

Catabrosa versus *Colpodium* (Poaceae: Poeae) in southern Africa, with a key to these genera and their species in Africa

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Summary. Differences between the genera *Colpodium* Trin. and *Catabrosa* P. Beauv. are discussed. *Colpodium drakensbergense* Hedberg & I. Hedberg is transferred to *Catabrosa drakensbergense* (Hedberg & I. Hedberg) Soreng & Fish and a lectotype is chosen for the species. This leaves only two *Colpodium* species in Africa (Ethiopia, Kenya and Tanzania), and extends the range of *Catabrosa* from northwestern Africa to southern Africa.

Key Words. Africa, *Catabrosa*, *Colpodium*, Miliinae, Poaceae, Poeae, Puccinelliinae.

Introduction

Colpodium drakensbergense Hedberg & I. Hedberg was described by Olov Hedberg and Inga Hedberg (1994), from specimens collected in high altitude bogs in Lesotho. Collections from Lesotho were initially identified as *Catabrosa aquatica* (L.) P. Beauv. (Anderson 1969), then, beginning with annotations as early as 1972 (on Weger 1614), as *Colpodium hedbergii* (Melderis) Tzvelev (van Zinderen Bakker & Werger 1974; Gibbs Russell *et al.* 1990), a species otherwise known from Mt Kilimanjaro to Ethiopia. The Hedbergs provided a discussion of the taxonomic history of the genus *Colpodium* Trin. s.l. (sensu Clayton & Renvoize 1986), along with a detailed analysis and key to the species of Africa. Tzvelev & Bolchovskich (1965) divided *Colpodium* into four genera: *Catabrosella* (Tzvelev) Tzvelev, *Colpodium*, *Hyalopoa* (Tzvelev) Tzvelev, and *Paracolpodium* (Tzvelev) Tzvelev. The three segregate genera are sometimes accepted (Alexeev 1980, 1988; Alexeev & Tzvelev 1981; Cope 1982; Tzvelev 1976; Mill 1985), and sometimes not (Bor 1970; Clayton & Renvoize 1986; Hedberg & Hedberg 1994; Dicoré 1995; Wu & Phillips 2006). *Colpodium* s.s., including *Keniochloa* Melderis (Tzvelev 1976; Hedberg & Hedberg 1994), sometimes recognised as *Colpodium* sect. *Keniochloa* (Melderis) E. B. Alexeev (Alexeev 1980) primarily based on the higher chromosome number Hedberg & Hedberg (1977) found in the two African species known at that time ($2n = 8$ versus $2n = 4$), is the only one of these genera found in Africa. At present, in *Colpodium* s.s. there are two species in southeast Europe and southwest Asia, *C. versicolor* (Steven) Schmalh. (Georgia, Iraq, Iran, Russia [Caucasus], and Turkey) and *C. violaceum* (Boiss.) Griseb. (Iran and Iraq), and three in Africa, *C.*

chionogeiton (Pilg.) Tzvelev (Kenya and Tanzania), *C. drakensbergense* (Lesotho), and *C. hedbergii* (Ethiopia, Kenya, Tanzania).

On receiving two specimens of *Colpodium drakensbergense* from Lesotho as a gift to US from PRE it was noticed that the glumes were unequal in length and some samples had numerous 2-flowered spikelets. Thus it looked as if these specimens belonged to *Catabrosa* P. Beauv. rather than to *Colpodium*. However, in Africa *Catabrosa* was known only from northwest Africa (Maire 1955; Clayton *et al.* 2006), and a study was therefore undertaken to examine the variation in this species, including the type material, in order to resolve the generic position of the southern African material.

The genus *Colpodium* was merged with *Catabrosa* by Boissier (1884) as *Catabrosa* sect. *Colpodium* (Trin.) Boiss. but nearly all other authors since Bentham & Hooker (1883) have kept the genera, s.s. or s.l., apart. Several characteristics differentiate *Catabrosa* from *Colpodium* (see Discussion and Table 1). *Catabrosa* has two widely accepted species: the polymorphic *C. aquatica* (circumboreal, with a few stations in southern Patagonia and Tierra del Fuego in Argentina and Chile) and *C. werdermannii* (Pilg.) Nicora & Rúgolo (Andes of central Argentina and Chile to southern Bolivia). Sometimes, *C. aquatica* subspecies (Tzvelev 1976) are treated as species: *C. capusii* Franch. (China, Iran, Iraq, Kyrgyz Republic, Tajikistan, Turkey, Uzbekistan) and *C. pseudaimoides* (J. C. G. Herrm.) Tzvelev (Azerbaijan, Iran, Iraq, Israel or Palestine, Russia (around the Caspian and Aral Seas), Syria, Turkey) (Czerepanov 1995; Mill 1985; Wu & Phillips 2006).

Tzvelev (1976), in the *Grasses of Soviet Union*, arranged these genera in the subtribe Poinae, in the

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Table 1. Comparison of *Colpodium*, *Catabrosa* and *Catabrosa drakensbergense*.

