Helictochloa Romero Zarco (Poaceae), a New Genus of Oat Grass

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Helictochloa Romero Zarco (Poaceae), a new genus of oat grass

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Abstract

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Morphological and anatomical characters used to separate the genera related to *Avena* L. *(Poaceae: Aveneae)* are analyzed. The taxonomic importance of these characters is discussed with regard to recent molecular studies. Six genera of perennial oats are recognized: *Arrhenatherum* P. Beauv., *Pseudarrhenatherum* Rouy*, Helictotrichon* Besser*, Avenula* (Dumort.) Dumort., *Tricholemma* (Röser) Röser and *Helictochloa* Romero Zarco (described here) is accepted. New combinations for the species included in *Helictochloa* are proposed. A key to *Avena* related genera from the Mediterranean region is given.

Key-words

POACEAE – Avena – Arrhenatherum – Pseudarrhenatherum – Avenula – Helictochloa – Tricholemma – Helictotrichon – Oat grasses – Taxonomy

Résumé

ROMERO-ZARCO, C. (2011). Helictochloa Romero Zarco (Poaceae), un nouveau genre d'avoine. *Candollea* 66: 87-103. En anglais, résumés anglais et français.

Les principaux caractères morphologiques et anatomiques sont présentés ici et utilisés pour servir à la délimitation des taxons les plus proches du genre *Avena* L. *(Poaceae: Aveneae).* L'importance taxonomique de ces caractères est discutée selon des études moléculaires récentes. Six genres d'avoines vivaces sont ainsi distingués: *Arrhenatherum* P. Beauv., *Pseudarrhenatherum* Rouy*, Helictotrichon* Besser, *Avenula* (Dumort.) Dumort., *Tricholemma* (Röser) Röser et *Helictochloa* Romero Zarco (décrit ici). Plusieurs nouvelles combinaisons pour les espèces incluses dans *Helictochloa* sont établies. Une clé de détermination est aussi donnée pour séparer les genres proches d'*Avena* pour la région méditerranéenne.

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Introduction

This article is especially focused on the so called "perennial oats" (Gervais, 1973), that is, *Avenula* (Dumort.) Dumort. plus *Helictotrichon* Besser *(Poaceae: Aveneae),* a group that has been circumscribed as a single genus (Holub, 1958; Röser, 1989, among others) or two (Holub, 1962; Gervais, 1973; Kerguélen, 1975; Romero-Zarco, 1984a, 1984b) or four genera (Röser & al., 2009). Nevertheless, it is also necessary to discuss their phylogenetic relationships with *Avena* L., *Arrhenatherum* P. Beauv. and *Pseudarrhenatherum* Rouy at the light of recent molecular studies (Röser & al., 2001; Grebenstein & al., 1995, 1998; Rodionov & al., 2005; Quintanar & al., 2007; Soreng & al., 2007; Winterfeld & Röser, 2007; Schneider & al., 2009; Winterfeld & al., 2009).

"Oats grasses" is used here as the appropriate common name for species belonging to *Avena, Helictotrichon, Avenula, Arrhenatherum* and *Pseudarrhenatherum.* Other genera with nomenclatural relations with *Avena* or *Helictotrichon*, such as *Amphibromus* Nees, *Danthoniastrum* (Holub) Holub, *Gaudinia* P. Beauv., *Ventenata* Koeler, *Deschampsia* P. Beauv., *Avenella* Parl., and *Trisetum* Pers., etc. are not considered here, as they do not pose taxonomic problems in relation to the limits of the genus *Avena.* The aim of this article is to ascertain relationships among oat grasses. For this purpose anatomical and morphological characters are summarized and discussed. Consequently, a taxonomic scheme for oat grasses is here established, accepting in general the monophyletic lineages suggested by molecular studies and supported by anatomical, morphological and biogeographical evidence.

Grebenstein & al. (1995), using highly repeated satellite DNA as a molecular marker, found differences between *Helictotrichon* s.s. and the remaining species investigated. A second study (Grebenstein & al., 1998) concludes that *Helictotrichon* s.l. is paraphyletic, if not polyphyletic according to ITS1 and ITS2 rDNA sequence analysis. Further evidence from physical mapping of 5S rDNA (Röser & al., 2001) and from plastid 'trnT-F' and nuclear ITS sequences (Quintanar & al., 2007) strongly suggest that the large genus *Helictotrichon* is paraphyletic or polyphyletic.

The anatomical characteristics of leaf blade in transverse section have been intensely investigated and used in the taxonomy of the group (Duval-Jouve, 1863; Potztal, 1951). It has been of special importance for the separation of *Avenula* with respect to *Helictotrichon* (Holub, 1962; Gervais, 1973; Kerguélen, 1975; Romero-Zarco, 1984b). Nevertheless, molecular studies suggest that *Avenula* is polyphyletic (Grebenstein & al., 1998; Röser & al., 2001; Quintanar & al., 2007). A taxonomic consequence is the description of the monospecific genus *Homalotrichon* Banfi, Galasso & Bracchi (Conti & al., 2005) including *H. pubescens* (Hudson) Banfi, Galasso & Bracchi (≡ *Avenula pubescens* (Hudson) Dumort. ≡ *Avena pubescens* Hudson, see below). This implies that the conduplicated leaf blades structure, a diagnostic character for the genus, could have evolved independently in three lineages. In order to investigate this possibility, the anatomical structure of blades were re-examined in more detail in *A. pubescens* (placed by recent molecular analyses in an isolated position near *Arctagrostis* Griseb. or *Milium* L.; see Quintanar & al., 2007), and *Avenula pratensis* (L.) Dumort., with strong affinity with the rest of European *Avenula* species, both clearly separated with respect to *Helictotrichon* and other *Aveneae* genera (Grebenstein & al., 1998; Röser & al., 2001).

Material and methods

Approximately 2600 sheets (herbarium specimens) were examined for this study. Leaf blade cross-sections from sterile innovations were obtained from nearly 260 samples, following methods in Saint-Yves (1931) and anatomical techniques described in previous papers (Romero-Zarco, 1984b, 1985b). Several root samples of different diameters were removed for study from one year old plants grown in pots. For each species lodicules were observed in 10 or more florets from at least three populations when possible. Two or three dried mature caryopses samples were studied in selected species. The caryopses were softened in fresh water during six hours and then embryos were dissected using an entomological needle and placed in 50% lactic acid. Most of the studied specimens belong to the main collection of the Servicio General de Herbarios de la Universidad de Sevilla (SEV). Vouchers cited in the figures are listed in table 1. Nomenclature used in the next section follows Romero-Zarco (1984a, 1984b, 1985a, 1985c, 1993).

Results and discussion

Root anatomy (Fig. 1)

The presence of a ring of sclerenchyma around endodermis in several European species of *Helictotrichon* and in *Pseudarrhenatherum longifolium* (Thore) Rouy was shown by Gervais (1968). This periendodermic ring does not appear in *Avena* species, *Arrhenatherum elatius* (L.) J. Presl & C. Presl, nor in *Avenula* species. A similar ring was described later in the roots of *Pseudarrhenatherum pallens* (Link) Holub by Romero-Zarco (1985c). In order to complete the data, this character was investigated in *Arrhenatherum album* (Vahl) W. D. Clayton and, for comparison, in *Pseudarrhenatherum pallens* and *Avenula hackelii* (Henriq.) Holub. The results obtained here are in agreement with those contributed by Gervais (1968, 1973) and by Röser (1989). The studied species of *Arrhenatherum* and *Avenula* lack a sclerenchymatic ring, whereas this ring is present in *Pseudarrhenatherum.*

Table 1. – Material cited in the figures. Nomenclature according to Romero-Zarco (1984a, 1984b, 1985a, 1985c, 1993).

Taxa	Locations	Vouchers
Arrhenatherum album var. *erianthum* (Boiss.) Romero Zarco	Spain. Córdoba, entre Torrecampo y Santa Eufemia, 8.VI.1978	E. F. Galiano & A. Ramos (SEV 78472)
Arrhenatherum elatius (L.) J. Presl & C. Presl subsp. *elatius*	Spain. Ávila, Circo de Gredos, 27.VII.1978	J. A. Devesa & al. (SEV 78612)
Arrhenatherum elatius subsp. *baeticum* Romero Zarco	Spain. Jaén, Valdepeñas de Jaén, 18.VI.1979	M. J. Díez & al. (SEV 78626)
Avenula hackelii (Enriq.) Holub	Portugal. Bajo Alentejo, Vila Nova de Milfontes [pinares de *P. pinaster* junto al camping], 17.IV.1981	C. Romero-Zarco (SEV 86752)
Avenula bromoides (Gouan) H. Scholz subsp. *bromoides*	Spain. Burgos, entre Pancorvo y Bujedo, 16.VII.1980	J. A. Devesa & al. (SEV 77484)
Avenula bromoides subsp. *pauneroi* Romero Zarco	Spain. Jaén, Sierra de Cazorla, Nava de San Pedro, 23.VI.1980	J. A. Devesa & al. (SEV 77506)
Avenula gervaisii Holub subsp. *gervaisii*	Spain. Málaga, entre Archidona y Salinas, 17.VI.1980	J. A. Devesa & al. (SEV 86683)
Avenula marginata (Lowe) Holub var. *marginata*	Spain. Asturias, Puerto de Tarnas, 12.VII.1980	J. A. Devesa & al. (SEV 79499)
Avenula pratensis subsp. *iberica* (St.-Yves) O. Bolòs & Vigo	Spain. Jaén, Sierra del Pozo, pico Cabañas, 24.VI.1980 Spain. Huesca, entre Aínsa y Campó, 21.VII.1980	J. A. Devesa & al. (SEV 77590) J. A. Devesa & al. (SEV 77573)
Avenula pubescens (Hudson) Dumort.	Spain. Burgos, entre Soncillos y Cubillos del Rojo, 16.VII.1980 Spain. Palencia, San Martín de Valdeiglesias, 10.VIII.1982	J. A. Devesa & al. (SEV 86747) P. Montserrat (SEV 86748)
Helictotrichon cantabricum (Lag.) Gervais	Spain. Huesca, Puente la Reina de Jaca, 25.VIII.1981	J. A. Devesa & al. (SEV 77605)
Helictotrichon sarracenorum (Gand.) Holub	Spain. Granada, Sierra Nevada, Fuente de San Jerónimo, 26.VI.1980	J. A. Devesa & al. (SEV 86651)
Helictotrichon sedenense (DC.) Holub subsp. *sedenense*	Spain. León, Valverde de la Sierra, Pico Espiguete, 14.VIII.1975 Spain. Huesca, Sallent de Gállego, El Respumoso, 9.VIII.1980	P. Montserrat & L. Villar (SEV 77616) P. Montserrat & L. Villar (SEV 77613)
Pseudarrhenatherum longifolium (Thore) Holub	Spain. Cádiz, Algeciras, Sierra de Ojén, 4.VII.1981	J. Arroyo & al. (SEV 66721)
Pseudarrhenatherum pallens (Link) Holub	Portugal. Estremadura, Setúbal, Sierra de Arrábida, 28.IV.1981	J. A. Devesa & C. Romero-Zarco (SEV 86754)

