; Saarela et al., 2010, 2017; Wölk & Röser, 2014, 2017).

Quintanar et al. (2007) included the species *Trisetum baregense* and *T. glaciale*, both collapsing in the nuclear topology into a polytomy with *Koeleria*, *T.* sect. *Trisetaera*, and *Graphephorum wolfii*, while in the plastid topology, were resolved as sisters to *Trisetaria panicea* and in the same clade with *Avellinia festucoides*, *Trisetum flavescens*, *T. gracile*, and *Rostraria*. Recently, Wölk & Röser (2017), in their study with the nuclear markers ITS and *topo6* and plastid *matK*, described a new Asiatic genus, *Tzveleviochloa*, morphologically intermediate between *Helictotrichon* and *Trisetum*. In their plastid topology, *Tzveleviochloa* was resolved together with *Trisetum glaciale*, while *T. distichophyllum* and *T. argenteum* were resolved as sister to *Koeleria*, *Gaudinia fragilis*, and *Trisetaria panicea*; in the ITS tree, *Trisetum altaicum* was sampled for the first time and placed in a group with *Trisetum cernuum*, *Graphephorum*, *Tzveleviochloa*, and *Helictotrichon sumatrense*, closely related to another lineages such as that of *Trisetum distichophyllum*, *T. argenteum*, and *T. glaciale*, and of *T. flavescens*, *Trisetaria aurea* and *Trisetaria linearis*. In the nuclear *topo6* topology, some clones of *Trisetum argenteum* were resolved as sister to *Koeleria* + *T. spicatum*, while the rest of them resulted as sister to *T. spicatum*, *Tzveleviochloa*, some *Graphephorum* and *Trisetum cernuum* clones, being *T. glaciale*, *T. distichophyllum*, and some clones of *K. litvinowii* at the base of this clade. Wölk & Röser (2017) indicated that the nuclear gene *topo6* phylogenies corroborated the close relationship of *Graphephorum* with *Trisetum cernnum*, obtaining some of the clones of these species as part of *Sphenopholis*, *Peyritschia*, and *Trisetopsis*, and other clones as part of the group with *Tzveleviochloa*, *Trisetum spicatum*, *T. argenteum*, clones of *K. litvinowii*, *Trisetum distichophylum*, and *T. glaciale*. According with their results, Wölk & Röser (2017) suggested that *T. cernuum* could possibly be a link between *Trisetum* and *Graphephorum*.

The ITS topology of Saarela et al. (2017) showed how *Trisetum glaciale* and *T. gracile* were resolved as sister to *Graphephorum*, *Trisetum cernuum*, and *T. distichophyllum* but with scarcely supported relationships, while in the plastid tree *T. distichophyllum* was resolved as sister to a large clade containing *Avellinia*, *Trisetum flavescens*, *Rostraria pumila*, *Gaudinia fragilis*, *Koeleria* sp. pl., and several species of *Trisetum* sect. *Trisetaera*. Saarela et al. (2017) also indicated that *Graphephorum* and *Trisetum cernuum* were incongruent in plastid and ITS topologies, belonging to Koeleriinae clade II in the plastid tree, while they were included together with *T. distichophyllum*, in Koeleriinae clade I, concluding that they are probably of hybrid origin, although the parental species from which they might have arisen in Koeleriinae clades I and II are unknown.

In our combined plastid and ITS tree, the abovementioned species of *Trisetum* sect. *Acrospelion* and *T.* sect. *Trisetum* p.p. are placed within a moderately to strongly supported clade, which includes *Tzveleviochloa parvifolia* together with two species of *Helictotrichon*, *H. sumatrense* and *H. delavayei.* The latter, according with molecular and morphological data, should be transferred to the genus *Tzveleviochloa.* However, all those species of *Trisetum* are not placed together in the ITS tree but they are separated into some weakly to strongly supported lineages, basal to the other Koeleriinae clade I, with scarce support for their inner relationships. In both, nuclear and plastid trees, the species of *Trisetum* sect. *Acrospelion* are grouped in two clades: 1) the Carpathian *T. macrotrichum*, the South-Iberian *T. velutinum*, and the Alpine *T. distichophyllum* and *T. argenteum*; 2) the Caucasian species *T. rigidum*, *T. teberdense, T. buschianum*, and *T. transcaucasicum* appear as a sister clade to the Apennine species *T. bertolonii* with scarce support. This species is easily differentiated from the rest of species of the genus mainly by its habit, with convolute or filiform leaves, pubescent culms, and by its long aristules and awns. Moreover, *Trisetum bertolonii* is the species of *T.* sect. *Trisetum* with the longest callus hairs and the most marked differences in length between palea and lemma, sharing these characters with other species of *T.* sect. *Acrospelion*. Also, in the ITS topology, *Tzveleviochloa* and *Trisetum altaicum* are grouped with the species before indicated and the ITS incongruence 3. These incongruent placements of this group of species have been previously indicated by earlier studies (Wölk & Röser, 2014, 2017; Saarela et al., 2017). Our results add some additional taxa to this lineage: the South American *Trisetum ambiguum* and *Koeleria mendocinensis*, and the North American *T. longiglume* var. *glabratum*, and *T. ortochaetum*. The topologies based on both plastid and ITS or low copy nuclear *topo6* markers show evidences of reticulation in the origin of the genus *Graphephorum, Koeleria mendocinensis* and these three species of *Trisetum*. Most of the species of the grouped taxa of the incongruence have hairy ovaries, instead of *Graphephorum melicoides* and *Trisetum longiglume* var. *glabratum*, with glabrous ones. This character is also present in three species of *Trisetum* in the clade E, the Alpine and Carpathian species *T. alpestre* and the Northern Spanish and Pyrenean *T. baregense* and *T. glaciale*. Another evidence of the reticulate origin of the species included the ITS incongruence 3 is the difference shape of their lemma apex, a good taxonomical character. It can have four short apical awns in *Trisetum ambiguum*, and *T. longiglume* var. *glabratum* as in some species of the complex *Calamagrostis/Deyeuxia*, entire to slightly bidentate in *Graphephorum*, *Trisetum ortochaetum*, *Koeleria mendocinensis*, and *Sphenopholis* (Molina 1993; Finot et al., 2004, 2005a, b), or bisetulate in *T. cernuum* (Molina, 1993; Finot et al., 2004, 2005a, b). The Argentinian *Koeleria mendocinensis* is the only representative of the genus not included in the clade L; it is singular due to its ovary with scattered hairs at the apex, and its marked elliptic hilum (Molina, 1993). The small North American genus *Graphephorum* have been included in *Trisetum* by some authors (Louis-Maire, 1928; Rumely, 2007) differing from this genera in having an entire lemma apex, the dorsal awn reduced to a subapical mucro, and paleas tightly enclosed by the margins of the lemma (Finot et al., 2005b). Therefore, those inconsistences in the resolution of species or genera between plastid and ITS analyses point out to hybridization and reticulate evolution between *Trisetum* and other Koeleriinae genera. Thus, the taxa included in the incongruence 3, as indicated by Saarela et al. (2017), could be treated as a putative hybrid genus, whose origin could be related to its speciation beyond a primary hybridization event, a common evolutionary process in other Poeae genera (Gillespine et al., 2008), and it could be considered a nothogenus.

As indicated before, E clade composed mainly by Eurasian perennial species of *Trisetum* is sister to the rest of species of Koeleriinae clade I, which form a clade in the combined plastid and ITS tree weakly supported. Thus, a deeper study is needed to confirm the hypothesis that this group of Eurasian plants shares a common ancestor with the Koeleriinae clade I.

Clades F, G, H, I, J, and K

The rest of the species included in Koeleriinae clade I mainly belong to the genera *Koeleria* and *Trisetum* sect. *Trisetaera*, plus some species of *T.* sect. *Trisetum* in addition to several small and annual genera adapted to the dry and open places of the Mediterranean area and surroundings, which are *Avellinia*, *Trisetaria*, *Rostraria*, and *Gaudinia*.

The clades F, G, and H are grouped into a larger and strongly supported clade, which includes the rest of Eurasian species of *Trisetum* sect. *Trisetum* (those not placed in the clade E), *Trisetaria* p.p., and *Rostraria* p.p. The type species of *Trisetaria, T. linearis,* is basal to two sister clades, the clade G with *Trisetum* sect. *Trisetum* p.p. (including the type species of the genus, *T. flavescens*, and the allied species *T. gracile*) plus *Trisetum bungei*; the clade H includes of *Trisetaria lapalmae* and several lineages of *Rostraria*, some of this last genus constituting the ITS incongruence 4. *Trisetaria linearis* is distributed from the northern Africa to the southwestern Asia and is characterized by its linear and spiciform panicles, 1 or rarely 2-flowered, subtended by an inflated leaf sheath, and by its lemma with long aristules and a short central awn inserted in the upper ¼ of the lemma (Cope, 2005; Ibrahim et al., 2016). This annual species was also included in the study of Wölk & Röser (2017) with the low copy nuclear gene *topo6*, and was placed into a strongly supported group with *Lagurus ovatus* and some clones of *Avellinia festucoides* and *Rostraria cristata*, while in the ITS topology was resolved as sister to *Trisetaria aurea* and *T. flavescens*, and in the plastid *matK* also including *Rostraria cristata*. Although we have not included samples of *Trisetaria aurea*, the inclusion of a higher number of specimens in our analyses provides new insight into their affinities. As in previous studies (Quintanar et al., 2007; Saarela et al., 2010, 2017), the endemic species *Trisetum gracile* from the mountains of South Corsica and Sardinia is sister to the *Trisetum flavescens* group (clade G). Apart from the different life cycle, *Trisetum gracile* shares morphological characters with the Mediterranean annual species *Trisetaria aurea*, being caespitose and with short culms, sheaths somewhat inflated, short upper culm leaves, lemma sometimes pubescent and with the dorsal awn inserted close to the middle (below it in *T. gracile*) (Jonsell, 1980a; Jeanmonod & Gamisans, 2007; Barberá et al., in review). Most of the subspecific ranks of the polymorphic and widely distributed *T. flavescens* have been sampled for this study and they were altogether placed into a monophyletic clade, which includes the endemic Iranian *Trisetum bungei*, a synonym of *T. flavescens* (Barberá et al., in review). Another species, *Trisetum turcicum* has been always related with *T. flavescens* in molecular studies (Grebenstein et al., 1998; Quintanar et al., 2007, 2010; Saarela et al., 2010, 2017) but this wrong relationship was due to a misidentification of the samples used by Grebenstein et al. (1998), which actually correspond to *T. flavescens*. The real *Trisetum turcicum* seems to be closely related to *T.* sect. *Sibirica* and is to be classified among the lineages of the Koeleriinae clade II (commented below).

The clade H is separated in two sister subclades. One of the subclades is strongly supported, including *Rostraria litorea* and *R. salzmannii*, which have been differentiated mainly by the awn length and the pattern of distribution of the indumentum of panicles and spikelets. Both species were classified by Domin (1907) in *Koeleria* subsect. *Aequiglumes*, and later by Jonsell (1980b) in *Lophochloa* subgen. *Aegialina*, being characterized by their subequal glumes and elongate anthers. Sherif & Siddiqi (1988) suggested their possible hybridization, due to the existence of intermediate specimens, thus their closeness here is not surprising. The other subclade is weakly to strongly supported, and includes *Trisetaria lapalmae*, *Rostraria pumila*, and the incongruence 4, which in the plastid topology includes *R. balansae*, *R. cristata*, *R. obtusiflora*, and *R. smyrnacea*. Domin (1907) classified *R. pumila* in *Koeleria* subsect. *Trisetiformes* because of its unequal glumes, subapical awns and densely hairy rachilla, and its affinities with the genus *Trisetaria* have been already pointed out (Sherif & Siddiqi, 1988). Thus it is not surprising its close relationship with *Trisetaria lapalmae*, which is mainly differentiated from *Rostraria pumila* by its longer aristules and geniculate awn, which is more deeply inserted at the lemma. Scholz & Böcker (1996) observed both species growing up sometime very close to each other as well as intermediate morphological characters. The plastid topology shows *R. cristata*, *R. obtusiflora*, *R. smyrnacea*, and *R. balansae* as sister to *R. pumila* with a weak support. Conversely, the ITS topology shows *R. cristata* and *R. obtusiflora* resolved, with a weak support, close to *R. hispida* and *Trisetaria panicea*, as well as to *Gaudinia* and the rest of species of *Trisetaria*, including *T. ovata*, a result pointed out in previous studies (Quintanar et al., 2007; Saarela et al., 2017). Those species of *Rostraria* belonging to incongruence 4 and *R. hispida* are characterized by having unequal glumes. Quintanar et al. (2007) named this group as “Trisetum ovatum group” a markedly xerophytic lineage with either strongly contracted panicles (*Trisetaria* p.p. and *R. hispida*) or more or less lax spiciform inflorescences

(*Gaudinia*). *Rostraria smyrnacea* and *R. balansae* have been included in our study only for the plastid topologies, being sampled for the first time. Both species are morphologically close to *R. cristata* and *R. obtusiflora*. *Rostraria cristata*, the type of the genus *Rostraria*, is a high polymorphic and widely distributed species. In the analysis with the low copy nuclear gene *topo6* (Wölk & Röser, 2017), some clones of *R. cristata* were resolved as sisters to *Trisetaria linearis* and the rest as sisters to *Gaudinia fragilis*, supporting the existence of reticulation in the group. Furthermore, Saarela et al. (2017) suggested the hybrid origin of at least some cytotypes of *R. cristata*, which is reinforced by the different levels of ploidy recorded for this species.

The clades I, J and K comprises the rest of the sampled annual taxa such as *Avellinia*, *Trisetaria* p.p., *Rostraria p.p.*, and *Gaudinia* (including *Rostraria cristata* and *R. obtusiflora* in the nuclear tree). The Mediterranean monospecific genus *Avellinia* (clade I) is resolved on a long branch in both, plastid and ITS topologies, as a sister group of the rest of the clades of Koeleriinae clade I (clades J, K and L). *Avellinia* has sometimes been associated to either *Trisetaria* (Clayton & Renvoize, 1986) or *Rostraria* (Romero-Zarco, 1996) and is characterized by its unequal glumes [noticeably difference in length if compared to the usual in *Rostraria* according with Romero-Zarco (1996)], contracted panicles and non- to slightly-keeled lemmas that are apically bifid and muticous to shortly and subapically awned. These results are consistent with the ITS and ITS+ETS topologies of earlier studies (Quintanar et al., 2007; Saarela et al., 2017). In their nuclear *topo6* topology of Wölk & Röser (2017), *Avellinia festucoides*, *Rostraria cristata*, *Lagurus ovatus*, and *Trisetaria linearis* form a strongly supported group. In previous plastid topologies with few samples of these groups (Quintanar et al., 2007; Saarela et al., 2010), *A. festucoides* resulted sister to three species of *Rostraria* (*R. litorea*, *R. obtusiflora*, *R. salzmanii*, and *R. pumila*), *Trisetum flavescens*, *T. baregense*, *T. glaciale*, and *Trisetaria panicea*.

The annual genus *Gaudinia* is characterized by having spicate unbranched inflorescence with a more or less fragile rachis at fruiting which disarticulates just above the spikelet (Stace & Tutin, 1978; Kellogg et al., 2015). This genus, represented in our study by *G. fragilis* and *G. hispanica*, appears as paraphyletic. The Iberian endemism *Gaudinia hispanica* is resolved as sister to *Trisetaria dufourei*, both with a very different morphology. Accordig to Catalán et al. (2007), in the Loliinae subtribe the "development of a spike inflorescence with a depressed or excavated rachis and loss of the lower glume, is inferred to have taken place in parallel in both the broad- (*Lolium*) and fine- leaved (*Psilurus*) lineages, as well as in Parapholiinae (*Hainardia*)". Within the broad-leaved clade of *Festuca* s.l., the monotipic *Micropyropsis* would represent an intermediated state in the evolution from a panicle (*Festuca* s.s.) to the spike of *Lolium*, with short-pedunculated spikelets that conserve two well developed, unequal glumes.Taking into account these precedents, a close phylogenetic relationship between the species of the genus *Gaudinia* and those of the *Trisetaria*-*Rostraria* complex of K clade is less surprising.

The same close relation between *Gaudinia* and *Trisetaria* and *Rostraria* were also obtained by Quintanar et al. (2007), but including a less number of samples. Soreng et al. (2007), in the plastid topologies, included the same two species of *Gaudinia*, resulting to be monophyletic due to the not inclusion of any species of *Trisetaria* or *Rostraria*. In previous nuclear topologies (Quintanar et al., 2007;

Saarela et al., 2017), *Gaudinia* resulted as sister to *Trisetum* sect. *Trisetaera* + *Koeleria* clade, or to *Rostraria cristata* (Wölk & Röser, 2017). Saarela et al. (2017) included in the *matK* tree the species *G. coarctata*, endemic to the Azores Islands (Galán de Mera et al., 2014), also resulting not monophyletic due to the inclusion of *Trisetaria loeflingiana* in the same clade. This species of *Gaudinia* was also included in a plastid tree, resulting as sister to *Rostraria azorica*, in a study in which they are the only representative of Koeleriinae (Grass Phylogeny Working Group II, 2012).

According to Röser (1997), the evolution of annual lineages from perennial ones in the Mediterranean-type climatic zone is recognized to be an important source of diversification in avenoid grasses, an adaptation facilitating the colonization of ephemeral or disturbed habitats (Quintanar et al., 2007). These annual genera have been historically threated to be close or included in *Trisetum* or *Koeleria* (Quintanar et al., 2007). The problematical classification of these genera indicates the morphological homoplasy of the Koeleriinae, before pointed out by Soreng et al. (2007) and Quintanar et al. (2007). As in previous studies, apart from the monospecific genus *Avellinia*, the genera *Trisetaria* and *Rostraria* are not resolved as monophyletic. Depending on the authors, *Trisetaria* and *Trisetum* have been treated as one genus (Paunero, 1950; Maire, 1953; Watson & Dallwitz, 1992) or as independent genera (Tzvelev, 1976; Clayton & Renvoize, 1986; Quintanar et al., 2007, 2010; Saarela et al., 2010, 2017; Barberá et al., 2017a, 2017b) separated by their life cycle, but having their spikelet structure essentially identical. Moreover, the strong resemblances between the lemma of *Trisetum* sect. *Trisetum* (*T. flavescens* group) and *Rostraria* have been indicated by earlier studies (Hubbard, 1937; Holub, 1974; Jonsell, 1975; Quintanar et al., 2007). The different placements for these groups has been explained by past reticulation, the main evolutionary process argued to explain misplacements of genera within lineages in tribe Poeae, obscuring taxon boundaries (Soreng & Davis, 2000; Quintanar et al., 2007, 2010; Gillespine et al., 2008). Up to the moment, this work includes the highest number of species of those genera.

The clade L

Our results confirm the close relationship existing between the genus *Koeleria* and *Trisetum* sect. *Trisetaera*, which species are all together in clade L, and in line to the previous phylogenetic studies with several markers (Soreng & Davis, 2000; Quintanar et al., 2007; Saarela et al., 2010, 2017; Wölk & Röser, 2017). The number of representatives of these two taxa in these studies was scarce and could not let go far away of this minimal insight. With the widest sampling up to now, Saarela et al. (2017) obtained different topologies in nuclear and plastid trees: on one hand, their nuclear topology presents all the species of *T.* sect. *Trisetaera* and *Koeleria* forming a single clade with little internal structure; on the other hand, in the plastid one, *T.* sect. *Trisetaera* form a clade with three species of *Koeleria* (*K. macrantha*, *K. permollis*, and *K. vallesiana*), while other three species of *Koeleria* (*K. capensis*, *K. lobata*, and *K. splendens*) are excluded from the clade and their affinities in Koeleriinae clade I are unresolved. Finally they pointed out the possibility of ancient hybridization events in these groups.

In our study, a very extensive sampling of these groups has been made and has let us to explore the relationships between this section of *Trisetum* and the different sections of *Koeleria*. Their systematic closeness has not only been appreciated in the last molecular studies including both taxa, but had previously been pointed out by various authors on a morphological basis, and focusing, above all, to the type and most widespread species of the section, *T. spicatum* (Reichenbach, 1830; Tzvelev, 2011). *Trisetum spicatum* and its allied species share with *Koeleria* very contracted panicles with short branches, pyramidal or frequently ovate in outline, as common characteristics. Moreover, the species of *T.* sect. *Trisetaera* do not have, noticeably and like many other species of *Trisetum*, long awns, habitually short aristules, sometime missing (Hultén, 1959; Tzvelev, 1976, 2011). This reduction of length in panicle branches and of both size and length of awns are, without any doubt, convergent characters with those of *Koeleria*, which generally presents very contracted panicles, and muticous lemmas, though, occasionally, a short apical awn can be observed (Quintanar & Castroviejo, 2013). Enuschenko (2011), in a revision of *Trisetum* for the Northern Asia, recently described a new subsection in *Trisetum* sect. *Trisetaera*, named subsect. *Koeleriformia*, including the species of *T. spicatum* complex, because of their resemblance with *Koeleria*. This group was separated from *T. altaicum* and *T. subalpestre* (named *T. agrostideum*), included in subsect. *Agrostidea* Prob. As indicated above, *T. altaicum* resulted to be included in E clade, together with other Eurasian *Trisetum*, and *T. subalpestre* at the base of one of the groups of L clade. Regarding to the American species of *T.* sect. *Trisetaera*, we have followed Finot et al. (2004, 2005a, b) taxonomical arrangement, where they recognized 18 species. Of them we included 11 species, of which six have been sampled for the first time, namely *T. ambiguum*, *T. barbinode*, *T. caudulatum*, *T. ligulatum*, *T. longiglume*, and *T. projectum*. Finot (2010) provided a more synthetic approach, reducing the number of species which would difficult a detailed analyses of the variability of some taxa.