Character\Taxon	<i>Colpodium</i>	<i>Catabrosa</i> (not counting <i>Cat. drak.</i>)	<i>Cat. drakensbergense</i>	<i>Cat. aquatica</i> subsp. <i>aquatica</i>	<i>Cat. aquatica</i> subsp. <i>uniflora</i>	<i>Cat. aquatica</i> subsp. <i>pseudatairoides</i>
Habit	caespitose	stooling (lateral shoots sometimes buried, frequently submerged), or caespitose	as in <i>Catabrosa</i>			
Upper culm sheath proportion fused	near base or up to 1/5	1/4 - 3/4	1/2			
Spikelet length (biflorate) (mm)		2 - 4.2	2.5 - 4.2	2.5 - 4.2		2 - 2.8 (3)
Spikelet length (uniflorate) (mm)	2.5 - 6.5	1.5 - 3.5	(1.9) 2.3 - 3.5	2.3 - 3.5	1.7 - 3.5	1.5 - 2.2
Number of florets per spikelet	1	1 - 4 (7)	1, 1 - (2), 1 - 2	1 - (2), 1 - 2, (1) 2 (3), 2 - 4 (7)	1	1 - 3 (4)
Floret number variable or not within panicle or among panicles	no	yes, within and among panicles	yes, within and among panicles	highly variable	probably variable	yes, within and among panicles
Rachilla extension in 1-flowered spikelets	suppressed	suppressed or short	suppressed, or up to 0.2 mm long			
Glumes	(subequal) equal	unequal	unequal			
Lower glume relative to first floret	(subequal) equal or exceeding	1/6 - 1/2	1/2 - 2/3 the proximal lemma	1/6 - 1/3 (1/2)		1/4 - 1/5
Upper glume relative to first floret	equal or exceeding	1/3 - 2/3 (3/4)	(2/3)3/4 to nearly equalling or slightly exceeding the proximal lemma	1/2 - 2/3 (3/4)		1/3 - 1/2
Glume shape	lanceolate to broadly lanceolate, obtuse or acute	broadly lanceolate to broadly ovate to elliptical to oblanceolate to obovate, apically slightly acute, obtuse, sub-flabellate, or truncate	broadly lanceolate to oblanceolate, apically obtuse or slightly acute	broadly lanceolate to broadly ovate to elliptical to oblanceolate to obovate, apically slightly acute, obtuse, sub-flabellate, or truncate	oblanceolate, apically obtuse or slightly acute	
Lemma texture relative to glumes	thinner than glumes	same as glumes or thicker	same as glumes or thicker			
Lemma length (mm)	2.5 - 6.5	1.5 - 3.5	1.9 - 2.5 (2-fld.), 2.2 - 3.5 (1-fld.)	2 - 3 (3.5)	1.7 - 3.5	1.5 - 2.2
Lemma shape	lanceolate to ovate, obtuse to acute	broadly lanceolate to oblong, truncate to acute	broadly lanceolate to oblong, acute or slightly obtuse	truncate to obtuse, margin irregular	acute or slightly obtuse	
Lemma no. of veins and vein prominence	3, relatively faint	3, prominent, rarely with faint laterals (5)	3, prominent	3	3	3
Lemma pubescence	glabrous or pubescent	glabrous or pubescent	glabrous or sparsely minutely pubescent	glabrous or sparsely minutely pubescent	glabrous or sparsely minutely pubescent	prominently short pubescent
Palea surfaces and keels	scarious to hyaline, or faintly green, keels slender, green or anthocyanic	subchartaceous, strongly coloured, keels prominent	subchartaceous, strongly coloured, keels prominent			
Lodicules	with a well developed upper portion	hyaline upper portion reduced	hyaline upper portion reduced			
Hilum	narrowly elliptic to oblong, little differentiated in colour from pale body	ovoid, elliptic, oblong, or round, darker than caryopsis body	elliptic to oblong, darker than caryopsis body			
Chromosome number: #=	2 (Asia), 4 (Africa)	(5) 10, 15, 21	10	5, 10, 15, 21		5

