A NEW CIRCUMSCRIPTION OF FESTUCA TRICHOPHYLLA (GAUDIN) K. RICHTER (GRAMINEAE)

by

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Resumen

AL-BERMANI, A.-K. K. A., P. CATALÁN & C. A. STACE (1992). Una nueva circunscripción de Festuca trichophylla (Gaudin) K. Richter (Gramineae). *Anales Jard. Bot. Madrid* 50(2): 209-220 (en inglés).

Se revisan la identidad y la posición taxonómica de diez táxones que, en un tiempo u otro, han sido considerados próximos a Festuca trichophylla (Drucros ex Gaudin) K. Richter. Se propone un nuevo concepto, el del grupo de F. trichophylla, que se compone de cuatro especies: F. nevadensis (Hackel) K. Richter, F. rothmaleri (Litard.) Markgr.-Dann., F. trichophylla y F. paucispicula Fuente García & Sánchez-Mata. La propia F. trichophylla incluye, en nuestra propuesta, cuatro especies distintas de las reconocidas por Markgraf-Dannenberg (1980) más una subespecie situada por la autora bajo F. rubra L.; nosotros distinguimos, dentro de la especie, tres subespecies: subsp. trichophylla, subsp. scabrescens (Hackel ex Trabut) Catalán & Stace, comb. nov., y subsp. asperifolia (St.-Yves) Al-Bermani, comb. nov. Se aporta un breve comentario sobre la sinonimia y la distribución geográfica de los seis táxones del grupo. F. rubra var. gaetula Maire ex St.-Yves se transfiere a F. nevadensis como var. gaetula (Maire ex St.-Yves) Al-Bermani & Stace, comb. nov.

Palabras clave: Festuca, grupo de F. trichophylla, Gramineae, taxonomía.

Abstract

AL-BERMANI, A.-K. K. A., P. CATALÁN & C. A. STACE (1992). A new circumscription of Festuca trichophylla (Gaudin) K. Richter (Gramineae). *Anales Jard. Bot. Madrid* 50(2): 209-220.

The identity and taxonomic disposition of ten taxa that have at one time or another been considered as close relatives of Festuca trichophylla (Ducros ex Gaudin) K. Richter are reviewed. A new concept, the F. trichophylla group, is presented in which are placed four species. F. nevadensis (Hackel) K. Richter, F. rothmaleri (Litard.) Markgr.-Dann., F. trichophylla and F. paucispicula Fuente García & Sánchez-Mata. F. trichophylla itself includes four separate species recognized by Markgraf-Dannenberg (1980) and a subspecies that she placed under F. rubra L.; we divide it into three subspecies: subsp. trichophylla, subsp. scabrescens (Hackel ex Trabut) Catalán & Stace, comb. nov., and subsp. asperifolia (St.-Yves) Al-Bermani, comb. nov. A brief synonymy and geographical range of the six taxa are given. F. rubra var. gaetula Maire ex St.-Yves is transferred to F. nevadensis as var. gaetula (Maire ex St.-Yves) Al-Bermani & Stace, comb. nov.

Key words: Festuca, F. trichophylla group, Gramineae, taxonomy.

Introduction

The Festuca rubra L. aggregate

Twenty-one species (nos. 56-89, excl. 57 and 62) of the 170 species recognized in

Flora Europaea by MARKGRAF-DANNEN-BERG (1980) would fall into 'Festuca rubra L. sensu amplissimo' as defined by HACKEL (1882: 128). Some of these 21 species (e.g. F. heterophylla Lam.) are very distinct

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from all the rest, while others form recognizable groupings within which specific limits are more difficult to describe. Two of these may be known as the *F. rubra* and the *F. trichophylla* (Ducros ex Gaudin) K. Richter groups. Together, these two groups have been called the *F. rubra* aggregate, and correspond with species 65-78 of MARK-GRAF-DANNENBERG'S (1980) treatment.

The Festuca trichophylla (Ducros ex Gaudin) K. Richter group

A future paper (AL-BERMANI & STACE, in prep.) will present a revision of the F. rubra aggregate and define precisely its two groups and give full descriptions of its segregates. The F. trichophylla group is characterized by a range of vegetative morphological and anatomical characters, which taken together set it apart from the F. rubra group. All the characters, however, are variable, and taken in isolation none of them can be regarded as absolutely diagnostic. The F. trichophylla group may be distinguished from the F. rubra group as follows:

 The leaf-blades are usually scabrid. The scabridity is caused by antrorsely directed prickle-hairs on the abaxial leaf surface. In the F. rubra group such

- prickle-hairs are absent or few and confined to the apical region of the leaf.
- The leaf-sheaths are mostly fused almost to the mouth, as in the F. rubra group, but usually a few of the tillers have free, overlapping leaf-sheaths (as in the F. ovina aggregate).
- 3. The abaxial leaf-blade surface usually possesses rows of small protuberances c.12-15 µm across where the files of longcells meet (fig. 1). We have never seen these in the *F. rubra* group.
- 4. The silica-cells are usually mostly kidney-shaped or rounded and each is characteristically infolded by the adjacent cork-cell, whereas they are usually rectangular or square and not infolded in the F. rubra group (fig. 2).
- 5. The longitudinal walls of the long-cells on the abaxial epidermis are usually thicker and more strongly sinuate than in the *F. rubra* group (fig. 2).
- 6. As seen in leaf-blade transverse section, the abaxial strands of sclerenchyma are markedly unequal in size: either the median strand alone, or sometimes the median as well as the two marginal strands, are conspicuously larger than the others (fig. 3).

