

Phylogenetics of *Piptatherum* s.l. (Poaceae: Stipeae): Evidence for a new genus, *Piptatheropsis*, and resurrection of *Patis*

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Abstract Historically, there has been taxonomic confusion among agrostologists regarding the short-spikeleted Stipeae. We refer to these as the *Oryzopsis/Piptatherum* complex which consists of short-spikeleted species with coriaceous to cartilaginous and often caducous-awned lemmas, and florets with a blunt callus. We conducted a phylogenetic analysis of 53 species that have been associated with this complex using four plastid regions (*ndhF*, *rpl32-trnL*, *rps16-trnK*, *rps16* intron) in combination with lemma micromorphology to infer evolutionary relationships. *Piptatherum* as currently circumscribed is polyphyletic and is found in five strongly supported clades in our maximum likelihood tree. Based on our phylogenetic and morphological evidence we recognize a Eurasian *Piptatherum* s.str., propose a new genus, *Piptatheropsis*, to include five North American species, and resurrect the genus *Patis* to include three species, two from Eurasia and one from North America. We provide morphological descriptions of *Patis*, *Piptatherum*, and *Piptatheropsis*, and provide keys to the genera and species of the *Oryzopsis/Piptatherum* complex. The following new combinations are made: *Patis obtusa*, *Patis racemosa*, *Piptatheropsis canadensis*, *Piptatheropsis exigua*, *Piptatheropsis micrantha*, *Piptatheropsis pungens*, *Piptatheropsis shoshoneana*, *Piptatherum brachycladum*, and *Piptatherum kopetdagense*.

Keywords classification; lemma micromorphology; plastid DNA sequences; phylogeny; Pooideae

Supplementary Material The alignment is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

■ INTRODUCTION

Of approximately 600 species currently ascribed to the tribe Stipeae Dumort., over 170 species have been attributed at various times to either *Oryzopsis* Michx. and/or *Piptatherum* P. Beauv. We refer to these as the *Oryzopsis/Piptatherum* complex, which consists of short-spikeleted species with coriaceous to cartilaginous and often caducous-awned lemmas, and florets with a blunt callus. The taxonomic history of species placed in this complex has been equivocal and controversial. The array of other genera that were subsequently invoked to represent the different members of this complex is also substantial. A partial list of these includes: *Stipa* L., *Agrostis* L., *Milium* L., *Urachne* Trin., *Achnatherum* P. Beauv., *Panicum* L., *Dilepyrum* Raf., *Eriocoma* Nutt., *Fendleria* Steud., *Garnotia* Brongn., *Caryochloa* Trin., *Ptilagrostis* Griseb., *Piptochaetium* J. Presl, *Anatherostipa* (Hack. ex Kuntze) Peñailillo, *Anemanthele* Veldkamp, and *Nassella* (Trin.) E. Desv. In modern treatments (Roshevitz, 1951; Freitag, 1975; Barkworth, 1993, 2007; Dorn, 2001) the name *Piptatherum* is reserved for about 25 species from the Old World and six species from the New World (chiefly from North America), while *Oryzopsis* s.str. is segregated as a monotypic genus confined to North America. However, despite providing a solid concept for *Piptatherum*, clearly distinguishing it from *Achnatherum* or *Stipa*, new molecular and micromorphological

data (Barkworth & Everett, 1987; Barkworth & al., 2008; Romaschenko & al., 2008, 2010) suggest that a reevaluation of the phylogenetic relationships among species of this complex is necessary.

The origin of confusion. — *Piptatherum* (from: πίπτω – fall, and ἀθήρ – awn) was described by Palisot de Beauvois (1812) to accommodate awn-bearing species of *Milium* which, as proposed by Linnaeus (1753), was considered an artificial assemblage. Initially, four species of *Milium* were recognized: *M. multiflorum* Cav. (= *Piptatherum miliaceum* (L.) Coss.), *M. coerulescens* Desf. (= *P. coerulescens* (Desf.) P. Beauv.), *M. paradoxum* (L.) L. (= *P. paradoxum* (L.) P. Beauv.), and *M. punctatum* L. (= *Eriochloa punctata* (L.) Desv. ex Ham.). An earlier counterpart to *Milium* in Linnaeus (1753, 1764) was the genus *Agrostis* in which *P. miliaceum* and *P. paradoxum* were placed. In the 1764 edition of *Genera Plantarum* the concept of *Agrostis* was altered to exclude the awned lemma from the set of defining generic features. It can be assumed that Linnaeus considered *Milium* (represented then only by *M. effusum* L.) an awnless genus, although this was not explicitly stated in the description. Moreover, since the 1764 edition, *Milium* has accommodated several species with awned lemmas including *Milium paradoxum* segregated from *Agrostis*. Based on a treatment of *Agrostis miliacea* by Gouan (1773), Cavanilles (1802) transferred this species into *Milium*, adding an ample