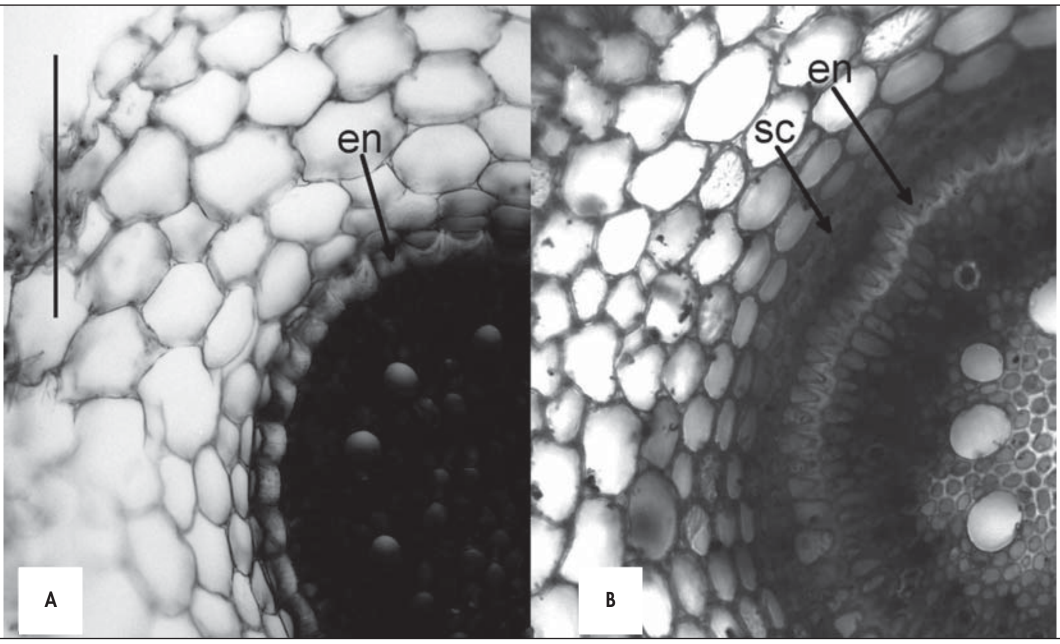

Fig. 1. – Root anatomy in cross-sections stained with safranin. **A.** *Avenula hackelii* (Henriq.) Holub (SEV [86752]) ; **B.** *Pseudarrhenatherum pallens* (Link) Holub (SEV [86754]). [en = endodermis ; sc = periendodermic sclerenchyma].

[Bar = 0.2 mm]

In *Arrhenatherum album* and *Avenula hackelii* (Fig. 1A) the endodermis is composed of approximately square cells, almost totally plugged by deposits of suberin, with a small lumen next to the outer wall. The sclerification of cortex cells was not observed. On the contrary in *Pseudarrhenatherum pallens* (Fig. 1B) the endodermis is formed by cells extended radially, with an inner 'V'-shaped suberin deposit leaving a lumen half as large as the cutting surface. A two to three row layer of sclerenchyma cells are observed around the endodermis. As asserted in Gervais (1973) the endodermis of *Pseudarrhenatherum* is different from those of *Arrhenatherum, Avenula* and *Helictotrichon.*

Leaf blade anatomy (Fig. 2)

Details of sclerenchyma girders and the arrangement of the chlorenchyma are shown in figure 2 for *Avenula pratensis* subsp. *iberica* (St.-Yves) O. Bolòs & Vigo and *A. pubescens.* In *Avenula pratensis* subsp. *iberica,* the subepidermal strands of sclerenchyma are substantially thinner than the marginal ones, and some of them are connected to the vascular strand forming thin, 'I'-shaped girders. In *A. pubescens* the marginal strands are less developed and the subepidermal strands of sclerenchyma are very robust, even more than the marginal ones, forming rounded girders with main lateral vascular strands. The differentiation of a palisade chlorenchyma is observed in *Avenula pratensis* subsp. *iberica,* whereas in *A. pubescens* all chlorenchyma cells are nearly isodiametric. Other *Avenula* taxa have palisade chlorenchyma (López & Devesa, 1991) and girders, when present, are 'I'-shaped (Gervais, 1973; Romero-Zarco, 1984b; Röser, 1989).

Morphology of lodicules (Fig. 3)

The morphological characteristics of lodicules in *Arrhenatherum elatius* subsp. *baeticum* Romero Zarco, *Pseudarrhenatherum pallens, Helictotrichon sarracenorum* (Gand.) Holub, *H. sedenense* (DC.) Holub subsp. *sedenense, Avenula bromoides* subsp. *pauneroi* Romero Zarco and *A. pubescens* are summarized in figure 3. *Avenula pubescens* differs remarkably from the others by having shorter (< 1 mm) and irregularly lobed lodicules (see also Romero-Zarco, 1984b: Fig. 5; Röser, 1989: Fig. 8). The remaining species have longer lodicules (> 1 mm), with a lanceolate membranous portion, with or without a

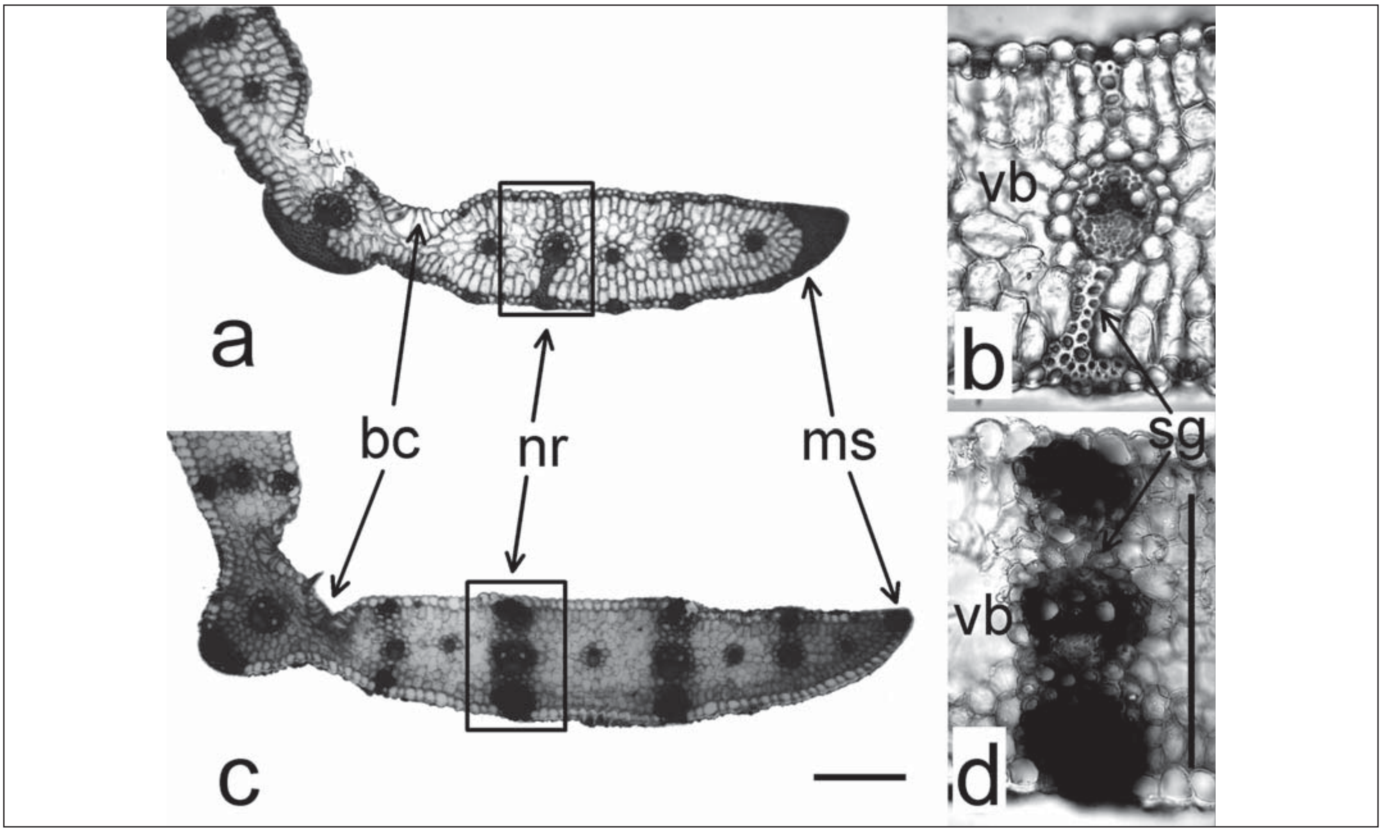

Fig. 2. – Leaf blade cross-sections from sterile innovations, stained with safranin. **A-B.** *Avenula pratensis* subsp. *iberica* (St.-Yves) O. Bolòs & Vigo (SEV [77590]); **C-D.** *Avenula pubescens* (Hudson) Dumort. (SEV [86747]). [bc = bulliform cells, ms = marginal sclerenchyma, nr = nerve region, sg = sclerenchyma girders, vb = vascular bundle].