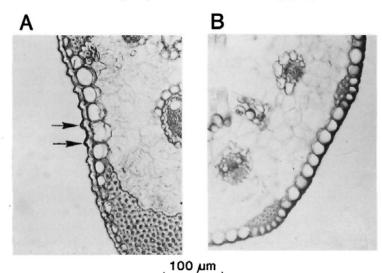


Fig. 1.—Leaf-sections: A, F. trichophylla subsp. trichophylla, to show abaxial protuberances (arrowed); B, F. rubra subsp. rubra.

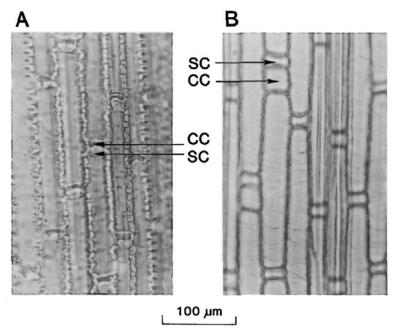


Fig. 2.—Abaxial epidermis to show silica-cells (SC) and cork-cells (CC): A, F. trichophylla subsp. trichophylla; B, F. arenaria.

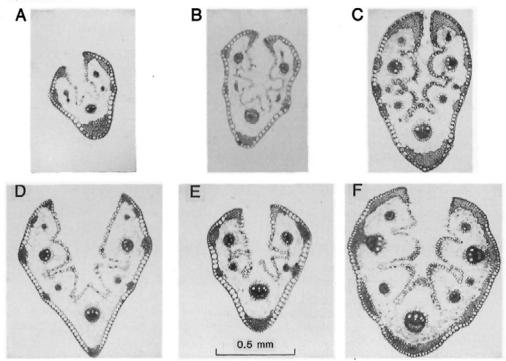


Fig. 3.—Leaf-sections: A, F. trichophylla subsp. trichophylla; B, F. nevadensis var. gaetula; C, F. nevadensis var. nevadensis; D, F. rubra subsp. rubra; E, F. rubra subsp. juncea; F, F. arenaria.

Sometimes the submarginal and marginal strands merge to form one larger strand at each margin, but otherwise the strands are distinct. In the *F. rubra* group, where the strands are discrete all are approximately of the same size, but in other members of the group the strands merge to varying degrees (fig. 3), in extreme cases (*F. arenaria* Osbeck) forming a continuous arc.

Our concept of the *F. trichophylla* group has gradually developed during taxonomic and biosystematic studies of the *F. rubra* aggregate; the numbers of taxa that we ascribed to it gradually grew as further binomials were investigated. Concurrently the number of species that we recognized decreased as more material was examined. At present we recognize four species: *F. nevadensis* (Hackel) K. Richter, *F. rothmaleri* (Litard.) Markgr.-Dann., *F. trichophylla* and *F. paucispicula* Fuente García & Sánchez-Mata.

All the taxa that we place under F. trichophylla sensu stricto are, as far as we know, hexaploid (2n = 42), but we have insufficient living material for a thorough cytological survey. Segregates that have been

studied in this respect are F. trichophylla, F. cyrnea (St.-Yves & Litard.) Markgr.-Dann. and F. iberica (Hackel) K. Richter. On the other hand, F. rothmaleri is octoploid (2n = 56) and F. nevadensis is decaploid (2n = 70) (table 1), and the stomatal length (mean 55 µm) of the type specimen of F. paucispicula suggests that this might also be at a higher level than hexaploid. The purpose of this paper is to review the F. trichophylla group and to present evidence for a new, wider circumscription of F. trichophylla sensu stricto that includes four separate species recognized by MARKGRAF-DANNENBERG (1980) (one of them placed by her outside the F. rubra aggregate) and a subspecies that she placed under F. rubra.

MATERIALS

We have examined herbarium material from BC, BM, G, GDAC, JACA, K, LISI, LTR, MA, MAF, P and W, including the type specimens of eight of the ten taxa discussed, and living material of F. trichophylla, F. cyrnea and F. iberica, as well as of F. nevadensis and F. rothmaleri.

Table 1 $egin{align*} \mbox{Origin of material providing new chromosome counts in the genus $\it Festuca$ $\it Table 1$ \\ \mbox{Origin of material providing new chromosome counts in the genus }\it Festuca$ \\ \mbox{Origin of material providing new chromosome counts in the genus }\it Festuca$ \\ \mbox{Origin of material providing new chromosome counts in the genus }\it Festuca$ \\ \mbox{Origin of material providing new chromosome counts in the genus }\it Festuca$ \\ \mbox{Origin of material providing new chromosome counts in the genus }\it Festuca$ \\ \mbox{Origin of material providing new chromosome counts in the genus }\it Festuca$ \\ \mbox{Origin of material providing new chromosome counts }\it The setucation $\it The setucati$

Festuca cyrnea (StYves & Litard.) MarkgrDann. 1. St. Zacharie, Var (France)	2n = 42 $2n = 42$
F. iberica (Hackel) K. Richter 1. Sierra Nevada, Granada (Spain) 2. Prado de las Pozas, Sierra de Gredos, Ávila (Spain) 3. Morcuera to Rascafría, Sierra de Guadarrama, Madrid (Spain)	2n = 42 $2n = 42$ $2n = 42$
F. nevadensis (Hackel) K. Richter 1. By road from Granada to Veleta, near Fuente Bajada, 1900 m, Granada (Spain).	2n = 70
F. rothmaleri (Litard.) MarkgrDann. 1. Puerto de la Peña Negra, Ávila (Spain)	2n = 56
F. rubra L. subsp. juncea (Hackel) K. Richter 1. Great Orme Copper Mine, Caernarvonshire (Wales) 2. Tarbat Ness, East Ross (Scotland) 3. Near Liège (Belgium)	2n = 42 $2n = 42$ $2n = 56$
F. trichophylla (Ducros ex Gaudin) K. Richter subsp. trichophylla 1. Montagne de Lachens, 1700 m, Var (France)	2n = 42

