Generic realignments in the grass tribe Aveneae (Poaceae)

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Abstract: Röser, M., Döring, E., Winterfeld, G. & Schneider, J. 2009: Generic realignments in the grass tribe Aveneae (Poaceae). Schlechtendalia **19**: 27–38.

Taxonomy and classification of 'core' genera of the grass tribe Aveneae are critically examined in view of recent molecular phylogenetic and cytogenetic studies. The previously broadly defined genera *Helictotrichon* and *Avenula* are polyphyletic and disintegrate into altogether at least four different genera including *Homalotrichon* and *Tricholemma*, stat. et gen. nov. None of these genera is sister to the other in the molecular phylogenies. *Pseudarrhenatherum* is reduced to synonymy with *Helictotrichon* s. str. Interestingly, none of the new generic alignments is in conflict with morphological and anatomical data that were the only basements of previous classifications and had led to a long-standing controversy in the taxonomy of these oats and the genus *Avena.* Important aspects of morphology and taxonomic history are surveyed and discussed for some genera and species. The following combinations are made: *Helictotrichon thorei*, comb. nov., *Tricholemma*, stat. et gen. nov., *T. jahandiezii*, comb. nov., *T. breviaristatum*, comb. nov.

Zusammenfassung: Röser, M., Döring, E., Winterfeld, G. & Schneider, J. 2009: Neue Gattungsumgrenzungen in der Gräser-Tribus Aveneae (Poaceae). Schlechtendalia **19**: 27–38.

Taxonomie und Klassifikation einiger 'Kern-'Gattungen der Gräsertribus Aveneae werden im Zusammenhang mit neueren molekular-phylogenetischen und -cytogenetischen Untersuchungen kritisch überprüft. Die zuvor breit definierten Gattungen *Helictotrichon* und *Avenula* sind polyphyletisch und zerfallen in mindestens vier unterschiedliche Gattungen, darunter *Homalotrichon* und *Tricholemma*, stat. et gen. nov. Keine dieser vier Gattungen bildet die Schwestergruppe von einer der anderen. Die Gattung *Pseudarrhenatherum* wird in *Helictotrichon* s. str. eingeschlossen. Interessanterweise stehen diese Veränderungen in den Gattungsumgrenzungen nicht in Konflikt mit morphologischen und anatomischen Daten, die bislang die einzige Grundlage der Klassifikation bildeten und zu einer langanhaltenden Diskussion über die Taxonomie dieser Gattungen und der Gattung *Avena* führten. Wichtige Aspekte zur Morphologie und taxonomischen Geschichte werden für einige Gattungen und Arten zusammengestellt und diskutiert. Die folgenden Umkombinationen werden durchgeführt: *Helictotrichon thorei*, comb. nov., *Tricholemma*, stat. et gen. nov., *T. jahandiezii*, comb. nov., *T. breviaristatum*, comb. nov.

Key words: *Avena*, *Avenula*, *Helictotrichon*, *Homalotrichon*, *Tricholemma*, taxonomy, classification.

Introduction

Genera of the tribe Aveneae (Poaceae subf. Pooideae) have been delineated quite differently during the past 200 years, especially those considered closely related with oat (*Avena sativa* L.). By the end of the 18th and the early 19th century, several genera had become segregated out of the broadly circumscribed genus *Avena* L., which included some species nowadays even recognized under different tribes or subfamilies

of grasses (e.g., trib. Stipeae, trib. Phaenospermateae, subf. Danthonioideae). The delineation of early described segregate genera of *Avena* still acknowledged to belong to subf. Pooideae [e.g., *Trisetum* Pers., *Arrhenatherum* P. Beauv., *Gaudinia* P. Beauv., *Avenastrum* Opiz, *Avenula* (Dumort.) Dumort., *Helictotrichon* Besser, *Amphibromus* Nees, *Pseudarrhenatherum* Rouy] was based mainly on few floral (spikelet) characters and on life form (annual versus perennial). Influenced especially by anatomical studies (e.g., Duval-Jouve 1863, 1871, 1875; Prat 1932), a wide range of different structures in leaf and awn anatomy was documented for these genera, which seemed to disagree with the previous genus treatments or infrageneric divisions. Gross spikelet structure, life form and characters of leaf anatomy seemed to display a complicated mosaic (Vierhapper 1914, Saint-Yves 1931, Holub 1958).