[Bars = 0.2 mm]

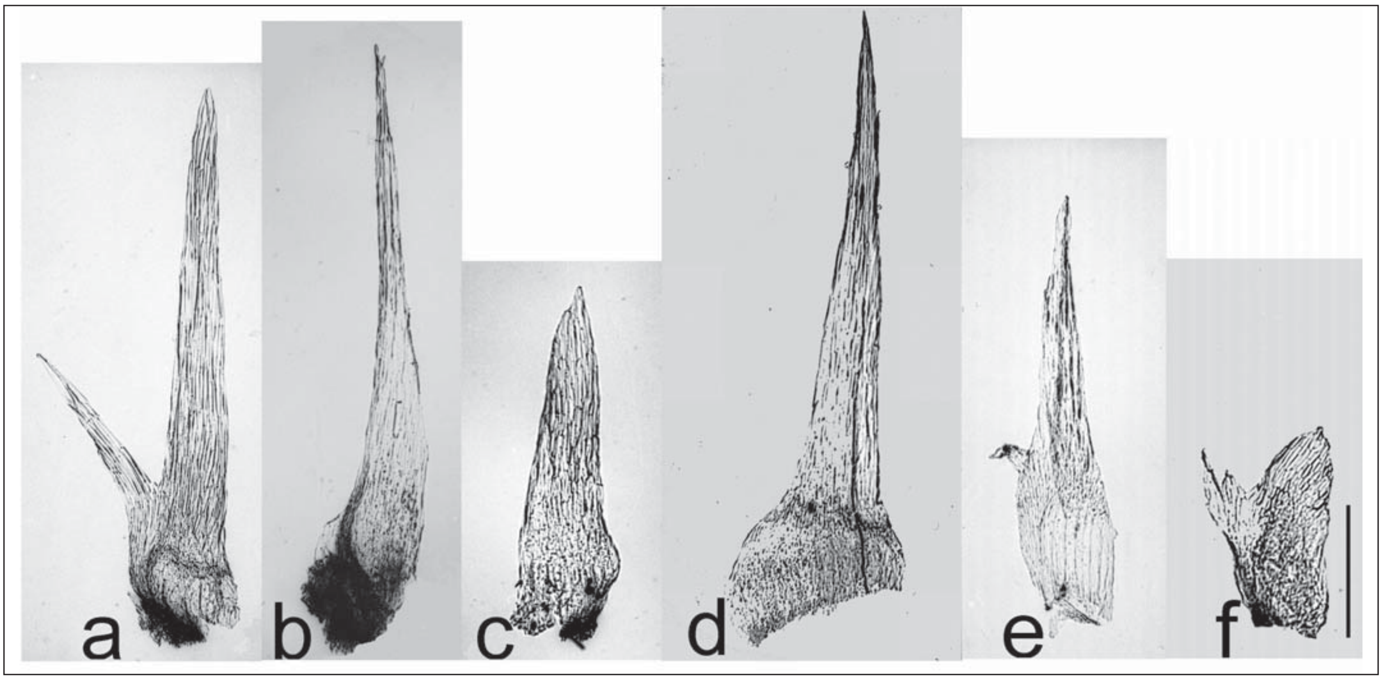

Fig. 3. – Morphology of the lodicules in perennial oat grasses. **A.** *Arrhenatherum elatius* subsp. *baeticum* Romero Zarco (SEV [78626]); **B.** *Pseudarrhenatherum pallens* (Link) Holub (SEV [86754]); **C.** *Helictotrichon sarracenorum* (Gand.) Holub (SEV [86651]); **D.** *Helictotrichon sedenense* (DC.) Holub subsp. *sedenense* (SEV [77616]); **E.** *Avenula bromoides* subsp. *pauneroi* Romero Zarco (SEV [77506]); **F.** *Avenula pubescens* (Hudson) Dumort. (SEV [86747]).

[Bar = 0.5 mm]

lateral lobe or tooth. In all *Arrhenatherum* taxa investigated, the presence of a lateral lobe or tooth is a variable character, even between the basal and apical floret within the same spikelet (Romero-Zarco, 1985a). This character is less variable in species of *Pseudarrhenatherum, Helictotrichon* s.s. and *Avenula*. A lobe is always observed in most Eurasian *Avenula* species (*A. pubescens* excluded); the lobe is located at or below the middle on the lateral margin facing the palea, and its size is variable. *Pseudarrhenatherum* and most Eurasian *Helictotrichon* taxa investigated have entire lodicules, with the exception of *H. sedenense* subsp. *sedenense*, that has a small lateral tooth in some cases (Romero-Zarco, 1984a; Röser, 1989). Lodicules in *Avena* s.s. (Baum, 1977; Romero-Zarco, 1996) are similar to *Helictotrichon,* containing a lanceolate membranous portion, and with or without a small (sometimes tiny) lateral tooth.

Morphology of the embryos (Fig. 4)

Some differences between species were observed in the morphology of epiblast. Several types of epiblasts have been described in *Avena,* some with rounded apical margins and others with more or less truncated margins (Baum, 1977). Figure 4 shows the morphology of embryos extracted from mature caryopses of the following perennial oats: *Arrhenatherum album* var. *erianthum* (Boiss. & Reut.) Romero Zarco, *A. elatius* subsp. *elatius*, *Pseudarrhenatherum longifolium*, *Helictotrichon sedenense* subsp. *sedenense, H. cantabricum* (Lag.) Gervais, *Avenula pubescens, A. pratensis* subsp. *iberica, A. gervaisii* Holub subsp. *gervaisii, A. bromoides* (Gouan) H. Scholz subsp. *bromoides* and *A. marginata* (Lowe) Holub var. *marginata.* Aside from the differences in size (probably attributable to the size of the caryopsis itself), variations in two characters are observed: the form of the epiblast and the apex of the scutellum.

The combination of both characters allows us to define three types of embryos in perennial oat grasses:

1. *"Arrhenatherum"* type, characteristic of this genus, with rounded epiblast and scutellum.
2. *"Helictotrichon"* type, with truncated or somewhat emarginated epiblast, and subobtuse or rounded scutellum, present in *Helictotrichon, Pseudarrhenatherum* and *Avenula pubescens*.
3. *"Avenula"* type, with epiblast similar to the *"Helictotrichon"* type and scutellum with nipple-shaped apex, present in most *Avenula* species (*A. pubescens* excluded).

According to Negbi & Sargent (1986: 252, Fig. 7), the scutellum of *Avena fatua* L. resembles the subobtuse one of *Helictotrichon sedenense* subsp. *sedenense* (Fig. 4D).