METHODS

All the established morphological and anatomical characters of value in *Festuca* taxonomy have been utilized. Spikelet length, as is normal, is taken to the tip of the fourth lemma only, excluding the awn. Leaf-sections and epidermal preparations were taken from the middle of a tiller leaf. Sections were made with a freezing microtome after the leaf had been boiled in water. Epidermises were obtained by the lactic acid/scraping method. Chromosome counts were made on root-tips of mature plants that were pre-treated in saturated aqueous hexachloro-cyclohexane (gammexane) and stained with acetic-orcein.

REVIEW OF TAXA IN THE F. TRICHOPHYLLA GROUP

The distinct and well-known species F. nevadensis and F. rothmaleri (see FUENTE GARCÍA & SANCHEZ-MATA, 1987) are not covered here, except in the key, but ten other taxa that fall into the F. trichophylla group or have been implicated in its taxonomy are discussed below.

1. F. rubra trichophylla Ducros ex Gaudin, Fl. Helv. 1: 288 (1828), variously interpreted as variety or subspecies, was described from wet places in the Jura and Swiss Alps. The leaves were said to be very narrow and to resemble those of F. ovina, from which it was distinguished by the presence of rhizomes. It was raised to specific status by Richter (1890: 100). F. trichophylla is a well-known species from the mountains of southern Europe and, although we have not been able to trace type material, we have examined many accurately determined specimens. We have living material from Var, France, which is hexaploid (2n = 42) (table 1). Kerguélen & Plonka (1989: 283) stated that the type (? lectotype) from Mont Reculet, Ain (Jura) had been seen by them in LAU.

Gaudin did not mention leaf scabridity, from which one could assume that it was absent or slight. In our experience this taxon is rarely strongly scabrid —usually

the scabridity is weak and/or confined to the apical part of the leaf. Material that we have seen almost always agrees with Gaudin's description in its very narrow leaf-blades (usually ≤0.6 mm diameter) and long, often numerous rhizomes.

F. rubra var. iberica Hackel, Monogr. Festuc. Eur.: 136 (1882) was described from Spain under F. rubra subsp. violacea (Schleicher ex Gaudin) Hackel, most variants of which were differentiated from ssp. eu-rubra in having the ovary hairy at the apex. The ovary of var. iberica, however, was rightly described as glabrous, and this variety was separated in Hackel's key from most varieties of subsp. eu-rubra by the densely tufted, scarcely rhizomatous habit and setaceous leaves. It was raised to specific rank by RICHTER (1890: 99) and kept within the F. violacea Schleicher ex Gaudin aggregate by MARKGRAF-DANNEN-BERG (1980). Hackel described the leaves as scabrid and as having three (central and two marginal) sclerenchyma strands conspicuously larger than the others. Material we have seen confirms all the above characters.

F. iberica occurs in the mountains of Spain and North Africa. We have living material from central and south-eastern Spain; this is hexaploid (2n = 42) (table 1).

Within his var. iberica, HACKEL (1882: 136-137) distinguished two subvarieties; typica and subscabra Hackel, the latter differing in its leaf-blades being scabrid only near the apex, its smaller spikelets and its smooth (not scabrid) lemmas; it was said to be confined to the Pyrenees, where subvar. typica was unknown. KERGUÉLEN & PLONKA (1989: 193) also recognized only subvar. subscabra from the Pyrenees; they claimed that it lacks rhizomes.

Var. iberica was lectotypified by FUENTE GARCÍA & al. (1988: 515): "Sierra Nevada, in valle sup. fluv. Jenil, 29.6.1876" (W no. 5182). Subvar. subscabra has been lectotypified by FUENTE GARCÍA & SÁNCHEZMATA (1986a: 170): "Gavarnie, Htes. Pyrénées, juillet 1877, Bordère" (W no. 5183). We have seen both lectotypes.

F. iberica in some ways comes at the opposite end of the spectrum from F. tri-

chophylla sensu stricto, as it is strongly scabrid and has a densely tufted growth-habit, making it a characteristic species of the southern and central Spanish mountains. It shares with F. trichophylla, however, the very narrow leaves (usually ≤ 0.55 mm) and it sometimes produces a few long rhizomes that eventually form further dense tufts (field note by P.C.). Subvar. subscabra has longer, much less scabrid leaves and is possibly less densely tufted, but we have not seen it in the field; it comes closer to F. trichophylla.