Several major floras thus continued to follow a rather broad concept of the genus *Avena* with numerous infrageneric subdivisions, e.g., Flore de l'Afrique du Nord (Maire 1953). Others kept *Avena* separate from *Helictotrichon*, e.g., Flora SSSR, Flora of tropical Africa, Flora of tropical East Africa or Flora of China (Roshevitz 1934, Hubbard 1937, Clayton 1970, Wu Zhenlan & Phillips 2006). In agreement with several taxonomic studies (Holub 1962, 1976; Romero Zarco 1984a, b), *Helictotrichon* was further split into *Helictotrichon* s. str. and *Avenula* in Flora europaea (Holub 1980), Flora of North America north of Mexico (Baum 2007, Tucker 2007a, b) and the Catalogue of New World grasses (Soreng et al. 2003). Other systematic treatments on *Helictotrichon* did not segregate *Avenula* as genus, but considered it under the different subgenera of *Helictotrichon* they acknowledged (e.g., Röser 1989, 1996; Lange 1995). An equivalent delineation of genus *Helictotrichon* was adopted by the treatments of the grasses of the Soviet Union and Central Europe (Tsvelev 1976, Conert 1979–1998). An even wider circumscription was chosen in the synopsis for the grass genera of the world (Clayton & Renvoize 1986) by including also *Amphibromus* within genus *Helictotrichon*.

Additionally, uncertainty prevailed concerning the generic affiliation of some species with unusual combination of characters, for example, the Algerian endemic *Avena macrostachya* Balansa ex Coss. & Durieu, which resembled in spikelet characters the typically annual species of this genus and was included within this genus despite its perennial life form (Baum 1968, 1974, 1977) or alternatively was treated under the perennial genus *Helictotrichon*, rendering *Avena* a genus of exclusively annual species (Holub 1958, Clayton & Renvoize 1986).

Pseudarrhenatherum, distributed in western Europe and northwestern Africa, was acknowledged as separate genus (e.g., Guinochet & Vilmorin 1978, Holub 1980, Romero Zarco 1985a, Watson & Dallwitz 1992) or became included with either *Helictotrichon* (Couderc & Guédès 1976) or *Arrhenatherum* (Clayton & Renvoize 1986).

Nomenclatural problems concerning the validity of the genus names *Avenastrum* Opiz, *Avenastrum* Jessen and *Avenochloa* Holub, connected with previously unclear nomenclatural rules for the lectotypification and illegitimacy of genus names (cf. Holub 1976, Lange 1995) have been settled by now: *Avenastrum* Opiz and *Avenastrum*

Jessen, although validly published, are later synonyms to *Helictotrichon*, such as is *Avenochloa* relative to *Avenula*.

Results and Discussion

Much progress has been made in these oat grasses during the past ca. ten years by in-depth investigation of chromosome and DNA characters (molecular cytogenetics, DNA sequencing of different nuclear and chloroplast DNA stretches, physical mapping of coding and highly repetitive non-coding DNA on the chromosomes; e.g., Grebenstein et al. 1996, 1998; Soreng & Davis 2000, Röser et al. 2001, Rodionov 2005, Winterfeld 2006, Döring et al. 2007, Quintanar et al. 2007, Winterfeld & Röser 2007a, b; Döring 2009, Schneider et al. 2009, Winterfeld et al. 2009). These results add a valuable new data set to the morphological, micromorphological, anatomical, and life form features studied to date. They contribute substantially to resolve the mosaic of morphological characters displayed by the Aveneae genera in question and aid to interpret the direction of evolutionary change(s). This implies also a re-circumscription of certain taxa and make some nomenclatural changes necessary. Notably, none of the realignments of taxa proposed in the following is really new. All of them have been envisaged already by some earlier authors, based on the morphological data they had at hand or they considered to have especial weight:

Helictotrichon (incl. *Pseudarrhenatherum*)

The genus *Helictotrichon* now receives a narrow circumscription by the exclusion of subgenera *Pratavenastrum* (Vierh.) Holub, *Pubavenastrum* (Vierh.) Holub and *Tricholemma* Röser, which are considered separate genera (see below). *Helictotrichon* s. str., however, is also expanded by enclosure of the species previously ascribed to the genus *Pseudarrhenatherum*. Inclusion of *Pseudarrhenatherum* with *Helictotrichon* had been suggested on morphological grounds already by Couderc & Guédès (1976). Recent nuclear DNA data show *Pseudarrhenatherum* nested within species of *Helictotrichon* s. str. (Röser et al. 2001, Quintanar et al. 2007, Schneider et al. 20009, Winterfeld et al. 2009) rather than as separate genus or affiliated with *Arrhenatherum*, as suggested by Clayton & Renvoize (1986) and based on the same way of disarticulation of the spikelet at maturity (only above the glumes, i.e., synaptospermy). This character is found occasionally also in other species of *Helictotrichon* s. str., i.e., the *H. parlatorei* species group in the Alps (Röser 1989, 1996) and also here coupled with reduction of the awns of the upper glumes of the spikelets, although usually [though sometimes encountered in *H. sempervirens* (Vill.) Pilg.] not coupled with entire loss as in *Pseudarrhenatherum*.

Pseudarrhenatherum contains two species, the more widespread *P. longifolium* (Thore) Rouy (western W Europe to NW Africa) and *P. pallens* (Link) Holub (endemic to the Serra da Arrábida in W Portugal). In transferring the species of *Pseudarrhenatherum* to *Helictotrichon*, Couderc & Guédès (1976: 188) misinterpreted Link's diagnosis and protologue of *Avena pallens* in J. Bot. (Schrader) vol. 2, Stück [= part] 2: 314,

1799 and also his later statement in Hort. Berol. 1: 124, 1827: "folia ... inferiora saltem[!] vaginae pubescente" in a way that the new combination *Helictotrichon pallens* (Link) Couderc & Guédès was applied to the widespread *P. longifolium* and a new combination, *Helictotrichon setifolium* (Brot.) Couderc & Guèdés, was created for the Arrábida endemic, based on Brotero's description of *Avena setifolia* Brot. in his Flora lusitanica 1: 108, 1804. Actually, Brotero l.c.: 108 stated "Hab. in collibus de Arrabida ... Comm. primum a Cl. P. Link", and later Link (1827: 124) cited "*Avena pallens* Linn. [= Link; typographic error] Schrad. Journ. 4. St. [= 4. Stück or vol. 2, part 2]: 314, 1799 " and "*Avena setifolia* Brot. lus. 1: 108" as synonym of his newly created combination *Arrhenatherum pallens* (Link) Link. Identity of *Avena pallens* Link and *A. setifolia* is further substantiated by a book review published by Link (1806) on Brotero's first volume of the Flora lusitanica in which he described how Hoffmannsegg and himself first met Brotero in the year 1798 in Coimbra and briefly reports on Brotero's botanical work. Link was delighted that Brotoro always mentioned in the Flora lusitanica whenever he had obtained a hint to a Portuguese species from him (Link) or from Hoffmannsegg: "Brotero gedenkt unser nicht allein in der Vorrede, sondern er führt auch fast immer bei jeder Pflanze an, dass er sie von uns erhalten habe" (p. 129). In translation: "Brotero remembers us not only in the preface, but lists also for most plants if he has obtained it from us." The antiquated German phrase is difficult to interpret. Most likely it does not mean the physical donation of a plant specimen, but rather a hint to an occurring plant species or the communication of knowledge about it. In the subsequent and very detailed comments on Brotero's flora, Link stated (p. 135): "*Av. setifolia* von mir dem Verfasser mitgetheilt und in diesem Journal als *A. pallens* aufgeführt, wird gut beschrieben." In translation: "*Av. setifolia* I had communicated to the author [= Brotero] and listed in this journal as *A. pallens* [= reference to Link's own publication of 1799 in J. Bot. (Schrader)] is well described". Thus, there is little doubt that *Avena pallens* Link and *A. setifolia* Brot. are the same taxon as argued already by Romero Zarco (1985a). Despite taxonomic misapplication, the combination *Helictotrichon pallens* (Link) Couderc & Guédès is formally correct and can be used further.