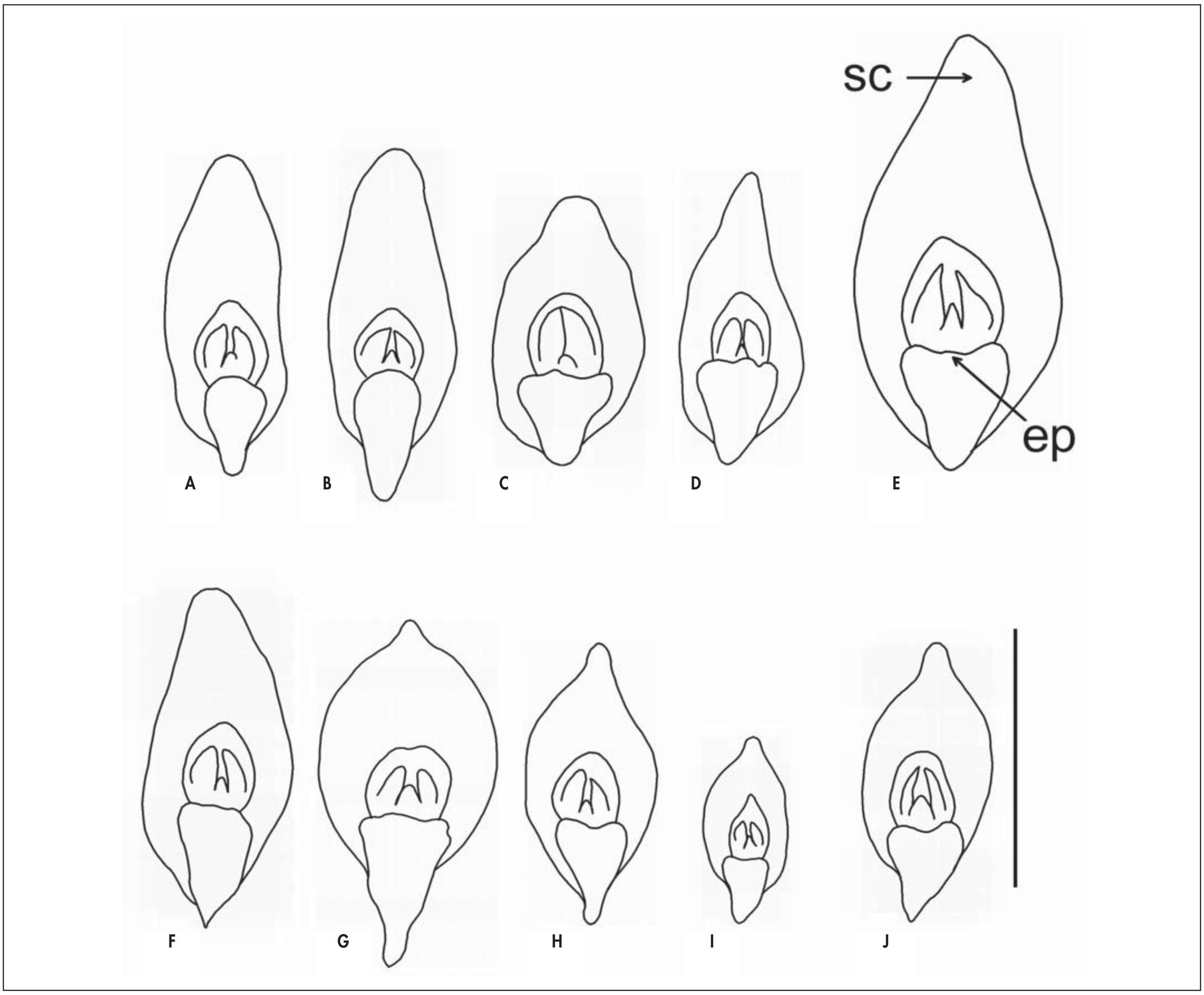

Fig. 4. – Morphology of the embryos in perennial oat-grasses (frontal view). **A.** *Arrhenatherum album* var. *erianthum* (Boiss.) Romero Zarco (SEV [78472]); **B.** *A. elatius* (L.) J. Presl & C. Presl subsp. *elatius* (SEV [78612]); **C.** *Pseudarrhenatherum longifolium* (Thore) Holub (SEV [66721]); **D.** *Helictotrichon sedenense* (DC.) Holub subsp. *sedenense* (SEV [77613]); **E.** *Helictotrichon cantabricum* (Lag.) Gervais (SEV [77605]); **F.** *Avenula pubescens* (Hudson) Dumort. (SEV [86748]); **G.** *Avenula pratensis* subsp. *iberica* (St.-Yves) O. Bolòs & Vigo (SEV [77573]); **H.** *Avenula gervaisii* Holub subsp. *gervaisii* (SEV [86683]); **I.** *Avenula bromoides* (Gouan) H. Scholz subsp. *bromoides* (SEV [77484]); **J.** *Avenula marginata* (Lowe) Holub var. *marginata* (SEV [79499]). [sc = scutelum; ep = epiblast].

[Drawn by author] [bar = 1mm]

Taxonomic treatment

1. *Avena s.s.*

Since the formal description of *Avena* by Linnaeus in 1753, many genera have been attributed to the tribe *Aveneae.* In the last 100 years the main subject of discussion in the taxonomy of *Avena* has focused on the separation of annual species (*Avena* s.s.) with respect to perennial ones *[Helictotrichon* s.l., that is: including *Avenula* (Holub, 1958; Röser, 1989), *Arrhenatherum* (Potztal, 1951), and *Pseudarrhenatherum* (Röser & al., 2009)]. The main stumbling block has been the existence of *Avena macrostachya* Coss. & Durieu, a perennial species, endemic to northwestern Africa, that has spikelets similar to other annuals in the genus. In the analysis of Röser & al. (2001), *A. macrostachya* appears as an isolated lineage, occupying a basal position with respect to *Helictotrichon* s.s. and not clustered with *A. sativa* L. Quintanar & al. (2007) included eight annual *Avena* species, and *A. macrostachya* is placed between two *Avena* s.s. clades.

These two clades are well defined based on morphological features of the spikelets:

1. the species near *A. ventricosa* Coss. (see *Avena* sect. *Ventricosa* Coss., Romero-Zarco, 1996);
2. the remaining species *(A. sativa*, *A. barbata* Link, etc.).

Avena macrostachya is found in a similar position in another phylogenetic tree (Rodionov & al., 2005), although sister to *A. ventricosa* group, and distantly related to *A. sativa*.

According to Winterfeld & al. (2009) karyotype features suggest that *A. macrostachya* is close to the C-genome species of *Avena* (i.e. *A. eriantha* Durieu). These results support retaining *A. macrostachya* in *Avena* s.s., as proposed by Baum (1968) who based his conclusion on morphological and anatomical characters (large glumes and sclerenchyma not present surrounding the endodermis in the root).

Avena L., Sp. Pl.: 79. 1753.

Lectotypus designated by Britton & Brown, 1913): *Avena sativa* L.

Diagnosis. – Annuals (with the exception of *A. macrostachya);* roots without sclerenchyma surrounding endodermis; culms with (2-)3-6 visible nodes; leaves convolute, relatively soft and flexible; cross-section with numerous secondary nerves, scarcely pronounced ribs, bulliform cells scarcely developed, forming several rows between the nerves, 'I'-shaped girders of colourless parenchyma, and subepidermal sclerenchyma in small, scarcely developed strands. Spikelets (12-)16-41(-48) mm long, (1-)2-4(-5) florets, completely developed, bisexual; equal or unequal glumes, almost as long as the whole spikelet, rounded on the back, glabrous, with (5-)7 or more nerves; lemma generally hairy towards the base, somewhat scabrous towards the apex; awn dorsal, generally with a strongly twisted column -exceptionally flattened or not developed in cultivated forms-; palea strongly 2-keeled, keels minutely ciliate; lodicules longer than ovary, lanceolate, entire or with a small lateral tooth. Caryopsis furrowed; hilum linear; embryo with a rounded or truncated epiblast and subobtuse scutellum.

Species and distribution. – 24-31 species, some of them cultivated derivatives; West Mediterranean and Macaronesia is the main centre of species diversity.

2. *Arrhenatherum* vs *Pseudarrhenatherum*

The delimitation of *Arrhenatherum* presents two problems. First its separation from *Helictotrichon* and second, the splitting of *Pseudarrhenatherum* as proposed by Rouy (1913, 1921). There are three traditional morpho-anatomical criteria used to delimit these genera.

The first criterion used is the composition of spikelets. *Arrhenatherum elatius* and related species are clearly separable from other perennial oats by having two unequal florets that are joined at maturity; the lower floret masculine, with a strong subbasal awn; the upper floret bisexual, with a rudimentary, subapical awn, sometimes absent. It is evident that this configuration must be understood as a specialized polyandry syndrome in the context of the family. The majority of the remaining species of the group have spikelets with several similar, bisexual florets, all of them articulated with the rachilla, so that the dispersal unit (diaspora) is a single floret. Nevertheless some *Avena* and *Helictotrichon* species have spikelets with a reduced number of florets (frequently only two of them well developed) remaining united at maturity, since only the lower floret is articulated with the rachilla. The result is the configuration of a synaptospermic diaspora. In *Avena* this phenomenon occurs in some species belonging to different sections *(A. sterilis* L., *A. murphyi* Ladizinsky and *A. eriantha;* see for example Romero-Zarco, 1996: Fig 1). Among the European *Helictotrichon* species, this specialized configuration of spikelets occurs in a small group of closely related, central European species, the group of *H. parlatorei* (J. Woods) Pilger (see Röser, 1989: 65-76). In all these cases the two florets of the spikelets are similar, both provided with a well developed, dorsal awn. However, in the two unique species included in the genus *Pseudarrhenatherum* (Holub, 1980; Romero-Zarco, 1985c), spikelets are formed by two different florets, both completely developed and bisexual, the lower floret with a well developed, dorsal awn, the upper floret without awn or with a reduced, straight subapical one.

Four kinds of major modifications in the structure of the spikelets occur in oats grasses:

1. reduction to two completely developed florets, rarely only one in some cultivars;
2. synaptospermy;
3. morphological differentiation between the lower floret and the upper one;
4. polyandry.

In synaptospermic *Avena* species, the spikelets have 2-4 (-5) florets (see Romero-Zarco, 1996), but only cultivated forms have two morphologically different florets. In *Arrhenatherum,* the spikelets reach the maximum degree of modification, with reduction, differentiation, and polyandry. Obviously, synaptospermy cannot occur in *Arrhenatherum,* since the spikelets contain a unique fruit, but the atrophy of the joint at the base of the second flower does occur. In *Pseudarrhenatherum* the three first phenomena occur together, but not polyandry. In the species of *Helictotrichon parlatorei* group (Röser, 1989), together with certain endemic atypical species from Atlas Range *(Avena Jahandiezii* Litard. and *A. breviaristata* Barratte, included by Holub, 1962, 1976 in *Avenula),* synaptorpermy occurs, occasionally accompanied by the reduction of spikelets to two fertile florets, but there is no clear upward differentiation as in *Pseudarrhenatherum.*

The second critieria used to separate species of *Arrhenatherum* from *Pseudarrhenatherum* is foliar anatomy. *Arrhenatherum* leaves are similar to those of *Avena,* i.e. relatively soft, with scarcely developed subepidermal sclerenchyma and less protruding ribs. The leaves of *Pseudarrhenatherum* are rigid, similar to those of Paleartic *Helictotrichon* species, with numerous, well-marked ribs above, with abundant subepidermal sclerenchyma forming 'T'-shaped girders and, in more xerophilic species, a continuous layer of subepidermal sclerenchyma beneath. The variability observed among *Pseudarrhenatherum* species is parallel to that occurring in *Helictotrichon* (see ROMERO-ZARCO, 1985c).