following order: *Poa* L., *Eremopoa* Roshev., *Catabrosella*, *Hyalopoa*, *Arctophila* Rupr., *Dupontia* R. Br., *Catabrosa*, *Paracolpodium*, *Colpodium*, *Phippsia* R. Br., *Puccinellia* Parl., *Sclerochloa* P. Beauv., and *Torreyochloa* G. L. Church. Since then other relationships for the above genera have been proposed taking DNA data into account. Choo *et al.* (1994) examined chloroplast DNA restriction-site data for the *Puccinellia* complex including *Catabrosa*, *Sclerochloa*, *Phippsia* and *Puccinellia*. Soreng & Davis (2000) provided additional restriction-site evidence for this group within the Pooideae. This led to the establishment of a new subtribe for the above genera and the *Colpodium* complex, namely Puccinelliinae Soreng & Davis (Soreng *et al.* 2003a), which was originally proposed to include *Catabrosa*, *Colpodium*, *Paracolpodium*, *Phippsia*, *Puccinellia* and *Sclerochloa*. Although there are published analyses of plastid and nuclear DNA sequences with *Colpodium versicolor* and/ or other members of the *Colpodium* complex (Döring *et al.* 2007; Rodionov *et al.* 2007; Gillespie *et al.* 2008, 2010; Kim *et al.* 2009; Schneider *et al.* 2009), along with representatives of the other genera in related subtribes (Alopecurinae, Cinninae, Miliinae, Phleinae, Poinae and Puccinelliinae), there are no DNA data for the endemic African taxa. The nuclear ribosomal DNA data place *Colpodium* s.s. as sister to and closely related to the genus *Zingeria* P. A. Smirn. (also $2n = 4, 8$ chromosomes). Both these genera are isolated from the other three genera sometimes included within *Colpodium*. Meldris (1956) initially compared his new genus *Keniochloa* with *Zingeria*, not *Colpodium*. In an analysis of nuclear ITS DNA, *Catabrosella*, *Hyalopoa pontica* (Balansa) Tzvelev, and *Paracolpodium* are a sister lineage to *Catabrosa*, and are embedded in a clade with *Phippsia*, *Puccinellia* and *Sclerochloa*, and this set of genera was included in the subtribe Puccinelliinae (Gillespie *et al.* 2008 (submerged in Coleanthinae based on newer Gillespie & Soreng unpubl. data; Soreng *et al.* 2003b, online classification)). A plastid DNA analysis placed *Hyalopoa lanatiflora* (Roshev.) Tzvelev in or near *Poa*, well isolated from a clade containing *Colpodium* s.s. and *Zingeria* as sister to *Phippsia*, *Puccinellia* and *Catabrosa* (Döring *et al.* 2007), but whatever these data indicate, the discordant results for the two *Hyalopoa* species need further investigation (see also Kim *et al.* 2009). Schneider *et al.* (2009) had similar results to Döring *et al.* (2007), but did not include *Hyalopoa*. *Colpodium* and *Zingeria* are possibly allied to *Milium* L., and were included in the subtribe Miliinae by Gillespie *et al.* (2008) and Soreng *et al.* (2007, 2003b) because they share several characteristics with *Milium*, such as similar panicles, spikelets strictly 1-flowered, weakly compressed, without rachilla extension, glumes as long or longer than spikelet and equal in length and chromosome number reduction ($2n = 8, 10, 14, 18$ in *Milium*). Possibly Miliinae are sister to Puccinelliinae. The basic

chromosome number in Poae is $x = 7$, and this is common, widespread (only a dozen or so small genera deviate from this) and evidently pleisomorphic in the tribe, as it is also characteristic of the sister tribal lineage Bromaeae plus Triticeae (Clayton & Renvoize 1986).

The molecular evidence supports the separation of *Colpodium* s.s. and *Catabrosa*. Here, the morphological and cytogenetic differences between *Colpodium* s.s. and *Catabrosa* will be evaluated with regard to the disposition of *Col. drakensbergense*.

Materials

The types and additional material of the African *Colpodium* taxa were borrowed from UPS and PRE. All cited specimens have been seen by the first author, the second author has seen all PRE specimens. These, and in addition material of *Catabrosa*, *Catabrosella*, *Colpodium*, *Hyalopoa* and *Paracolpodium* at US, were examined under a dissecting microscope. African specimens examined, with chromosome vouchers indicated, are as follows:

***Colpodium chionogeiton*. TANZANIA.** Kilimanjaro: Mawenzi hut, 2 March 1953, G. H. Wood 923 (UPS V-235556; $2n = 8$); saddle between Kibo and Mawenzi, W slope of Mawenzi, 4830 m, at small brook, 17 June 1948, O. Hedberg 1253 (UPS V-235556; $2n = 8$); SW slope, upper Umbwe Valley, 4150 m, in the lowermost part of the alpine belt, in bog, 7 Dec. 1963, S. W. Bie 135 (UPS V-235557); greenhouse voucher, 22 July 1964, O. Hedberg s.n. (cultivated from: c. 3800 m, in the lowermost part of the alpine belt, in bog, Sept. 1963, S. W. Bie 35) (UPS V-235558; $2n = 8$).

***Colpodium drakensbergense*. LESOTHO.** 27 km from Oxbow on road to Letseng la Terai, 3200 m, 5 Feb. 1987, D. J. B. Killick 4506 (US-3396868); 3050 m, 27 Jan. 1982, D. J. B. Killick 4414 (PRE-616759); 33 km NW of Mokhotlong, semi-floating in tarn in peat bog, 4000 m, 6 April 1972, M. J. A. Werger 1614 (PRE-62659); Butha-Butha: along the road from Oxbow Lodge to the diamond mine, at a pond, 27 Jan. 1982, O. Hedberg 82009 (UPS V-061120); Pone Valley, Mothae Mts, in pools, 2750 m, 8 Jan. 1958, W. J. Lutjeharms 808 (PRE-91696); Maluti Mts, on plateau in westerly direction from Sani Pass, bank of river, stony soil, 3000 m, 15 Feb. 1987, M. D. Panagos 121 (US-3396878); Qacha's Nec: next to dam and road in stream coming from Hodson's Peak, 19 Jan. 1977, P. C. V. du Toit 2328 (PRE-489449); Sani Pass, Sani Pass Lodge, 2850 m, in small dried-out pools, 1 Feb. 1982, O. Hedberg 82088 (holotype UPS-V-061119; isotype UPS-V-061121, PRE-805594) (UPS-V-061121 was cultivated from seed of O. Hedberg 82088; $2n = 20$); near the Lodge, 2900 m, in small rivulet, 3 Feb. 1982, O. Hedberg 82146 (UPS-V-