Only *Pseudarrhenatherum longifolium* (Thore) Rouy is without a correct name under *Helictotrichon*. Use of this epithet under *Helictotrichon* is prevented by of the valid name *Helictotrichon longifolium* (Nees) Schweick. for a S African species (Schweickerdt 1937). Instead of coining a new species epithet, the name *Avena thorei* Duby is suggested to be used here for several reasons: Duby (1828), in honoring with this epithet J. Thore, who first described this species as *Avena longifolia* Thore in the Prom. Golfe Gascogne: 92, 1810, also gave an excellent description in his widespread and influential botanical treatment. Additionally the epithet "*thorei* Duby" had been used under *Avena* or *Arrhenatherum* in many botanical treatments before Rouy (1913, 1921) re-animated the forgotten epithet *longifolia* Thore. The following combination is proposed:

Helictotrichon thorei (Duby) Röser, **comb. nov.**
Bas.: *Avena thorei* Duby, Bot. Gall. 1: 512, 1828.

Avenula

Avenula is segregated out from genus *Helictotrichon*, but is not maintained in its previous broad circumscription, i.e., comprising the subgenera *Pratavenastrum* (Vierh.) Holub, *Pubavenastrum* (Vierh.) Holub and the species of the N African *H.* subg. *Tricholemma*. The latter subgenus has not been formally transferred to *Avenula* to date, but its species (*Avena jahandiezii* Litard. in Jahand. & Maire and most likely *A. breviaristata* Barratte in Batt. & Trab; cf. below) had always been considered belonging to *Avenula* [HOLUB (1976); under its synonym *Avenochloa* by HOLUB (1962)]. Alternatively, it was treated collectively together with *Avena pubescens* Huds. and the species kept in this study under genus *Avenula* under *Avena* sect. *Avenastrum* Koch subsect. *Ecostatae* St.-Yves (cf. SAINT-YVES 1931) or *Avena* subg. *Avenastrum* (Koch) Rouy sect. *Ecostatae* St.-Yves (cf. MAIRE 1953). The type species of *Avenula* is *Avena pratensis* L. (HOLUB 1958; cf. RÖSER 1995). *Avenula* subg. *Pubavenastrum* and *Helictotrichon* subg. *Tricholemma* are excluded here from genus *Avenula* and considered separate genera:

Homalotrichon

This genus name, *Homalotrichon* Banfi, Galasso & Bracchi, coined in CONTI et al. (2005: 28) marks the transfer of the traditional *Helictotrichon* subg. *Pubavenastrum* or *Avenula* subg. *Pubavenastrum* to a separate genus, consisting of the single species *H. pubescens* (Huds.) Banfi, Galasso & Bracchi. The type species thus is *Avena pubescens. Homalotrichon* as a genus is well delineated against *Helictotrichon* and *Avenula* as narrowly circumscribed in this study by morphological characters of the spikelets (paleas with glabrous instead of hairy keels, lodicules very short, apically and laterally crenate; cf. SAINT-YVES 1931, HOLUB 1958, RÖSER 1989, LANGE 1995), an uncommon karyotype structure (WINTERFELD 2006, WINTERFELD & RÖSER 2007a, WINTERFELD et al. 2009), and its deviant representation of highly repetitive DNA repeat types in the genome (GREBENSTEIN 1996, WINTERFELD & RÖSER 2007b). Additionally, all molecular phylogenetic analyses based on DNA sequencing or restriction site mapping revealed consistently a separate position of *Homalotrichon pubescens* [syn. *Helictotrichon pubescens* (Huds.) Pilger, *Avenula pubescens* (Huds.) Dumort.] relative to *Helictotrichon* s. str. and *Avenula* s. str. (GREBENSTEIN et al. 1998, SORENG & DAVIS 2000, RÖSER et al. 2001, WINTERFELD et al. 2009).