The third criterion is based on the anatomical characteristic of the root as described by GERVAIS (1968, 1973). The endodermis is surrounded by a more or less heavy layer of sclerenchyma cells in the roots of the European *Helictotrichon* species, as well as in *Pseudarrhenatherum.* This character does not occur in *Avena* species (including *A. macrostachya), Avenula,* or *Arrhenatherum* s.s. In addition, the form of the endodermic cells are different in *Helictotrichon* when compared with *Pseudarrhenatherum:* in the former, the cells are ± rounded, with a thick internal reinforcements of suberin and a reduced lumen, whereas in the later the cells are extended radially and have a broad lumen. This detail was observed by GERVAIS (1973) in *P. longifolium* and is verified here in *P. pallens.*

Two additional criteria are added here: the morphology of the embryos and the presence of macrohairs on the back of lemmas (excluding the callus). The embryos of *Arrhenatherum* differ by having rounded epiblasts, not truncated or emarginated epiblasts, like the other genera studied (Fig. 4). Macrohairs are present on lemmas of *Pseudarrhenatherum, Arrenatherum* and some *Avena* and *Avenula* s.l. species and not in Eurasian and American species of *Helictotrichon* (FINOT & al., 2005; ROMERO-ZARCO, 1984a, 1984b, 1985a, 1985c, 1996).

Four schemes regarding the classification are:

1. to maintain a broad criterion for *Helictotrichon,* including *Arrhenatherum* and *Pseudarrhenatherum;*
2. to separate *Arrhenatherum* and *Helictotrichon* maintaining *Pseudarrhenatherum* within the first;
3. the same but including *Pseudarrhenatherum* in *Helictotrichon;*
4. to completely separate these three genera.

How have molecular studies contributed to these questions? GREBENSTEIN & al. (1995, 1998) have demonstrated with different molecular markers, that *Arrhenatherum elatius* clearly occupies a different position from *Avena* and from European *Helictotrichon* s.s. species. However, no *Pseudarrhenatherum* species where included in these studies. RÖSER & al. (2001) concluded that *Pseudarrhenatherum* should be included in *Helictotrichon* s.s. on the basis of its 5S rDNA sequence, but only the most common species, *P. longifolium,* was studied, and no *Arrhenatherum* species were included in their analysis. A study of the whole group would have supported their conclusion in this respect. QUINTANAR & al. (2007) in their phylogram on nuclear ITS data, separate clearly *Arrhenatherum elatius* from *Helictotrichon* s.s., but *Pseudarrhenatherum longifolium* is nested in *Helictotrichon.* Similar relationships are seen in recent studies (SCHNEIDER & al., 2009; WINTERFELD & al., 2009). One might assume that *Pseudarrhenatherum longifolium* should not be included in *Arrhenatherum*, but it could be included in *Helictotrichon* if the phylogenetic position of *Pseudarrhenatherum pallens* were clarified. Meanwhile, the most coherent position according to available data is to maintain the independence of these three genera until an analysis including all taxa with more molecular markers is completed.

Arrhenatherum P. Beauv., Ess. Agrostogr. 55: 1812.

Lectotypus (designated by PFEIFFER, 1872: 274): *Avena elatior* L. (≡ *Arrhenatherum elatius* (L.) J. Presl & C. Presl).

Taxonomic characters and diagnosis. – See ROMERO-ZARCO (1985a).

Species and distribution. – Only five species, primarily found in the Mediterranean Basin and SW Asia. The polymorphic *A. elatius* is the most frequent species, extending from Macaronesia to Siberia and introduced elsewhere.

Pseudarrhenatherum Rouy in Bull. Soc. Bot. France 68: 401. 1921.

≡ *Thorea* Rouy, Fl. France 14: 142. 1913 (non *Thorea* Bory in Ann. Mus. Hist. Nat. 12: 127. 1808 [nom. illeg.].

Typus: *Avena longifolia* Thore (≡ *Pseudarrhenatherum longifolium* (Thore) Rouy).

Nomenclature. – See ROUY (1921) and ROMERO-ZARCO (1985c).

Taxonomic characters and diagnosis. – See ROMERO-ZARCO (1985c).

Species and distribution. – Two species: the West-European, acidophilic *P. longifolum,* with the southernmost known populations in South Spain and Morocco, and *P. pallens,* endemic from a few localities near Lisbon, growing on calcareous substrates.

3. *Avenula* vs *Helictotrichon*

The question of recognizing *Avenula* as separate from *Helictotrichon* has been suitably discussed by several authors using morphological and anatomical characters (GERVAIS, 1973; HOLUB, 1962; ROMERO-ZARCO, 1984b). Most distinguishing characteristics of the former with respect to the later are based on leaf and root anatomy. The Eurosiberian and Mediterranean species of *Helictotrichon* s.s. have a layer of sclerenchyma surrounding the endodermis that is not present in *Avenula* s.l. (that is, including *Tricholemma* (Röser) Röser). Moreover, leaf blades are bilaterally symmetrical in *Avenula* s.l., since there are no ribs, and bulliform cells form rows along each side of the adaxial midrib. Other important characters such as palea hairiness, lodicule shape and the form of awn columns are heterogeneous in *Avenula* s.l.*, A. pubescens* has glabrous paleas, short, ovate or obovate lodicules and terete or square awn column in cross-section; *A. jahandiezii* (here included in *Tricholemma* together with *A. breviaristata*) has similar lodicules and awn columns, but minutely ciliate paleas found in many grasses; the remaining *Avenula* species have ciliate paleas, long, lanceolate lodicules, and flattened awn column with pale margins.

Therefore, Röser (1989) in his first treatment, maintained a broad concept of *Helictotrichon* by recognizing four subgenera:

1. *Helictotrichon* subgen. *Helictotrichon,* includes species with ribbed leaves and strongly twisted awn columns, terete or square in cross-section, from Europe, N Africa, Western Asia and one North American species.
2. *Helictotrichon* subgen. *Pubavenastrum* (Vierh.) Holub, monospecific, includes only *H. pubescens* (Hudson) Pilger, a species with a wide distribution but isolated morphologically and phylogenetically, with conduplicate leaf blades as in *Avenula* species, awn like in *Helictotrichon* s.s., short *Trisetum* type lodicules (Baum, 1968), and palea with smooth keels, a unique configuration in the group.
3. *Helictotrichon* subgen. *Tricholemma* Röser includes two rare species from NW Africa, characterized by lemmas with the central nerve prominent and hairy at the base; awn like in *Helictotrichon* s.s., and leaf blades very similar to those of *Avenula.*
4. *Helictotrichon* subgen. *Pratavenastrum* (Vierh.) Holub includes species with conduplicate leaf blades and ± flattened awn columns; distributed mainly in the Mediterranean basin.

All molecular analyses published to date agree in separating *Helictotrichon* s.s. from most *Avenula* species (that is, excluding *Tricholemma).* The results of Quintanar & al. (2007) are compatible with the hypothesis that the four subgenera defined by Röser (1989) constitute separate phylogenetic clades. According to morphological and anatomical characters and molecular analyses, I think the simplest taxonomic solution is to recognize four genera. Coming to the same conclusion Röser & al. (2009) established the generic category for the four groups: *Helictotrichon* subgen. *Tricholemma* is upgraded to generic rank as *Tricholemma* and *Homalotrichon* is accepted for *Helictotrichon* subgen. *Pubavenastrum* as an independent genus.

So, in the author's opinion, the species at present classified under *Avenula* must be separated into the following three genera *Tricholemma, Avenula* and the new *Helictochloa* Romero Zarco. A nomenclature summary, diagnoses and diversity are proposed for the following four genera formerly included in *Helictotrichon* s.l. (sensu Röser, 1989):

1. *Tricholemma,* its generic rank has been well defended by Röser & al. (2009);
2. *Avenula,* a monotypic genus including *A. pubescens.* The separation of *A. pubescens* in a monotypic genus (apart from the rest of species at present classified under *Avenula)* is according to morphological and anatomical characters analyzed above;
3. *Helictochloa* Romero Zarco, a large and new genus including the remaining *Avenula* species *(Avenula* subgen. *Avenula* sensu Romero-Zarco, 1984b);
4. *Helictotrichon* s.s.

Tricholemma (Röser) Röser in Schlechtendalia 19: 34. 2009.

≡ *Helictotrichon* subgen. *Tricholemma* Röser in Diss. Bot. 145: 46. 1989.

Typus: *Avena jahandiezii* Litard. (≡ *Tricholemma jahandiezii* (Litard.) Röser)

Diagnosis. – Perennials, densely caespitose; roots without sclerenchyma surrounding endodermis; culms with 1-2 visible nodes, sometimes subbulbous at the base. *Leaf* blades flat, conduplicate or junciform, not furrowed above, with or without thin ribs beneath, very hard or relatively soft, but rigid, with several or numerous secondary nerves; abaxial midrib and margins outstanding, without long hairs; bulliform cells forming a row each side of the adaxial midrib; without girders and subepidermal sclerenchyma *(T. jahandiezii)* or with subepidermal sclerenchyma forming 'I'-shaped girders at the lateral nerves *(T. breviaristatum* (Barratte) Röser). *Spikelets* 13-18 mm long, with 2-3 developed bisexual florets, two upper floret not or scarcely exceeding the upper glume, apical floret reduced; glumes slightly unequal, keeled in the back, glabrous, 3-nerved; rachilla disarticulating only above the glumes; lemmas with a row of hairs on the back, along the lower part of the central nerve, the rest glabrous; awn without pale margins, dorsally inserted and with a strongly twisted column, or reduced and subapically inserted, with or without a slightly twisted column; palea strongly 2-keeled, keels minutely ciliate; lodicules as long or shorter than the ovary, ovate or obovate, with a ± truncate, usually dentate apex. *Caryopsis* furrowed; hilum linear; embryo not seen.