3. F. scabrescens (Hackel ex Trabut) Batt. & Trabut was described by Trabut, Fl. Algérie Mon.: 215 (1895) and BATTANDIER & TRABUT (1904) from 1900 m on Djebel Mzi, Sud Oranais, Algeria. We have been unable to trace any type or authentic material, but have examined two specimens in P collected by R. Maire in the Grand and Moyen Atlas in 1921 and 1923 respectively. The basionym (TRABUT, 1895) was written "F. [RUBRA] SCABRESCENS Hackel, in litt", and reference to the Introduction (p.ix) and to the footnote on p. 4 of the Dicotylédones volume of Flore de l'Algérie (1888) suggests that the rank intended was race or subspecies. St.-Yves (1922: 17) referred to it as a variety and considered that in its acuminate young leaves, pubescent leaf-sheaths, presence of well-developed bulliform cells and scabrid leaf-blades it shows affinity with F. nevadensis (a member of the F. trichophylla group in our sense). St.-Yves (1913: 125) earlier stated that he had received material sent by Trabut from Diebel Mzi, some of which possessed the diagnostic characters "peu devéloppés". He also (ST.-YVES, 1922: 17) saw the same Maire material from Grand Atlas that we have seen.

This taxon is close to *F. iberica* and we here unite them; at subspecific level we believe *scabrescens* is the earliest epithet to have been used.

4. F. rubra subvar. asperifolia St.-Yves, Annuaire Conserv. Jard. Bot. Genève 17: 125 (1913) was described from the Alpes Maritimes, France under subsp. eu-rubra var. genuina. It was said to differ from other subvarieties of var. genuina in its glaucous, scabrid leaves, and from var. trichophylla in its flat culm-leaves. Other characters stressed were the presence of rhizomes, the well developed leaf-blade sclerenchyma strands, the relatively thick (0.7-0.8 mm diameter) leaf-blades, and the long (8-10 mm) spikelets. ST.-YVES (1913: 125) remarked that his subvar. asperifolia is "trés distinct" from F. (rubra) scabrescens, the latter having larger, auriculate ligules and well developed bulliform cells, although these characters were not always well developed.

This taxon was raised to subspecific level by Markgraf-Dannenberg (1976: 143).

We have seen many specimens in G, and of the syntypes we select the following as lectotype: "Alpes Maritimes, St. Etienne de Tinée, à Cascai, points frais, silice, 1500 m, 18.VII.1908, St.-Yves". Our examinations confirm the characters given by St.-Yves. This taxon shares the rhizomatous habit with F. trichophylla and the leafblade scabridity with F. iberica, but it has much thicker leaf-blades than either. Other characters placing it in the F. trichophylla group rather than the F. rubra group are the leaf-blade sclerenchyma pattern and the presence of abaxial protuberances, characteristic silica-bodies and some overlapping leaf-sheaths.

ST.-YVES (1913: 125) noted specimens from the Alpes Maritimes that were intermediate between subsp. asperifolia and subsp. juncea (Hackel) K. Richter, and others intermediate between subsp. asperifolia and F. trichophylla. According to MARKGRAF-DANNENBERG (1980) subsp. asperifolia is endemic to mountains of southern Europe, but Kerguélen & Plonka (1989) also gave localities north to Switzerland and Bretagne. KERGUÉLEN & PLONKA (1989) suggested that decaploid (2n = 70)plants from the Pyrénées Atlantiques "rapprochent un peu" F. rubra subsp. asperifolia but suggested that they might be F. rubra subsp. megastachys Gaudin or a new taxon (see under F. nevadensis var. gaetula for further discussion).

5. F. rubra var. yvesiana, Litardière & Maire, Mém. Soc. Sci. Nat. Maroc 4: 25

(1924) was described from the Grand and Moyen Atlas under subsp. eu-rubra. The leaves were said to be scabrid, setaceous and in exposed habitats with very strong marginal and central strands of sclerenchyma; the plants were described as densely tufted with few short rhizomes. It was raised to specific rank by PATZKE (1964: 195) as F. pseudotrichophylla; this was accepted and placed next to F. trichophylla by MARK-GRAF-DANNENBERG (1980), who gave the distribution as endemic to mountains of France, Spain and Portugal. LITARDIÈRE (1945: 134) gave records from Var and Basses-Pyrénées, France, and said that forms transitional to F. trichophylla occur in Spain. Kerguélen & Plonka (1989: 149), however, implied that the Var records were errors for F. cyrnea, and those from the Pyrénées for F. trichophylla. According to MARKGRAF-DANNENBERG (1980), F. pseudotrichophylla (and F. cyrnea) differ from F. trichophylla in their more densely tufted habit with shorter rhizomes and more persistent leaf-sheaths. We have seen a specimen in P that we select as lectotype: "Maroc, Grand Atlas, Ourika, pentes N.N.W. du Djebel Tachdirt, porphyre, 3200 m, 25.VII.1922, R. de Litardière". This specimen has poorly developed sclerenchyma strands, but the small abaxial protuberances are evident.

This taxon is close to F. iberica.

6. F. rubra var. cyrnea St.-Yves & Litard., Bull. Soc. Bot. France 71: 122 (1924) was described from Corsica (ST.-Yves. 1924), under subsp. eu-rubra, and was raised to specific rank by MARKGRAF-DANNENBERG (1978: 237). The leaves were said to be ca-pillary to subsetaceous, glaucous and very smooth, and transitional plants to F. rubra subvar. glaucescens Wahlenb. and to F. trichophylla were noted. (The precise identity of subvar. glaucescens is unknown, but is probably referable to F. rubra.)

F. cyrnea differs from F. pseudotrichophylla in its longer rhizomes and smoother leaf-blades. KERGUÉLEN & PLONKA (1989: 149), however, said that the latter character is very variable in F. cyrnea, which may have leaves "plus ou moins scabre". We agree.