Homalotrichon pubescens was mostly found to be sister to genus *Avenula*, however, most of these molecular studies suffered from a rather sparse sampling of further taxa, which would cast the segregation of *Homalotrichon* as separate genus into doubt, as it could be unified again with *Avenula* and eventually treated as a subgenus. Based on a broader sampling of Aveneae genera for nuclear and chloroplast DNA sequence data (QUINTANAR et al. 2007, DÖRING 2009), evidence was obtained just recently that *Homalotrichon* and *Avenula* s. str. are not sister, thus supporting their recognition as separate genera.

Tricholemma

The former *Helictotrichon* subg. *Tricholemma* (cf. Röser 1989) is here raised to genus rank as *Tricholemma*. It is morphologically characterized by a set of uncommon characters: main nerve of the lemma protruding from the back of the lemma below the exsertion of the awn and bearing a row of stiff and long hairs (a character not found in any other of the taxa discussed here except *A. breviaristata*; cf. below); rachilla of the spikelet disarticulating only above the glumes; lodicules short, truncate and crenate at the apex. The rachilla of the spikelets of *Avena jahandiezii*, type species of *Tricholemma*, had erroneously been described as disarticulating below each floret in the original description (Jahandiez & Maire 1925: 67: "floribus articulatis") and subsequent studies (Saint-Yves 1931, Maire 1953). The disarticulation actually only above the glumes corresponds with that found in the Alpine *Helictotrichon parlatorei* species group (see above). Together with the other uncommon characters, this induced Röser (1989) to abandon the genus *Avenula* as circumscribed at that time, i.e., comprising subg. *Pratavenastrum* (= *Avenula* in the sense of the present study) and subg. *Pubavenastrum* (with only *Avenula pubescens*), because *Avena jahandiezii* did not fit any of these acknowledged subgenera and further inclusion of this species would have made *Avenula* in this broad sense impossible to define morphologically. Returning to a broader delineated genus *Helictotrichon* with *Avena jahandiezii* constituting a further subgenus seemed a better solution. As it now seems, this conservative approach was exactly the wrong of two equally likely solutions possible at that time:

Recent molecular phylogenetic studies unambiguously support a segregation of the former *Helictotrichon* subg. *Tricholemma* (*Avena jahandiezii*) as a further genus in addition to *Helictotrichon*, *Avenula* and *Homalotrichon*. Based on all analyses conducted to date on chloroplast and nuclear DNA stretches in the Aveneae, *Avena jahandiezii* is separated from all of these genera and is not even sister to any of it (Grebenstein et al. 1998, Röser et al. 2001, Döring et al. 2007, Quintanar et al. 2007, Döring 2009, Schneider et al. 2009, Winterfeld et al. 2009). It represents a morphologically and molecularly well defined separate lineage.

It is an unresolved question whether the genus *Tricholemma* is monotypic (with only *Avena jahandiezii*, an endemic species of the Moyen Atlas in Morocco) or if it comprises a second species in North Africa, i.e., *Avena breviaristata* known from only the type collection made in 1882 by Letourneux in the Algerian Hauts Plateaux (Battandier & Trabut 1895, Saint-Yves 1931, Maire 1953). This grass was never recollected since (cf. Quézel & Santa 1962) and, unfortunately, also the type collection had become lost. It was part of Cosson's herbarium and Saint-Yves (1931: 487f) has seen and studied the plant(s), giving a brief but detailed description in Latin with anatomical illustrations of the leaf blade and awn in transverse section (Figs. 37, 38). The later description of Maire (1953) in the Flore de l'Afrique du Nord vol. 2. is much more extended relative to Saint-Yves' diagnosis. It contains a reproduction of Saint-Yves' figures, but additionally illustrates the spikelet and the florets, which had not been illustrated by Saint-Yves (1931). At the same time it was stated "Cette plante n'est connue que par un pied unique conservé dans l'Herbier Cosson. Ni nous, ni nos collaborateurs n'avons pu jusqu'ici la retrouver" (Maire 1953: 308). Since all