Species and distribution. – Two endemic species in NW Africa: *T. jahandiezii* from Morocco (Middle Atlas) and *T. breviaristatum,* endemic from E Algeria.

Nomenclature and taxonomy. – See Röser & al. (2009).

Avenula (Dumort.) Dumort. in Bull. Soc. Bot. Belg. 7: 68. 1868.

≡ *Trisetum* sect. *Avenula* Dumort., Observ. Gramin. Belg.: 122. 1823.

≡ *Avena* sect. *Avenastrum* W. D. J. Koch, Syn. Fl. Germ. Helv.: 795. 1837 [nom. illeg.].

≡ *Homalotrichon* Banfi, Galasso & Bracchi in F. Conti, G. Abbate, Aless. & C. Blasi, Annot. Cheklist Italian Vasc. Fl.: 18. 2005 [nom. illeg.].

Lectotypus (designated by CHASE, 1939): *Avena pubescens* Hudson (≡ *Avenula pubescens* (Hudson) Dumort.).

Perennial, loosely caespitose; roots without sclerenchyma surrounding endodermis; culms with 1-3 visible nodes. *Leaf* blades flat or ± conduplicate, not furrowed, relatively soft but rigid, with long hairs; bulliform cells forming a row each side of the adaxial midrib; with abaxial midrib and margins scarcely evident; secondary nerves few; well developed subepidermal sclerenchyma forming 'O'-shaped girders at lateral nerves. *Spikelets* 14-20 mm long, with 3-4 developed bisexual florets, two upper floret not or scarcely exceeding the upper glume, apical floret reduced; glumes unequal, keeled on the back, somewhat scabrid on the central nerve at the base, the lower glume 1-3-nerved, the upper glume 3-nerved; rachilla disarticulating above the glumes and between the florets; lemmas glabrous (except for the callus); awned dorsally, with a strongly twisted, rounded column, without pale margins; palea scarcely 2-keeled, with glabrous keels; lodicules as long or shorter than the ovary, ovate or obovate, 2-3-lobed or with a irregularly dentate apex. *Caryopsis* furrowed; hilum linear; embryo with a truncated epiblast and obtuse scutellum.

Nomenclature. – See ROMERO-ZARCO (1984b), RÖSER (1989: 44) and HOLUB (1976: 288).

Lectotypification. – There are two different lectotopyfications of the generic name *Avenula:* a) *Avena pubescens* Hudson, designated by CHASE (1939: 568) and ignored by most European taxonomists (HOLUB, 1977; ROMERO-ZARCO, 1984b; RÖSER, 1989; RÖSER & al., 2009) and b) *A. pratensis* L., designated by BREISTROFFER (1966). Only these two species were cited by DUMORTIER (1824) in the original description of *Trisetum* sect. *Avenula,* the basyonim of *Avenula*, and both fit the protologue. According to MCNEILL & al. (2006, art. 10.5), the first lectotypification is accepted, and the correct name for the monotypic genus including *A. pubescens* is *Avenula.* The name *Homalotrichon* is then illegitimate (MCNEILL & al., 2006, art. 52.1).

Species and distribution. – Only the diploid *Avenula pubescens*, extends from Spain to China: from submediterranean Europe through Central Europe to continental regions of Middle Asia and Central Siberia (cf. RÖSER, 1997: 109).

Helictochloa Romero Zarco, **gen. nov.**

Typus: *Avena bromoides* Gouan (≡ *Helictochloa bromoides* (Gouan) Romero Zarco).

= *Avena* sect. *Pratenses* Rouy, Fl. France 14: 132. 1913. **Typus:** *A. pratensis* L.

= *Avena* subsect. *Ecostatae* St.-Yves in Candollea 4: 374. 1931. **Lectotypus** (designated here): *A. pratensis* L.

= *Avenastrum* ser. *Pratenses* Roshev. in Kom. & al., Fl. CCCP 2: 273. 1934. **Typus:** *Avena pratensis* L. (≡ *Avenastrum pratense* (L.) Opiz).

= *Avenastrum* sect. *Pratavenastrum* Vierh. in Verh. Ges. Deutsch. Naturf. 85: 672. 1914. ≡ *Helictotrichon* subgen. *Pratavenastrum* (Vierh.) Holub in Nemec. & al., Philipp Maxmillian Opiz Bedeut. Pflanzentaxon.: 125. 1958. **Typus:** *Avena pratensis* L. (≡ *Avenastrum pratense* (L.) Opiz).

= *Avenochloa* Holub in Acta Horti Bot. Prag. 1962: 82. 1962 [nom. illeg]. **Typus:** *Avena planiculmis* Schrad. (≡ *A. planiculmis* (Schrad.) Holub).

= *Helictotrichon* sect. *Scleravenastrum* Holub in Nemec. & al., Philipp Maxmillian Opiz Bedeut. Pflanzentaxon.: 126. 1958. ≡ *Avenula* sect. *Scleravenastrum* (Holub) Holub in Folia Geobot. Phytotax. 11: 294. 1976. **Typus:** *Avena hackelii* Henriq. (≡ *Helictotrichon hackelii* (Henriq.) Henrard).

– *Avenula* mult. auct.

Ab Helictotricho sensu stricto praecipue differt foliis conduplicatis, nervo medio dorsaliter notato, margine incrassato. Ab Avenulae sensu stricto praecipue differt foliis glabris vel scabridis; carinis paleae ciliolatis; lodiculis lanceolatis. A Tricholemmate praecipue differt lemmate nervo mediano non prominente instructo. A generibus praecedentibus atque differt columella aristae sectione transversa applanata. Gramina ob folia in sicco saepe helica Helictochloa nominata.

Perennials, loosely or densely caespitose; roots without sclerenchyma surrounding endodermis; culms with 1-3 visible nodes. *Leaf* blades flat, conduplicate or ± junciform, not furrowed above, sometimes with thin ribs beneath, relatively hard and rigid; bulliform cells forming a row each side of the adaxial midrib; margins and abaxial midrib prominent, cartilaginous; secondary nerves numerous or not; with or without 'I'-shaped girders of sclerenchyma and/or colourless parenchyma; subepidermal sclerenchyma in ± developed small islands, rarely forming a continuous layer beneath. *Spikelets* 10-36 mm long, with (2-)3-9(-12) developed, bisexual florets, two or more upper florets exceeding the glumes, apical floret reduced; glumes unequal, keeled on the back, somewhat scabrous on the nerves, the lower glume with (1-)3-5 nerves, the upper glume with 3-5(-7) nerves; rachilla disarticulating above the glumes and between the florets; lemmas glabrous or sericeous towards the base, awned dorsally; awn with a loosely twisted column, ± flattened in cross-section, with pale margins; palea strongly 2-keeled, keels minutely ciliate; lodicules longer than the ovary, lanceolate, with a lateral, ± developed lobe. *Caryopsis* furrowed; hilum linear; embryo with a truncate or somewhat emarginate epiblast, scutellum with a nipple-shaped apex.

Etymology. – From Greek *helictos,* by the spirally twisted leaves when dry, and *chloe*, green grass.

Nomenclature and taxonomy. – See HOLUB (1976) for *Avenochloa* Holub. According to MCNEILL & al. (2006, art. 22.6) *Avena pratensis* is the type species of infrageneric names derived or similar to its epithet.

According to the taxonomic criteria here defended, a number of 40 taxa (25 species) accepted by DOGAN (1985), RÖSER (1989, 1996), SAUER (1984), SAUER & CHMELITSCHEK (1976), ROMERO-ZARCO (1984b), ROSHEVITS & SHISHKIN (1934) or WU & PHILLIPS (2006) must be transferred to the new genus (see Appendix 1).

SAINT-YVES (1931) included in his *Avena* subsect. *Ecostatae* 8 species belonging to 3 different genera:

1. *Avena jahandiezii* (classified here within *Tricholemma*) is discarded as a possible lectotypus because he considered it an intermediate species (SAINT-YVES, 1931: 425);
2. *Avena pubescens* (type species of *Avenula*), discarded as lectotype by the same reason;
3. *A. hackelii* Henriq. (genus *Helictochloa*); this species was considered by SAINT-YVES (1931: 435) an atypical species in the group or even a possible hybrid between two species belonging to different subsections;
4. *Avena pratensis* (genus *Helictochloa*), the most complex and extended species of this group in Europe;
5. *A. versicolor* Vill. (genus *Helictochloa*);
6. *A. blaui* Asch. & Janka ["Blavii"] (genus *Helictochloa*);
7. *A. bromoides* (genus *Helictochloa),* another species complex, extended around the Mediterranean basin;
8. *A. breviaristata* (classified here within *Tricholemma*) considered by SAINT-YVES (1931: 489) of doubtful classification due to some affinities with his subsect. *Anomalae.*

So, only species 4 to 7 can be properly selected as lectotype. *Avena pratensis* have been designated here because it was previously selected by VIERHAPPER (1906), ROUY (1913), and ROSHEVITS & SHISHKIN (1934) as the type species for other infrageneric taxa including this species group.

Species and distribution. – Several polyploid species complexes and some ± isolated endemic species previously classified as *Avenula* or *Helictotrichon*. The number of species ranges from 20 to 30 according to different taxonomic treatments. Two main centres of diversity: West Mediterranean and Balkan-Aegean region. A secondary centre is in the European Alpes. Some species extending north and east in Europe to Asia. Only one species in N America.

Helictotrichon Besser in Schultes & Schultes fil., Mant. 3: "326" [526]. 1827.