One important feature of this clade is the polyphyly of the type species of the involved taxa, *K. pyramidata* and *T. spicatum*. The different samples of this two species appear dispersed in this big clade, in more or less supported subclades. They would be specific complexes rather than species, with the highest morphological plasticity and widest distribution area of their respective genera, as it has previously been indicated by some authors (Hultén, 1959; Jonsell et al., 1975; Quintanar & Castroviejo, 2013). Both, *K. pyramidata* and *T. spicatum* are polyploidy species and inhabit large areas from cold and temperate zones of North America and Eurasia, being *T. spicatum* also extended to Central and South America, New Guinea, Borneo, Australia, and New Zealand (Domin, 1907; Hultén, 1959; Jonsell et al., 1975; Finot, 2004, 2005a, 2005b; Weiller et al., 2009; Quintanar & Castroviejo, 2013). The infraspecific diversity of *T. spicatum* and *K. pyramidata* has been unambiguously circumscribed, due to the absence of good morphological characters for its classification, which is relationated with the great reduction of the spikelet structure in both species, especially in *K. pyramidata*, and the role of polyploidy in their evolution (Jonsell et al., 1975; Pecinka et al., 2006). Because of all these reasons, it can be supposed that these species conserve the higher number of plesiomorphic characters of the group.

The representatives of *Koeleria* and *Trisetum* sect. *Trisetaera* of clade L have been structured into several more or less supported subclades or nested subclades (L1 to L4). In our combined plastid and ITS tree, most of the species of *T.* sect. *Trisetaera* are grouped in two strongly supported groups of L clade

(L3 and L4), while most of the species of *Koeleria* are included in basal subclades partially well supported (L1 and L2).

The L1 and L2 groups contain most of the sampled species of *Koeleria*, including Eurasian and African species. The most recent classifications of the around 50 species of *Koeleria* recognize five sections, following the previous one made by Domin (1907): *K.* sect. *Africanae* Domin, *K.* sect. *Bulbosae* Domin, *K.* sect. *Imbricatae* (Domin) Tzvelev, *K.* sect. *Koeleria*, and *K.* sect. *Reticulatae* (Domin) Quintanar & Castrov. (Quintanar et al., 2010; Tzvelev, 2011; Quintanar & Castroviejo, 2013). *Koeleria* sect. *Africanae*, characterized by its densely tufted habit and more or less narrow leaves (Domin, 1907), is represented in our study by *K. capensis*, which samples are together in one of the subclades. L1 also contains species of *Koeleria* from the Balkans, Caucasus, Middle East, and surrounding areas. Those species are mainly *K. glaucovirens* and *K. kurdica*, representatives of *Koeleria* group “Nitidulae” Domin, which are characterized by being densely tufted, glabrous, pyramidal panicles slightly lax, and with usually narrow spikelets; they are also accompanied by *K. caucasica* and *K. eriostachya*, which are high mountain species with tufted habit, by two species adapted to xeric habitats and with the base of the culms conspicuously swollen, *K. splendens* (*Koeleria* sect. *Koeleria*), and *K. glauca* (*Koeleria* subsect. *Glaucae* Domin; not included in Quintanar's (2010) treatment) (the latest usually conspicuously with blunt glumes and lemma apex), and as indicated above, *K. pyramidata* p.p. With those groups, other species are intermingled, some from Central and with caespitose habit, like *K. altaica* and *K. transiliensis*, and other with a more restricted distribution, like *K. brevis* distributed from the North of the Black See basin and having swollen culms at the base and extremely contracted panicles (Domin, 1907; Tzvelev, 1976; Dogan, 1985).

The L2 group composed mainly by species of Mediterranean *Koeleria*, is basally surrounded by unsupported clades with *K. loweana*, *Trisetum hispidum*, and *K. pyramidata* p.p. *Koeleria loweana* is a robust species with a very high ploidy level (near 25*x*), endemic to Madeira (Quintanar et al., 2006), while *T. hispidum* is endemic to the Northwest Iberian Peninsula, and also has a robust habit, being densely villous. *Trisetum hispidum* is resolved separated from rest of *Trisetum* and it clearly has morphological affinities with *Koeleria*, like its narrowly cylindrical and shortly branched panicles, and lemma shorty awned and with the awn inserted on the upper part (Jonsell, 1980a; Humphries, 1980). Apart from several European or Iberian specimens of *K. pyramidata* (including *K. pyramidata* subsp. *schroeteriana* and *K. pyramidata* subsp. *arenaria*), this second group (L2) includes representatives of *K.* sect. *Koeleria*, *K. crassipes* and *K. dasyphylla*, two Ibero-African species with culms swollen at the base, and also representatives of the conspicuous *K.* sect. *Reticulatae*, including samples of Ibero-North African species *K. vallesiana* and the Central Spanish *K. castellana*, two species with also culms swollen at the base but characterized by having a reticulate appearance due to rests of old leaf sheaths (Quintanar & Castroviejo, 2013). None of monophyly of the species of this clade above commented, most of them with a high number of samples in our analysis, like *K. crassipes* or *K. vallesiana*, beside the specimens of *K. pyramidata*, all of them supported by the morphology, have resulted with any support. In the other hand, one of the clades weakly supported, containing several specimens of European *K. pyramidata*, also includes the North American *T. spicatum* subsp. *pilosiglume* and *T. spicatum* subsp. *molle*. These two infraspecific taxa were described by Hultén (1959) but the lack of morphological discontinuities, as in the rest of infraspecific taxa described for North America leads not to recognize infraspecific delimitations (Randall & Hilu, 1986; Finot et al., 2005b).

The L3 group, including a high number of the sampled *T.* sect. *Trisetaera*, is strongly supported, being also surrounded by a weakly supported sample of *K. hirsuta*. *Koeleria hirsuta* is an Alpinian endemism included in *K.* sect. *Imbricatae*, characterized by its basal swollen culms, recovered by numerous leaf sheaths tightly imbricated, by its hirsute spikelets and lemma with a longer subapical awn (Domin, 1907; Humphries, 1980). This group (L3) includes the Asiatic species *T. clarkei*, which boundary with *T. spicatum* is obscured by intermediates, tending to be taller and to have a slightly looser panicle of narrower spikelets with well-exerted awns (Wu & Phillips, 2006). Part of the representatives of North and South American *T. spicatum* are included here, as well as other species belonging to *T.* sect. *Trisetaera*, which are the North American *T. ligulatum*, *T. projectum* and *T. rosei,* and the South American *T. barbinode*, *T. caudulatum*, and *T. preslei*, all of them closely to two species of *Koeleria* from Southern America, *K. fueguinea* and *K. vurilochensis*. The New Zealanders species *Trisetum tenellum* and *T. younguii*, with less dense but spike like panicles, and *T. drucei*, with more or less lax panicles with longer branches, have been resolved in this clade, of which only the nuclear topology has been included in our tree, indicating again the closeness of these lineages and the well-studied biogeographical relationship between both areas (Edgar, 1998; Ezcurra et al., 2008). Moreover, the nuclear topology of two species of *T.* sect. *Trisetum* from Central and South America, *T. foliosum* and *T. irazuense*, have been resolved in this clade, specifically in a clade weakly supported with *T. rosei*. Saarela et al. (2017) indicated the possible hybrid origin *T. irazuense* and the South American *T. macbridei* (*T.* sect. *Trisetaera*), being not congruent the nuclear topology with the plastid one. In the nuclear topology, *T. irazuense* and *T. macbridei* were included with the group formed by *T.* sect. *Trisetaera* + *Koeleria* (Koeleriinae clade I), while in the plastid one *T. irazuense* is part of *Trisetum* and *Calamagrostis* from Central America, and *T. macbridei* is part of a large clade of South American species *Calamagrostis*/*Deyeuxia* (Koeleriinae clade II). Our results support these results, but only for *T. irazuense*, not including *T. macbridei*. However, we include the endemism from Venezuela, *T. foliosum*, sampled for the first time, which is together with *T. irazuense* in incongruence 6. In the ITS topology, as indicated above, both species are included in L clade, together with *T. rosei*, while in the plastid one it is included in P clade as a group of the polytomy with other *Trisetum*/*Calamagrostis* from Central America.

Finally, a well-supported group L4 basally surrounded by samples of the Scandinavian and Northern Asian *Trisetum subalpestre*, included by Enuschenko (2011), as indicated before, in *T.* sect. *Trisetaera* subsect. *Agrostidea*, morphologically similar to the rest of species of *T.* sect. *Trisetaera*, being laxly caespitose plants with spiciform dense panicles, and awn inserted in the upper part of the lemma (Jonsell, 1980a). The L4 also contains a large group of Eurasian and American *T. spicatum*, including the infraspecific taxa *T. spicatum* subsp. *virescens*, *T. spicatum* subsp. *pilosiglume*, *T. spicatum* subsp. *wrangelense*, and *T. spicatum* subsp. *ovatipaniculatum*, followed by the Central Asian taxa *K. litvinowii*, *Trisetokoeleria taymirica* and *Trisetokoeleria gorodkowii*. Wölk & Röser (2017) included in their nuclear *topo6* tree samples of *K. litvinowii*, resulting that part of the clones were resolved together with *Trisetum* ones (*T. distichophyllum*, *T. argenteum*, and *T. glaciale*), indicating that these results support that *K. litvinowii* is an intermediate between *Trisetum* and *Koeleria*. Those groups of species are followed by the New Zealander *T. antarcticum*, and the Hawaiians *T. inaequale* and *T. glomeratum*. The inclusion in this group of the North American species *T. montanum*, included in *T.* sect. *Trisetum* by Finot et al. (2005b), is also supported by Saarela et al. (2017). This species has panicles open to more or less contracted, and lemma awned in the upper third or fourth, similar characters to *T. spicatum* complex. Other South American species of *T.* sect. *Trisetaera* (including North and South American samples of *T. spicatum)*, *T. orephilum* and *T. andinum*, are part of this group, as well as the *Koeleria* species *K. kurtzii* and *K. boliviensis*.

Koeleriinae clade II

The clade M

A strongly supported lineage, the clade M, has been here identified for the first time and resolved as a sister to the rest of the Koeleriinae clade II in the combined plastid and ITS tree, and the combined plastid tree (results not shown). However, the ITS topology (results not shown) showed this group as a sister clade of the Koeleriinae clade I, a weakly supported relationship as in other previous studies with ITS (Saarela et al., 2017; Wölk & Röser, 2017) and with the also nuclear gene *topo6* (Wölk & Röser, 2017). Saarela et al. (2017) previously identified this lineage on two species, the widespread *T. sibiricum* and the southeastern Asian *T. bifidum*, pointing out the necessity of characterizing and delimiting this group. In our study, we have also sampled two Himalayan species, *T. aeneum* and *T. scitulum*, and all together account for four of the six species of this section. Both *T. bifidum* and its sister species *T. scitulum* appear as sister to *T. aeneum*, and all of them are grouped apart of all the sampled specimens of *T. sibiricum*. Further studies with low copy nuclear genes in the *T. sibiricum* complex are likely to be insightful in the relationships among *T. sibiricum* subsp. *litorale* and *T. sibiricum* subsp. *sibiricum*.

All the species included into this lineage, together with *T. henryi* and *T. turcicum*, were recently grouped by Barberá et al. (2017b) in *Trisetum* sect. *Sibirica*, a section distributed from the Eastern Europe to Alaska and Canada and center of diversity in ethe astern Asia. *Trisetum* sect. *Sibirica* is characterized by having goldish-brown spikelets, lemmas with callus glabrous or shortly hairy (up to 0.7 mm), and ovary glabrous (Barberá et al., 2017b). *Trisetum turcicum* has not been yet sampled for this study, though, as it was indicated before, has been related in previous molecular studies to *T. flavescens* on the basis of misidentified specimens. Following previous morphological studies (Probatova, 1979; Barberá et al., 2017b), we support the inclusion of *T. turcicum* in *T.* sect. *Sibirica*. Therefore, these results could support the recognizement of *T.* sect. *Sibirica* as a separate genus, as previously suggested by Saarela et al. (2017).

The clade N

The monospecific genus *Limnodea* is endemic from the southeastern United States and adjacent areas from Mexico and its affinities have remained uncertain til now. Tucker (1996) wrongly included *Limnodea* in the genus *Cinna*, and then both were separated by Brandenburg and Thieret (2000) because of their different morphological traits. Later, it was included in either the Agrostidinae (Soreng et al., 2015) or the Poinae (Kellogg, 2015). Döring (2009) sampled *Limnodea arkansana* for the first time and got a moderately to strongly supported plastid lineage with representatives of the genera *Sphenopholis*, *Graphephorum*, *Helictotrichon*, *Peyritschia*, and *Trisetum*. The nuclear multi-gene study of Hochbach et al. (2015) supported the inclusion of *Limnodea* in the Aveneae/Poeae complex, belonging to a lineage comprising *Gaudinia*, *Koeleria*, *Sphenopholis*, and *Briza*. Saarela et al. (2017) only sampled *Limnodea* in the *matK* tree, indicating that it belongs to the Koeleriinae clade II, but its affinities with *Sphenopholis* and all other taxa in the clade remained unresolved. In our combined plastid and ITS topology, a strongly supported clade including five specimens of *Limnodea arkansana* is showed, though with a moderate support, as sister to the representatives of the genus *Sphenopholis*. The tufted annual genus *Limnodea* is mainly characterized by its 1-flowered spikelets, coriaceous glumes and lemmas with a long, subterminal awn. The spikelets of *Sphenopholis* and *Limnodea* disarticulate below the glumes, a character not shared with the rest of species of the Koeleriinae and the Aveninae that has consistently been used to separate *Sphenopholis* from *Trisetum* (Finot et al., 2004). *Sphenopholis* and *Limnodea* also share entire or more or less bifid lemmas, with the awn, when present in *Sphenopholis*, inserted just below the apex, and liquid endosperm (Erdman, 1965; Finot et al., 2004; Daniel, 2007; Snow, 2007; Kellogg, 2015).

The clade O

According to Soreng et al. (2003, 2017), the perennial genus *Sphenopholis* includes seven species, distributed in North and Central America. Quintanar et al. (2007) sampled a single species of *Sphenopholis*, *S. intermedia*, confirming its placement in the Koeleriinae for the first time. Later, Saarela et al. (2010), using the same sample of *S. intermedia*, resolved *Sphenopholis* in a lineage which also included species of the Koeleriinae clade II. This result was supported by recent studies which include four species of *Sphenopholis*, resulting a monophyletic genus in the topologies of nuclear marker *topo6* by Wölk & Röser (2014, 2017), and in the ITS+ETS and the combined plastid trees of Saarela et al. (2017). Moreover, Saarela et al. (2017), in the combined plastid tree, showed the close alliance *Graphephorum wolfii* and *Trisetum cernuum* subsp. *canescens* joined into a polytomy close to the *Sphenopholis* clade.

Our study includes, finally, the two species that were still missing of *Sphenopholis* in these sorts of studies, including four samples of *S. interrupta* and two of *S. longiflora*, all of them resolved together into a strongly supported clade (the clade O). *Sphenopholis* results to be a non monophyletic genus, neither in ITS nor in the combined plastid topologies. Our results resolve the placement of *S. interrupta* in *Sphenopholis*, instead of *Trisetum*, in agreement with the normal criteria (Scribner, 1906; Finot et al., 2004; Soreng et al., 2003, 2017). The same type of spikelet disarticulation, the structure of the pieces of the spikelets, besides of the micro-epidermal characters of *S. interrupta* and the rest of species of

Sphenopholis (Finot et al., 2004, 2006a), support our results. In our ITS topology, as well as in the combined plastid and ITS tree, the four samples of *S. filiformis* falls together into a clade which is sister to the rest of species of the genus, as it was previously indicated by Saarela et al. (2017). However, the representative of *Deyeuxia rupestris* f. *pilosa* is also included within the *Sphenopholis* clade, in particular together with *Sphenopholis pensylvanica*, while the plastid topology shows it in company of the rest of species of *Deyeuxia* sect. *Viridiflavescentia* (the clade T). *Deyeuxia rupestris* f. *pilosa*, sometimes synonymized with *Calamagrostis leonardii*, is distributed throughout Brazil, Haiti and the Dominican Republic (Rúgolo de Agrasar, 2006). The specimen studied was collected in the Dominican Republic. More samples of this widely distributed species are necessary to clarify its variability and relationships, at least regarding the ITS topology. As it has been commented above, the plastid topology includes part of the plastid incongruence 3, which consists of *Graphephorum melicoides* and a part of the included representatives of *Trisetum cernuum*, likely due to reticulate evolution.

The clade P

A moderately supported clade, here named as the clade P, includes representatives from Mexico, Central and South America of the *Calamagrostis*/*Deyeuxia* species complex and *Trisetum* p.p. (including *Trisetum* subg. *Deschampsioidea*), *Peyritschia*, and most of the species of the plastid incongruences 3 and 6. Our results agree with previous studies that already informed about these incongruences between plastid and ITS topologies realted to this group, as it is indicated above.

Moreover, our results also confirm the polyphyly of the *Calamagrostis*/*Deyeuxia* complex as indicated previously with ITS, plastid and *topo6* data (Saarela et al., 2010; Wölk & Röser, 2014, 2017), wider sampling, comparable with that presented by Saarela et al. (2017). Saarela et al. (2017) got a strongly supported clade in the plastid and nuclear topologies, which included representatives of four species from *Trisetum* subg. *Deschampsioidea* (*T. durangense*, *T. palmeri*, *T. viride*, and *T. virletii*), and five of the *Calamagrostis*/*Deyeuxia* species complex from Mexico (*C. divaricata*, *C. pringlei*, *C. erectifolia*, *C. eriantha*, and *C. vulcanica*). On the other hand, two or three species of the genus *Peyritschia* (*P. deyeuxoides*, *P. koelerioides*, and/or *P. pringlei*) had been included in some previous studies (Saarela et al., 2010; Wölk & Röser, 2014, 2017), in which a clade with unresolved affinities in the Koeleriinae clade II was shown in nuclear and plastid trees. Saarela et al. (2017) included a single representative of *P. deyeuxoides* in their analysis, plus another of *P. pringlei* in the ITS topology. In their study, *Peyritschia* was not closely related to any of the Mexican species of *Trisetum*, and formed a weakly supported clade with five species of the *Calamagrostis/Deyexia* species complex from Central to South America. In our study, several groups of this lineage collapse into a polytomy. The first ones is the plastid incongruence 3, which corresponds to *T. cernuum*, *T. ortochaetum*, *Graphephorum wolfii*, and in a moderately supported clade, *T. ambiguum*, *T. longiglume* var. *glabratum*, and *Koeleria mendocinensis*. *Trisetum cernuum* var. *canescens*, also a part of the incongruence, is placed into a group with *Trisetum pringlei* and *Calamagrostis coahuilensis*. *Trisetum pringlei*, a species from Mexico, Guatemala, Costa Rica, and Panama, has not been assigned to a section, even its generic assignment is not clear. This species, sampled in our study for the first time, differs from a typical representative of *Trisetum* by having entire and mucronate lemma apices, linear lodicules with entire apices, and solid endosperm (Finot et al., 2004), as well as by some micromorphological characters of the lemma (Finot et al., 2006a). *Trisetum angustum*, not assigned to any section by Finot et al. (2004), has not been sampled yet, but is morphologically very similar to *T. pringlei;* both are differentiated by the panicle shape and the hairs of the lemma (Swallen, 1955). This species has been only studied from Guatemala, and was suggested to be a variety of *T. pringlei* by Pohl & Davidse (1994). The Mexican species *Calamagrostis coahuilensis* has an awned lemma, with the awn inserted near the base, and lemma apex acute, entire or bifid, being morphologically similar to *C. purpurascens* according with some authors (Peterson et al., 2004). However, *C. purpurascens* has been resolved with the rest of northern American *Calamagrostis* in other studies (Saarela et al., 2017; Barberá et al., unpublished).

The rest of the lineages of this polytomy correspond to species of *Calamagrostis* from Mexico, Central and South America. A moderately to strongly supported clade includes representatives of *Calamagrostis pittieri*, *C. killipii* (both sampled here for the first time), and *C. planifolia*. *Calamagrostis pittieri* and *C. planifolia*,most of them clearly morphologically similar taxa, having lax panicles, bilobed lemma apex and lemma awned above the middle, as well as two anthers, though *C. killipii* has appressed panicles, lemmas deeply bifid and awned at the middle, and three anthers (Swallen, 1948; Pohl & Davidse, 1994; Renvoize, 1998; Hammel et al., 2003). The rest of species are *C. vulcanica* and *C. mcvaughii*, both placed in one group, and *C. tolucensis* and *C. eriantha* in another one. These four species are densely tufted grasses and have lax panicles and a lemma with the awn inserted slightly below the middle or just at the middle (Swallen, 1955; McVaugh, 1983; Pohl & Davidse, 1994).

The sampled representatives of *Peyritschia*, *Trisetum filifolium*, *T. curvisetum*, *T.* subg. *Deschampsioidea*, and the three *Calamagrostis* from Central America (*C. pringlei, C. erectifolia*, and *C. orizabae*), are all together grouped into a strongly supported clade, sister to the series of polytomies indicated before, which also includes the plastid incongruence 6 (*T. irazuense* and *T. foliosum)* in the plastid topology. The Central and South American genus *Peyritschia* include seven species, which were treated under *Trisetum* by Hernández-Torres & Koch (1987). *Peyritschia* differs from *Trisetum* by having isomorphic glumes, bilobed lemmas with awn inserted at the middle of the lemma or near its base, sometime reduced to a subapical mucro, paleas tightly enclosed by the margins of the lemma, only two stamens, and by many epidermal features of the lemma (Finot et al., 2004, 2006a, 2006b). Our combined plastid and ITS tree shows these previously sampled three species together in a moderately supported and monophyletic clade. In contrast with Saarela et al. (2017), here the clade of *Peyritschia* is sister to a strongly supported clade which includes the representatives of *T.* subg. *Deschampsioidea*, *T. filifolium* (not assigned to a section), *T. curvisetum* and plastid topologies of *T. irazuense* and *T. foliosum*, the three belonging to *T.* sect. *Trisetum*, and some Central American *Calamagrostis*, indicating their close relationship. Finot et al. (2004) upgraded *T.* subsect. *Deschampsioidea* as a subgenus, which included eight Mexican and Central American species. Later, after the inclusion of *T. pinetorum* in *Peyritschia* (Finot, 2006b), seven species are considered to be included in this subgenus: *T. durangense*, *T. martha-*

gonzaleziae, *T. palmeri*, *T. spellenbergii*, *T. tonduzii*, *T. viride*, and *T. virletii*. We have sampled representatives of six of the seven species of this taxon, being *T. spellenbergii* and *T. tonduzii* sampled for the first time. *Trisetum* subg. *Deschampsioidea* is characterized by having lax panicles, lemmas with hyaline apex and margin, without nerves or with intermediate and marginal nerves protruded beyond the apex as four awnlets and the awn inserted at the middle of the lemma (Finot et al., 2004), as well as by leaf epidermal characters, which noticeably differ between this subgenus and the rest of the genus (Finot, 2006a). The three endemic Mexican species of *Calamagrostis* included in this group share characters of the lemma and the panicle with *Trisetum* subg. *Deschampsioidea*. *Calamagrostis orizabae* has been sampled for the first time; however, some author considerated it to be very close to *C. erectifolia*, scarcely separated by some differences of the habits, though they may be considered synonymous (MacVaugh, 1983). Finally, *Trisetum curvisetum* and *T. filifolium,* both endemics to Mexico, also present lax panicles, as well as lemmas with entire apex and nerves extending as 2-4 awnlets. Thus, all these morphological characters related to the lemma features are undoubtfully important to characterize these lineages.