061118, PRE-805578); seepage area on summit of Drakensberg, 2750 m, Jan. 1966, *D. J. B. Killick & J. Vahrmeyer* 3730 (PRE-107065) (originally determined as *Catabrosa aquatica* (Anderson 1969), with 1 or rarely 2-flowered spikelets); summit, 1 – 2 km W of chalet, next to main road, 2865 m, 16 Jan. 1977, *D. J. B. Killick* 4154 (PRE-489446); stream and swampy area below dam next to road in valley leading from Hodson's Peak, 2900 m, 19 Jan. 1977, *P. C. V. du Toit* 2329 (PRE-489450); Sani R. flats, 2300 m, 14 Feb. 1987, *D. J. B. Killick* 4596 (PRE-708719); stream junction — Sani R., in sedge meadow, 19 Jan. 1977, *P. C. V. du Toit* 2327 (PRE-489448); stream leading to the Sani R. in sedge meadow, 19 Jan. 1977, *P. C. V. du Toit* 2326 (PRE-489447); Thabana Ntlenyana, 29°29'15"S 29°32'04"E, wetland, 3225 m, 2 Feb. 1988, *C. Schwabe* 6a (PRE-734772).

Colpodium hedbergii. ETHIOPIA. Bale Prov.: Bale Region, Bale Mts N.P., Saneti Plateau, 4000 m, along small stream, 8 Nov. 1982, *O. Hedberg* 9067 (UPS V-235559; $2n = 8$); on crest S of Garba Goracha, 4100 m, in shallow lakelet, growing in shallow water, 2 Nov. 1973, *O. Hedberg* 5645 (UPS V-235560; $2n = 8$); N.P., Saneti Plateau, between Garba Goracha and Tullu Deemtu, 4150 m, 1 Nov. 1973, *O. Hedberg* 5618 (UPS V-235561; PRE-969393; $2n = 8$); Gonder Begemdir Prov.: Simien Geech, 3600 m, in shallow water in a small stream, 16 Oct. 1973, *O. Hedberg & Getachwe Aweke* 5361 (UPS-V-235562; $2n = 8$); N of the camp, 3700 m, in a small stream, in water c. 5 cm depth, 19 Oct. 1973, *O. Hedberg & Getachwe Aweke* 5492 (UPS-V-235563, PRE-969392; $2n = 8$). KENYA. Mt Elgon, in the crater, at Maji ya Moto (hot spring), 3580 m, on moist ground at a small stream from the spring, 13 May 1948, *O. Hedberg* 908 (holotype UPS V-139997; $2n = 8$; Melderis 1956: fig. 2 — photo).

Results

Examination of type material of *Colpodium drakensbergense*.

Holotype: *O. Hedberg* 82088 (UPS-V-061119) (Fig. 1)

The holotype has four separate flowering shoots of two forms:

Form "A" includes three more robust, taller samples, with one 1-flowered spikelet (two with rare 2-flowered spikelets), lemmas usually with a few to several hairs on the sides and keel (anthers 1.2 mm).

Form "B" is more slender and lower growing, 2-flowered spikelets about as common as 1-flowered spikelets, lemmas infrequently with one or a few hairs on the sides (anthers 0.8 mm).

Isotype: PRE-805594.

The isotype includes six isolated flowering culms and one complete flowering shoot of medium stature

(panicles 7 – 15 cm long), and one short plant with four inflorescences c. 4 cm long.

Four of the medium stature shoots have 1-flowered spikelets. The inflorescences of these medium stature plants are mostly fairly mature and shattered so we cannot know for sure if they lacked 2-flowered spikelets or how many they had, except that two of the shoots have rare 2-flowered spikelets. These six are considered to be of form "A". These have anthers 1.0 – 1.2 mm, and lemma hairs that are short and very sparse between the veins or absent.

One additional medium stature shoot is a little younger than the other six, and has frequent 2-flowered spikelets with glabrous lemmas, and is thus transitional between forms "A" and "B".

The short plant looks like form "B" on the holotype. It has rare 2-flowered spikelets, anthers 1.0 mm, and rare lemma hairs are visible.

Clearly, from the description, the Hedbergs intended the 1-flowered plants to be the new species, as they specify the genus is 1-flowered in Africa. However, they also indicate the lemmas are "glabrous", which they clearly are not in the 1-flowered inflorescence specimens they selected for the type (82088). The lemmas in the frequently 2-flowered forms on the types are glabrous or nearly so, but some sparse hairs may be found in most inflorescences. Lemma hairs were not illustrated in Hedberg & Hedberg (1994: fig. 3), drawn from Hedberg 82009 (see notes below).

Some additional material examined by the Hedbergs:

O. Hedberg s.n. (UPS-V-061121) was grown at Uppsala University from seed of *O. Hedberg* 82008. This plant is like the "A" form in having only 1-flowered spikelets, and lemmas with sparse hairs primarily between the veins. It reaches 30 cm in height and is quite pale green. All of the field collected plants are less than 25 cm tall, and are distinctly, although not darkly, anthocyanic.

O. Hedberg 82009 UPS is 1-flowered, and a bit immature. There are no hairs on the lemmas. This medium stature plant is the one illustrated in Hedberg & Hedberg (1994, fig. 3), and matches the description of the species.