Lectotypus (designated by SCHWEICKERDT, 1937: 185): *Avena sempervirens* Vill. (≡ *Helictotrichon sempervirens* (Vill.) Pilger).

Perennials, densely or loosely caespitose, sometimes mat forming; roots with sclerenchyma surrounding endodermis; culms with 1-3 visible nodes. *Leaf* blades convolute, ± flattened, involute, junciform or setaceous, furrowed above, with protruding ribs, very hard or relatively soft, but rigid, with several or numerous lateral nerves; abaxial midrib and margins not outstanding; bulliform cells forming several rows between the nerves, sometimes reduced or not developed between the distal nerves; sclerenchyma forming 'T'-shaped girders across the main nerves and 'I'-shaped or incomplete girders at the secondary nerves; subepidermical sclerenchyma frequently forming a continuous layer beneath. *Spikelets* 7.5-20 mm long, with 2-4 developed bisexual florets, apical floret reduced; glumes unequal, keeled in the back, somewhat scabrous on the keel near the apex, the lower glume 1-3-nerved, the upper glume 3-5-nerved, almost as long as the spikelet; rachilla disarticulating only above the glumes or between the florets too; lemmas 7-18 mm long, generally 2-dentate, glabrous (except for the callus) or somewhat scabrous towards the apex; awns ± equally developed, without pale margins, dorsally inserted and with a strongly twisted column, terete or square in cross-section; palea strongly 2-keeled, keels minutely ciliate; lodicules longer than the ovary, lanceolate, generally entire, rarely with a small lateral tooth. *Caryopsis* furrowed; hilum linear; embryo with truncate epiblast and obtuse or subobtuse scutellum.

Nomenclature. – See RÖSER (1989: 44) (under *Helictotrichon* subgen. *Helictotrichon*).

Species and distribution. – Approximately 42 species following different regional taxonomic treatments, some of then recently described (COPE, 2006; ROMERO-ZARCO, 2007). A well-know Mediterranean-Balkanic group of approximately 12 species, some of them forming polyploid complexes (ROMERO-ZARCO, 1984a, 1985b; RÖSER, 1989). At least 20 species in Tropical and South Africa, with two different diversity centres: E Africa and

Cape Region. Perhaps only nine species in Asia, but some of them polymorphic, as *H. junghuhnii* (Buse) Henrard. Only one species in N America: *H. mortonianum* (Hitchc.) Parodi, and the South American *H. bulbosum* (Hitchc.) Parodi.

Key for *Avena* related genera present in the Mediterranean region

1. Leaf blades not furrowed above; bulliform cells forming a row each side of the adaxial midrib 2

1a. Leaf blades furrowed above; bulliform cells forming several rows between the nerves, sometimes reduced or not developed between the distal nerves 4

2. Awns with a loosely twisted column, ± flattened in cross-section, with pale margins. Spikelets with (2-)3-9(-12) florets, two or more upper florets exceeding the glumes. Lodicules lanceolate, generally with a subbasal lateral lobe. Mainly Mediterranean, sub-Mediterranean or alpine species .... ***Helictochloa***

2a. Awns with a strongly twisted column, rounded or quadrangular in cross-section (rarely very reduced), rarely with pale margins. Spikelets with (2-)3-4 florets, two upper floret not or scarcely exceeding the upper glume. Lodicules ovate or obovate, 2 or 3-lobed or with a dentate apex. Eurosiberian or Atlasic species 3

3. Leaf blades with long hairs. Lemmas glabrous (except for the callus). Eurosiberian species .... ***Avenula***

3a. Leaf blades without long hairs. Lemmas with a row of hairs on the back, along the lower part of the central nerve. Endemic species from Algeria and Morocco .... ***Tricholemma***

4. Annuals, very rarely perennial. Lower glumes with (5-)7 or more nerves. Lemmas (10-)12-33(-36) mm long. Mediterranean or Eurosiberian species .... ***Avena***

4a. Perennials. Lower glumes 1-3-nerved. Lemmas 5-17 (-18) mm long 5

5. Lemmas glabrous (except for the callus) or somewhat scabrous towards the apex. Spikelets 7.5-20 mm long, with 2-4 florets; rachilla disarticulating only above the glumes or between the florets too. Awns ± equally developed, dorsally inserted .... ***Helictotrichon***

5a. Lemmas hairy. Spikelets 5-12(-14) mm long, with two developed florets. Rachilla disarticulating only above the glumes. Awn of the lower floret inserted near the base or near the middle, awn of the upper floret reduced, subapically inserted 6

6. Awn of the lower floret inserted near the middle of the lemma. Leaf blades with very protruding ribs, relatively hard and rigid. Culms without corms. Subatlantic species .... ***Pseudarrhenatherum***

6a. Awn of the lower floret inserted near the base of the lemma. Culms frequently with the basal internodes swollen into globose corms. Leaf blades relatively soft and flexible. Mediterranean, Iranoturanian and Eurosiberian species .... ***Arrhenatherum***

General discussion

According to the taxonomic scheme adopted here, the conduplicate structure of the leaf blade, with two rows of bulliform cells flanking the central nerve, a character usually used to the separate *Avenula* s.l. from *Helitotrichon*, does not have a unique origin in the group. This is not surprising for researchers of leaf anatomy. In figure 2 the anatomical characters of the leaf blade in *Avenula pubescens* and in *A. pratensis* subsp. *iberica* (now classified in the new genus *Helictochloa*) have been compared. In species here included within *Helictochloa*, the strands of subepidermal sclerenchyma are much thinner than marginal strands, and in many species (*H. pratensis* (L.) Romero Zarco, *H. marginata* (Lowe) Romero Zarco, and related species) these strands are united to the vascular bundles forming relatively thin, 'I'-shaped girders. In *Avenula pubescens* the marginal strands are less developed and the subepidermal strands are very robust, forming 'O'-shaped girders. Beside this, differentiation of a palisade chlorenchyma is found in *Helictochloa pratensis* but not in *Avenula pubescens*. López & Devesa (1991) also found palisade chlorenchyma in *Helictochloa bromoides* subsp. *bromoides* (sub. *Avenula)*. The remaining species of *Helictochloa* all have palisade chlorenchyma according to many figures previously published (Romero-Zarco, 1984b; Röser, 1998). The anatomical structure of the leaf blade in *Avenula pubescens* may be the result of analogous changes also having originated in the typical leaves of *Helictochloa* and *Tricholemma.*

In the genus *Tricholemma,* the two known species present very different leaf blade structures. In *T. jahandiezii,* the leaves have only sclerenchyma in front of the central nerve (beneath) and in the margins, a unique pattern of sclerenchyma distribution in oat grasses (see Röser, 1989: 31, Fig. 4). However, in *T. breviaristatum* the distribution of sclerenchyma in cross-section (see Saint-Yves, 1931: Fig. 37) is similar to that of certain xeromorphic populations of *Helictochloa pruinosa* (Hackel & Trabut) Romero Zarco from Middle Atlas, originally described by Saint-Yves (1931: 485, Fig. 36) as *Avena bromoides* subvar. *dolosa* St.-Yves. This remarkable difference between two closely related species, can be seen in the different development of the sclerenchymatous tissue probably in response to habitat. In the case of *T. jahandiezii,* the absence of subepidermal strands in front of lateral nerves can be explained by an extreme reduction of the sclerenchyma, perhaps as an adaptation to the relatively humid habitat where it grows: "garriga" schrublands at the Middle Atlas up to 1600 m above see level in deep calcareous soils, with autumnal precipitations of 1000 mm or more and frequent fog (Röser, 1996: 214). On the contrary, *Tricholemma breviaristatum* is an endemic xeromorphic species of the Djebel Sahari, in NW Algeria, zone of median height mountains with Mediterranean type vegetation, containing elements of the *Quercetea ilicis* A. Bolòs & O. Bolòs 1950 (Röser, 1996: 214). A similar relationship between humidity and development of sclerenchyma in the leaves has been described between mesomorphic and xeromorphic *Helictochloa* species (Röser, 1989, 1996, 1997, sub *Helictotrichon* subg. *Pratavenastrum*) and in *Pseudarrhenatherum* species (Romero-Zarco, 1985c).

The remarkable development of the marginal strands of sclerenchyma is a shared characteristic between *Tricholemma* and *Helictochloa.* A detailed phylogenetic analysis will be necessary to find out if this foliar structure has arisen independently in both genera or is the result of common descent. The molecular analyses available do not clarify the question. Nuclear ITS sequences studies (Grenbenstein & al., 1998; Quintanar & al., 2007) align *T. jahandiezii* closer to *Helictotrichon* s.s. than to *Avenula* or *Helictochloa.* Nevertheless Röser & al. (2001) in his analysis of 5S rDNA sequences proposed an isolated and basal situation of this species in respect to the group. Both results are not absolutely contradictory and they could be resolved if *T. breviaristatum* were studied. Unfortunately, *T. breviaristatum* has not been collected since May 1882 (Röser & al., 2009). In conclusion, the so called "Avenastrum type" leaf structure (Potztal, 1951), may be the result of convergent processes resulting in anatomical simplification.

The splitting of species showing a unique combination of morphological characters within monotypic genera or genera with 2-3 taxa, is frequently encountered in the *Aveneae* tribe *(Avenella, Danthoniastrum*, *Lagurus* L., *Mibora* Adans., *Ventenata*, among others). Some cases, like the new *Tricholemma* genera, are possibly, relics of a substratum of diversity from which other genera, at present in the diversification process arose, and may be a significant example of the otherwise poor supraspecific endemism in the orophytic Mediterranean flora of N Africa Röser (1996: 245). The distribution of *Tricholemma* species corresponds to the southern edge of the Mediterranean vegetation in N Africa, where orophytic taxa were isolated at the end of the Tertiary. This, together with the great differences (possibly quantitative) in leaf anatomy and spikelet morphology (*T. breviaristatum* has very reduced awns) suggests an ancient derivation and a long history for this genus, which would support its basal position with respect to the group as shown in the dendrogram of Röser & al. (2001).