The clades Q, R, S and T

The representatives of the *Deyeuxia*/*Calamagrostis* species complex from South America have been classified in five sections (Rúgolo de Agrasar, 1986; Villavicencio, 1995), recently revised by Rúgolo de Agrasar (2006). As it is indicated above, the previous molecular studies included few of these species using nuclear and plastid markers (Saarela et al., 2010; Wölk & Röser, 2014, 2017); recently Saarela et al. (2017) greatly widened the sampling of this complex. They were able to indicate a common origin for *Deyexia* sect. *Stylagrostis* and *Deschampsia* (subtribe Aristaveninae, Poeae chloroplast group 2), thus combining seven species of this section in *Deschampsia* (Saarela et al., 2017). Apart of this, only the nuclear topology presented by Saarela et al. (2017) provided some support for the sectional classification of the South American *Deyeuxia*/*Calamagrostis*species complex. *Deyeuxia* sect. *Chamaecalamus*, which includes *D. heterophylla*, *D. nana*, *D. rigescens*, and *D. vicunarum,* were placed together in a poorly supported clade in the ITS+ETS tree, as well as *D. fibrovaginata* (named *D. coarctata*), and *D. lagurus*. *Deyeuxia* sect. *Pungentes* and *Deyeuxia* sect. *Deyeuxia* form a poorly to weakly supported clade in the ITS+ETS tree, except *D. rigida*, *D. recta*, *D. planifolia*, *D. tarmensis*, and *D. intermedia*, all of them included in "Rigida Group" (Villavicencio, 1995), forming a common clade with *Peyristchya deyeuxoides*. Saarela et al. (2017) included three representatives of *Deyeuxia* sect. *Viridiflavescentia* (*D. rupestris, D. viridiflavescens*, and *D. viridis*), which were placed together in plastid and ITS trees in a strongly supported clade in the company of *T.* subg. *Deschampsioidea* and *Leptophyllochloa*. *Leptophyllochloa* was sampled by Wölk & Röser (2017) for the first time, and it was resolved in the Poeae chloroplast group 2 in plastid and nuclear topologies. Saarela et al. (2017) suspected that one of them was wrong, although the morphology-based classifications had considered it to be closely related to the Koeleriinae. Our results have also provided support to the South American *Deyeuxia*/*Calamagrostis* sectional classification. *Deyexia* sect. *Stylagrostis,* characterized by having the spikelets raised on a lemma stipe (Escalona, 1988), is resolved into the *Deschampsia* clade, as indicated by Saarela et al. (2017). Our data include one more species of this section (*C. gayana*) that is now to be combined (Barberá et al., unpublished). All the included representatives of *Deyeuxia* sect. *Chamaecalamus* (except *D. boliviensis*) belong to a poorly supported lineage (the clade Q), plus *D. fuscata,* which is at the base of this clade, and *D. recta*, both included in *Deyeuxia* sect. *Deyeuxia*, and three species that have not ever classified in any sections, *D. macrophylla*, *C. rauhii*, and *D. fibrovaginata*. *Deyeuxia* sect. *Chamaecalamus* is characterized by short callus hairs (up to 1 mm), lemma apex with four teeth or awnlets, glabrous rachillas or with scattered hairs, and small anthers (up to 0.6 mm) (Villavicencio, 1995; Rúgolo de Agrasar, 2006). Apart from the four species of the section included in Saarela et al. (2017), two more species have been sampled here for the first time, such as *D. minima* and *D. setiflora*. *Deyeuxia macrophylla*, *C. rauhii*, and *D. fibrovaginata* share short callus hairs, 3-4-toothed lemma apex, and rachillas with scattered hairs. *Deyeuxia lagurus*, also included in Saarela et al. (2017), was classified in *Deyeuxia* sect. *Deyeuxia* and shares with *Deyeuxia* sect. *Chamaecalamus* the type of lemma apex, short anthers and short callus hairs, while it rachilla has long hairs. Although *Deyeuxia boliviensis* belongs to *D.* sect. *Chamaecalamus*, it is here shown, followed by *D. jamesonii* (no classified by section), to be at the base of the clade that includes most of the species of *Deyeuxia* sect. *Deyeuxia* and *Deyeuxia* sect. *Pungentes*. The species of these two sections collapsed into a large polytomy, sister to the clade before explained and at the base of *Leptophyllochloa*, *Deyeuxia* sect. *Viridiflavescentia* and the South African *Trisetopsis*. Unlike Saarela et al. (2017) nuclear topology, *D. rigida*, *D. recta*, *D. tarmensis*, and *D. intermedia* are included in this polytomy with most of the species of *Deyeuxia* sect. *Deyeuxia*. However, *D. planifolia* was resolved, as in Saarela et al. (2017), in a polytomy with other *Calamagrostis* from Mexico and Central America, sister to *Peyritschia* and *Trisetum* subg. *Deschampsioidea* (clade P), as it is indicated above. In our combined plastid and ITS tree, our two representatives of *Leptophyllochloa* are resolved to be at the base of a clade. *Deyeuxia* sect. *Viridiflavescentia* is defined by having recurved callus, rachilla always prolonged close to the palea, short anthers, and soft endosperm (Rúgolo de Agrasar, 2006). In our study, the same three representatives of *Deyeuxia* sect. *Viridiflavescentia* sampled by Saarela et al. (2017) have been resolved together in a poorly supported clade. The monospecific *Leptophyllochloa*, which has been previously classified either in *Trisetum* or in *Koeleria*, is characterized by having lax panicles, 3-nerved lemmas with an entire or slightly cleft apex and straight awn inserted subapically, short anthers, and punctiform hilum (Rúgolo de Agrasar, 2012). Therefore, our results support those by Saarela et al. (2017) and shows *Leptophyllochloa* in the Koeleriinae clade II, solving the issue caused by the results of Wölk & Röser (2017). Additionally, the plastid topology shows the Asiatic *Trisetopsis junghuhnii* in closeness with the rest of the African *Trisetopsis*, but in *Leptophyllochloa* clade, as explained above.

In sum, in major agreement with Saarela et al. (2017), this phylogenetic scenario of poorly to weakly supported clades, including the *Calamagrostis*/*Deyeuxia* complex, indicates the low molecular variation existing among them, which could have resulted because of a rapid radiation in South America.

The clade U

Wölk & Röser (2013) described *Trisetopsis* including a series of taxa from tropical to subtropical Africa, Madagascar, and the Arabian Peninsula, and previously classified in *Helictotrichon* (Schweickerdt, 1937), which has resulted to be a polyphyletic genus. *Trisetopsis* is separated morphologically from *Helictotrichon* mainly by its lemma apically deeply bifid (2-lobed) with the incision usually reaching down to the awn insertion, sparsely ciliate at the apex ovary, and apically narrowed or bi- to trifid lodicules (Wölk & Röser, 2013, 2014). In the ITS, *topo6*, and plastid topologies of Wölk & Röser (2014), *Trisetopsis* resulted to be placed close to some South American *Deyeuxia*/*Calamagrostis*, *Sphenopholis*, and *Peyritschia*, in the Koeleriinae clade II. *Topo6* marker suggested an allopolyploid origin of most of *Trisetopsis* species, having two different copy types (A and B), as indicated above, which are strongly different from the rather uniform copies that are characteristic of the Eurasian species of *Helictotrichon*. Copy type A formed a strongly supported lineage with the genus *Arrhenatherum* (Aveninae), while copy type B was part of a clade with New World representatives of *Calamagrostis*, *Graphephorum*, *Peyritschia* and *Sphenopholis*. In a more recent study, the two copy types of *topo6* were also found in two Southeast Asian species (Wölk & Röser, 2017). In agreement with the morphological data, both species were combined in *Trisetopsis* (*T. junghuhnii* and *T. virescens*), expanding the distribution of the genus. Saarela et al. (2017) did not sample any additional species of *Trisetopsis*, only indicating that the genus was resolved in the Koeleriinae clade II.

Our dataset includes 22 of the 27 species of the genus *Trisetopsis*, including one from China (belonging to the incongruence 7) as indicated above. In our combined plastid and ITS tree, a strongly supported clade corresponding to *Trisetopsis* (clade U) was placed close to the South American representatives of the *Deyeuxia*/*Calamagrostis* species complex and *Leptophyllochloa*, specifically below the *Deyeuxia* sect. *Viridiflavescentia* group. One important morphological character that *Trisetopsis* shares with this section of *Deyeuxia* is the linear or elliptic hilum, instead of the punctiform hilum of most of the species of the Koeleriinae. Additionally, *Trisetopsis namaquensis* has a recurved callus, which characterizes the species of *Deyeuxia* sect. *Viridiflavescentia*. In any case, it seems to be clear that further studies to found more characters to support the placement of *Trisetopsis* in the Koeleriinae would be advisable.

ACKNOWLEDGEMENTS

This work was financed by *Flora iberica* CGL2014–52787–C3–1–P, CGL2012–32914 and CGL2015–66161–P, projects of the Spanish Government, supported by FEDER funds, and through the FPI fellowship BES-2012-053754 to P. Barberá. We are indebted to the curators and staff of the herbaria mentioned in Material and Methods for kindly providing specimens. Alberto Herrero and Emilio Cano (LSM) of Real Jardín Botánico de Madrid, and Gabriel Johnson (LAB) of the Smithsonian Institution for their assistance with laboratory work. We thank Ramón Morales for translations of manuscripts in German. Irene Villa, Kina, Javier Fernández, Miguel Ángel García, Laura Martín, Alicia Agudo, and Toni Buira for their technical support. Maria Vorontsova (K) for supplying a sample from her Institution.

To the personal from the Komarov Institute (LE), N.N. Tzvelev, Dmitry Geltman, Elena Glazkova, Denis Melnikov, for their help and their welcoming attitude during our stay.

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SUPPORTING INFORMATION

Appendix 1. Voucher information for new DNA sequence data. Information is present in the following order: taxon, provenance, voucher, ITS, *rps16-trnK*, *rps16 intron*, *rpl32-trnL*. A dash indicates no sequence was obtained.

Agropyron cristatum (L.) Gaertn.: CANADA, Western Canada, *P. M. Peterson et al. 18365* (US), X, X, X, X. ***Agrostis curtisii*** Kerguélen: SPAIN, A Coruña, *T. Gil Gil s.n.* (MA-649795), X, X, X, X. ***Agrostis trachyphylla*** Pilg.: TANZANIA, Kilimanjaro, *P.M. Peterson et al. 24374* (US-1446248), X, X, X, X. ***Agrostis truncatula*** Parl.: SPAIN, Palencia, *P. Barberá & A. Quintanar 916* (MA-871546), X, X, X, X. ***Aira caryophyllea*** L.: TANZANIA, Njomba Region, *P.M. Peterson et al. 24013* (US), X, X, —, X. ***Aira uniaristata*** Lag. & Rodr.: SPAIN, Zamora, *P. Bariego 2566* (MA-792644), X, X, X, X. ***Airopsis tenella*** Coss. & Durand: SPAIN, Ciudad Real, *A. Quintanar 3656* (MA-836414), X, X, X, X. ***Amphibromus nervosus*** (Hook. f.) Baill.: AUSTRALIA, Western Australia, *P. M. Peterson et al. 14303* (US-3422357), X, X, X, X. ***Anthoxanthum aristatum*** Boiss.: ITALY, Cerdeña, *C. Navarro et al. 4668* (MA-708063), X, X, X, X. ***Anthoxanthum nivale*** K. Schum.: TANZANIA, Kilimanjaro, *P. M. Peterson et al. 24351* (US), X, X, X, X. ***Apera spica-venti*** (L.) P. Beauv.: BULGARIA, *J. J. Aldasoro et al. 8781* (MA-727679), X, X, —, X. ***Arrhenatherum album*** (Vahl) Clayton: SPAIN, Madrid, *P. Barberá s.n.* (MA-865113), X, X, X, X; SPAIN, Guadalajara, *L. Medina et al. 5010* (MA-838195), X, X, X, X. ***Arrhenatherum calderae*** A. Hansen: SPAIN, Tenerife, *S. Castroviejo & Marrero 17370* (MA), X, X, X, X. ***Arrhenatherum elatius*** (L.) P. Beauv. ex J. Presl & C. Presl: ARMENIA, Vayots Dzor, *A. Herrero et al. 2759* (MA-744548), X, X, X, X; AUSTRIA, Niederösterreich, *E. Vitek 05-1325* (MA-833020), X, X, X, X; USA, Virginia, *F. R. Fosberg 45437* (US-2685717), —, —, —, X. ***Arrhenatherum elatius* var. *biaristatum*** (Peterm.) Peterm.: USA, California, *L. White s.n.* (US-2116098), —, —, —, X. ***Arrhenatherum elatius* subsp. *bulbosum*** (Willd.) Schübl. & G. Martens: SPAIN, A Coruña, *J. Rodriguez Oubiña & Louzán s.n.* (MA-730645), X, X, X, X; SPAIN, Granada, *R. J. Soreng & N. Soreng 3709b* (US-3565353), —, —, —, X; SPAIN, Valladolid, *C. Aedo 18463* (MA-839932), X, X, X, X; USA, Delaware, *C. F. Reed 31513* (US-2151975), —, —, —, X. ***Arrhenatherum elatius*** (L.) P. Beauv. ex J. Presl & C. Presl **subsp. *elatius***: ANDORRA, *S. Castroviejo et al. 11932* (MA-512176), X, X, X, X; FRANCE, Aude, *J. Calvo & T. Buira 3725* (MA-793632), X, X, X, X; SPAIN, Zaragoza, *C. Aedo 19258* (MA-864180), X, X, X, X. ***Arrhenatherum elatius* subsp. *sardoum*** (E. Schmid) Gamisans: ITALY, Cerdeña, *S. Castroviejo et al. 17004* (MA-707757), X, X, X, X. ***Arrhenatherum kotschyi*** Boiss.: IRAN, Isfahan, *M. R. Parishani 14503* (MA-749111), X, X, X, X. ***Arrhenatherum nebrodense*** Brullo, Minissale & Spampinato: ITALY, Sicily, *C. Aedo et al. 5629* (MA-646653), X, X, X, X; ITALY, Sicily, *A. Herrero et al. 790* (MA-647269), X, X, X, X. ***Avellinia festucoides*** (Link) Valdés & H. Scholz: SPAIN, Menorca, *C. Aedo et al. 20029* (MA), X, X, X, X; SPAIN, Menorca, *J. L. Fernández Alonso et al. 30318* (MA), X, X, X, X. ***Avena barbata*** Pott ex Link: PORTUGAL, Ribatejo, *M. A. García et al. 6225* (MA-863948), X, X, X, X; SPAIN, Alicante, *C. Aedo 17304* (MA-805730), X, X, X, X; SPAIN, Lugo, *C. Aedo 17029* (MA-796524), X, X, X, X; SPAIN, Toledo, *A. Quintanar & M. Vega 2362* (MA-803505), X, X, X, X; TURKEY, Sinop, *V. Valcárcel et al. 259VV01* (MA-689616), X, X, X, X; USA, California, *R. F. Hoover 6035* (US-1984717), —, —, —, X. ***Avena fatua*** L.: CANADA, Ontario, *W. G. Dore et al. 8716* (US-2076085), —, —, —, X; SPAIN, Burgos, *P. Galán Cela & Martín 592* (MA-640306), X, X, —, X; USA, Oregon, *R. R. Halse 6488* (US-3476300), —, —, —, X. ***Avena barbata*** Poit. ex Link: SPAIN, Alicante, *A. Quintanar & M. Vega 2453* (MA-783698), X, X, —, X; TUNISIA, Nabeul, *A. Quintanar et al. 3262* (MA-798192), X, X, —, X. ***Avena nuda*** L.: CHINA, North West China, *[unknown 875]* (US-1722147), —, —, —, X. ***Avena prostrata*** Ladiz.: SPAIN, Almeria, *J. Calvo et al.*

4374 (MA-805595), X, X, X, X. ***Avena sativa*** L.: MEXICO, Zacatecas, *P. M. Peterson et al. 21280* (US-3555808), —, —, —, X; SPAIN, Islas Baleares, *J. Calvo & A. Quintanar 6075* (MA-859226), X, X, X, X; USA, Missouri, *P. C. Standley s.n.* (US-869624), —, —, —, X. ***Avena sterilis*** L.: ARMENIA, Syunik, *R. Gonzalo et al. 157* (MA-742907), X, X, X, X; PORTUGAL, Ribatejo, *C. Aedo et al. 18937* (MA-865200), X, X, X, X; PORTUGAL, Estremadura, *C. Aedo et al. 19075* (MA-865023), X, X, X, X. ***Avena strigosa*** Schreb.: RUSSIA, Leningrad, *V. Nekrasova & Litwinow s.n.* (US-2119662), —, —, —, X; SWEDEN, *J. B. Bengtsson s.n.* (US-1866663), —, —, —, X. ***Avenella flexuosa*** (L.) Drejer: USA, Tennessee, *P. M. Peterson & J. M. Saarela 20793* (US-3539391), —, —, —, X. ***Avenula pubescens*** (Huds.) Dumort.: CANADA, Ontario, *W. G. Dore 1430* (US-1760108), X, —, —, X. ***Briza minor*** L.: SPAIN, Cádiz, *C. Aedo 15654* (MA-769628), X, X, X, X. ***Bromus densus*** Swallen: MEXICO, Coahuila, *P. M. Peterson et al. 21128* (US-3554616), X, X, —, X. ***Calamagrostis amoena* var. *festucoides*** (Wedd.) Soreng: BOLIVIA, La Paz, *S. G. Beck 14731* (US-3198959), X, X, X, X; PERU, Puno, *H. H. Iltis et al. 1461* (US-2543111), X, X, X, X. ***Calamagrostis arundinacea*** (L.) Roth: RUSSIA, Kabardino-Balkariya, *R. J. Soreng et al. 7949* (US-3600758), X, X, X, X. ***Calamagrostis coahuilensis*** P.M. Peterson, Soreng & Valdés-Reyna: MEXICO, Nuevo León, *McDonald 2185* (TEX), X, X, X, X. ***Calamagrostis coarctata*** (Torr.) Torr. ex Eaton: USA, Maryland, *P. M. Peterson et al. 24440* (US), X, X, X, X. ***Calamagrostis epigeios*** (L.) Roth: ARMENIA, Syunik, *R. Gonzalo et al. 243* (MA-743077), X, X, X, X. ***Calamagrostis erectifolia*** Hitchc.: MEXICO, Jalisco, *P. M. Peterson & Sánchez Alvarado 19105* (US-3496197), X, X, X, X; MEXICO, Jalisco, *P. M. Peterson & Sánchez Alvarado 19106* (US-3496196), X, X, X, X; MEXICO, Jalisco, *P. M. Peterson & Sánchez Alvarado 19109* (US-3496194), X, X, X, X. ***Calamagrostis eriantha*** (Kunth) Steud.: MEXICO, Veracruz, *M. H. Nee et al. 33190* (US-3338286), X, X, X, X. ***Calamagrostis fibrovaginata*** Lægaard: COLOMBIA, Santander, *M. C. Gómez MCG-37* (US-3534975), X, X, X, X; PERU, *W. Rauh & Hirsch P1866* (US-2180808), X, X, X, X. ***Calamagrostis gayana*** (Steud.) Soreng: ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17225* (US-3450931), X, X, X, X; ARGENTINA, Neuquen, *P. M. Peterson et al. 17448* (US-3450392), X, X, X, X; CHILE, *A. Pirion 117* (US-1445584), —, X, X, X. ***Calamagrostis killipii*** Swallen: VENEZUELA, Mérida, *J. P. Schulz 669* (US-2474395), X, X, X, X. ***Calamagrostis mcvaughii*** Sohns: MEXICO, *J. H. Beaman 3215* (US), —, X, —, X. ***Calamagrostis menhoferi*** Govaerts: BOLIVIA, La Paz, *M. Cárdenas 5821* (US-2954230), X, X, X, X. ***Calamagrostis orizabae*** (Rupr. ex E. Fourn.) Beal: MEXICO, *M. Saint Pierre 832* (US-1537754), X, —, X, X. ***Calamagrostis pittieri*** Hack.: COSTA RICA, San Jose, *W. E. Booth 105* (US-3480612), X, X, —, X; COSTA RICA, San Jose, *R. W. Pohl & Davidse 11138* (US-3578574), X, X, —, X. ***Calamagrostis pringlei*** Scribn. ex Beal: MEXICO, Chihuahua, *R. Bye et al. 31949* (US-3588287), X, X, X, X; MEXICO, Chihuahua, *P. Tenorio et al. 23971* (US-3589176), X, X, X, —; MEXICO, Durango, *P. M. Peterson et al. 15440* (US-3459919), X, X, —, X. ***Calamagrostis pseudophragmites* subsp. *tartarica*** (Hook.f.) Tzvelev: KYRGYZ REPUBLIC, Oblast of Chu, *R. J. Soreng et al. 7534* (US-3491820), X, X, X, X. ***Calamagrostis rauhii*** Tovar: PERU, *R. Hirsch s.n.* (US-2180785), X, X, X, X. ***Calamagrostis scabrescens*** Griseb.: CHINA, Xizang, *Tibet-MacArthur et al. 3228* (US-3601577), X, X, X, X. ***Calamagrostis tolucensis*** (Kunth) Trin. ex Steud.: MEXICO, *J. H. Beaman 3481* (US-2381684), X, X, X, X; MEXICO, *H. H. Iltis et al. 1004a* (US-2380084), X, X, —, X; MEXICO, *G. Mick & Roe 194* (US-2630285), X, X, X, X. ***Calamagrostis vulcanica*** Swallen: GUATEMALA, San Marcos, *M. E. Veliz et al. 8874* (MEXU-1043593), X, X, X, X; MEXICO, *J. H. Beaman 3155* (US), X, X, —, X. ***Catabrosa aquatica*** (L.) P. Beauv.: USA, *E. E. Terrell 4962* (US), X, X, X, X. ***Catapodium rigidum*** (L.) C.E. Hubb.: [Unknown locality], *J. H. Thomas 9511* (US), X, X, X, X. ***Cinna poiformis*** (Kunth) Scribn. & Merr.: MEXICO, Ixtapaluca, *S. D. Koch & Magaña 75186* (US-3643235), —, X, X, X. ***Colpodium chionogeiton*** (Pilg.) Tzvelev: TANZANIA, Kilimanjaro, *P. M. Peterson et al. 24357* (US), X, X, —, X. ***Cutandia memphitica*** (Spreng.) K. Richt.: KUWAIT, *A. Rawi 11543* (US-2970919), X, —, —, X. ***Cynosurus echinatus*** L.:

USA, California, *P. M. Peterson et al. 19712* (US-3539853), —, —, —, X. ***Deschampsia cespitosa*** (L.) P. Beauv. **subsp.** ***cespitosa***: CANADA, Alberta, *P. M. Peterson et al. 18410* (US-3514255), X, X, X, X. ***Deschampsia eminens*** (J. Presl) Saarela: BOLIVIA, La Paz, *T. Killeen 2643* (US-3254759), X, X, X, X. ***Deschampsia ovata*** (J. Presl) Saarela: PERU, Cusco, *W. Rauh & Hirsch P1155* (US-2180710), X, X, X, X. ***Desmazeria sicula*** (Jacq.) Dumort.: [Unknown locality], *C.R. Ball s.n.* (US), X, —, —, X. ***Deyeuxia boliviensis*** (Hack.) Villav.: BOLIVIA, La Paz, *E. Asplund 6491* (US-1099480), X, X, —, X. ***Deyeuxia breviaristata*** Wedd.: BOLIVIA, Oruro, *P. M. Peterson et al. 12756* (US-3265406), X, X, X, X; BOLIVIA, Potosi, *P. M. Peterson et al. 12921* (US-3276889), X, X, X, X; CHILE, Region I, *P. M. Peterson & R. J. Soreng 15672* (US-3444661), X, X, X, X; PERU, Tacna, *P. M. Peterson et al. 14742* (US-3449446), X, X, X, X. ***Deyeuxia brevifolia*** J. Presl: BOLIVIA, Potosi, *P. M. Peterson et al. 12936* (US-3276495), X, X, X, X; BOLIVIA, Oruro, *P. M. Peterson et al. 13161* (US-3264977), X, X, X, X; CHILE, Region II (Antofagasta), *P. M. Peterson et al. 15563* (US-3445683), X, X, X, —. ***Deyeuxia cabrerae*** (Parodi) Parodi: BOLIVIA, Potosi, *P. M. Peterson et al. 13006* (US-3276611), X, X, X, X; CHILE, Region II (Antofagasta), *P. M. Peterson et al. 15531* (US-3445663), X, X, X, X; CHILE, Region II (Antofagasta), *P. M. Peterson et al. 15533* (US-3445664), X, X, X, X. ***Deyeuxia calderillensis*** (Pilg.) Rúgolo: BOLIVIA, Tarija, *K. Fiebrig 3172* (US-81684), —, X, —, —. ***Deyeuxia chrysophylla*** Phil.: BOLIVIA, Potosí, *P. M. Peterson et al. 13020* (US-3276628), X, X, X, X. ***Deyeuxia ciliata*** Rúgolo & Villav.: BOLIVIA, Cochabamba, *M. Cárdenas 5604* (US-2954261), X, X, —, —. ***Deyeuxia crispa*** Rúgolo & Villav.: BOLIVIA, Potosí, *P. M. Peterson et al. 13007* (US-3276612), X, X, X, X; BOLIVIA, Potosí, *P. M. Peterson et al. 13054* (US-3277149), X, X, X, X; CHILE, Region II (Antofagasta), *P. M. Peterson et al. 15527* (US-3445660), X, X, X, X. ***Deyeuxia curvula*** Wedd.: ARGENTINA, *L. R. Parodi 9642* (US), X, X, —, X; CHILE, Region I, *P. M. Peterson & R. J. Soreng 15724* (US-3444537), X, X, X, X. ***Deyeuxia densiflora*** J. Presl: PERU, Junín, *K. Cook & Cook 22* (US-3098626), X, X, X, X; PERU, Ancash, *P. M. Peterson & Refulio-Rodriguez 17957* (US-3491345), X, X, X, X; PERU, Lima, *P. M. Peterson et al. 20300* (US), X, X, X, X. ***Deyeuxia deserticola*** Phil.: BOLIVIA, Potosí, *P. M. Peterson et al. 13007a* (US-3479005), X, X, X, X; BOLIVIA, Potosí, *P. M. Peterson et al. 13042* (US-3276642), X, X, X, X; CHILE, Region I, *P. M. Peterson & R. J. Soreng 15764* (US-3444549), X, X, X, X. ***Deyeuxia fiebrigii*** (Pilg.) Rúgolo: BOLIVIA, Potosí, *P. M. Peterson et al. 12966* (US-3277020), X, X, X, X. ***Deyeuxia filifolia*** Wedd.: BOLIVIA, Potosí, *P. M. Peterson & Annable 11841* (US-3481480), X, X, X, X; BOLIVIA, La Paz, *P. M. Peterson et al. 13196* (US-3264875), X, X, X, X. ***Deyeuxia fuscata*** J. Presl: PERU, Junin, *P. M. Peterson & Tovar 14093* (US-3421435), X, X, X, X. ***Deyeuxia glacialis*** Wedd.: BOLIVIA, La Paz, *P. M. Peterson et al. 12608* (US-3279308), X, X, X, X; BOLIVIA, La Paz, *J. C. Solomon 8289* (US-3097946), —, X, X, X; PERU, Yauli, *W. Rauh & Hirsch s.n.* (US-2180609), X, X, X, X. ***Deyeuxia heterophylla*** Wedd.: BOLIVIA, La Paz, *P. M. Peterson et al. 12609* (US-3279309), X, X, X, X; CHILE, Region I, *P. M. Peterson & R. J. Soreng 15715* (US-3444530), X, X, X, X; PERU, Moquegua, *P. M. Peterson et al. 14547* (US-3428495), X, X, X, X; PERU, Puno, *P. M. Peterson et al. 20615* (US), X, X, X, X; VENEZUELA, Mérida, *J. P. Schulz 256* (US-2951755), X, X, X, X. ***Deyeuxia hieronymi*** (Hack.) Türpe: ARGENTINA, Tucumán, *S. Venturi 7889* (US-1547366), X, X, —, X. ***Deyeuxia intermedia*** J. Presl: BOLIVIA, Oruro, *P. M. Peterson et al. 12767* (US-3265414), X, X, X, X; BOLIVIA, Potosí, *P. M. Peterson et al. 12822* (US-3277076), X, X, X, X; BOLIVIA, La Paz, *S. A. Renvoize 4209* (US), —, X, —, X; PERU, Ancash, *P. M. Peterson & Refulio Rodriguez 13887* (US-3423036), X, X, X, X. ***Deyeuxia jamesonii*** (Steud.) Munro ex Wedd.: ECUADOR, Pichincha, *L. B. Holm-Nielsen 24232* (US-3450184), —, X, —, X; ECUADOR, Pichincha, *P. M. Peterson et al. 9083* (US-3237444), X, X, X, X. ***Deyeuxia macrophylla*** Pilg.: PERU, Junin, *P. M. Peterson & Tovar 14130* (US-3421329), X, X, X, X; PERU, Cajamarca, *D. N. Smith & Cabanillas 7318A* (US-3310223), X, X, —, X. ***Deyeuxia malamalensis*** (Hack.) Parodi: BOLIVIA, Cochabamba, *M. Cárdenas 3424* (US-1564515), X, —, —, X. ***Deyeuxia mandoniana*** Wedd.:

BOLIVIA, La Paz, *P. M. Peterson & Laegaard 13197* (US-3264877), X, X, X, X. ***Deyeuxia minima*** (Pilg.) Rúgolo: BOLIVIA, La Paz, *P. M. Peterson et al. 13205* (US-3264885), X, X, X, X; BOLIVIA, La Paz, *J. C. Solomon & Moraes 13444* (US-3072329), X, X, —, X. ***Deyeuxia nana*** Rúgolo: PERU, Pasco, *P. M. Peterson & Tovar 14100* (US-3421437), X, X, X, X. ***Deyeuxia nitidula*** (Pilg.) Rúgolo: BOLIVIA, La Paz, *J. C. Solomon 13638* (US-3071954), X, X, X, X; PERU, Cusco, *W. Rauh & Hirsch P1207* (US-2180732), X, X, X, X. ***Deyeuxia orbignyana*** Wedd.: BOLIVIA, Santa Cruz, *L. Spiaggi 60* (US-2184991), X, —, —, —. ***Deyeuxia planifolia*** Kunth: COLOMBIA, Boyacá, A. *M. Cleef 8577* (US-2785781), —, X, X, X; ECUADOR, Loja/Zamora-Chinchipe, *S. Laegaard & Lozano 20710* (US-3588248), X, X, X, X. ***Deyeuxia polygama*** (Griseb.) Parodi: PERU, Cusco, *P. M. Peterson et al. 20585* (US), X, X, X, X. ***Deyeuxia polygama*** **subsp.** ***filifolia*** Rúgolo & Villav.: BOLIVIA, Cochabamba, *M. Cárdenas 771* (US-1764679), X, X, X, X. ***Deyeuxia recta*** Kunth: BOLIVIA, La Paz, *S. A. Renvoize 4524* (US-3480805), X, X, —, X. ***Deyeuxia rigescens*** (J. Presl) Türpe: BOLIVIA, Potosi, *P. M. Peterson et al. 12994* (US-3276602), X, X, X, X; ECUADOR, Napo, *L. B. Holm-Nielsen & Balslev 23798* (US-3450183), X, X, X, X; PERU, Ancash, *P. M. Peterson & Refulio Rodriguez 13812* (US-3423059), X, X, X, X. ***Deyeuxia rigida*** Kunth: BOLIVIA, Potosi, *P. M. Peterson et al. 12963* (US-3277017), X, X, X, X; PERU, Junin, *P. M. Peterson & Tovar 14027* (US-3421388), X, X, X, X. ***Deyeuxia rupestris*** (Trin.) Rúgolo: BOLIVIA, La Paz, *O. Buchtien 8906* (US-1538048), X, X, —, X; BRAZIL, Rio de Janeiro, *A. Chase 8444* (US-1257208), X, X, X, X; BRAZIL, Río Grande do Sul, *L. Scur 920* (US-3432533), X, X, —, X. ***Deyeuxia rupestris*** **f.** ***pilosa*** (Kämpf) Rúgolo: DOMINICAN REPUBLIC, La Vega, *A. H. Liogier 13127* (US-3138764), X, —, —, X. ***Deyeuxia setiflora*** Wedd.: CHILE, Region I, *P. M. Peterson & R.J. Soreng 15727* (US-3444540), X, X, X, X. ***Deyeuxia spicigera*** J. Presl: BOLIVIA, La Paz, *P. M. Peterson et al. 13195* (US-3264873), X, X, X, X; BOLIVIA, La Paz, *J. C. Solomon 13645* (US-3072068), X, X, X, X. ***Deyeuxia spicigera*** **var.** ***cephalotes*** (Wedd.) Rúgolo: PERU, Huarochiri, *P. C. Hutchison & Tovar 4264* (US-2473232), —, X, X, X. ***Deyeuxia tarmensis*** (Pilg.) Sodiro: BOLIVIA, Chuquisaca, *R. R. B. Cordech 32* (US-3250603), X, X, X, X; BOLIVIA, Oruro, *P. M. Peterson et al. 12768* (US-3265415), X, X, X, X; PERU, Ancash, *P. M. Peterson & Refulio Rodriguez 13930* (US-3423011), —, X, X, X. ***Deyeuxia tianschanica*** (Rupr.) Bor: CHINA, Xizhang (Tibet), *R. J. Soreng et al. 5542* (US-3491846), X, X, —, X. ***Deyeuxia trichodonta*** Wedd.: BOLIVIA, Potosi, *P. M. Peterson et al. 12891* (US-3276853), X, X, X, X; BOLIVIA, Potosi, *P. M. Peterson et al. 12934* (US-3276491), X, X, X, X; BOLIVIA, Potosi, *P. M. Peterson et al. 12960* (US-3277014), X, X, X, X. ***Deyeuxia velutina*** Nees & Meyen: ARGENTINA, San Juan, *R. Kiesling et al. 7959* (US-3288285), X, X, X, X; CHILE, Region III, *P. M. Peterson et al. 15481* (US-3445711), X, X, X, X; CHILE, Region III, *P. M. Peterson et al. 15484* (US-3445713), X, X, X, X. ***Deyeuxia vicunarum*** Wedd.: BOLIVIA, La Paz, *P. M. Peterson et al. 12610* (US-3279310), X, X, X, X; PERU, Ancash, *P. M. Peterson & Refulio Rodriguez 13815* (US-3423061), X, X, X, X. ***Deyeuxia violacea*** Wedd.: BOLIVIA, La Paz, *S. G. Beck 14703* (US-3198958), X, X, X, X; BOLIVIA, La Paz, *J. C. Solomon 13757* (US-3198792), X, X, X, X. ***Deyeuxia violacea*** **var.** ***puberula*** Rúgolo & Villav.: BOLIVIA, La Paz, *E. Valenzuela 974* (US-3198949), X, X, X, X. ***Deyeuxia viridiflavescens*** (Poir.) Kunth: BRASIL, Paraná, *L.T.D. Dombrowski 6716* (US-2847560), X, X, X, X. ***Deyeuxia viridiflavescens*** **var.** ***montevidensis*** (Nees) Cabrera & Rúgolo: BRAZIL, Río Grande do Sul, *L. Scur 1150* (US-3486684), X, X, X, X. ***Deyeuxia viridiflavescens*** (Poir.) Kunth **var.** ***viridiflavescens***: BRAZIL, Río Grande do Sul, *G. Grazziotin 6281* (US-3173507), X, X, —, X. ***Deyeuxia viridis*** Phil.: ARGENTINA, Neuquen, *P. M. Peterson et al. 17371* (US-3451012), X, X, X, X; CHILE, Valdivia, *J. L. Morrison 17627* (US-2434600), —, —, —, X. ***Dichelachne crinita*** (L. f.) Hook. f.: AUSTRALIA, Western Australia, *P. M. Peterson et al. 14489* (US-3422328), X, —, —, X. ***Elymus caninus*** (L.) L.: RUSSIA, Krasnodar, *R. J. Soreng et al. 8056* (US-3600700), X, —, —, X. ***Gaudinia fragilis*** (L.) P. Beauv.: ARGENTINA, *G. Seijo et al. 2557* (US), X, —, —, X; GREECE, Crete, *R. J. Soreng & N. Soreng 3790*

(US-3561064), X, —, —, X; SPAIN, Huelva, *A. Quintanar 1916* (MA-772223), X, X, X, X; SPAIN, Segovia, *R. García 1243* (MA-828347), X, X, X, X. ***Gaudinia hispanica*** Stace & Tutin: SPAIN, Huesca, *B. F. Garrido & Pérez s.n.* (MA-806230), X, X, X, X. ***Graphephorum melicoides*** (Michx.) Desv.: CANADA, Ontario, *W. G. Dore & Gorham* 45-884 (US-2013905), X, —, —, X; CANADA, Ontario, *A. Dutilly & Lepage* 16059 (US-1935710), X, —, —, X; CANADA, Ontario, *C. V. Morton 11449* (US-2306540), X, —, —, X. ***Graphephorum wolfii*** (Vasey) Vasey ex Coult.: CANADA, Alberta, *W. G. Dore 12163* (US-2076128), X, X, X, X; USA, Montana, *J. S. Shelly & King 1228* (US-3062155), X, X, X, X; USA, Montana, *J. R. Swallen 6500* (US-2303885), X, X, X, X. ***Helictochloa hackelii*** (Henriq.) Romero Zarco: PORTUGAL, Algarve, *T. Buira et al. 2617* (MA), X, X, X, X. ***Helictotrichon cantabricum*** (Lag.) Gervais: SPAIN, Asturias, *M. A. Del Collado 1625* (MA-800933), X, X, X, X. ***Helictotrichon convolutum*** (C. Presl) Henrard: GREECE, Peloponeso, *L. Medina et al. 4063* (MA-761434), X, X, X, X; ITALY, Sicily, *A. Herrero et al. 881* (MA-646751), X, X, X, X. ***Helictotrichon delavayi*** (Hack.) Henrard: CHINA, Yunnan, *Tibet-MacArthur et al. 1089* (US), X, X, X, X. ***Helictotrichon filifolium*** (Lag.) Henrard **subsp. *filifolium***: SPAIN, Valencia, *P. Barberá & A. Quintanar 1612* (MA), X, X, X, X; SPAIN, Alicante, *L. Serra 8929* (MA-866283), X, X, X, X. ***Helictotrichon filifolium* subsp. *velutinum*** (Boiss.) Romero Zarco: SPAIN, Granada, *A. Quintanar & E. Glazkova 4000* (MA-836828), X, X, X, X. ***Helictotrichon mortonianum*** (Scribn.) Henrard: USA, *R.K. Gierisch 2842* (US), X, —, —, X; USA, Colorado, *R. J. Soreng & N. Soreng 7427* (US), X, X, X, X. ***Helictotrichon pallens*** (Link) J. M. Couderc & Guédès: PORTUGAL, Estremadura, *J. A. Devesa & C. Romero-Zarco s.n.* (MA-371107), X, X, X, X. ***Helictotrichon sedenense*** (Clar. ex Lam & DC.) Holub **subsp. *sedenense***: ANDORRA, *C. Aedo & Pedrol 19268* (MA-857577), X, X, X, X; SPAIN, Gerona, *J. Calvo 5690* (MA-840202), X, X, X, X; SPAIN, León, *M. L. Gil Zuñiga & Alejandre 1534-90* (MA-547460), X, X, X, X; SPAIN, Palencia, *C. Aedo & Pedrol 19176* (MA-863916), X, X, X, X. ***Helictotrichon thorei*** Röser: SPAIN, Asturias, *C. Aedo 18385* (MA-835099), X, X, X, X; SPAIN, Cádiz, *C. Aedo 15651* (MA-769625), X, X, X, X. ***Helictotrichon tianschanicum*** (Roshev.) Henrard: KYRGYZSTAN, Issyk-Kul, *R. J. Soreng et al. 7580* (US-3500051), X, X, X, X. ***Helictotrichon tibeticum* var. *laxiflorum*** Keng ex Z.L. Wu: CHINA, Qinghai, *R. J. Soreng et al. 5450* (US-3491824), X, X, X, X; CHINA, Sichuan, *R. J. Soreng et al. 5684* (US-3491115), X, X, X, X. ***Helictotrichon tibeticum* var. *tibeticum*** (Roshev.) Keng: CHINA, Sichuan, *R. J. Soreng et al. 5380* (US-3482595), X, X, X, X. ***Holcus lanatus*** L.: USA, California, *P. M. Peterson et al. 19682* (US-3539901), X, —, —, X. ***Koeleria altaica*** (Domin) Krylov: CHINA, Inner Mongolia, *R. J. Soreng et al. 5139* (US-3468991), X, —, —, X. ***Koeleria asiatica*** Domin: USA, *S. G. Shetler & Stone 3439* (US), —, —, —, X. ***Koeleria boliviensis*** (Domin) A.M. Molina: BOLIVIA, Tomás Frías, *P. M. Peterson & Annable 11839* (US-3479035), X, X, X, X; BOLIVIA, Tomás Frías, *P. M. Peterson et al. 12924* (US-3276893), X, X, X, X. ***Koeleria brevis*** Steven: RUSSIA, Crimea, *P. A. Smirnow 14* (US-2554578), X, X, X, X; TURKEY, Bursa, *L. Gillespine et al. 10419* (US), X, X, X, X. ***Koeleria capensis*** Nees: SOUTH AFRICA, Natal, *L. Smook 1371* (US-2988227), X, X, —, X; SOUTH AFRICA, Eastern Cape, *L. Smook 10302* (US-3428003), X, X, X, X; TANZANIA, Kilimanjaro, *P. M. Peterson et al. 24336* (US), X, X, —, X; ZIMBABWE, *S. Laegaard 16082* (US-3292436), X, X, X, X. ***Koeleria castellana*** Boiss. & Reut.: SPAIN, Madrid, *A. Quintanar 997* (MA-735762), X, X, X, X. ***Koeleria caucasica*** (Trin. ex Domin) B. Fedtsch.: ARMENIA, Gegharkunik, *C. Aedo et al. 11603* (MA-743258), X, X, X, X; ARMENIA, Syunik, *A. Quintanar et al. 1582* (MA-743850), X, X, X, X. ***Koeleria crassipes*** Lange: MOROCCO, Agadir, *W. Lippert 25333* (US-3430084), —, X, —, X; MOROCCO, Souss-Massa, *A. Quintanar et al. 3582* (MA), X, X, X, X; PORTUGAL, Beira Baixa, Silva & Silva 5812 (US-2237563), X, X, X, X; PORTUGAL, Estremadura, *M. Á. García et al. 6115* (MA-865676), X, X, X, X; PORTUGAL, Tras-Os-Montes, *C. Aedo et al. 17564* (MA-823359), X, X, X, X; SPAIN, Ávila, *A. Quintanar 1424* (MA-735748), X, X, X, X; SPAIN, Madrid, *A. Quintanar 1430* (MA-735853), X, X, X, X; SPAIN, Málaga, *A. Quintanar & E. Glazkova 4090* (MA-836944), X, X, X, X.