O. Hedberg 82146 UPS is like 82009, a slender plant, with lemmas glabrous throughout.

O. Hedberg UPS-V-061121 cultivated from 82088 is presumably the chromosome voucher, $2n = 20$. It is etiolated, "grown from seeds from the type collection" (thus it is not an isotype). A separate tag says "Chromosome number counted in this specimen/collection" (i.e., not from this specimen); a similar tag is on the holotype sheet. UPS did not send a sheet that said "counted in this specimen". Perhaps the voucher was held back by UPS, or it does not exist. However, this cultivated specimen, or one grown from the same batch of seed, is material from which the chromosome number was obtained. This specimen has four isolated inflorescences

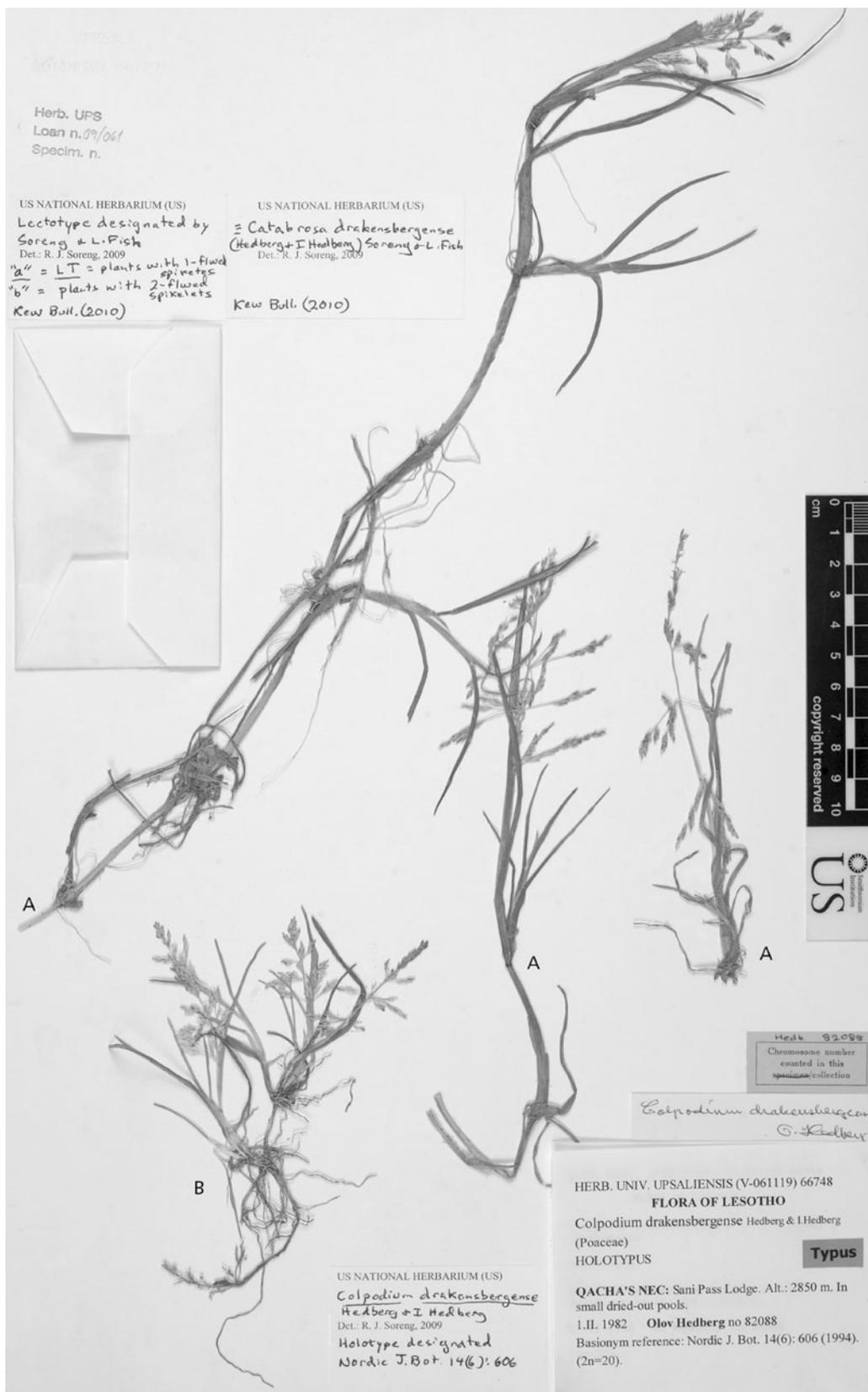


Fig. 1. Lectotype of *Catabrosa drakensbergense* (Hedberg & I. Hedberg) Soreng & Fish, O. Hedberg 82088 "A" (UPS). The specimen marked "B" has about equal numbers of 2-flowered spikelets, both florets well developed and fertile, and 1-flowered spikelets. 2-flowered spikelets are rare in two shoots, and absent in one shoot.

and one tuft with four inflorescences that appear uniform: these have infrequent 2-flowered spikelets, and the lemmas are pubescent as in holotype form “A”.