MARKGRAF-DANNENBERG (1980) stated that F. cyrnea was endemic to Italy and but Markgraf-Dannenberg Corsica, (1982: 491) added Sardinia, KERGUÉLEN (1983: 10) added Bouches-du-Rhône, and KERGUÉLEN & PLONKA (1989: 149) added south-eastern France (Var and Alpes Maritimes). We have living material from Var and Bouches-du-Rhône; both are hexaploid (2n = 42) (table 1). We have also seen the lectotype (G), designated by KERGUÉ-LEN (1983). When grown side-by-side in the garden with F. trichophylla no differences were detected, and the rhizomatous habit of both was conspicuous.

F. rubra subsp. font-queri Litardière, Candollea 10: 133 (1945) was described from Tarragona, Spain as having a pubescent ovary apex, long rhizomes, and capillary, smooth leaf-blades. It was said to be "valde distincta" but with affinity "satis remota" to F. pyrenaica Reuter and F. violacea Schleicher ex Gaudin. Its most distinctive character is the very depauperate panicle with only 2-4 spikelets, and it was raised to specific rank as F. paucispicula by Fuente García & Sánchez-Mata (1986b: 443), who designated the lectotype in BC. They provided drawings of leaf-sections which showed a strongly pronounced median sclerenchyma strand, and stated that the leaf-blades were slightly scabrid.

The only material or record known to us are the syntypes, which we have seen. Our observations confirm those of FUENTE GARCÍA & SANCHEZ-MATA (1986b). In addition we can confirm that the ovary is sparsely pubescent, a character unknown in either the F. trichophylla or F. rubra groups (except for F. cretacea T. Popov & Proskorj.). Despite this, its scabrid leaves with abaxial protuberances and trichophylla-like sclerenchyma pattern and silica-bodies suggest to us that it is a member of the F. trichophylla group, but probably a distinct species. The collection of more material is highly desirable.

8. F. duriotagana Franco & Rocha Afonso, Bol. Soc. Brot., sér. 2, 54: 91 (1980) was described from the valleys of the Douro and Tagus in Portugal. It was said to

have been included in F. rubra by previous Portuguese authors, but to have leaves \pm sacabrid near the apex and to be closer to F. trichophylla, from which it differs in its thicker stems and longer upper glume. The rhizomes were described as long.

The only material we have seen is the type in LISI. The leaf-blade sclerenchyma pattern, the lack of abaxial protuberances, and the very weakly developed scabridity place this taxon closer to *F. rubra* than to *F. trichophylla*. In silica-cell shape and long-cell wall sinuation it is more or less intermediate between the *F. rubra* and *F. trichophylla* groups. The leaf-sheaths, however, present a mixture of open and closed, and hence suggest a closer affinity with *F. trichophylla*. Assignation of this taxon to one group or the other must await the acquisition of further material.

9. F. rubra subvar. juncea was described by Hackel, Monogr. Festuc. Eur.: 139 (1882) under subsp. eu-rubra var. genuina from a range of localities on lake and river banks in central Europe and Sweden. It was raised to subspecific level by RICHTER (1890: 99) and accepted at that rank by MARKGRAF-DANNENBERG (1980) and Ker-GUÉLEN & PLONKA (1989). Hackel described it as strongly creeping, with thick, Juncus-like leaf-blades with strong sclerenchyma strands. Since then it has been recorded more widely in central Europe, extending to the British Isles (MARKGRAF-Dannenberg, 1952). Fuente García & SANCHEZ-MATA (1989: 248) found that it also occurs in the Pyrenees (Gerona to Huesca), and they compared the Spanish material with the syntypes in W, but without making a lectotypification. We have also examined the syntypes and select the lectotype as follows: "Böhmen. Prag. Im Bergschutte am Fusse des Kuchelbader Berger. 15.VI.1879".

As noted previously, ST.-YVES (1913: 125) recorded specimens intermediate between *F. rubra* subsp. *asperifolia* and subsp. *juncea*. However, in all characters (except perhaps leaf sclerenchyma, q.v.) subsp. *juncea* comes much nearer *F. rubra* than *F. trichophylla*, and we are convinced that it

belongs within the former species, whereas subsp. asperifolia falls much closer to F. trichophylla. In fact A.-K. A.-B. and C. A. S. consider subsp. juncea indistinguishable from F. rubra subsp. pruinosa (Hackel) Piper, for which it is an earlier name. Its pattern of leaf-sclerenchyma (fig. 3E) often resembles that of F. trichophylla rather than that of F. rubra, with the median and marginal strands conspicuously larger than the others, as shown in the drawings of Hackel on the lectotype sheet and FUENTE GARCÍA & SÁNCHEZ-MATA (1989: 250), and less so in those of Kerguélen & Plonka (1989: 267). We have taken leaf-sections from many specimens, and find that the drawings of Fuente García & Sánchez-Mata and Hackel represent the extreme of the range. the other extreme of which is typical of the F. rubra group.

F. rubra subsp. juncea is hexaploid (2n = 42) or octoploid (2n = 56) (table 1).

10. F. rubra var. gaetula Maire ex St.-Yves, Candollea 1: 17 (1922) was described from 2000 m in Morocco under subsp. nevadensis Hackel (= F. nevadensis). This was raised to specific level by KERGUÉLEN (1979: 545).