Koeleria dasyphylla Willk.: SPAIN, Cádiz, *A. Quintanar 994* (MA-735754), X, X, X, X. ***Koeleria dasyphylla* subsp. *nevadensis*** (Hack.) A. Quintanar & Romero García: SPAIN, Almeria, *A. Quintanar 990* (MA-735757), X, X, X, X. ***Koeleria eriostachya*** Pančić: RUSSIA, Adygeya, *R. J. Soreng et al. 8042* (US-3600723), X, X, X, X; RUSSIA, Stavropol, *R. J. Soreng et al. 7934* (US-3600764), X, X, X, X; TURKEY, Nigde, *R. J. Soreng et al. 8156* (US), X, X, X, X. ***Koeleria fueguina*** C.E. Calderón ex Nicora: ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17142* (US-3453548), X, X, X, X; CHILE, Aysén, *R. J. Soreng & N. Soreng 7302* (US-3483191), X, X, X, X. ***Koeleria glauca*** (Spreng.) DC.: RUSSIA, Bryansk, *E. Glazkova s.n.* (MA-744204), X, X, X, X; SLOVAQUIA, Senica, *F. Slavonovsky 1498* (US-2574144), —, —, X, X; SLOVAQUIA, Senica, *F. Slavonovsky 1498* (US-3472891), X, X, —, X. ***Koeleria glaucovirens*** Domin: BULGARIA, *J. J. Aldasoro et al. 8786* (MA-727794), X, X, X, X; BULGARIA, A. *Quintanar et al. 1167* (MA-721296), X, X, X, X; BULGARIA, *A. Quintanar et al. 1360* (MA-721303), X, X, X, X; TURKEY, Izmir, *L. Gillespine et al. 10446* (US), X, X, X, X; TURKEY, Afyon, *L. Gillespine et al. 10635* (US), X, X, X, X. ***Koeleria hirsuta*** Gaudin: SWITZERLAND, Ticino, *P. Schönswetter et al. s.n.* (MA-735738), X, X, X, X. ***Koeleria kurdica*** Ujhelyi: ARMENIA, Aragatsotn, *L. Medina et al. 3116* (MA-742230), X, X, X, X; ARMENIA, Ararat, *C. Navarro et al. 5628* (MA-743854), X, X, X, X; ARMENIA, Syunik, *A. Quintanar et al. 1465* (MA-743670), X, X, —, X; ARMENIA, Vayots Dzor, *A. Herrero et al. 2732* (MA-744638), X, X, X, X; ARMENIA, Vayots Dzor, *A. Quintanar et al. 1635* (MA-743811), X, X, X, X; TURKEY, Bilecik, *R. J. Soreng & Davis 4050* (US-3483172), X, X, X, X; TURKEY, Nigde, *R. J. Soreng et al. 8157* (US-3628906), X, X, X, X; TURKEY, Manisa, *L. Gillespine et al. 10474* (US), X, X, X, X. ***Koeleria kurtzii*** Hack. ex Kurtz: ARGENTINA, Mendoza, *P. M. Peterson & Annable 11428* (US-3479036), X, X, X, X; BOLIVIA, Oruro, *P. M. Peterson et al. 12732* (US-3265382), X, X, X, X; BOLIVIA, La Paz, *S. A. Renvoize & Cope 4106* (US-2931105), X, X, X, X; CHILE, Region I, *P. M. Peterson & Soreng 15658* (US), X, X, X, X; ECUADOR, Bolívar, *P. M. Peterson & Judziewicz 9293* (US-3237249), X, —, —, —; PERU, Puno, *P. M. Peterson et al. 14662* (US-3428549), X, X, X, X. ***Koeleria litvinowii* subsp. *argentea*** (Griseb.) S.M. Phillips & Z.L. Wu: INDIA, Kashmir, *W. Koelz 2352a* (US-1537047), X, X, X, X; INDIA, Kashmir, *W. Koelz 5542a* (US-1607505), X, X, X, X. ***Koeleria litvinowii*** Domin **subsp. *litvinowii***: CHINA, Gansu, *R. J. Soreng et al. 5386* (US-3482586), X, X, X, X; RUSSIA, *Ikonnikov 540* (LE), —, X, X, X. ***Koeleria loweana*** A. Quintanar, Catalán & Castrov.: PORTUGAL, Madeira, *M. Sequeira & P. Catalán 4532* (MA-725995), X, X, X, X. ***Koeleria mendocinensis*** (Hauman) C.E. Calderón: ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17203* (US-3450912), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17235* (US-3450938), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17257* (US-3453527), X, X, X, X. ***Koeleria nitidula*** Velen.: BULGARIA, Smolyan, *A. Herrero et al. 2280* (MA-721277), X, X, X, X. ***Koeleria pyramidata*** (Lam.) P. Beauv.: AUSTRIA, Lower Austria, *L. Arnow 6368* (US-3623980), X, X, X, X; AUSTRIA, *L. Arnow 6389* (US), —, —, —, X; FRANCE, Ardennes, *J. Duvigneaud 78F531* (MA-359011), X, X, X, X; MEXICO, Durango, *P. M. Peterson & Sánchez Alvarado 19119* (US-3483188), —, —, —, X; MEXICO, Coahuila, *P. M. Peterson & Valdés-Reyna 18798* (US-3483178), X, X, X, X; MEXICO, Coahuila, *P. M. Peterson et al. 21025* (US), X, X, X, X; MEXICO, Coahuila, *P. M. Peterson & Romaschenko 24525* (US), X, —, —, X; MEXICO, Nuevo León, *P. M. Peterson & Valdés-Reyna 18947* (US-3483189), —, —, —, X; RUSSIA, Stavropol, *R. J. Soreng et al. 7892* (US-3600725), X, X, X, X; SPAIN, Barcelona, *A. Quintanar & G. García 1436* (MA-735774), X, X, X, X; SPAIN, Castellón, *A. Quintanar & G. García 1434* (MA-735837), X, X, X, X; SPAIN, Gerona, *A. Quintanar & G. García 1439* (MA-735839), X, X, X, X; SPAIN, Huesca, *A. Quintanar & M. Vega 978* (MA-735752), X, X, X, X; SWITZERLAND, Valais, *S. Castroviejo et al. 11380* (MA-490269), X, X, X, X; SWITZERLAND, Waadt, *H. Bührer s.n.* (MA-358970), X, X, X, X; USA, California, *P. M. Peterson & Annable 2755* (US-3483187), X, X, X, X; USA, California, *P. M. Peterson et al. 19783* (US-3523936), X, X, X, X; USA, Colorado, *P. M. Peterson &*

Annable 7829 (US-3483185), X, X, X, X. ***Koeleria pyramidata* subsp. *arenaria*** (Dumort.) A. Quintanar & Castrov.: SPAIN, Cantabria, *J. Calvo & A. Quintanar 1807* (MA-774753), X, X, X, X. ***Koeleria pyramidata* subsp. *schroeteriana*** (Domin) A. Quintanar & Castrov.: SPAIN, Cantabria, *A. Quintanar & G. García 1449* (MA-735766), X, X, X, X; SPAIN, Cantabria, *A. Quintanar & G. García 1450* (MA-735767), X, X, X, X; SPAIN, Palencia, *J. Calvo & A. Quintanar 1813* (MA-774757), X, X, X, X. ***Koeleria rodriguez-graciae*** A. Quintanar & Castrov.: PORTUGAL, Tras os Montes, *C. Aedo et al. 17602* (MA), X, X, X, X. ***Koeleria splendens*** C. Presl: GREECE, Peloponnissos, *L. Medina et al. 4053* (MA-761427), X, X, X, X; GREECE, Peloponnissos, *R. J. Soreng 3813b* (US-3561041), X, X, X, X; GREECE, Thessaly, *R. J. Soreng et al. 7491* (US-3555907), X, X, X, X. ***Koeleria trachyantha*** Phil.: PERU, Arequipa, *Universidad San Agustin s.n.* (US-3375727), X, X, X, X. ***Koeleria transiliensis*** Reverd. ex Pavlov: KYRGYZSTAN, Chu, *R. J. Soreng et al. 7538* (US-3500034), X, X, X, X. ***Koeleria vallesiana*** (Honck.) Gaudin: FRANCE, Aude, *R. J. Soreng & Maumont 4005b* (US-3483168), X, X, X, X; MOROCCO, Tanger-Tétouan, *A. Quintanar & J. Calvo 2761* (MA-782637), X, X, X, X; PORTUGAL, Estremadura, *M. A. García et al. 6045* (MA-864760), X, X, X, X; SPAIN, Barcelona, *A. Quintanar & García 1435* (MA-735834), X, X, X, X; SPAIN, Castellón, *A. Quintanar & García 1433* (MA-735842), X, X, X, X; SPAIN, Huesca, *A. Quintanar 1428* (MA-735848), X, X, X, X; SPAIN, Madrid, *A. Quintanar 1425* (MA-735855), X, X, X, X; SPAIN, Madrid, *A. Quintanar 1426* (MA-735846), X, X, X, X; SPAIN, Madrid, *A. Quintanar 1427* (MA-735847), X, X, X, X; SPAIN, Teruel, *C. Aedo et al. 4633* (MA-611915), X, X, X, X. ***Koeleria vurilochensis*** C.E. Calderón ex Nicora: ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17220* (US-3450926), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17258* (US-3453528), X, X, X, X. ***Lagurus ovatus*** L.: ARGENTINA, Chubut, *A. A. Beetle 395* (US), —, —, —, X; SOUTH AFRICA, Eastern Cape, *G. Davidse 33570* (US), —, —, —, X; SPAIN, Córdoba, *C. Aedo 12734* (MA-738597), X, X, X, X; SPAIN, Gerona, *A. Quintanar & García 1446* (MA), X, X, X, X; SPAIN, Menorca, *J. L. Fernández Alonso et al. 30298* (MA), X, X, X, X. ***Leptophyllochloa micrathera*** (E. Desv.) C. E. Calderón: ARGENTINA, Neuquen, *P. M. Peterson et al. 17395* (US-3452778), X, X, X, X; ARGENTINA, Neuquen, *P. M. Peterson et al. 17403* (US-3452785), X, X, X, X. ***Limnodea arkansana*** (Nutt.) L.H. Dewey: MEXICO, Coahuila, *F. W. Gould 11223* (US-2473978), X, X, X, X; MEXICO, Coahuila, *F. W. Gould 11130* (US-2474029), X, X, X, X; USA, Mississippi, *R. J. Soreng 7860* (US-3683654), X, X, X, X; USA, Texas, *C. L. Lundell & Lundell 8948* (US-1818926), X, —, —, —; USA, *S. D. Correll 15570* (US), X, —, —, —. ***Mibora minima*** (L.) Desv.: SPAIN, Valladolid, *C. Aedo et al. 18781* (MA-855702), X, X, X, X. ***Oreochloa confusa*** (Coincy) Rouy: SPAIN, Palencia, *J. Calvo & A. Quintanar 1816* (MA-772357), X, X, —, X. ***Peyritschia deyeuxioides*** (Kunth) Finot: MEXICO, Chihuahua, *P. M. Peterson et al. 17695* (US-3470480), X, X, X, X; MEXICO, Chihuahua, *P. M. Peterson & J. M. Saarela 22058* (US), X, X, X, X. ***Peyritschia koelerioides*** (Peyr.) E. Fourn.: GUATEMALA, *M. De Koninck 209* (US-2153274), X, X, —, X; MEXICO, Mexico, *S. D. Koch 76206* (US-2989662), X, X, X, X. ***Peyritschia pringlei*** (Scribn.) S.D. Koch: MEXICO, Chihuahua, *P. M. Peterson et al. 7994* (US-3436730), X, X, X, X; MEXICO, San Luis Potosí, *E. R. Sohns 1162* (US-2154424), X, X, X, X; MEXICO, *E. R. Sohns 525* (US-2118507), —, X, X, —. ***Phalaris arundinacea*** L.: POLAND, Biebzra, *J. Calvo & Unió 4848* (MA-821959), X, X, X, X. ***Phippsia algida*** (Sol.) R. Br.: CANADA, Northwest Territories, *H.A. Senn & Calder* 3810 (US), —, —, —, X. ***Poa kilimanjarica*** (Hedberg) Markgr.-Dann.: TANZANIA, Kilimanjaro, *P. M. Peterson et al. 24361* (US), X, X, —, X. ***Psilurus incurvus*** (Gouan) Schinz & Thell.: CHIPRE, *Iter Mediterraneum IV Chipre 767* (MA-496455), X, X, X, X. ***Puccinellia andersonii*** Swallen: [Unknown locality], *L. J. Gillespie 8377* (US), X, —, —, X. ***Relchela panicoides*** Steud.: ARGENTINA, Chubut, *P. M. Peterson et al. 17318* (US-3450671), X, X, —, X. ***Rostraria balansae*** (Coss. & Durand) Holub: ALGERIA, *Faure s.n.* (MA-9435), —, X, —, —. ***Rostraria cristata*** (L.) Tzvelev: GREECE, Peloponnissos, *C. Navarro et al. 6899* (MA-765839), X, X, X, X; IRAQ, Baghdad Liwa, *F. A.*

Barkley & Brahim 1325 (US-2381402), X, X, X, X; ISRAEL, Coastal Galilee, *A. Danin et al. 54-39* (MA-499549), X, X, X, X; PORTUGAL, Tras-Os-Montes, *R. Morales et al. 2243* (MA-824240), —, —, X, —; SPAIN, Asturias, *G. Hernández Palacios s.n.* (MA-866475), X, X, X, X; SPAIN, Gerona, *J. Calvo 4324* (MA-805534), X, X, X, X; TURKEY, Antalya, *R. J. Soreng & Cabi 9072* (US), X, X, X, X; TURKEY, Gümüshane, *A. Herrero et al. 1207* (MA-688010), X, X, X, X; TURKEY, Sinop, *V. Valcárcel et al. 250VV01* (MA-689608), X, X, X, X. ***Rostraria hispida*** (Savi) Doğan: SPAIN, Huelva, *E. Valdés Bermejo et al. 3914* (MA-3914), X, X, —, X; SPAIN, Sevilla, *A. Quintanar 995* (MA-735857), X, X, X, X. ***Rostraria litorea*** (All.) Holub: ITALY, Cerdeña, *A. Quintanar et al. 934b* (MA-709393), X, X, X, X; ITALY, Cerdeña, *A. Quintanar & G. Vacca 3368* (MA), X, X, X, X; SPAIN, Islas Baleares, *R. Morales et al. 2527* (MA), X, X, X, X. ***Rostraria obtusiflora*** (Boiss.) Holub: ISRAEL, Sharon Plain, *A. Danin s.n.* (MA-498402), X, X, —, X. ***Rostraria pumila* subsp. *fuscescens*** (Pomel) H. Scholz & Valdés: MOROCCO, Figuig, *J. Lambinon & van Den Sande 95/169* (MA-590485), X, X, —, X. ***Rostraria pumila* subsp. *pumila*** (Desf.) Tzvelev: AUSTRALIA, Western Australia, *P. M. Peterson et al. 14444* (US-3423163), X, X, —, X; PORTUGAL, Madeira, *C. Aedo et al. 13710* (MA-757732), X, X, X, X; SPAIN, Gran Canaria, *C. Aedo et al. 12408* (MA-751313), X, X, X, X; TUNISIA, Gafsa, *J. Calvo et al. 3109* (MA-797927), X, X, X, X; TUNISIA, Kasserine, *J. Calvo et al. 3318* (MA-798203), X, X, X, X; TUNISIA, Sfax, *C. Aedo et al. 16178* (MA-796930), X, X, —, X. ***Rostraria salzmannii*** (Boiss.) Holub: TUNISIA, Gabès, *C. Aedo et al. 16252* (MA-797210), X, X, X, X; TUNISIA, Medenine, *C. Aedo et al. 16278* (MA-796771), X, X, —, X; TUNISIA, Medenine, *J. Lambinon & Margot 99/T/107* (MA-693894), X, X, —, X. ***Rostraria smyrnacea*** (Trin.) H. Scholz: ISRAEL, *A. T. Semple 16* (US-2241801), —, X, X, X. ***Sclerochloa dura*** P. Beauv.: USA, Mississippi, *C.T. Bryson 17876* (US), —, —, —, X. ***Scolochloa festucacea*** (Willd.) Link: [Unknown locality], *W.H. Harvey 3896* (US), X, —, —, X. ***Sesleria albicans*** Kit. ex Schult. **subsp.** ***albicans***: FRANCE, Hautes Alpes, *C. Aedo 18426* (MA-839875), X, X, X, X. ***Sphenopholis filiformis*** (Chapm.) Scribn.: USA, Texas, *C. L. Lundell 13358* (US-1913232), X, X, X, X; USA, Texas, *L. H. Shinners 7021* (US-2079457), —, X, X, X; USA, Virginia, *M. L. Fernald & Long 11747* (US-1912851), X, X, X, X; USA, *A. J. Cronquist 5037* (US-1937277), X, —, —, —. ***Sphenopholis intermedia*** (Rydb.) Rydb.: USA, Iowa, *T. S. Cooperrider & Cooperrider 1350* (US-2382141), X, X, X, X; USA, Maryland, *P. M. Peterson et al. 23719* (US), X, X, X, X; USA, Maryland, *R. J. Soreng & P. Barberá 9333* (US), X, X, X, X; USA, Virginia, *M. L. Fernald & Long 9818* (US-1810382), X, X, X, X. ***Sphenopholis interrupta*** (Buckley) Scribn.: USA, Texas, *L. C. Hinckley & Hinckley 400* (US-2115223), —, X, X, X; USA, Texas, *J. C. Johnson & Webster 528* (US-2078855), —, X, —, —; USA, Texas, *W. A. Silveus 2709* (US-72649), X, X, X, X; USA, Texas, *J. R. Swallen 10330* (US-1980235), —, X, X, —. ***Sphenopholis longiflora*** (Vasey ex L.H. Dewey) Hitchc.: USA, Arkansas, *D. Demaree 16808* (US-1761162), X, X, X, X; USA, Texas, *R. L. Crockett s.n.* (US-2078830), X, X, X, X. ***Sphenopholis nitida*** (Biehler) Scribn.: USA, Georgia, *A. Cronquist 5051* (US-1937278), X, X, X, X; USA, Maryland, *P. M. Peterson et al. 23755* (US), X, X, X, X; USA, North Carolina, *B. A. Sorrie 12924* (US-3674421), X, X, X, X; USA, Virginia, *M. L. Fernald & Long 11748* (US-1912852), —, X, —, X. ***Sphenopholis obtusata*** (Michx.) Scribn.: USA, Georgia, *W. Knapp et al. 3505* (US-3675409), X, X, X, X; USA, Nebraska, *W. Kiener 29463* (US-2151127), X, X, —, X; USA, Nevada, *A. Tiehm 15908* (US-3590839), X, X, X, X. ***Sphenopholis pensylvanica*** (L.) Hitchc.: USA, North Carolina, *B. A. Sorrie 13175* (US-3669599), X, X, X, X; USA, Ohio, *F. Bartley 2635* (US-3465263), X, X, X, X; USA, Virginia, *T. F. Wieboldt & R. J. Soreng 6360* (US-3541637), X, X, X, X. ***Torreyochloa pallida*** (Torr.) G.L. Church: USA, Indiana, *C. C. Deam 47046* (US-1445500), X, —, —, X. ***Triplachne nitens*** (Guss.) Link: SPAIN, Almeria, *F. Sanz Fábregas s.n.* (MA-492206), X, X, X, X. ***Trisetaria dufourei*** (Boiss.) Paunero: SPAIN, Cádiz, *R. Auriault s.n.* (MA-628175), X, X, —, X; SPAIN, Huelva, *E. Valdés & G. López 5488* (MA-445702), X, X, X, X. ***Trisetaria lapalmae*** H. Scholz: SPAIN, Gran Canaria, *C. Aedo et al. 12541* (MA), X, X, X, X; SPAIN, Gran