Among the 15 different collections of *Colpodium drakensbergense* studied, five have one or more panicles with at least one 2-flowered spikelet (*Killick* 4404, 4506; *Panagos* 121; *du Toit* 2326; *Hedberg* 82088). The first two have rare 2-flowered spikelets. The latter three have some panicles with frequent 2-flowered spikelets, which are referred to as form “B” or transitional to “B”. Plants of form “B” are all less than 10 cm tall, whereas wild plants of form “A” range up to 25 cm tall (to 30 cm in the greenhouse sample), and form “B” proximal lemmas are shorter on average than in plants of form “A” (averaging 2.5 mm, versus averaging 3 mm and up to 3.5 mm). Both the proximal and distal florets in the 2-flowered spikelets appear well developed and fertile.

Discussion

Colpodium s.s., including *Keniochloa*, but excluding *Col. drakensbergense*, differs from *Catabrosa* in habit, sheath openness, several spikelet bract and rachilla characteristics, lodicule and hilum shape, and chromosome numbers. Differences between *Colpodium*, *Catabrosa*, and some species and infraspecies of *Catabrosa* are summarised in Table 1.

Tzvelev (1976) describes *Colpodium* as forming fairly dense tufts (“turf”), and *Catabrosa* as often stoloniferous or rhizomatous. All the plants of *Col. drakensbergense* are stoloniferous (the lateral culms are former aerial shoots that became submerged and rooted at the nodes, so we call them stoloniferous, rather than rhizomatous, as rhizomes are by definition subterranean), with exclusively extravaginal branching, and quite curly roots, features typical of *Catabrosa aquatica*. Although additional study of specimens is warranted, we agree with Clayton (1970) that *Col. chionogeiton* and *Col. hedbergii* are tufted, not stoloniferous. It appears to us that both the latter taxa are tufted, but field work is needed to verify whether lateral or deep arising shoots seen in a few specimens are normal productions, or resulted from environmental modifications (such as burial or emergence around solid objects), or were aberrancies of pressing.

Tzvelev (1976) indicates the sheaths of *Colpodium* s.s. are closed (= margins united) only near the base, and in *Catabrosa* they are closed for $\frac{1}{4}$ – $\frac{3}{4}$ of their length. In *Col. chionogeiton* and *Col. hedbergii* sheaths are closed about $\frac{1}{5}$ – $\frac{1}{6}$ of their length; while those of *Col. drakensbergense* are closed about $\frac{1}{2}$ of their length. (This sheath characteristic is given as measured on the upper culm leaf).

In *Colpodium* s.s. the glumes are equal (to subequal) in length, and as long (or subequal), or longer than the spikelet. Unlike *Colpodium* s.s., but like *Catabrosa*, the glumes in *Col. drakensbergense* are distinctly unequal in length and mostly shorter than the proximal lemma

and are commonly broadest at or above the middle. The glumes are papillate in both genera and of about the same consistency, but the lemmas and paleas are more delicate than the glumes in *Colpodium*, and firmer than them in *Catabrosa* and *Col. drakensbergense*.

In *Colpodium* s.s. spikelets are strictly 1-flowered, and a rachilla extension is absent. In *Catabrosa aquatica* spikelets vary from 1-flowered (with or without a minute vestigial rachilla extension) to 2 or more-flowered. Some specimens have only panicles with 1-flowered spikelets, while other specimens have mixtures of 1 and 2-flowered, sometimes up to 7-flowered, spikelets within a panicle. Within individual specimens with more than one panicle some panicles may exhibit only 1-flowered spikelets while others show mixtures of 1 and 2-flowered spikelets. In *Col. drakensbergense*, unlike *Colpodium* s.s., but like *Cat. aquatica*, the spikelets vary in number of florets, and even 1-flowered spikelets sometimes produce a minute (up to 0.2 mm), but distinct, rachilla extension.

The hilum in *Colpodium* s.s. is narrowly elliptic to oblong, and little differentiated in colour from the body of the caryopsis, whereas in *Col. drakensbergense* the hilum is elliptic to oblong and darker than the caryopsis. In *Catabrosa* the hilum is oblong, elliptic to round, and darker than the caryopsis.

Chromosome numbers in *Colpodium drakensbergense* match those in *Catabrosa*. *Col. drakensbergense* has $2n=20$ (Hedberg & Hedberg 1994), as is found in the majority of counts for *Catabrosa* (for chromosome numbers see Goldblatt & Johnson 1979). Tzvelev (1976) gives the base number for *Catabrosa* as $x=5$ based on a count for *Catabrosa aquatica* subsp. *pseudairioides* (J. C. G. Herrm.) Tzvelev ($2n=10$), and another from *C. aquatica* var. *atrata* Tzvelev. *Colpodium* s.s., in contrast, has $2n=4$ in Asia [*Col. versicolor*] (see Kotseruba *et al.* 2005), and $2n=8$ in the two other African species [*Col. hedbergii* and *Col. chionogeiton*; Hedberg & Hedberg 1977]. In summary, there is no doubt in our minds that *Col. drakensbergense* belongs in *Catabrosa*. We have also compared *Col. drakensbergense* with *Catabrosella*, *Hyalopoa*, *Paracolpodium*, and again it is clear that it belongs to *Catabrosa* s.s.