characters described for *A. breviaristata* by Saint-Yves reiterate in Maire's much extended French description without any modification, it may be that Maire's additional descriptive characters have been included according to expectation and to make the description compatible to that of the other species treated in this work. Additionally, the illustration of spikelet and florets was most likely inspired by Saint-Yves description rather than based on an actual study of plant(s) that were already lost at that time. Several recent attempts to relocate the lost voucher(s) of *A. breviaristata* were unsuccessful to date (Röser 1989, Lange 1995).

Based on the morphological description of this species (Battandier & Trabut 1895, Saint-Yves 1931, Maire 1953), the short-awned lemmas with seemingly a total loss of the columella and a much reduced subula were considered as most conspicuous character and served to circumscribe *A. breviaristata*. The species has spikelets with a rachilla disarticulating only above the glumes (as *A. jahandiezii* and some species in genus *Helictotrichon* s. str.; cf. above). The lemmas are described as "secus nervum medianum usque ad exsertionem subulae dense villosae" (Saint-Yves 1931: 488) or "densément et longuement villeuse le long de la nervure médiane jusqu'à l'arête, due reste glabre" (Maire 1953: 308). Following these descriptions, *Avena breviaristata* shares several further characters, which otherwise are rarely encountered, with *A. jahandiezii*. The leaf sheaths of vegetative shoots are almost entirely fused, densely hairy at least in their lower part, the inflorescence branches slender and not or just slightly thickened below the spikelets. Thus there is good reason to consider *A. breviaristata* closely related with *A. jahandiezii*, although this remains rather speculative without having seen a specimen of the former species.

The reduction of the awns in all lemmas of the spikelet is a unique feature of *A. breviaristata* among the taxa discussed in this study. *Avena breviaristata* was sometimes treated therefore under a monotypic section, i.e., *Helictotrichon* subg. *Pratavenastrum* sect. *Brevitrichon* Holub, *Avenochloa* subg. *Avenochloa* sect. *Brevitrichon* (Holub) Holub or *Avenula* subg. *Avenula* sect. *Brevitrichon* (Holub) Holub (cf. Holub 1958, 1962, 1976).

This change of awn structure is remarkable with respect to dispersal biology. It occurs in a species with dispersal units consisting of all florets of the spikelet keeping together. Other species with the same type of dispersal units also show changes in awn structure, most frequently the reduction or complete loss of the awn only in the upper lemmas, whereas the awn of the lowermost lemma remains fully developed (cf. above comments on the *Helictotrichon parlatorei* species group and the species of the traditional genus *Pseudarrhenatherum*). An additional example would be the genus *Arrhenatherum*: Its species have the same type of rachilla disarticulation only above the glumes and carry a fully developed awn only on the lemma of the lowermost floret, which additionally is unisexual and male in this instance (cf., e.g., Conert 1979–1998, Romero Zarco 1985b).

Species with spikelet rachillas disarticulating below each lemma, by contrast, always have fully developed awns on the back of each lemma and the florets are always female-fertile (all species of genera *Avenula* and *Homalotrichon* and most of genus *Helictotrichon* as delineated in this study). Single florets with the awned lemma as

outer structure act as dispersal units here, making the awn with its basal part (columella) capable of hygroscopic movement (twisting) an efficient instrument to bury the fruit(s) in the soil. Although this has never been really documented for these grasses, the mechanism is most likely the same as well-known in the feathergrasses (*Stipa*).