ST.-YVES (1922: 20) considered that the taxa 'nevadensis', 'gaetula', 'scabrescens', 'cyrnea' and 'rubra' formed a 'chaîne' connecting F. rubra subsp. rubra and subsp. nevadensis, 'gaetula' differing from typical 'nevadensis' mainly in its more angular leafsection and smaller, more equal-sized sclerenchyma strands. LITARDIÈRE (1945: 137) recognized intermediates in all three combinations between 'rubra', 'gaetula', and typical 'nevadensis', and recorded F. nevadensis from France (Pyrenees, Cevennes and Alpes). Later (LITARDIÈRE 1947: 121) he identified plants from the region between the Cevennes and Alpes (Drôme, Vaucluse) as intermediate between F. rubra subsp. eu-rubra and F. rubra subsp. nevadensis var. gaetula. Subsequently (e.g. CLAUStres, 1960; Kerguélen, 1979, 1983), all French and Pyrenean material referred to F. nevadensis was considered to represent var. gaetula. The combination F. nevadensis var. gaetula, used by Fuente García &

SANCHEZ-MATA (1987: 371), appears not to have been made validly before now. The latter two authors considered that *F. nevadensis* (including var. *gaetula*) does not occur north of south-eastern Spain.

FUENTE GARCÍA & SÁNCHEZ-MATA (1989) reviewed the Pyrenean records of var. gaetula, and concluded that they represent F. rubra subsp. juncea. According to Kerguélen & Plonka (1989: 297) some of the French Pyrenean material that has been placed under F. nevadensis is referable to F. rubra subsp. asperifolia (q.v.), and some to subsp. juncea. KERGUÉLEN (1983: 13) stated that plants named F. nevadensis from the Alps and Cevennes need checking; we have not seen specimens nor a subsequent reference to them, and similary do not know the source of MARKGRAF-DAN-NENBERG's (1980) record of the species from Corsica.

One collection from the Pyrénées Atlantiques is, like F. nevadensis, decaploid (2n=70) (KERGUÉLEN & PLONKA, 1988: 226). It was originally collected as var. gaetula (KERGUÉLEN 1975: 178) but in our opinion it is F. rubra subsp. megastachys (=F. diffusa Dumort. = F. heteromalla Pourret), a possibility also mentioned by KERGUÉLEN & PLONKA (1989: 297). In cultivation it has flat leaves and a diffuse inflorescence.

An isotype of F. rubra var. gaetula in P has been examined by us. It bears a Université d'Alger label in Maire's writing agreeing in all repects with the locality given in the protologue: "Djebel Beni Smir, forêts de *Quercus*, grès, 2000 m, R. Maire, 2.VI.1918". The specimen also agrees closely with the type description. In our opinion it clearly belongs to F. nevadensis; it has some open leaf-sheaths, slightly scabrid leaves with very hairy adaxial ribs and abaxial protuberances, and rounded silicabodies. The stomatal length (50-70 µm, mean 61.5 μm) is typical of a decaploid. It differs from typical F. nevadensis in the characters emphasized by St.-Yves, and in the adaxial sclerenchyma strands mostly being absent or rudimentary. We do not, however, consider that these characters merit the description by St.-Yves of the taxon as

"exactement intermediaire" between F. rubra and F. nevadensis. It would be more accurate to describe it as intermediate between F. nevadensis and F. trichophylla subsp. trichophylla.

We have seen specimens in herb. St.-Yves (G) collected by Sennen in Pyrenées Orientales, France (Angoustrine and Odeillo) that were determined by St.-Yves as F. rubra subsp. nevadensis var. gaetula. We fully agree with these determinations, and consider that this taxon should be regarded as a variety of F. nevadensis. We have not seen specimens from the Spanish Pyrenees, but surely they exist.

DISCUSSION

As with many groups, taxa in the past have often been based solely on a few herbarium specimens that show distinctive characters, and when a much greater range of specimens is examined and material is grown in the botanic garden the distinctions tend to break down. It has become very noticeable to us that characters such as sclerenchyma development, leaf rigidity and scabridity, leaf-sheath persistence, rhizome length and panicle size and shape are greatly affected by cultural conditions.

Other characters that have been stressed by some authors in this group, such as leaf-blade or sheath pubescence and various spikelet characters, are in our experience not valuable in taxon recognition as they vary in a parallel fashion across many taxa. For example, populations frequently contain both glabrous and pubescent individuals; hybridization experiments have shown these characters to be genetically fixed, but they are of no taxonomic value.

The anatomical characters used by previous authors to separate taxa within this group have not been found by us to be consistently useful. Bulliform cells are, for example, well developed in at least some individuals of all taxa, despite the considerable reliance on their presence or absence placed by ST.-YVES (1913 and later) and MARKGRAF-DANNENBERG (1980, key), who used the character also within the *F. rubra* group.

The key in Flora Europaea (MARKGRAF-DANNENBERG, 1980) was not actually constructed by Markgraf-Dannenberg but was compiled from the descriptions supplied by her; it is highly unsatisfactory in many respects. The three characters (sheath decay; vein number; presence of intravaginal shoots) used in the key (couplet 58) to separate F. iberica from the rest of the taxa in this group are totally unreliable.

From our studies involving many characters of a large number of specimens, we conclude that F. nevadensis, F. rothmaleri, F. paucispicula and F. trichophylla are four related species together forming what we call the F. trichophylla group. Other taxa that we include within F. trichophylla itself are F. iberica, F. scabrescens, F. pseudotrichophylla, F. cyrnea and F. rubra subsp. asperifolia. These were obviously considered closely related by MARKGRAF-DANNENBERG (1980) also, except for F. rubra subsp. asperifolia, which was placed in the F. rubra group, and F. iberica, which was placed outside the whole F. rubra aggregate. Although the latter two taxa, especially F. iberica, are quite distinct in their typical or extreme state, they are linked to F. trichophylla by intermediates. It is unfortunate that under our new classification the name iberica has to be replaced by scabrescens.