Within *Catabrosa*, *Colpodium drakensbergense* can be compared with other elements of the genus. In *Cat. aquatica* subsp. *pseudairioides* the spikelets are 1 – 5-flowered, 1.5 – 2.2 mm to the tip of the proximal lemma, the lower glume is $\frac{1}{4}$ – $\frac{1}{5}$ and upper glume $\frac{1}{3}$ – $\frac{1}{2}$ to the proximal lemma in length; the lemmas are distinctly pilose along the keel and marginal veins and usually between them (Tzvelev 1976; R. J. Soreng pers. obs.). In the *Col. drakensbergense* material the spikelets are mostly 1-flowered and generally larger, (1.9) 2.3 – 3.5 mm long, glabrous or only sparsely hairy, and the glumes are distinctly longer and proportionally longer when compared to the proximal lemma.

In *Catabrosa aquatica* subsp. *aquatica* spikelets are most commonly (1) 2 (3)-flowered, but are occasionally 1-flowered (usually with a few 2-flowered spikelets),

or are 2 – 4-flowered, and rarely are up to 7-flowered (Maire 1955; Bor 1970). Plants with predominantly 1-flowered spikelets are occasional in collections from across Eurasia and are infrequently found in North America. Although such plants are sometimes taxonomically recognised as subsp. *minor* (Bab.) F. H. Perring & P. D. Sell, var. *uniflora* Gray, var. *littoralis* Parn., or var. *laurentiana* Fern. (Scoggan 1978; Sell & Murrell 1996), the single-flower state is generally regarded as variation within individual inflorescences, within plants, or within populations, and is generally considered as taxonomically of minor significance (Bor 1970; Tzvelev 1976; Tutin 1980; Mill 1985; Barkworth 2007). We consider the 1-flowered depauperate plants from high elevations and northern latitudes to be variations within *Cat. aquatica* subsp. *aquatica*.

About a quarter of the European and Asian specimens examined at US have sparse short vermiform pubescence on the keel and marginal veins, infrequently a few hairs between the veins. The species has glabrous lemmas in the New World.

In *Catabrosa aquatica* the lower glumes are $1/6 - 1/2$ to the proximal lemma, and the upper glumes $1/2 - 2/3$ ($3/4$) the proximal lemma. In *Col. drakensbergense* the lower glumes $1/2 - 2/3$ the proximal lemma, and upper glumes $(2/3)^{3/4}$ to nearly equalling or slightly exceeding the proximal lemma.

Specimens at US from central Asia and trans-Caucasia, show that shorter spikelets (uniflorate 1.5 – 2.2 mm, biflorate 2 – 2.8 mm (up to 4 or 5-flowered as illustrated in the original publication of *Poa pseudairoides* J. C. G. Herrm. (Herrmann 1812)) with proportionally shorter glumes can be found combined with short lemmas (1.5 – 2.2 mm) that have moderately dense pilose hairs on and sometimes between the veins (Tzvelev 1976). These plants correspond to *Catabrosa aquatica* subsp. *pseudairoides*. *Catabrosa aquatica* subsp. *pseudairoides* occurs in Azerbaijan, Iran, Iraq, Palestine, South-Central Russia, Syria, Turkey, Uzbekistan (Tzvelev 1976; Mill 1985). Mill indicated it intergrades with subsp. *aquatica* in Turkey. Specimens at US from across Europe and Asia that are larger-flowered than subsp. *pseudairoides* frequently have sparse hairs on the lemma keel and veins and between veins. There seems to be no sharp line of demarcation between these forms and they are frequently mounted together on herbarium sheets. Another subspecies, *Cat. aquatica* subsp. *capusii* (Franch.) Tzvelev, of south central Asia, is excluded from the discussion as it has linear appressed and short branched panicles, unlike other *Catabrosa* taxa or *Col. drakensbergense*.

Catabrosa aquatica has highly variable upper glume and lemma shapes, which are indicated in the genus name: “Greek *catabrosis*, an eating, referring to the erose or ‘nibbled’ glumes” (Fernald 1950: 127), or, “Gr. *katabrosis*, an eating up or devouring or gnawing, an obscure allusion, but supposed to refer to the erose tips of the lemmas which are membranous and torn” (Bor

1970: 58). The glumes are commonly lanceolate, oblanceolate or obovate, apically acute, obtuse, sub-flabellate, or truncate, often with irregular margins. The lemmas tend to be apically truncate to sub-flabellate, but also range to obtuse or acute, and are often erose. In *Colpodium drakensbergense* the glumes are oblanceolate, and apically obtuse or slightly acute, and the lemmas tend to be acute or slightly obtuse. But this is also true of the glumes and lemmas of 1-flowered specimens of *Cat. aquatica* in Eurasia. In *Col. drakensbergense*, although the spikelets are predominantly 1-flowered within inflorescences, isolated 2-flowered spikelets, or zones of predominantly 2-flowered spikelets occur in some inflorescences of the same plants. Actually, it is fairly remarkable how within *Catabrosa* (including *Col. drakensbergense*) the morphology of bracts changes in length and shape with the reduction to 1-flowered spikelets, and how the rachilla extension varies between vestigial and absent in those spikelets. This demonstrates how plastic grass spikelet morphology can be (Soreng *et al.* 2007).

In the type collection of *Colpodium drakensbergense* we separate forms “A” and “B” on the grounds that someone may decide in the future that they represent different taxa, or variations within a hybrid swarm, and it should be clear which form is represented by the type. The species stands only slightly apart from *Catabrosa aquatica*. However, as it has longer glumes and this expands the circumscription of *Catabrosa* and would expand it for *C. aquatica* for this trait, we treat it as a distinct species here.