This burying mechanism does probably not work well in dispersal units consisting of all florets of the spikelet when all lemmas should carry fully developed awns capable of hygroscopic movement, as their movements may counteract each other. Keeping just a single fully developed awn on one of the lemmas could have been one of the solutions to this problem, the other was reduction of all awns (*Avena breviaristata*) most likely coupled with loss of the burying mechanism. Aspects of dispersal biology are not sufficiently known in these grasses, but most likely the awn structure of *A. breviaristata* has something to do with specialization in the production of dispersal units as similarly encountered in other species with the same type of rachilla disarticulation in the spikelets (*Helictotrichon parlatorei* species group, *Pseudarrhenatherum*, *Arrhenatherum*). It does not seem mandatory therefore to ascribe a separate supraspecific rank to *A. breviaristata*. The species is tentatively included here with *Avena jahandiezii* under the same genus with the following nomenclatural changes made:

Tricholemma (Röser) Röser, **stat. et gen. nov.**
Bas.: *Helictotrichon* subg. *Tricholemma* Röser, Diss. Bot. 145: 46, 1989.

Tricholemma jahandiezii (Litard.) Röser, **comb. nov.**
Bas.: *Avena jahandiezii* Litard. in Jahand. & Maire, Bull. Soc. Hist. Nat. Afr. N. 16: 67, 1925.

Tricholemma breviaristatum (Barratte) Röser, **comb. nov.**

Bas.: *Avena breviaristata* Barratte, in Batt. & Trab., Flore de l'Algér. (Monoc.): 184, 1895.

Avena

Inclusion of perennial *Avena macrostachya* within this genus of ca. 29 otherwise annual species (Baum 1977) is now well substantiated by nuclear 18S–26S rDNA (ITS and intergenic spacer IGS), 5S rDNA and chloroplast *mat*K gene and *trn*L intron DNA sequence data (Röser et al. 2001, Rodionov et al. 2005, Döring et al. 2007, Nikoloudakis & Katsiotis 2008, Nikoloudakis et al. 2008, Döring 2009, Winterfeld et al. 2009). Like *A. sativa*, the type species of genus *Avena*, also *A. macrostachya* carries none of the high-repeat non-coding satellite DNA sequences in the nuclear genomes that are typical of *Helictotrichon* and *Avenula* as circumscribed above (Grebenstein et al. 1996, Winterfeld 2006, Winterfeld et al. 2007b, Winterfeld et al. 2009). Because of its perennial habit, *Avena macrostachya* had occasionally been treated under *Helictotrichon* (Holub 1958, Clayton & Renvoize 1986) as a separate subgenus, i.e., *H.* subg. *Avenotrichon* Holub (cf. Holub 1958). Based on spikelet morphology and micromorhological characters (Baum 1968, 1974, 1977), it was transferred to *Avena* in which it was treated as a monotypic section, i.e., *A.* sect. *Avenotrichon* (Holub) B.R. Baum (cf. Baum 1974, 1977].

With regard to karyotype and molecular cytogenetic characters, *A. macrostachya* deviates conspicuously from the annual species of *Avena* and shares a number of structural chromosome characters with the strictly perennial oat genera, for example, *Tricholemma* as circumscribed in this study (cf. Rajhathy & Thomas 1974, Baum & Rajhathy 1976, Winterfeld 2006, Winterfeld & Röser 2007a, Winterfeld et al. 2009). It seems likely that in genus *Avena* only *A. macrostachya* has retained some kind of plesiomorphic chromosome structure shared with other, strictly perennial oat genera, whereas the karyotypes of *Avena* annuals are rather derived (cf. Rodionov 2005, Winterfeld et al. 2009). Most molecular phylogenetic studies currently conducted on different nuclear DNA stretches in *Avena* corroborate a separate position of *A. macrostachya* relative to the annual species and closest, though remote affinity to the C-genome species (Rodionov et al. 2005, Nikoloudakis & Katsiotis 2008, Nikoloudakis et al. 2008, Peng et al. 2008), suggested also by chromosome painting studies (*in situ* hybridization with total genomic DNA; Leggett & Markhand 1995).

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