Within F. trichophylla there are three nodes of variation that we consider worth recognizing as subspecies. They are less distinct than the four species that we recognize, but almost all specimens can be placed within one or the other, and there is some geographical distinction between them.

KEY TO TAXA IN THE F. TRICHOPHYLLA GROUP

- 1'. Tiller leaf-blades with marginal sclerenchyma strands smaller than to slightly larger than those of main lateral veins 4
- 2. Adaxial ribs of leaf-blades sparsely pubescent; panicle rather diffuse ... F. rothmaleri
- 2'. Adaxial ribs of leaf-blades densely pubescent; panicle rather contracted 3

- Tiller leaf-blades with well-developed sclerenchyma strands in adaxial ridges; leafblades not or scarcely angular in section . . .
- 4. Panicle with 2-4 spikelets; ovary sparsely pubescent F. paucispicula
- 4'. Panicle with many spikelets; ovary glabrous (F. trichophylla) 5
- 5. Leaf-diameter mostly 0.65-1.3 mm 6
- 5'. Leaf-diameter mostly 0.3-0.6 mm 7
- Leaf-blades strongly scabrid throughout abaxial surface, with scabrid or sparsely pubescent adaxial ridges; stomatal length (37.5-)41.5-46.5(-50) μm
- 6'. Leaf-blades weakly scabrid or scabrid only towards apex on abaxial surface, with densely pubescent adaxial ridges; stomatal length 50(-61.5-)75 μm... F. nevadensis var. gaetula
- F. trichophylla subsp. trichophylla
 Plant not or sparsely rhizomatous, forming large tufts; leaves usually moderately to strongly scabrid along whole length
 F. trichophylla subsp. scabrescens

TAXONOMIC TREATMENT OF THE F. TRICHOPHYLLA GROUP

1. F. nevadensis (Hackel) K. Richter, Pl. Eur. 1: 101 (1890)

Basionym: F. rubra subsp. nevadensis Hackel, Monogr. Festuc. Eur. 146 (1882).

Lectotypified by Fuente García & SANCHEZ-MATA (1986a).

- a. var. nevadensis (fig. 3B)
 Synonym: F. rubra [subsp. nevadensis] var. hackelii Litard. & Maire ex Litard., Arch. Bot. 1 (Bull. Mens. 4): 56 (April 1927), nom. nov. pro "subsp. nevadensis Hack. s. str.".
 South-eastern Spain; north-eastern Morocco.
- b. var. gaetula (Maire ex St.-Yves)
 Al-Bermani & Stace, comb. nov. (fig. 3C)

Basionym: F. rubra [subsp. nevaden-

sis] var. gaetula Maire ex St.-Yves, Candollea 1: 17 (1922).

Other synonym: F. gaetula (Maire ex St.-Yves) Claustres ex Kerguélen, Fl. Descr. Illustr. France, Suppl. 5: 545 (1979).

North-eastern Morocco, Spain, French Pyrenees.

- F. rothmaleri (Litard.) Markgr.-Dann., Bot. J. Linn, Soc. 76: 325 (1978)
 Basionym: F. rubra [subsp. eu-rubra] var. rothmaleri Litard., Cavanillesia 8: 57 (1936).
 - Central and north-western Spain; northern Portugal;? Corsica.

Lectotypified by Fuente García & Sánchez-Mata (1986b).

- 3. F. trichophylla (Ducros ex Gaudin) K. Richter, Pl. Europ. 1: 100 (1890) Basionym: F. rubra trichophylla Ducros ex Gaudin, Fl. Helv. 1: 288 (1828). Other synonym: F. rubra var. trichophylla (Ducros ex Gaudin) Hackel, Monogr. Festuc. Eur. 142 (1882).
 - a. subsp. trichophylla (fig. 3A)
 Synonyms: F. rubra [subsp. violacea var. iberica] subvar. subscabra Hackel, Monogr. Festuc. Eur. 137 (1882); F. iberica subsp. subscabra (Hackel) K. Richter, Pl. Eur. 99 (1890); F. rubra [subsp. eu-rubra] var. cyrnea St. Yves & Litard., Bull. Soc. Bot. France 71: 122 (1924); F. cyrnea (St. Yves & Litard.) Markgr.-Dann., Bot. J. Linn. Soc. 76: 327 (1978). Central and south-central Europe, from Spain to Romania; ? North Africa.
 - b. subsp. scabrescens (Hackel ex Trabut) Catalán & Stace, comb. nov. Basionym: F. rubra [subsp.] scabrescens Hackel ex Trabut, Fl. Algérie Mon. 215 (1895).

 Other synonyms: F. rubra [subsp. violacea] var. iberica Hackel (incl. subvar. typica), Monogr. Festuc. Eur. 136 (1882); F. iberica (Hackel) K. Richter, Pl. Eur. 99 (1890); F. scabrescens (Hackel ex Trabut) Batt. & Trabut, Fl. Algérie Tunisie 384 (1904); F. rubra [subsp. eu-rubra]

- var. yvesiana Litard. & Maire, Mém. Soc. Sci. Nat. Maroc 4: 25 (1924); F. pseudotrichophylla Patzke, Decheniana 117: 195 (1964). Spain and North Africa;? France and Portugal.
- c. subsp. asperifolia (St.-Yves) Al-Bermani, comb. nov.
 Basionym: F. rubra [subsp. eu-rubra var. genuina] subvar. asperifolia St.-Yves, Annuaire Conserv. Jard. Bot. Genève 17: 125 (1913).
 Synonym: F. rubra subsp. asperifolia

Synonym: F. rubra subsp. asperifolia (St.-Yves) Markgr.-Dann., Veröff. Geobot. Inst. Rübel Zürich 56: 143 (1976).