Catabrosa drakensbergense (Hedberg & I. Hedberg) Soreng & Fish **comb. nov.** Lectotypus: Lesotho, Sani Pass, Sani Pass Lodge, 2850 m, in small dried-out pools, 1 Feb. 1982, O. Hedberg 82088 “A” (lectotype UPS-V-061119 p.p. “A”, **selected here**; isotype PRE-805594 p.p. “A”) Fig. 1.

<http://www.ipni.org/urn:lsid:ipni.org:names:77111274-1>

Colpodium drakensbergense Hedberg & I. Hedberg, *Nordic J. Bot.* 14: 606 (1994).

DISTRIBUTION. Lesotho (see [Materials](#) section).

SPECIMENS EXAMINED. (see [Materials](#) section).

HABITAT. Alpine bogs and shallow streams.

CONSERVATION STATUS. We have seen 16 different collections from northeastern Lesotho in the Drakensberg Mts. Ten of these are from the vicinity of Sani Pass. None of the sites are in national or conservation parks. Overgrazing and human activities that affect wet lands are very real threats.

NOTES. Plants like the lectotype (form “A”) have: 1-flowered spikelets (rare 2-flowered spikelets within some inflorescences); a rachilla extension absent or sometimes present but vestigial (up to 0.2 mm long); mature lemmas usually sparsely pubescent between the veins

and sometimes on the keel and marginal veins (immature lemmas are glabrous within the same inflorescence); spikelets 2.5 – 3.5 mm long; lower glume $1/2 - 2/3$, and the upper glume $3/4$ to nearly equalling or slightly exceeding, the proximal lemma in length.

Plant “B” on the lower left hand side of the lectotype is excluded from the type as: the spikelets are 1 or (in at least half of the spikelets) 2-flowered; lemmas mostly glabrous (rarely with a few hairs on the sides between the veins), generally purple tinged, 1.9 – 2.5 mm long (to the tip of the proximal lemma); lower glumes $1/2 - 2/3$ and upper glumes $2/3$ to nearly equal to the proximal lemma in length.

In all this material the upper glumes are slightly longer and generally more pointed than is typical for *Catabrosa aquatica* (lower $1/6 - 1/2$ and upper $1/2 - 2/3$ the proximal lemma).

Except for a report of a single Drakensberg collection as *Catabrosa aquatica* (Anderson 1969), this and all subsequent gatherings of the taxon from Lesotho have been reported as *Colpodium* (van Zinderen Bakker & Werger 1974; Gibbs Russell *et al.* 1990; Hedberg & Hedberg 1994). Beyond Lesotho, the genus *Catabrosa* is known in Africa only from infrequent collections of *Catabrosa aquatica* from northwest Africa (Algeria, Libya, Morocco; Clayton, Harman & Williamson online). *Cat. aquatica* was treated for North Africa by Maire (1955: fig. 418), and the description and figure clearly apply to the typical form of the species, subsp. *aquatica*, with 2 or more florets per spikelet and typically short glumes. Here we provide a key to the four species of *Catabrosa* and *Colpodium*, as we understand them, that are found in Africa.

Key to species of *Catabrosa* and *Colpodium* in Africa

1. Glumes equal (or slightly unequal) in length, lanceolate to broadly lanceolate, as long or longer than the lemma (sometimes just slightly shorter in some spikelets); spikelets strictly 1-flowered, rachilla extension absent; palea surfaces scarious hyaline, with thin keels; hilum narrowly elliptical to oblong (c. 0.1 mm wide), little differentiated from the caryopsis in colour; upper culm sheaths closed up to $1/5$ their length; plants tufted, not stoloniferous. (*Colpodium* s.s.) 2
1. Glumes distinctly unequal in length, upper glume broadly lanceolate to oblanceolate or obovate, usually shorter than the proximal lemma; spikelets 1 or more flowered, rachilla extension present or absent in 1-flowered spikelets (vestige up to c. 0.2 mm long), rachilla well developed in spikelets with 2 or more florets; palea surfaces subchartaceous, with thick keels; hilum oblong, elliptical to round (c. 0.15 – 0.25 mm wide), distinctly darker than the caryopsis; upper culm sheath closed $1/4 - 3/4$ or more the length; plants stoloniferous or tufted. (*Catabrosa*) 3
2. Spikelets (3.5) 3.7 – 6.5 mm long; panicle usually contracted, if open then with all branches erect (rarely one reflexed); palea distinctly shorter than lemma; (Kenya, and Tanzania) ***Colpodium chionogeiton***
2. Spikelets 2.4 – 3.5 (4.1) mm long; panicle branches spreading soon after emergence, mature panicle open with at least some reflexed branches; palea equal or subequal lemma in length; (Ethiopia, Kenya, and Tanzania) ***Colpodium hedbergii***
3. Upper glume ($2/3$) $3/4$ to equalling the proximal lemma in length; spikelets mostly 1-flowered, sometimes 1 – 2 flowered; (Lesotho) ***Catabrosa drakensbergense***
3. Upper glume $1/3 - 2/3$ ($3/4$) the length of the lemma; spikelets 2 – 4 (7)-flowered; (Algeria, Libya, and Morocco) ***Catabrosa aquatica***

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