The next challenge in the taxonomy of the group would be to investigate the phylogenetic relationship between Paleartic, Paleotropical and South African species of *Helictotrichon*. The species from south and east Africa, together with some from SE Asia, differ from Paleartic species in several characters; specifically in the morphology of the lemma, but also by a greater variability in the morphology of lodicules, awns and leaves. New data are needed for a clear delimitation of *Helictotrichon* outside of Europe.

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Appendix 1. – New combinations for *Helictochloa* Romero Zarco

Helictochloa adsurgens (Simonk.) Romero Zarco, **comb. nova**
≡ *Avena adsurgens* Simonk., Enum. Fl. Transsilv.: 574. 1887.

Helictochloa adsurgens subsp. *ausserdorferi* (Asch. & Graebn.) Romero Zarco, **comb. nova**
≡ *Avena alpina* subsp. *ausserdorferi* Asch. & Graebn., Syn. Mitteleur. Fl. 2(1): 261. 1899.

Helictochloa aetolica (Rech. fil.) Romero Zarco, **comb. nova**
≡ *Avenastrum aetolicum* Rech. fil. in Beih. Bot. Centralbl., Abt. 2, 54: 680. 1936.

Helictochloa agropyroides (Boiss.) Romero Zarco, **comb. nova**
≡ *Avena agropyroides* Boiss., Diagn. Pl. Orient. 13: 50. 1854.

Helictochloa albinervis (Boiss.) Romero Zarco, **comb. nova**
≡ *Avena albinervis* Boiss., Voy. Bot. Espagne 2: 656. 1844.

Helictochloa albinervis var. *gaditana* (Romero Zarco) Romero Zarco, **comb. et stat. nov.**
≡ *Avenula sulcata* subsp. *gaditana* Romero Zarco in Lagascalia 13: 124. 1984.

Helictochloa armeniaca (Schischk.) Romero Zarco, **comb. nova**
≡ *Avena armeniaca* Schischk. in Izv. Tomsk. Gosud. Univ. 81: 418. 1929.

Helictochloa blaui (Asch. & Janka) Romero Zarco, **comb. nova**
≡ *Avena blaui* Asch. & Janka in Természetrajzi Füz. 1: 99. 1877.

Helictochloa blaui subsp. *aenigmatica* (D. Lange) Romero Zarco, **comb. nova**
≡ *Helictotrichon blaui* subsp. *aenigmaticum* D. Lange in Biblioth. Bot. 144: 181. 1995.

Helictochloa bromoides (Gouan) Romero Zarco, **comb. nova**
≡ *Avena bromoides* Gouan, Hort. Monsp.: 52. 1762.

Helictochloa bromoides subsp. *pauneroi* (Romero Zarco) Romero Zarco, **comb. nova**
≡ *Avenula bromoides* subsp. *pauneroi* Romero Zarco in Lagascalia 13: 114. 1984.

Helictochloa cincinnata (Parl.) Romero Zarco, **comb. nova**
≡ *Bromus cincinnatus* Ten., Fl. Med. Univ. 1: 52. 1823.

Helictochloa cintrana (Röser) Romero Zarco, **comb. nova**
≡ *Helictotrichon cintranum* Röser in Taxon 41: 60. 1992.

Helictochloa compressa (Heuff.) Romero Zarco, **comb. nova**
≡ *Avena compressa* Heuff. in Flora 18: 244. 1835.

Helictochloa crassifolia (Font Quer) Romero Zarco, **comb. nova**
≡ *Avena crassifolia* Font Quer in Butl. Inst. Catalana Hist. Nat. 20: 189. 1920.

Helictochloa dahurica (Kom.) Romero Zarco, **comb. nova**
≡ *Avena planiculmis* subsp. *dahurica* Kom., Fl. Kamtschatka 1: 159. 1927.
≡ *Avenastrum dahuricum* (Kom.) Roshev. in Kom. & al., Fl. CCCP 2: 275. 1934.

Helictochloa gervaisii (Holub) Romero Zarco, **comb. nova**
≡ *Avenula gervaisii* Holub in Preslia 49: 205. 1977.

Helictochloa gervaisii subsp. *arundana* (Romero Zarco) Romero Zarco, **comb. nova**
≡ *Avenula gervaisii* subsp. *arundana* Romero Zarco in Lagascalia 13: 108. 1984.

Helictochloa hackelii (Henriq.) Romero Zarco, **comb. nova**
≡ *Avena hackelii* Henriq. in Bol. Soc. Brot. 20: 87. 1905.

Helictochloa hackelii var. *algarbiensis* (Romero Zarco) Romero Zarco, **comb. nova**
≡ *Avenula hackelii* var. *algarbiensis* Romero Zarco in Lagascalia 13: 136. 1984.

Helictochloa hookeri (Scribn.) Romero Zarco, **comb. nova**
≡ *Avena hookeri* Scribn. in Hackel, True Grasses: 123. 1890.

Helictochloa hookeri subsp. *schelliana* (Hackel) Romero Zarco, **comb. nova**
≡ *Avena schelliana* Hackel in Trudy Imp. S.-Peterburgsk. Bot. Sada 12: 419. 1892.
≡ *Helictotrichon hookeri* subsp. *schellianum* (Hackel) Tzvelev in Novosti Sist. Vyssh. Rast. 8: 68. 1971.

Helictochloa levis (Hackel) Romero Zarco, **comb. nova**
≡ *Avena levis* Hackel in Oesterr. Bot. Z. 27: 122. 1877.

Helictochloa lusitanica (Romero Zarco) Romero Zarco, **comb. nova**
≡ *Avenula pratensis* subsp. *lusitanica* Romero Zarco in Lagascalia 13: 95. 1984.
≡ *Helictotrichon lusitanicum* (Romero Zarco) Röser in Flora 193: 438. 1998.

Helictochloa marginata (Lowe) Romero Zarco, **comb. nova**
≡ *Avena marginata* Lowe in Trans. Cambridge Philos. Soc. 6: 529. 1838.

Helictochloa marginata var. *font-queriana* (St.-Yves) Romero Zarco, **comb. nova**
≡ *Avena pratensis* var. *font-queriana* St.-Yves in Candollea 4: 465. 1931.

Helictochloa murcica (Holub) Romero Zarco, **comb. nova**
≡ *Avenula murcica* Holub in Preslia 49: 206. 1977.

Helictochloa planiculmis (Schrad.) Romero Zarco, **comb. nova**
≡ *Avena planiculmis* Schrad., Fl. Germ. 1: 381. 1806.

Helictochloa planiculmis subsp. *angustior* (Holub) Romero Zarco, **comb. nova**
≡ *Avenula planiculmis* subsp. *angustior* Holub in Preslia 49: 209. 1977.

Helictochloa praeusta (Rchb.) Romero Zarco, **comb. nova**
≡ *Avena praeusta* Rchb., Fl. Germ. Excurs.: 140(5). 1831.

Helictochloa pratensis (L.) Romero Zarco, **comb. nova**
≡ *Avena pratensis* L., Sp. Pl.: 80. 1753.

Helictochloa pratensis subsp. *amethystea* (Br.-Bl.) Romero Zarco, **comb. nova**
≡ *Avena pratensis* subsp. *amethystea* Br.-Bl. in Commun. Stat. Int. Géobot. Médit. Montpellier 87: 223. 1945.

Helictochloa pratensis subsp. *gonzaloi* (Sennen) Romero Zarco, **comb. nova**
≡ *Avena gonzaloi* Sennen, Pl. Espagne 1925: nº 5454. 1925-1926 [in sched., cum notula].
≡ *Avenula pratensis* subsp. *gonzaloi* (Sennen) Romero Zarco in Lagascalia 13: 86. 1984.

Helictochloa pratensis subsp. *iberica* (St.-Yves) Romero Zarco, **comb. nova**
≡ *Avena pratensis* subsp. *iberica* St.-Yves in Candollea 4: 435. 1931.

Helictochloa pratensis subsp. *hirtifolia* (Podp.) Romero Zarco, **comb. nova**
≡ *Avenastrum pratense* subsp. *hirtifolium* Podp. in Cas. Morav. Zemsk. Mus. Brne 12: 272. 1912.

Helictochloa pruinosa (Hackel & Trabut) Romero Zarco, **comb. nova**
≡ *Avena pruinosa* Hackel & Trabut in Bull. Soc. Bot. France 36: 411. 1889.

Helictochloa ×*talaverae* (Romero Zarco) Romero Zarco, **comb. nova**
≡ *Avenula* ×*talaverae* Romero Zarco in Lagascalia 13: 138. 1984.

Helictochloa versicolor (Vill.) Romero Zarco, **comb. nova**
≡ *Avena versicolor* Vill., Prosp. Hist. Pl. Dauphiné: 17. 1779.

Helictochloa versicolor subsp. *caucasica* (Holub) Romero Zarco, **comb. nova**
≡ *Helictotrichon versicolor* prol. *caucasicum* Holub in Preslia 31: 51. 1959.
≡ *Avenula versicolor* subsp. *caucasica* (Holub) H. Scholz & Valdés in Willdenowia 36: 663. 2006.

Helictochloa versicolor subsp. *praetutiana* (Arcang.) Romero Zarco, **comb. nova**
≡ *Avena scheuchzeri* subsp. *praetutiana* Arcang., Comp. Fl. Ital.: 777. 1882.