Southern Europe; ? exact range.

4. F. paucispicula Fuente García & Sánchez-Mata, Candollea 41: 443 (1986)

Nom. sust.: F. rubra subsp. font-queri
Litard., Candollea 10: 133 (1945).

Tarragona (Spain).

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BIBLIOGRAPHIC REFERENCES

- BATTANDIER, J. A. & L. C. TRABUT (1904). Flore Analytique et Synoptique de l'Algérie et de la Tunisie. Alger.
- CLAUSTRES, G. (1960). Festuca des Pyrénées, 1. La répartition géographyque des taxa dans l'ensemble de la chaine. Bull. Soc. Hist. Nat. Toulouse 95: 111-123.
- FUENTE GARCÍA, V. DE LA & D. SÁNCHEZ-MATA (1986a). Tipificación de algunos táxones ibéricos del género Festuca L. (Gramineae) descritos por E. Hackel. Candollea 41: 163-171.
- FUENTE GARCÍA, V. DE LA & D. SANCHEZ-MATA (1986b). Datos taxonómicos sobre el género Festuca L. (Gramineae) en la Península Ibérica. *Candollea* 41: 441-448.
- FUENTE GARCÍA, V. DE LA & D. SÁNCHEZ-MATA (1987). Datos sobre Festuca rothmaleri (Litard.) Markgr.-Dannenb. y F. nevadensis (Hackel) K. Richter (Gramineae). *Anales Jard. Bot. Madrid* 43: 361-373.

- FUENTE GARCÍA, V. DE LA & D. SANCHEZ-MATA (1989). Sobre Festuca rubra L. subsp. juncea (Hackel) K. Richter en la Península Ibérica. *Collect. Bot.* (*Barcelona*) 17: 247-253.
- FUENTE GARCÍA, V. DE LA, D. SANCHEZ-MATA & J. C. MORENO SAIZ(1988). Sobre el género Festuca L. (Gramineae). Tipificaciones en el herbario original de E. Hackel. *Candollea* 43: 513-520.
- HACKEL, E. (1882). Monographia Festucarum Europaearum. Kassel & Berlin.
- KERGUÉLEN, M. (1975). Les Gramineae (Poaceae) de la flore française. Essai de mise au point taxonomique et nomenclaturale. *Lejeunia*, n. sér., 75.
- KERGUÉLEN, M. (1979). Flore Descriptive et Illustrée de la France. Cinquième Supplement: Graminées. Paris
- KERGUÉLEN, M. (1983). Les Graminées de France au travers de 'Flora Europaea' et de la 'Flore' du C.N.R.S. Lejeunia, n. sér., 110.
- KERGUÉLEN, M. & F. PLONKA (1988). Festuca des Pyrenées. Du nouveau sur quelques taxons. Monogr. Inst. Pir. Ecología [Homenaje a Pedro Montserrat] 4: 225-229.
- KERGUELEN, M. & F. PLONKA (1989). Les Festuca de la Flore de France (Corse Comprise). Bull. Soc. Bot. Centre-Ouest, n. sér., num. spéc. 10.
- LITARDIERE, R. DE (1945). Contribution à l'étude du genre Festuca. Candollea 10: 103-146.
- LITARDIÈRE, R. DE (1947). Festuca nouveaux ou rares de France et d'Espagne, principalement des Pyrenées. Bull. Soc. Hist. Nat. Toulouse 82: 110-122.

- MARKGRAF-DANNENBERG, I. (1952). Studien an Irischen Festuca-Rassen. Veröff. Geobot. Inst. Rübel Zürich 25: 114-142.
- MARKGRAF-DANNENBERG, I. (1976). Die Gattung Festuca in Griechenland. Veröff. Geobot. Inst. Rubel Zürich 56: 92-182.
- MARKGRAF-DANNENBERG, I. (1978). New taxa and names in European Festuca (Gramineae). *Bot. J. Linn, Soc.* 76: 322-328.
- MARKGRAF-DANNENBERG, I. (1980). Festuca. In: T. G. Tutin & al. (eds.), Flora Europaea 5: 125-153. Cambridge.
- MARKGRAF-DANNENBERG, I. (1982). Festuca. In:
 S. Pignatti (ed.), Flora d'Italia 3: 478-501. Bologna.
- PATZKE, E. (1964). Gliederung der Festuca rubra L. in Deutschland. *Dechemana* 117: 191-196.
- RICHTER, K. (1890). Plantae Europeae 1. Leipzig.
- ST.-YVES, A. (1913). Les Festuca de la section Eu-Festuca et leurs variations dans les Alpes Maritimes. Annuaire Conserv. Jard. Bot. Genève 17: 1-218.
- ST.-YVES, A. (1922). Les Festuca (subg. Eu-Festuca) de l'Afrique du Nord et des Iles Atlantiques. Candollea 1: 1-63.
- ST.-YVES, A. (1924). Festucarum varietates novae (subg. Eu-Festuca). Bull. Soc. Bot. France 71: 28-43, 110-125
- Trabut, L. C. (1985). In: J. A. Battandier & L. C. Trabut, Flore de l'Algérie. 2. Monocotylédones. Paris & Alger.

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