Canaria, *A. Marrero & González-Martín s.n.* (MA-564162), X, X, X, —; SPAIN, Gran Canaria, *A. Marrero & González-Martín s.n.* (MA-564163), X, X, X, X; SPAIN, Gran Canaria, *A. Quintanar et al. 1850* (MA-750862), X, X, X, X. ***Trisetaria linearis*** Forssk.: AZERBAIJAN, *V. Ivanova s.n.* (LE), X, X, X, X; EGYPT, Northern Sinai, *L. Boulos 19858* (K), X, X, X, X. ***Trisetaria loeflingiana*** (L.) Paunero: SPAIN, Madrid, *P. Barberá s.n.* (MA-865101), X, X, X, X; TURKEY, Konya, *R. J. Soreng & Cabi 9251* (US), X, X, X, X. ***Trisetaria ovata*** (Pers.) Paunero: PORTUGAL, Tras-Os-Montes, *C. Aedo et al. 17622* (MA-823590), X, X, —, X. ***Trisetaria panicea*** (Lam.) Paunero: SPAIN, Cádiz, *C. Aedo 15643* (MA-769630), X, X, —, X; SPAIN, Cádiz, *P. Barberá & Quintanar 765* (MA), X, X, X, X; SPAIN, Madrid, *P. Barberá s.n.* (MA-865105), X, X, X, X; SPAIN, Madrid, *P. Barberá s.n.* (MA-865106), X, X, X, X; SPAIN, Menorca, *C. Aedo et al. 19940* (MA-874785), X, X, X, X. ***Trisetaria scabriuscula*** (Lag.) Paunero: PORTUGAL, Tras-Os-Montes, *R. Morales et al. 2310* (MA-824145), X, X, X, X; SPAIN, Madrid, *J. C. Moreno s.n.* (MA-480138), X, X, —, X; SPAIN, Segovia, *R. García Ada 5115* (MA-795679), —, X, —, X. ***Trisetokoeleria gorodkowii*** (Roshev.) Tzvelev: RUSSIA, *A. A. Gorobkov & Mikhaylova s.n.* (LE), X, X, X, X. ***Trisetokoeleria taymirica*** Tzvelev: RUSSIA, *E. B. Pospelova 93-179* (LE), X, X, X, X. ***Trisetopsis angusta*** (C.E. Hubb.) Röser & A. Wölk: KENYA, *A. Bogdan AB3051* (US-2307080), —, X, —, X; KENYA, *L. D. E. F. Vesey-Fitzgerald 5329* (US-2640049), X, X, X, X. ***Trisetopsis capensis*** (Schweick.) Röser & A. Wölk: SOUTH AFRICA, Eastern Cape, *C. Aedo et al. 15094bis* (MA), X, X, X, X. ***Trisetopsis elongata*** (Hochst. ex A. Rich.) Röser & A. Wölk: TANZANIA, Mbeya, *P. M. Peterson et al. 24122* (US), X, X, —, X; TANZANIA, Njomba Region, P. M. *Peterson et al. 24042* (US), X, X, —, X; TANZANIA, Njomba Region, *P. M. Peterson et al. 24047* (US), X, X, —, X; TANZANIA, Rukwa, *P. M. Peterson et al. 24090* (US), X, X, —, X; TANZANIA, Ruvuma Region, *P. M. Peterson et al. 23965* (US), X, X, —, X. ***Trisetopsis hirtula*** (Steud.) Röser & A. Wölk: SWITZERLAND, Thurgau, *Hugentobler s.n.* (US-2181529), X, X, —, —. ***Trisetopsis imberbis*** (Nees) Röser, A. Wölk & Veldkamp: SOUTH AFRICA, Natal, *L. Smook 1547* (US-3003611), —, X, X, X; SOUTH AFRICA, Transvaal, *Liebenberg 8509* (US-3004905), —, X, —, X; SOUTH AFRICA, Transvaal, *L. Smook 2560* (US-3184964), X, X, X, X. ***Trisetopsis junghuhnii*** (Buse) Röser & A. Wölk: CHINA, Sichuan, *Tibet MacArthur et al. 1727* (US-3528173), X, X, X, X. ***Trisetopsis lachnantha*** (Hochst. ex A. Rich.) Röser & A. Wölk: TANZANIA, Kilimanjaro, *P. M. Peterson et al. 24345* (US), X, X, —, X. ***Trisetopsis longifolia*** (Nees) Röser & A. Wölk: SOUTH AFRICA, Orange Free State, *G. Davidse 6962* (US-2769171), X, X, X, —. ***Trisetopsis mannii*** (Pilg.) Röser & A. Wölk: EQUATORIAL GUINEA, Bioko, *M. Carvalho 3651b* (MA-539964), X, X, —, X. ***Trisetopsis milanjiana*** (Rendle) Röser & A. Wölk: KENYA, *R. L. Piemeisel & Kephart 169* (US-1386847), —, X, X, X; TANZANIA, Njomba Region, *P. M. Peterson et al. 24018* (US), X, X, —, X; TANZANIA, Njomba Region, *P. M. Peterson et al. 24034* (US), X, X, —, X. ***Trisetopsis natalensis*** (Stapf) Röser & A. Wölk: SOUTH AFRICA, Natal, *H. G. Schweickerdt 1510* (US-2462051), X, —, —, —. ***Trisetopsis umbrosa*** (Hochst. ex Steud.) Röser & A. Wölk: MALAWI, *G. Jackson 1939* (US-2462157), X, X, X, X. ***Trisetum aeneum*** (Hook. f.) R.R. Stewart: INDIA, Kashmir, *R. R. Stewart 18314a* (US-1982222), X, X, X, X; INDIA, Kashmir, *R. R. Stewart 18448* (NY), X, —, —, X. ***Trisetum alpestre*** (Host) P. Beauv.: ITALY, Belluno, *SC s.n.* (FI), X, X, X, X. ***Trisetum altaicum*** Stephan ex Roshev.: RUSSIA, Siberia, *L. Malyshev & Pezhemskiy s.n.* (LE), X, X, X, X; RUSSIA, *G. Pavlova & Penkovskaya s.n.* (LE), X, X, X, —. ***Trisetum ambiguum*** Rúgolo & Nicora: ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17134* (US-3452772), X, X, X, X. ***Trisetum andinum*** Benth.: ECUADOR, Pichincha, P. *Sklenar & Kosteckova 9-3* (US-3338677), X, X, —, X. ***Trisetum antarcticum*** (G. Forst.) Trin.: AUSTRALIA, Victoria, *R. A. Black 1214-002* (US-1868259), —, X, —, X. ***Trisetum argenteum*** (Willd.) Roem. & Schult.: ITALY, Bolzano, *G. van Buggenhout s.n.* (MA-366782), X, —, X, —; ITALY, Veneto, *C. Aedo 20898* (MA), X, X, X, X. ***Trisetum barbinode*** Trin.: ARGENTINA, Neuquen, *P. M. Peterson et al. 17417* (US-345794), X, X, X, —; CHILE, Bio-Bio, *R. J. Soreng &*

N. Soreng 7125 (US), X, X, —, X. ***Trisetum baregense*** Laffitte & Miégev.: SPAIN, Burgos, P. *Barberá et al. 956* (MA), X, X, X, X. ***Trisetum bertolonii*** Jonsell: ITALY, Pescara, *C. Navarro et al. 4234* (MA-699433), X, X, —, X; ITALY, Pesaro, *H. Merxmüller & Wiedmann 19570* (M-223256), X, X, X, X. ***Trisetum bifidum*** (Thunb.) Ohwi: JAPAN, Honshu, *S. Tsugaru 14332* (MO-4338294), X, X, X, X. ***Trisetum bungei*** Boiss.: IRAN, *W. Koelz 16514* (US-1983148), X, X, X, —. ***Trisetum buschianum*** Seredin **subsp.** ***buschianum***: RUSSIA, Balkaria, *E. A. Bush & Bush s.n.* (LE), X, X, X, X. ***Trisetum buschianum*** **subsp.** ***transcaucasicum*** (Seredin) Mosul.: GEORGIA, Tush-Psav-Khevsureti, *H.-J. Zündorf & Gerth 25658* (JE), X, X, X, X. ***Trisetum caudulatum*** Trin.: ARGENTINA, Neuquen, *P. M. Peterson et al. 17358* (US-3451001), X, X, X, X; ARGENTINA, Neuquen, *P. M. Peterson et al. 17374* (US-3451014), X, X, X, X; CHILE, Valparaiso, *P. C. Hutchinson 45* (US-2381280), X, —, X, —. ***Trisetum cernuum*** **subsp.** ***canescens*** (Buckley) Calder & Roy L. Taylor: USA, California, *P. M. Peterson et al. 19686* (US-3539875), X, X, X, X; USA, California, *G.L. Stebbins 3826* (US-2014431), X, —, —, X; USA, Oregon, *P. M. Peterson et al. 19720* (US-3525166), X, —, —, X; USA, Oregon, *R. J. Soreng 5956* (US), X, X, X, X. ***Trisetum cernuum*** Trin. **subsp.** ***cernuum***: CANADA, Alberta, *F. J. Hermann 13048* (US-2209559), X, —, —, X; CANADA, British Columbia, *F. J. Hermann 12914* (US-2209483), X, —, —, X; CANADA, British Columbia, *P. M. Peterson et al. 18723* (US-3500293), X, —, —, X; USA, Montana, *J. S. Shelly & King 1229* (US-3062156), X, X, X, X. ***Trisetum clarkei*** (Hook. f.) R.R. Stewart: INDIA, Kashmir, *R. R. Stewart & Stewart 5594* (NY), X, X, —, X; PAKISTAN, *G. Miehe & Miehe 1374* (GOET), X, X, X, X. ***Trisetum curvisetum*** Morden & Valdés-Reyna: MEXICO, Nuevo León, *P. M. Peterson et al. 16719* (US-3536859), X, X, X, X; MEXICO, Nuevo León, *P. M. Peterson et al. 16723* (US-3536860), X, X, X, X; MEXICO, Nuevo León, *P. M. Peterson et al. 16764* (US-3536861), X, X, X, X. ***Trisetum distichophyllum*** (Vill.) P. Beauv.: AUSTRIA, Tyrol, *D. Podlech s.n.* (MA-873223), X, X, X, X; SWITZERLAND, Valais, *S. Castroviejo et al. 11213* (MA-490966), X, X, X, X. ***Trisetum durangense*** Finot & P.M. Peterson: MEXICO, Durango, *P. M. Peterson & Brothers 16964* (US-3536866), X, X, X, X; MEXICO, Durango, *P. M. Peterson & Sánchez Alvarado 19114* (US-3496190), X, X, X, X. ***Trisetum filifolium*** Scribn. ex Beal: MEXICO, Hidalgo, *H. E. Moore 3250* (US-1963112), —, X, —, X. ***Trisetum filifolium*** **var.** ***aristatum*** Scribn. ex Beal: MEXICO, Durango, *P. M. Peterson & Sánchez Alvarado 19144* (US-3496176), X, X, X, X. ***Trisetum flavescens*** **subsp.** ***africanum*** (H. Lindb.) Dobignard: MOROCCO, *R. Gonzalo et al. 1209* (MA-801008), X, X, —, X. ***Trisetum flavescens*** **subsp.** ***corsicum*** (Rouy) Cif. & Giacom.: FRANCE, Corsica, *P. Barberá & A. Quintanar 1599* (MA), X, X, X, X. ***Trisetum flavescens*** (L.) P. Beauv. **subsp.** ***flavescens***: ARGENTINA, *Gallinal PE-5594* (US-1914250), X, —, —, X; SPAIN, Almeria, *P. Barberá et al. 1219* (MA), X, X, X, X; TURKEY, Mus/Erzurum, *F. Ehrendorfer et al. 787-79-24* (WU), X, X, —, X; USA, Missouri, *B. F. Bush s.n.* (US-868240), X, —, —, X. ***Trisetum flavescens*** **subsp.** ***griseovirens*** (H. Lindb.) Dobignard: MOROCCO, Marrakech, *A. Herrero et al. 2985* (MA-7469779), X, X, —, X. ***Trisetum flavescens*** **subsp.** ***parvispiculatum*** Tzvelev: ARMENIA, Aragatsotn, *L. Medina et al. 2606* (MA), X, X, X, X; ARMENIA, Syunik, *A. Quintanar et al. 1512* (MA-743574), X, X, —, X. TURKMENISTAN, *Nikitin & Ivanov s.n.* (LE), X, X, X, X. ***Trisetum flavescens*** **subsp.** ***purpurascens*** (DC.) Arcang.: BULGARIA, Kosovo, *C. Aedo et al. 10371* (MA), X, X, X, X. ***Trisetum flavescens*** **subsp.** ***tenue*** (Hack. ex Formánek) Strid: GREECE, Peloponnissos, *R. J. Soreng 3818* (US), X, X, X, X. ***Trisetum foliosum*** Swallen: VENEZUELA, Merida, *G. Davidse 3226* (US-2977421), X, X, —, X. ***Trisetum glaciale*** (Bory) Boiss.: SPAIN, Granada, *P. Barberá et al. 937* (MA), X, X, X, X; SPAIN, Granada, *A. Quintanar & M. Vega 2198* (MA), X, X, X, X. ***Trisetum glomeratum*** (Kunth) Trin. ex Steud.: USA, Hawaii, *C. R. Annable & Gagne 3551* (US-3447638), X, X, —, X; USA, Hawaii, *H. H. Iltis & Iltis 179* (US-2624904), —, X, —, X; USA, Hawaii, *P. Rubtzoff 3724* (US-2624835), X, X, —, X. ***Trisetum gracile*** **subsp.** ***conradiae*** (Gamisans) Gamisans: FRANCE, Corsica, *P. Barberá & A. Quintanar 1439* (MA), X, X, X, X. ***Trisetum hispidum*** Lange: SPAIN, Palencia, *P. Barberá & A.*

Quintanar 909 (MA), X, X, X, X. ***Trisetum inaequale*** Whitney: USA, Hawaii, *K. R. Wood & Oppenheimer 12089* (US-3621941), X, X, X, X; USA, Hawaii, *K. R. Wood & Perlman 4217* (US-3334161), X, X, X, X. ***Trisetum irazuense*** (Kuntze) Hitchc.: GUATEMALA, Quiche, *E. Contreras 5124* (US-2486072), X, X, X, X; MEXICO, *J. Rzedowski 28717* (US-3320111), —, X, X, X; VENEZUELA, Trujillo, *B. Stergios et al. 20323* (US-3449835), —, X, X, X. ***Trisetum ligulatum*** Finot & Zuloaga: MEXICO, Nuevo León, *C. Ritchie Bell & Duke 16572* (US-2461599), —, X, —, X. ***Trisetum longiglume* var. *glabratum*** Nicora: ARGENTINA, Neuquen, *P. M. Peterson et al. 17456* (US-3450401), X, X, X, —. ***Trisetum macrotrichum*** Hack.: ROMANIA, *A. von Degen s.n.* (US), X, X, —, X. ***Trisetum montanum*** Vasey: CANADA, Alberta, *P. M. Peterson et al. 18397* (US-3500358), X, X, X, X; USA, Arizona, *K. F. Parker & Mc Clintock 7533* (US-2078220), X, X, —, X; USA, Colorado, *R. C. Rollins 1522* (US-1647755), X, —, —, X; USA, Colorado, *P. A. Rydberg 2481* (US-868255), X, —, —, X. ***Trisetum oreophilum*** Louis-Marie: ECUADOR, Chimborazo, *P. M. Peterson et al. 9239* (US-3237370), X, X, X, X; PERU, Ayacucho, *P. M. Peterson & Refulio Rodriguez 18209* (US-3482533), X, X, X, X. ***Trisetum orthochaetum*** Hitchc.: USA, Montana, *J. S. Shelly & King 1230* (US), X, —, —, X. ***Trisetum palmeri*** Hitchc.: MEXICO, Coahuila, *P. M. Peterson & Valdés-Reyna 15953* (US-3536849), X, X, X, X; MEXICO, Coahuila, *P. M. Peterson & Valdés-Reyna 18783* (US-3496166), X, X, X, X; MEXICO, Coahuila, *P. M. Peterson & Valdés-Reyna 18815* (US-3496142), X, X, X, X; MEXICO, Durango, *P. M. Peterson & Sánchez Alvarado 20004* (US), X, X, X, X; MEXICO, Nuevo León, *P. M. Peterson & Valdés-Reyna 18960* (US-3496247), X, X, X, X. ***Trisetum phleoides*** (d'Urv.) Kunth: ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17256* (US-3453526), X, X, X, X. ***Trisetum preslii*** (Kunth) E. Desv.: ARGENTINA, Mendoza, *P. M. Peterson & Annable 11467* (US-3478841), X, X, X, X; ARGENTINA, Mendoza, *P. M. Peterson et al. 19207* (US-3502194), X, X, X, X. ***Trisetum pringlei*** (Scribn. ex Beal) Hitchc.: COSTA RICA, Cartago, *W. E. Booth CR 91* (US-3480618), —, X, X, X; [Unknown locality], *Pohl 10694* (US), X, X, X, X. ***Trisetum projectum*** Louis-Marie: USA, California, *H. Bailey & Bailey 2924b* (US-2115959), X, —, —, X; USA, Nevada, *A. S. Hitchcock 3184* (US-868300), —, X, —, —. ***Trisetum rigidum*** (M. Bieb.) Roem. & Schult. **subsp. *rigidum***: ARMENIA, Vayots Dzor, *A. Herrero et al. 2718* (MA), X, X, X, X; AZERBAIJAN, Nakhichevan ASSR, *T. V. Egorova et al. 433* (LE), X, X, X, X. ***Trisetum rigidum* subsp. *teberdense*** (Litv.) Tzvelev: RUSSIA, Karacheyevo-Cherkessiya, *R. J. Soreng et al. 8009* (US-3600681), X, X, X, X. ***Trisetum rosei*** Scribn. & Merr.: MEXICO, Puebla, *P. Dávila et al. 391* (US-3625456), X, X, X, X; MEXICO, Puebla, *J. H. Beaman 1993* (US-2381561), X, X, —, X; MEXICO, Puebla, *S. D. Koch 76205B* (US-2989681), X, X, X, X; MEXICO, Puebla, *S. D. Koch 76231* (US-2989680), X, X, X, X. ***Trisetum scitulum*** Bor: NEPAL, Mahalangur Himal, *J. Poelt 6303* (M-223308), X, X, X, X. ***Trisetum sibiricum* subsp. *litorale*** Rupr. ex Roshev.: RUSSIA, *Bogdanovskaya-Gienef & Verlichenko s.n.* (LE), X, X, X, X; RUSSIA, *V. V. Vasilkova et al. s.n.* (LE), X, X, X, X; USA, Alaska, *E. Hultén s.n.* (US-2382235), —, X, X, X. ***Trisetum sibiricum*** Rupr. **subsp. *sibiricum***: KYRGYZSTAN, Chu, *R. J. Soreng et al. 7543* (US-3500012), X, —, —, X; KYRGYZSTAN, Naryn, *R. J. Soreng et al. 7652* (US-3500053), X, X, X, X; KYRGYZSTAN, Naryn, *R. J. Soreng et al. 7666* (US-3500035), X, X, X, X; MONGOLIA, *M. Neyburg s.n.* (LE), X, X, X, X; RUSSIA, Kabardino-Balkariya, *R. J. Soreng et al. 7950* (US-3600759), X, X, X, X; RUSSIA, *M. G. Popov s.n.* (LE), X, X, X, X. ***Trisetum spellenbergii*** Soreng, Finot & P.M. Peterson: MEXICO, Chihuahua, *R. W. Spellenberg et al. 6854* (US-3459114), X, X, X, X. ***Trisetum spicatum*** (L.) K. Richt.: ARGENTINA, Mendoza, *P. M. Peterson et al. 19212* (US-3502186), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17051* (US-3450457), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17058* (US-3450428), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17065* (US-3450452), X, X, X, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17095* (US-3452615), X, X, —, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17096* (US-3452616), X, X, —, X; ARGENTINA, Santa Cruz, *P. M. Peterson et al. 17220 a* (US-3478838), X, X, X, X;

CANADA, Labrador, *J. Gillett 8611* (US-2236539), X, —, —, X; CANADA, Labrador, *J. Gillett & Findlay 5635* (US-2206719), X, —, —, X; CHILE, Bio-Bio, *R. J. Soreng & N. Soreng 7122* (US), X, X, X, X; FINLAND, *Söyrinki s.n.* (H-167031), X, X, X, X; INDIA, Kashmir, *W. Koelz 5906* (US-1607515), —, X, —, —; KAZAKHSTAN, *V. P. Goloskokov s.n.* (LE), X, —, X, X; MEXICO, Coahuila, *P. M. Peterson et al. 10051* (US-3436717), X, X, —, X; PERU, Ayacucho, *P. M. Peterson et al. 20504* (US), X, X, X, X; USA, Oregon, *P. M. Peterson & Annable 4849* (US-3478840), X, X, X, X. ***Trisetum spicatum*** **var.** ***cumingii*** (Nees ex Steud.) Finot: CHILE, X Región de Los Lagos, *R. Morales et al. 2737* (MA-886331), X, X, X, X. ***Trisetum spicatum*** **subsp.** ***molle*** (Kunth) Piper: CANADA, *E. Rouleau 5090* (US), X, —, —, X. ***Trisetum spicatum*** **subsp.** ***ovatipaniculatum*** Hultén ex Jonsell: SPAIN, Huesca, *P. Barberá et al. 1035* (MA), X, X, X, X. ***Trisetum spicatum*** **subsp.** ***pilosiglume*** (Fernald) Hultén: GREENLAND, Disko, *J. Eugenius s.n.* (US-1625744), X, —, —, X; GREENLAND, *J. Grontved 86* (US-1625672), X, —, —, X. ***Trisetum spicatum*** (L.) K. Richt. **subsp.** ***spicatum***: CANADA, British Columbia, *P. M. Peterson et al. 18457* (US-3500301), —, X, X, —; RUSSIA, *V. A. Gavriliuk & Gagarina s.n.* (LE), X, X, X, X. ***Trisetum spicatum*** **subsp.** ***virescens*** (Regel) Tzvelev: KAZAKHSTAN, *V. P. Goloskokov s.n.* (LE), X, X, X, X; KYRGYZSTAN, Naryn, *R. J. Soreng et al. 7667* (US-3500000), X, X, X, X. ***Trisetum spicatum*** **subsp.** ***wrangelense*** V.V. Petrovsky: RUSSIA, Far Eastern, *V. V. Petrovskiy s.n.* (LE), X, X, X, X. ***Trisetum subalpestre*** (Hartm.) Neuman: FINLAND, Lapland, *S. Tynys s.n.* (H-810643), X, X, X, X; RUSSIA, *A. A. Korobkov & Yurtsev s.n.* (LE), X, X, X, —. ***Trisetum tonduzii*** Hitchc.: COSTA RICA, San Jose, *R. K. Godfrey 66654* (US-2580681), X, X, —, X. ***Trisetum viride*** (Kunth) Kunth: MEXICO, Durango, *S. D. Koch & Sánchez Vega 78155* (US-2989684), X, X, X, X. ***Trisetum virletii*** E. Fourn.: MEXICO, *P. López Marroquín 54* (US-2926534), X, X, X, X; MEXICO, Jalisco, *R. McVaugh 11614* (US-2115907), X, X, X, X. ***Trisetum velutinum*** Boiss.: SPAIN, Granada, *P. Barberá et al. 941* (MA), X, X, X, X; SPAIN, Valencia, *P. Barberá & A. Quintanar 1617* (MA), X, X, X, X. ***Vahlodea atropurpurea*** (Wahlenb.) Fr. ex Hartm.: USA, Alaska, *S. S. Talbot DUT008-50* (US-3520730), X, —, —, X.

Appendix 2. GenBank ITS accession numbers for previously published sequences included.

Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl, **JF904803**. ***Arrhenatherum palaestinum*** Boiss., **AJ632238**. ***Calamagrostis*** (***Deyeuxia) minima*** (Pilg.) Rúgolo, **FJ377641**. ***Calamagrostis coahuilensis*** P.M. Peterson, Soreng & Valdés-Reyna, **FJ377633**. ***Calamagrostis eriantha*** (Kunth) Steud., **FJ377653**. ***Calamagrostis vulcanica*** Swallen, **FJ377662**. ***Gaudinia fragilis*** (L.) P. Beauv., **DQ539600**. ***Hainardia cylindrica*** (Willd.) Greuter, **KJ598947**. ***Helictotrichon desertorum*** **subsp.** ***altaicum*** Holub., **FM956103**. ***Helictotrichon fedtschenkoi*** (Hack.) Henrard, **HG797509**. ***Helictotrichon hideoi*** (Honda) Ohwi, **HG797511**. ***Helictotrichon hissaricum*** (Roshev.) Henrard, **HG797512**. ***Helictotrichon mongolicum*** (Roshev.) Henrard, **HG797516**. ***Helictotrichon mortonianum*** (Scribn.) Henrard, **HG797517**. ***Helictotrichon pallens*** (Link) J. M. Couderc & Guédès, **HG797518**. ***Helictotrichon parlatorei*** (J. Woods) Pilg., **FM956105**, **FM179408**. ***Helictotrichon sarracenorum*** (Gand.) Holub, **FM956462**, **HG797519**. ***Helictotrichon sempervirens*** (Vill.) Pilg., **EU792325**. ***Helictotrichon setaceum*** **subsp.** ***petzense*** (H. Melzer) Röser, **FM956468**. ***Helictotrichon tianschanicum*** (Roshev.) Henrard, **HG797524**. ***Helictotrichon tibeticum*** (Roshev.) Holub, **HG797525**. ***Helictotrichon x krischae*** Melzer, **FM958415**. ***Koeleria capensis*** Nees, **FM179413**. ***Koeleria castellana*** Boiss. & Reut., **DQ539601**. ***Koeleria dasyphylla*** Willk., **DQ336825**. ***Lagurus ovatus*** L., **DQ539598**. ***Rostraria litorea*** (All.) Holub, **DQ539611**. ***Rostraria obtusiflora*** (Boiss.) Holub, **DQ539612**. ***Rostraria salzmannii*** (Boiss.) Holub, **DQ539613**. ***Sphenopholis obtusata*** (Michx.) Scribn., **HG797532**. ***Tricholemma jahandiezii*** (Litard. ex Jahand. & Maire) Röser, **FM179407**, **FM956101**. ***Trisetaria loeflingiana*** (L.) Paunero, **DQ539608**. ***Trisetaria ovata*** (Pers.) Paunero, **DQ336832**. ***Trisetopsis barbata*** (Nees)

Röser & A. Wölk, **HG797538**. ***Trisetopsis capensis*** (Schweick.) Röser & A. Wölk, **HG797555**. ***Trisetopsis dodii*** (Stapf) Röser & A. Wölk, **HG797565**. ***Trisetopsis elongata*** (Hochst. ex A. Rich.) Röser & A. Wölk, **HG797566**. ***Trisetopsis friesiorum*** (Pilg.) Röser & A. Wölk, **HG797573**. ***Trisetopsis galpinii*** (Schweick.) Röser & A. Wölk, **HG797574**. ***Trisetopsis imberbis*** (Nees) Röser, A. Wölk & Veldkamp, **HG797636**. ***Trisetopsis lachnantha*** (Hochst. ex A. Rich.) Röser & A. Wölk, **HG797585**. ***Trisetopsis leonina*** (Steud.) Röser & A. Wölk, **HG797586**. ***Trisetopsis longa*** (Stapf) Röser & A. Wölk, **HG797597**. ***Trisetopsis longifolia*** (Nees) Röser & A. Wölk, **HG797596**. ***Trisetopsis mannii*** (Pilg.) Röser & A. Wölk, **HG797598**. ***Trisetopsis namaquensis*** (Schweick.) Röser & A. Wölk, **HG797607**. ***Trisetopsis natalensis*** (Stapf) Röser & A. Wölk, **HG797616**. ***Trisetopsis roggeveldensis*** (Mashau, L. Fish & A.E. van Wyk) Röser & A. Wölk, **HG797622**. ***Trisetopsis umbrosa*** (Hochst. ex Steud.) Röser & A. Wölk, **HG797637**.***Trisetum baregense*** Laffitte & Miégev., **DQ539605**. ***Trisetum bifidum*** (Thunb.) Ohwi, **KF713286**. ***Trisetum drucei*** Edgar, **AY752485**. ***Trisetum glaciale*** (Bory) Boiss., **DQ539614**. ***Trisetum gracile*** (Moris) Boiss. **subsp. *gracile***, **DQ539607**. ***Trisetum hispidum*** Lange, **DQ336831**. ***Trisetum spicatum*** (L.) K. Richt., **FJ377674**, **KC691715**. ***Trisetum tenellum*** (Petrie) A.W. Hill, **AY752487**. ***Trisetum youngii*** Hook. f., **AY752488**.

DISCUSIÓN

Tratamiento taxonómico

Tras el estudio del abundante material de herbario existente del género *Trisetum* en el Paleártico, el tratamiento estadístico de las variables morfoanatómicas asociadas a los especímenes conservados o recolectados de nuevo y la revisión nomenclatural de todos los nombres publicados para esta región, pensamos haber logrado una simplificación de la clasificación propuesta por Chrtek (1965, 1967a, 1968), sobre la base del tratamiento publicado por Tzvelev (1976). De todo ello, resulta una clasificación más práctica y manejable de los distintos táxones que constituyen este género, en la que reconocemos 25 táxones específicos y subespecíficos. Se han excluido del presente tratamiento algunas especies que hasta ahora formaban parte del género *Trisetum* (Apéndice 1) y estaban incluidas en *T.* sect. *Trisetaera*, debido a la nueva información obtenida acerca de sus relaciones filogenéticas, que indican el mayor parentesco de estas con el género *Koeleria*. Por lo tanto, a nivel mundial, sólo queda fuera de la clasificación seccional propuesta *T.* subg. *Deschampsioidea*, un subgénero de especies de México y América Central, cuya revisión se ha llevado a cabo en la década pasada (Finot et al., 2004).

Las especies del género que cuentan con una distribución más amplia son *T. flavescens*, que pertenece a *T.* sect. *Trisetum* y es la especie tipo del género, y *T. sibiricum*, especie tipo de *T.* sect. *Sibirica*. Estas dos especies, que cuentan con una elevada variabilidad morfológica a lo largo de sus áreas de distribución, han sido constantemente confundidas a pesar de sus diferencias morfológicas, lo que ha resultado en la descripción de numerosos táxones específicos e infraespecíficos, basados principalmente en caracteres foliares, que han complicado su taxonomía. Hemos comprobado que muchos de estos caracteres son muy variables y tienen escaso valor diagnóstico, por lo que hemos reducido el número de especies y subespecies reconocidas –dos especies, cada una con una subespecie además de la típica–, cuya separación se apoya en caracteres más sólidos.

Trisetum sect. *Trisetum* se caracteriza por tener las panículas normalmente laxas, las espiguillas verdosas o purpúreas, a veces amarillentas, los pelos del callo cortos, la arista acodada o curvada, rara vez recta, y el ovario glabro, a veces con pelos dispersos o densamente pilosos en el ápice. Se trata de la sección del género que cuenta con un mayor número de especies y está distribuida en las regiones templadas de Europa, el norte de África y el centro y el sur de Asia y América. En nuestra zona de estudio, el Paleártico, se reconocen ocho especies, de las cuales seis son endémicas de las diferentes cadenas montañosas europeas, excepto *T. flavescens* –que se extiende desde el oeste de Europa y el norte de África hasta el oeste de Asia (introducido en otras partes de Asia y en el norte y el sur de América)–, y *T. altaicum* –que crece en las montañas asiáticas de Altai y Tien Shan, además de en las montañas del norte de Mongolia y el sur de Rusia–. *Trisetum flavescens* subsp. *griseovirens*, es la única subespecie reconocida además de la típica y es endémica de las montañas del Alto Atlas; se diferencia de la subespecie típica por sus hojas enrolladas y filiformes, sus panículas más pequeñas, por sus espiguillas, lemas y aristas más largas y su pequeño tamaño. Chrtek (1967c) y Jonsell (1978) indicaron que *T. bertolonii*, especie endémica de los Apeninos, estaba estrechamente relacionada con *T. flavescens* subsp. *griseovirens* debido a su hábito similar, la forma y la anatomía de las hojas y la longitud de las aristas; sin embargo, *Trisetum bertolonii* muestra suficientes diferencias como para ser reconocido en el rango de especie. Por otro lado, el estudio de sus morfologías apoya la sinonimización de *T. baregense* con *T. alpestre*, ya que los caracteres diagnósticos utilizados para separar ambos –sobre todos destacamos la presencia de indumento en el ápice del ovario– son muy variables, como reconocía el propio Chrtek (1967b).

Trisetum sect. *Sibirica* se caracteriza principalmente por la tonalidad dorada de sus espiguillas, en ocasiones simplemente amarillentas, el callo glabro o con pelos muy cortos y las aristas recurvadas, raramente acodadas. Esta sección presenta una distribución más restringida que *T.* sect. *Trisetum*: cuatro de las seis especies que la forman son endémicas del este de Asia (*T. bifidum* alcanza la isla de Nueva Guinea). *Trisetum sibiricum* tiene el mayor área de distribución de la sección y se expande desde el este de Eurasia hasta Alaska y el oeste del Canadá; *T. sibiricum* subsp. *litorale* se diferencia de la subespecie tipo por sus panículas más densas y pequeñas y sus más reducidas dimensiones; se distribuye a lo largo de la costa rusa, desde la península de Kanin hasta la de Kamchatka y el archipiélago de las Kuriles, más Alaska y el oeste del Canadá. Por otro lado, *T. turcicum*, una especie afín a *T. sibiricum*, como fue reconocido ya por Probatova (1979), vive en Turquía, el Cáucaso y el norte de Irán.

De las tres secciones reconocidas para el Paleártico, sólo una de ellas es endémica de Eurasia, *T.* sect. *Acrospelion*, en la que reconocemos siete especies, en total nueve táxones contando las subespecies. Esta sección se caracteriza principalmente por la disposición dística de las hojas de los tallos jóvenes y por los largos pelos de la raquilla y del callo. La mayor diversidad de esta sección se encuentra en las montañas del Cáucaso, con *T. rigidum* y *T. buschianum*, y en los Alpes, con *T. distichophyllum* y *T. argenteum*. *Trisetum rigidum* es la especie más polimorfa y cuenta con la distribución más amplia de la sección, al igual que *T. flavescens* y *T. sibiricum* lo son en sus secciones correspondientes: se extiende desde el este de Anatolia en Turquía, hasta las montañas del nordeste de Irán. Hemos reconocido una subespecie para *T. rigidum* además de la típica, *T. rigidum* subsp. *teberdense*, endémica del oeste del Cáucaso y con hojas de mayor longitud, la superior a menudo alcanzando la panícula y, en general, unas dimensiones mayores que la típica. Además de las anteriores, esta sección incluye *T. tamonanteae*, endémica de la isla de Fuerteventura (Canarias), *T. velutinum*, del sureste de la Península Ibérica y *T. macrotrichum*, de los Cárpatos. Por último, *T. transcaucasicum* se ha tratado como subespecie de *T. buschianum* de acuerdo a lo ya recomendado por algunos autores (Tzvelev, 1976; Mosulishvili, 1991), tratamiento que nos parece el más adecuado. *Trisetum buschianum* subsp. *transcaucasicum* se separa de la subespecie tipo principalmente por su hábito, siendo de menor tamaño y con los nodos concentrados en la parte inferior del tallo.

Relaciones filogenéticas

El análisis filogenético de los marcadores moleculares estudiados confirma la estructura general obtenida por otros estudios previos para el clado denominado "Poeae chloroplast group 1", que incluye el género *Trisetum* y corresponde a la subtribu Aveninae s.l., grupo hermano de otras subtribus afines, como son Agrostidinae, Anthoxanthinae, Brizinae, Echinopogoninae, Phalaridinae y Torreyochloinae (Quintanar et al., 2007; Saarela et al., 2017; Wölk & Röser, 2017). Aveninae s.l. ha resultado ser un grupo monofilético e incluye tres linajes con un apoyo estadístico sólido: 1) Aveninae s.s. –restringida a los géneros *Avena*, *Helictotrichon* y *Tricholemma*, además de la subtribu Sesleriinae y las especies asiáticas de *Trisetopsis* en la topología nuclear–, 2) Koeleriinae –*Trisetum*, *Koeleria* y géneros afines–, y 3) Lagurinae (solo *Lagurus*). El tipo de relación del género *Lagurus* con el resto de grupos de Aveninae s.l., es decir, principalmente con Aveninae s.s. y Koeleriinae, ha variado en los diferentes trabajos moleculares. Nuestros resultados apoyan su carácter de grupo hermano de Koeleriinae, lo que está en consonancia con el mayor número de caracteres morfológicos compartidos por ambas, como son el ovario glabro y la cariopsis con endosperma más o menos líquido e hilo corto (Quintanar et al., 2007, 2010).

El reconocimiento de la subtribu Koeleriinae como subtribu diferenciada de Aveninae s.s. ha sido ya previamente señalado por autores previos, debido tanto a las singularidades morfoanatómicas de sus géneros como a los resultados obtenidos en análisis filogenéticos recientes (Tzvelev, 1976; Clayton & Renvoize, 1986; Quintanar et al., 2007, 2010; Saarela et al., 2010, 2017). Al igual que Saarela et al. (2017), hemos identificado dos clados en Koeleriinae con un apoyo estadístico de moderado a fuerte, aquí denominados "Koeleriinae clado I" y "Koeleriinae clado II" [clados A y B en Saarela et al. (2017)]. Ambos incluyen representantes del género estudiado, *Trisetum*, que como tal demuestra ser un taxon no monofilético en consonancia con lo que ya venían advirtiendo otros estudios anteriores (Quintanar et al., 2007; Saarela et al., 2010, 2017; Wölk & Röser, 2014, 2017). "Koeleriinae clado I" incluye el gran género de gramíneas perennes *Koeleria* y parte de *Trisetum*, así como el género híbrido centroasiático de ambos ×*Trisetokoeleria*, los géneros de gramíneas anuales y circunmediterráneas *Trisetaria*, *Rostraria*, *Avellinia* y *Gaudinia*, y del género asiático recientemente descrito *Tzveleviochloa*. "Koeleriinae clado II" también incluye las especies restantes de *Trisetum*, así como el género norteamericano anual y monoespecífico *Limnodea*, los también americanos pero perennes *Sphenopholis*, *Graphephorum*, *Peyritschia* y *Leptophyllochloa*, el complejo de especies mexicanas y del centro y sur de América de los géneros *Calamagrostis* o *Deyeuxia*, y el recientemente descrito *Trisetopsis*. Además, dos clados toman posiciones incongruentes en la topología nuclear y plastidial, donde se asocian a clados distintos de Koeleriinae, probablemente debido a procesos de hibridación en su origen. Estos clados de posición incongruente se corresponden con el género *Graphephorum*, la especie argentina *Koeleria mendocinensis* y algunas de las especies americanas del género *Trisetum* (*T. ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, *T. longiglume* y *T. ortochaetum*).

Discusión

Las especies de *T.* sect. *Acrospelion*, al igual que aquellas con distribución paleártica de *T.* sect. *Trisetum* forman parte de "Koeleriinae clado I". *Trisetum* sect. *Acrospelion* constituye forma parte de un clado hermano de "Koeleriinae clado I". Esta sección ha sido muestreada prácticamente en su totalidad, exceptuando la especie canaria *T. tamonanteae*. Este clado, cuyas relaciones internas carecen de apoyo estadístico sólido, incluye también tres especies eurasiáticas de *T.* sect. *Trisetum –T. bertolonii*, *T. glaciale* y *T. altaicum*– y las asiáticas *Helictotrichon delavayei*, *H. sumatrense* y *Tzveleviochloa parviflora*; además, en la topología nuclear, también incluye la llamada "ITS incongruence 3", que incluye parte de los táxones señalados anteriormente, *Graphephorum* y *Koeleria mendocinensis*, y a las especies *Trisetum ambiguum*, *T. cernuum*, *T. longiglume* y *T. ortochaetum*. "ITS incongruence 3" aparece en "Koeleriinae clado II" en las topologías cloroplásticas, lo que resulta indicativo del papel de la hibridación en el origen de los táxones que se mencionan. Saarela et al. (2017) incluyó parte de estos táxones en su estudio y sus resultados le permitieron deducir que el clado podría interpretarse como un nuevo género híbrido, cuyo origen podría estar relacionado con su especiación más allá de un evento primario de hibridación, un proceso evolutivo común en otros géneros de la tribu Poeae (Gillespine et al., 2008). Parece claro que será necesario investigar este grupo de manera más intensiva, aplicando el estudio de genes nucleares de baja copia, que confirmen y esclarezcan más su sistemática.

El resto de especies eurasiáticas de *T.* sect. *Trisetum* se agrupan en un clado junto a las especies del género *Rostraria* y *Trisetaria lapalmae*, sin que ninguno de estos dos géneros –*Rostraria* y *Trisetaria*– sean monofiléticos. La especie tipo de *Trisetaria*, *T. linearis*, distribuida por el norte de África hasta el sudoeste de Asia, tiene una posición basal con respecto a estos dos clados. La mayor parte de la variabilidad subespecífica de *T. flavescens* ha sido muestreada en el estudio y se reúne en este clado junto a *T. gracile* como elemento hermano de la misma y al igual que en estudios anteriores (Quintanar et al., 2007; Saarela et al., 2010, 2017). En otros trabajos que incluyen la especie mediterránea anual *Trisetaria aurea* en la topología de ITS (Wölk & Röser, 2017), dicha especie apareció junto a *T. flavescens*. Aunque no se ha incluido esta *Trisetaria* en nuestro estudio, es notable que comparta con *Trisetum gracile* caracteres morfológicos como el hábito cespitoso, los tallos cortos, las vainas de las hojas algo infladas, las hojas superiores cortas, el lema piloso y la arista dorsal inserta por debajo de la mitad del mismo (Jonsell, 1980; Jeanmonod & Gamisans, 2007).

En línea con los anteriores estudios filogenéticos, nuestros resultados confirman la estrecha relación entre el género *Koeleria* y el género *Trisetum* (Soreng & Davis, 2000; Quintanar et al., 2007; Saarela et al., 2010, 2017; Wölk & Röser, 2017). *Koeleria* y la mayor parte de especies incluidas hasta el momento en *T.* sect. *Trisetaera* (excepto algunas americanas) pertenecen a un mismo clado. Su afinidad sistemática no solo ha sido evidenciada en dichos estudios, sino que ha sido previa y repetidamente señalada con criterios morfológicos y en alusión a la especie tipo de *T.* sect. *Trisetaera*, *T. spicatum* (Reichenbach, 1830; Tzvelev, 2011). *Trisetum spicatum* y sus especies afines comparten con *Koeleria* las panículas muy contraídas, piramidales o frecuentemente ovadas y las ramas cortas. Además, las especies de *T.* sect. *Trisetaera* tienen, al contrario que la mayoría de las especies de *Trisetum*, el lema con la arista y arístulas cortas, a veces incluso carecen de estas últimas (Hultén, 1959; Tzvelev, 1976, 2011). Esta reducción de las ramas de la panícula y de la longitud de las aristas, son, sin duda, caracteres convergentes con los de *Koeleria*, la cual tiene generalmente las panículas muy contraídas y el lema mútico, aunque ocasionalmente con una arista apical corta (Quintanar & Castroviejo, 2013). El extenso muestreo realizado de representantes de *Koeleria* y *T.* sect. *Trisetaera* permite estructurar de manera fiable el conjunto en cuatro subclados anidados con un apoyo estadístico por lo general razonablemente sólido. Es preciso destacar que los representantes de las especies tipo de ambos táxones no parecen ser monofiléticos y aparecen dispersos en estos subclados. También es notable la aparición en este clado de *T. montanum*, una especie norteamericana clasificada en *T.* sect. *Trisetum* por Finot et al. (2005), pero que, a pesar de tener panículas de abiertas a más o menos contraídas, su el lema con arista dorsal inserta en el tercio superior de lema lo asemeja a las especies de *T.* sect. *Trisetaera*. Además, la topología nuclear también muestra en este clado dos especies americanas de *T.* sect. *Trisetum –T. foliosum* y *T. irazuense*– que aparecen asociados a algunos *Calamagrostis* y *Trisetum* subg. *Deschampsioidea* en la topología plastidial.

Por otro lado, las especies de *T.* sect. *Sibirica* aparecen agrupadas en un clado con sólido apoyo estadístico dentro de "Koeleriinae clado II", a la vez que hermano del resto de los grupos incluidos en este clado de Koeleriinae. *Trisetum turcicum*, especie que no ha sido muestreada en este estudio, se relaciona en los trabajos moleculares anteriores con *T. flavescens* (Grebenstein et al., 1998; Quintanar et al., 2007, 2010; Saarela et al., 2010, 2017); tras la revisión del material utilizado en estos estudios se ha comprobado que realmente se trataba de especímenes de *T. flavescens*. Los estudios morfológicos realizados para caracterizar la sección apoyan su pertenencia a este grupo. *Trisetum* sect. *Sibirica* tiene sólidos caracteres distintivos que apoyan su tratamiento como género aparte, tanto desde el punto de vista molecular como desde el morfológico, como ya hemos comentado. Saarela et al. (2017), que insinuó esta separación en su trabajo, estudió solo dos especies y tan solo desde el punto de vista molecular, por lo que no llegó a publicarlo como tal.

El resto de especies de *Trisetum* incluidas en el trabajo son especies americanas principalmente de *T.* subg. *Deschampsioidea*, además de *T. filifolium* y *T. pringlei* –no asignados por el momento a una sección– y *T. curvisetum*, que pertenece a *T.* sect. *Trisetum*. Todas estas especies forman parte de un mismo clado dentro de "Koeleriinae clado II", que está formado únicamente por especies de México y el centro y el sur de América de los géneros *Calamagrostis, Deyeuxia* y *Peyritschia*.

La especie de mesoamericana *T. pringlei* ha sido muestreada en nuestro estudio por primera vez y ha resultado afín a ciertas especies de *Calamagrostis* del centro y el sur de América. Se distingue de otros *Trisetum* por tener el lema con ápice entero y mucronado, las lodículas lineares y con ápices enteros y el ovario con endosperma sólido, así como diferentes caracteres micromorfológicos del lema, lo que ha llevado a dudar de su pertenencia al género (Finot et al., 2004, 2006a).

Por otro lado, en este gran clado se ubican los representantes de *T.* subg. *Deschampsioidea*, cuyas especies se caracterizan por tener panícula laxa, el lema con el ápice y los márgenes hialinos, sin nervios o con nervios intermedios o marginales que sobresalen más allá del ápice de la misma como cuatro arístulas, y una arista inserta en la mitad del lema (Finot et al., 2004), así como también caracteres epidérmicos foliares que las diferencian del resto de especies del género *Trisetum* (Finot et al., 2006a). Sus representantes se encuentran en el mismo subclado que tres especies mexicanas de *Calamagrostis* y dos especies de *Trisetum* también endémicas de México, *T. curvisetum* y *T. filifolium;* todas ellas comparten los caracteres de la panícula y del lema con las de *T.* subg. *Deschampsioidea*. El clado formado por todas estas especies meso y sudamericanas, es hermano del clado formado por el género *Peyritschia*, el cual también se diferencia de *Trisetum* por sus glumas iguales, lemas con ápice bilobulado con la arista inserta del centro del mismo o cercano a la base, a veces reducida a un mucrón subapical, páleas encerradas por los márgenes del lema, androceo con dos estambres y por numerosas características epidérmicas del lema (Finot et al., 2004, 2006a, 2006b).

Tras la obtención de los primeros resultados de nuestro estudio filogenético, se ha realizado una clasificación preliminar de la subtribu Aveninae s.l. basada en la publicada anteriormente por Soreng et al. (2015), y se ha comparado con la publicada por Kellogg (2015) con la vista puesta en los estudios moleculares recientes sobre el grupo (Wölk & Röser, 2014, 2017; Wölk et al., 2015; Saarela et al., 2017). A la subtribu Aveninae sensu Kellogg, habría que añadir al menos tres géneros adicionales al expandido género *Trisetaria* sensu Kellogg (2015) –*Graphephorum*, *Sphenopholis* y *Trisetopsis*–, lo que suma un total de más de 260 especies para la subtribu. Para conservar los nombres *Koeleria*, *Trisetum*, *Gaudinia*, *Rostraria*, *Avellinia*, *Peyritschia*, *Graphephorum*, *Sphenopholis* y *Trisetopsis* no integrados en *Trisetaria* como proponía Kellogg (2015), se ha sugerido agrupar en *Acrospelion* varias especies eurasiáticas de *Trisetum* –lo que por el momento no se ha podido justificar desde el punto de vista morfológico– y, por otro lado, resucitar el género *Cinnagrostis* para la mayoría de especies de *Calamagrostis*/*Deyeuxia* de Sudamérica. Además, se adelantó la decisión de expandir *Koeleria*, mediante la inclusión en este género de *T.* sect. *Trisetaera* –alrededor de unas 25 especies–, al igual que el género *Graphephorum* –con origen híbrido y posible nothogénero con unas seis especies– y *Peyritschia* –con alrededor de 27 especies, entre ellas las de *T.* subg. *Deschampsioidea*–.

Estos resultados suponen un significativo avance en el esclarecimiento de la sistemática genérica e infragenérica de los distintos táxones agrupados en el llamado “Poeae chloroplast group 1” y, más en particular, la que se refiere a los elemento de la subtribu Koeleriinae, en la que *Trisetum* se incluye. Como se ha referido anteriormente, son precisos más trabajos, estudios tanto morfológicos como moleculares con genes nucleares de baja copia, que confirmen y completen la información disponible acerca de la evolución de los táxones implicados, muy especialmente sobre aquellos que toman posiciones incongruentes en las topologías filogenéticas, unas incongruencias relacionadas con la hibridación y la evolución reticulada de los mismos. Parece razonable que la información presentada en el presente estudio colabora notablemente en la confección de una nueva clasificación más natural y sólida que la disponible para los grupos implicados, resultado final que será publicado en un futuro próximo junto a los estudios filogenéticos incluidos en el último capítulo de la presente tesis doctoral.

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CONCLUSIONES

1. Las especies del género *Trisetum* Pers. en la región paleártica se clasifican en tres secciones, *T.* sect. *Trisetum*, *T.* sect. *Acrospelion* y *T.* sect. *Sibirica*, que reúnen un total de 21 especies, cuatro de ellas con dos subespecies cada una. Se han realizado un total de 42 lectotipificaciones y 2 neotifipificaciones.

2. En *Trisetum* sect. *Trisetum* se reconocen ocho especies de Eurasia y norte de África: *T. alpestre*, *T. altaicum*, *T. bertolonii*, *T. flavescens*, *T. fuscum*, *T. glaciale*, *T. gracile* y *T. laconicum*. *Trisetum* sect. *Trisetum* se caracteriza por tener panículas generalmente laxas, espiguillas verdosas o purpureas, a veces amarillentas, los pelos del callo cortos, la arista acodada o curvada, rara vez recta, y el ovario glabro, a veces con pelos dispersos o densamente peloso en el ápice. *Trisetum rechingeri* se ha sinonimizado con *T. laconicum*, *T. antonii-josephii* con *T. glaciale* y *T. baregense* con *T. alpestre*. Se trata de la sección con mayor número de especies, distribuida en las regiones templadas de Europa, norte de África, centro y sur de Asia y América. *Trisetum flavescens* es la especie más polimorfa del género y de más amplia distribución. Se ha reconocido tan solo la subespecie tipo, en la que se han incluido numerosos táxones localmente aceptados, así como *T. flavescens* subsp. *griseovirens*, endémica de las montañas del Alto Atlas.

3. *Trisetum* sect. *Acrospelion* es una sección endémica de Eurasia que incluye siete especies: *T. argenteum*, *T. buschianum* (con dos subespecies, *T. buschianum* subsp. *buschianum* y *T. buschianum* subsp. *transcaucasicum*), *T. distichophyllum*, *T. macrotrichum*, *T. rigidum* (con dos subespecies, *T. rigidum* subsp. *rigidum* y *T. rigidum* subsp. *teberdense*), *T. tamonanteae* y *T. velutinum*. *Trisetum persicum* se sinonimiza con *T. rigidum* subsp. *rigidum* y *T. cavanillesianum* con *T. velutinum*. Son características de esta sección la disposición dística de las hojas de los tallos jóvenes y los pelos del callo y de la raquilla largos. La mayor diversidad de esta sección se encuentra en las montañas del Cáucaso, con *T. rigidum* y *T. buschianum*, y en los Alpes, con *T. distichophyllum* y *T. argenteum*. *Trisetum rigidum* es la especie más polimorfa y con la distribución más amplia de esta sección.

4. *Trisetum* sect. *Sibirica* incluye seis especies: *T. aeneum*, *T. bifidum*, *T. henryi*, *T. scitulum* y *T. sibiricum* (con dos subespecies, *T. sibiricum* subsp. *sibiricum* y *T. sibiricum* subsp. *litorale*) y *T. turcicum*. En función de los resultados obtenidos, *T. pauciflorum*, *T. sikkimense* y *T. umbratile* se sinonimizan con *T. sibiricum* subsp. *sibiricum*. Esta sección se caracteriza principalmente por el color dorado de sus espiguillas, el callo glabro o con pelos muy cortos y las aristas recurvadas, rara vez acodadas. Cuatro de las seis especies de la sección son endémicas del este de Asia y Nueva Guinea, mientras que *T. turcicum* crece en Turquía y el Cáucaso y *T. sibiricum*, la de distribución más amplia y polimorfa de la sección, se extiende del este de Europa a Alaska y el oeste del Canadá.

5. Según nuestros estudios filogenéticos, el género *Trisetum* aparece incluido junto a toda una serie de géneros afines en un clado monofilético que corresponde a la subtribu Aveninae s.l.; esta subtribu se organiza en tres grupos monofiléticos a su vez: Aveninae s.s. (incl. *Avena*, *Helictotrichon* y *Tricholemma*, más Sesleriinae en el análisis con el marcador nuclear), Koeleriinae (incl. *Trisetum*, *Koeleria* y géneros afines) y Lagurinae (*Lagurus*). La subtribu Lagurinae es grupo hermano de la subtribu Koeleriinae y ambas de Aveninae s.s. Estos tres grupos forman un clado que tiene como grupo hermano a otros miembros del llamado "Poeae chloroplast group 1" (subtribus Agrostidiinae, Anthoxanthinae, Brizinae, Echinopogoninae, Phalaridiinae y Torreyochloinae).

6. La subtribu Koeleriinae merece un estatus independiente de Aveninae s.s. e incluye *Trisetum*, que ha resultado ser un género polifilético. Koeleriinae se divide en dos grandes subclados, ambos con representantes de *Trisetum*: i) "Koeleriinae clado I": *Avellinia*, *Gaudinia*, *Helictotrichon* p.min.p., *Koeleria*, *Rostraria*, *Trisetaria*, *Trisetum* sect. *Acrospelion*, *T.* sect. *Trisetum* p.p., *T.* sect. *Trisetaera* y *Tzveleviochloa*; ii) "Koeleriinae clado II": *Calamagrostis* p.p. y *Deyeuxia* p.p. (especies distribuidas desde México hasta Sudamérica), *Leptophyllochloa*, *Limnodea*, *Peyritschia*, *Sphenopholis*, *Trisetopsis*, *Trisetum* subg. *Deschampsioidea*, *T.* sect. *Trisetum* p.p. y *T.* sect. *Sibirica*. La situación de *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, *T. longiglume* y *T. ortochaetum* es incongruente en las topologías nuclear y plastidial, circunstancia que delata el posible origen híbrido de estos táxones.

7. Las especies de *T.* sect. *Acrospelion* conforman un clado con razonable apoyo estadístico, no ocurriendo lo mismo con sus relaciones internas, junto a algunas especies eurasiáticas de *T.* sect. *Trisetum* (*T. alpestre*, *T. altaicum*, *T. bertolonii* y *T. glaciale*), *Helictotrichon delavayei*, *H. sumatrense* y *Tzveleviochloa parviflora*, además de parte del grupo americano de táxones mencionado anteriormente en la topología nuclear (i.e., *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. longiglume* y *T. ortochaetum*). Todo este clado es grupo hermano del resto de táxones incluidos en "Koeleriinae clado I".

8. Las especies de *T.* sect. *Sibirica*, una sección morfológicamente bien caracterizada, se agrupan en un clado segregado del resto de grandes subclados y es grupo hermano de "Koeleriinae clado II", lo que podría justificar su tratamiento en un género aparte de *Trisetum*.

9. Las especies eurasiáticas de *T.* sect. *Trisetum* no incluidas en el mismo clado que *T.* sect. *Acrospelion* (*T. flavescens* y *T. gracile*), forman un grupo propio y hermano del que corresponde a parte de las especies de *Rostraria* estudiadas (*Rostraria litorea*, *R. pumila*, *R. salzmanii*, además de *R. balansae*, *R. cristata*, *R. obtusiflora* y *R. smyrnacea* en la topología plastidial) y a *Trisetaria lapalmae*. *Trisetaria linearis*, especie tipo de *Trisetaria*, aparece en una posición basal con respecto a estos dos grupos anteriores.

10. Las especies de *Trisetum* sect. *Trisetaera* aparecen incluidas en el mismo clado que agrupa a las del género *Koeleria*, lo que es congruente con sus similitudes morfológicas y apoya su posterior estudio en el marco de este último género.

11. El resto de especies de *Trisetum* incluidas en el estudio filogenético son especies americanas, principalmente clasificadas en *T.* subg. *Deschampsioidea*, además de *T. filifolium* y *T. pringlei* (no asignados por el momento a una sección) y *T. curvisetum*, que pertenece a *T.* sect. *Trisetum*. Todas ellas forman parte de un mismo grupo con suficiente apoyo estadístico en “Koeleriinae clado II”, junto a otras especies americanas (de México a Sudamérica) de *Calamagrostis* y *Deyeuxia*, y el género *Peyritschia*.

12. Nuestro estudio de las relaciones filogenéticas existentes entre los distintos miembros que componen la subtribu Koeleriinae, en la que está incluido *Trisetum*, muestra la necesidad de revisar la circunscripción y la taxonomía de los mismos con el objeto de conseguir una clasificación más natural para la subtribu. La sistemática de la subtribu es muy compleja, sobre todo porque la mayoría de los géneros de la misma no han resultado monofiléticos y la hibridación parece haber jugado su papel en el origen de un número no pequeño de géneros y especies. Las incongruencias que revelan el papel de la hibridación aparecen tanto en “Koeleriinae clado I” (i.e., *Gaudinia*, *Rostraria* p.p., *Trisetaria* p.p.), como entre “Koeleriinae clado I” y “Koeleriinae clado II” (i.e. *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, *T. longiglume* y *T. ortochaetum*). Estimamos necesario desarrollar más estudios con genes nucleares de baja copia para esclarecer con más detalle la sistemática de estos géneros y avanzar así en la clasificación de los diferentes grupos de la subtribu.

CONCLUSIONS

1. The species of the genus *Trisetum* Pers. in the Palearctic region are classified into three sections, *T.* sect. *Trisetum, T.* sect. *Acrospelion*, and *T.* sect. *Sibirica*, which bring together a total of 21 species, four of them with two subspecies each. A total of 42 lectotypifications and two neotypifications have been made.

2. In *Trisetum* sect. *Trisetum* eight species from Eurasia and Northern Africa are recognized: *T. alpestre*, *T. altaicum*, *T. bertolonii*, *T. flavescens*, *T. fuscum*, *T. glaciale*, *T. gracile*, and *T. laconicum*. *Trisetum* sect. *Trisetum* is generally characterized by lax panicles, greenish spikelets, short callus hairs, geniculate or bent awns, rarely straight, and glabrous ovary, sometimes with scattered hairs or densely hairy at the apex. *Trisetum rechingeri* has been synonymized with *T. laconicum*, *T. antonii-josephii* with *T. glaciale* and *T. baregense* with *T. alpestre*. This section has the highest number of species in the genus, and is distributed in the temperate regions of Europe, North Africa, Central and South Asia, and America. *Trisetum flavescens* is the most polymorphic species and it has the widest distribution of the genus. It has been recognized the type subspecies, in which numerous locally accepted taxa have been included, as well as *T. flavescens* subsp. *griseovirens*, endemic to the mountains of the High Atlas.

3. *Trisetum* sect. *Acrospelion* is a section endemic to Eurasia and includes seven species: *T. argenteum*, *T. buschianum* (with two subspecies, *T. buschianum* subsp. *buschianum*, and *T. buschianum* subsp. *transcaucasicum*), *T. distichophyllum*, *T. macrotrichum*, *T. rigidum* (with two subspecies, *T. rigidum* subsp. *rigidum*, and *T. rigidum* subsp. *teberdense*), *T. tamonanteae*, and *T. velutinum*. *Trisetum persicum* is synonymized with *T. rigidum* subsp. *rigidum*, and *T. cavanillesianum* with *T. velutinum*. This section is characterized by the distichous disposition of the leaves of the young shoots and the long hairs of the callus and rachilla. The highest diversity of this section is found in the mountains from the Caucasus, with *T. rigidum* and *T. buschianum,* and in the Alps, with *T. distichophyllum* and *T. argenteum*. *Trisetum rigidum* is the most polymorphic species and has the widest distribution of this section.

4. *Trisetum* sect. *Sibirica* includes six species: *T. aeneum*, *T. bifidum*, *T. henryi*, *T. scitulum,* and *T. sibiricum* (with two subspecies, *T. sibiricum* subsp. *sibiricum* and *T. sibiricum* subsp. *litorale*), and *T. turcicum*. Based on the results obtained, *T. pauciflorum*, *T. sikkimense* and *T. umbratile* are synonymous with *T. sibiricum* subsp. *sibiricum*. This section is mainly characterized by golden spikelets, glabrous callus or with very short hairs, and recurved awns, rarely geniculate. Four of the six species in the section are endemic to the Eastern Asia and New Guinea, while *T. turcicum* grows in Turkey and the Caucasus and *T. sibiricum*, the one with the broadest and most polymorphic distribution of the section ranges from the Eastern Europe to Alaska and the Western Canada.

5. According to our phylogenetic studies, the genus *Trisetum* is included along with a whole set of related genera in a monophyletic clade corresponding to the subtribe Aveninae s.l.; this subtribe is organized into three monophyletic groups in turn: Aveninae s.s. (including *Avena*, *Helictotrichon*, and *Tricholemma*, plus Sesleriinae in the analysis with the nuclear marker), Koeleriinae (including *Trisetum*, *Koeleria*, and related genera) and Lagurinae (*Lagurus*). The Lagurinae subtribe is sister to Koeleriinae and both are sister to Aveninae s.s. These three groups form a sister clade to the other members of the so-called "Poeae chloroplast group 1" (subtribes Agrostidiinae, Anthoxanthinae, Brizinae, Echinopogoninae, Phalaridiinae, and Torreyochloinae).

6. The subtribe Koeleriinae deserves an independent status from Aveninae s.s. and includes *Trisetum*, which has been resolved as a polyphyletic genus. Koeleriinae is divided into two large subclades, both with representatives of *Trisetum*: i) “Koeleriinae clade I”: *Avellinia*, *Gaudinia*, *Helictotrichon* p.min.p., *Koeleria*, *Rostraria*, *Trisetaria*, *Trisetum* sect. *Acrospelion*, *T.* sect. *Trisetum* p.p., *T.* sect. *Trisetaera*, and *Tzveleviochloa*; ii) “Koeleriinae clade II”: *Calamagrostis* p.p. and *Deyeuxia* p.p. (species distributed from Mexico to South America), *Leptophyllochloa*, *Limnodea*, *Peyritschia*, *Sphenopholis*, *Trisetopsis*, *Trisetum* subg. *Deschampsioidea*, *T.* sect. *Trisetum* p.p., and *T.* sect. *Sibirica*. The situation of *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, T. longiglume, and *T. ortochaetum* is incongruent in the nuclear and plastid topologies, a circumstance that reveals a likely hybrid origin of these taxa.

7. The species of *T.* sect. *Acrospelion* are part of a clade reasonably supported, unlike its internal relationships, together with some Eurasian species of *T.* sect. *Trisetum* (*T. alpestre*, *T. altaicum*, *T. bertolonii*, and *T. glaciale*), *Helictotrichon delavayei*, *H. sumatrense*, and *Tzveleviochloa parviflora*, as well as part of the American group of taxa mentioned above in the nuclear topology (i.e., *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. longiglume*, and *T. ortochaetum*). All this clade is sister to the rest of taxa included in "Koeleriinae clade I".

8. The species of *T.* sect. *Sibirica*, a morphologically well characterized section, have been grouped into a clade segregated from the rest of the large subclades and it is sister to "Koeleriinae clade II", which could justify its treatment as a separate genus from *Trisetum*.

9. The Eurasian species of *T.* sect. *Trisetum* which are not grouped in the same clade of those belonging to *T.* sect. *Acrospelion* (*T. flavescens* and *T. gracile*), form their own clade, sister to a part of the studied species of *Rostraria* (*Rostraria litorea*, *R. pumila*, *R. salzmanii*, además de *R. balansae*, *R. cristata*, *R. obtusiflora*, and *R. smyrnacea* in the plastid topology), and to *Trisetaria lapalmae*. *Trisetaria linearis*, type species of *Trisetaria*, appears in a basal position with respect to these two previous groups.

10. The species of *Trisetum* sect. *Trisetaera* appear included in the same clade that groups those of the genus *Koeleria,* which is consistent with their morphological similarities and supports their subsequent study in the frame of this last genus.

11. The rest of the species of *Trisetum* included in the phylogenetic study are American species, mainly classified in *T.* subg. *Deschampsioidea*, in addition to *T. filifolium* and *T. pringlei* (not assigned to any section up to now), and *T. curvisetum*, which belongs to *T.* sect. *Trisetum*. All of them are grouped into a reasonably supported subclade in "Koeleriinae clade II", along with other American species (from Mexico to South America) of *Calamagrostis* and *Deyeuxia*, as well with the genus *Peyritschia*.

12. Our study of the phylogenetic relationships existing among the different members of the subtribe Koeleriinae, in which *Trisetum* is included, shows the necessity to review the circumscription and the taxonomy of them in order to achieve a more natural classification for the subtribe. The systematics of the subtribe is very complex, mainly because most of its genera have not been resolved as monophyletic and hybridization seems to have played its role in the origin of a non-small set of genera and species. The incongruences suggesting the existence of past hybridization events linked to the origin of taxa appear in "Koeleriinae clade I" (i.e., *Gaudinia, Rostraria* p.p., *Trisetaria* p.p.), as well as between "Koeleriinae clade I" and "Koeleriinae clade II" (i.e., *Graphephorum*, *Koeleria mendocinensis*, *Trisetum ambiguum*, *T. cernuum*, *T. foliosum*, *T. irazuense*, *T. longiglume* y *T. ortochaetum*). We consider necessary to carry out more studies with low copy nuclear genes to clarify with more detail the systematic of these taxa and thus to advance in the classification of the different groups of the subtribe.

APÉNDICE 1

Apéndice 1. Táxones paleárticos excluidos del presente tratamiento taxonómico debido a la nueva información sistemática disponible acerca de los mismos.

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