description of the gross morphology. The last addition to the set of the *Milium* species that was used by Palisot de Beauvois (1812) to establish a new genus was made by Desfontaines (1798) when he described *M. coerulescens*, providing a thorough description of the generative parts of the plant including such characters as caducous awn, obtuse, black, shiny lemma, and purplish glumes. Desfontaines (1798) acknowledged a close affinity of this species to *M. paradoxum*, which presumably enabled Palisot de Beauvois (1812) to outline the concept and scope of *Piptatherum*. The main set of the characters applied to define the genus thus included coriaceous lemma and palea, caducous awn and subemarginate apex of the lemma. Considering the set of species attributed to the genus this pattern was inconsistent since the awn of *P. paradoxa* is persistent, the lemma apex of *P. coerulescens* is not emarginate, and the lemma of *P. miliaceum* is not coriaceous. Moreover, *P. miliaceum* was simultaneously merged into a new genus, *Achnatherum*, as *Achnatherum miliaceum* (L.) P. Beauv. The confusion might have arisen from using different basionyms—*Milium multiflorum* and *Agrostis miliacea*, and from working with inexplicit descriptions of the species. In agreement with the description of *Achnatherum*, *P. miliaceum* indeed possesses stiff membranous lemmas with emarginate apices. These features were not listed in the previous accounts but have recently been verified by personal observation of the senior author. Nevertheless, in the description of *Milium multiflorum*, Cavanilles (1802) clearly stated that his diagnosis was based on *Agrostis miliacea*, the name that Palisot de Beauvois (1812) used to establish his *Achnatherum miliaceum*. Whatever the reason for double placement of *P. miliaceum* in *Agrostis* and *Piptatherum*, this example illustrates the transitional nature of generic descriptions resulting in ambiguity, and ultimately affecting the taxonomic usage for the next 200 years (Roshevitz, 1951; Freitag, 1975; Tzvelev, 1977; Barkworth & Everett, 1987; Romaschenko & al., 2010). However, the taxonomic position of *Piptatherum paradoxum*, or its eastern counterpart, *P. virescens* (also with emarginate lemma apices), has never been questioned.

Oryzopsis (from: $\rho\rho\upsilon\zeta\alpha$ – rice, and $\rho\upsilon\tau\iota\varsigma$ – aspect) was described from steep and rocky soils of mountainous regions of Quebec near Hudson Bay by Michaux (1803). Palisot de Beauvois (1812) acknowledged close affinity of *Oryzopsis* to his newly described *Piptatherum* but preserved it as a separate taxon partly because it had a single style versus two in *Piptatherum*. However, Palisot de Beauvois (1812: 19) said he did not have the opportunity to examine the *Oryzopsis* material on which Michaux based his description.

History of the *Oryzopsis/Piptatherum* complex. — The first attempts at classifying all known short-spikeleted Stipeae were made by Trinius (1820, 1824, 1834) and Trinius & Ruprecht (1842) who described *Oryzopsis* as differing from *Piptatherum* by having a prominent ring of dense, long hairs at the base of the lemma. Initially, *Oryzopsis* was aligned with *Stipa*, but then was transferred to *Urachne* (Trinius, 1824, 1834). *Urachne* thus became the first union of the elements of the *Oryzopsis/Piptatherum* complex. These were placed in five subgenera: Old World—*Urachne* subg. *Piptatherum* (P. Beauv.) Trin. & Rupr. (with short styles, laterally exerted at anthesis);

New World—subg. *Oryzopsis* (Michx.) Link (with long styles and apically exerted at anthesis), subg. *Eriocoma* (Nutt.) Trin. & Rupr. (a single species, currently recognized as *Achnatherum hymenoides*), subg. *Nassella* Trin., and subg. *Piptochaetium* (J. Presl.) Trin. & Rupr. (Trinius & Ruprecht, 1842). In addition to the species previously included in *Piptatherum* by Palisot de Beauvois (1812), *Urachne* subg. *Piptatherum* included: *U. songarica* Trin. & Rupr. (= *P. songaricum* (Trin. & Rupr.) Roshev. ex Nikitina) and *U. grandiflora* Trin. (= *P. holciforme* (M. Bieb.) Roem. & Schult.); and *Urachne* subg. *Oryzopsis* included: *U. asperifolia* Trin. (= *Oryzopsis asperifolia* Michx.), *U. micrantha* Trin. & Rupr. (= *Piptatherum micranthum* (Trin. & Rupr.) Barkworth), *U. brevicaudata* Trin. (= *P. pungens* (Torr.) Dorn), and *U. racemosa* Trin. (= *P. racemosum* (Sm.) Eaton). Without regard to the inclusion of *Oryzopsis asperifolia*, Trinius & Ruprecht (1842) were the first to recognize the New World lineage of *Piptatherum* as a natural entity.

Piptatherum was not recognized by Link (1827) in his treatment of *Urachne* where he split the genus into two subgenera: *Urachne* subg. *Verae* Link (analog of Trinius' subg. *Piptatherum*) and subg. *Oryzopsis*. His *Urachne* subg. *Oryzopsis* included *U. melanosperma* Link. (= *Piptatherum racemosum*) and *U. leucosperma* Link (= *Oryzopsis asperifolia*). The subgenera roughly represented Old World and New World branches of the *Oryzopsis/Piptatherum* complex. However, the characters used to differentiate among them, i.e., lax panicles with multi-spikeleted branches versus contracted panicles with single to few-spikeleted branches, had limited utility. Nevertheless, the treatment of *Urachne* by Link (1827) still reflected a general tendency to associate this genus with *Milium*, based on having short, elliptic and coriaceous florets, rather than with *Stipa* and *Achnatherum*. In Link's scheme *Urachne* was placed in his "division" Miliaceae along with *Milium* while *Stipa*, *Aristida* L., and *Lasiagrostis* Link (= *Achnatherum*) were placed in Stipaceae. With the exception of having awnless lemmas and two lodicules, *Milium* indeed bears striking resemblance to some species of *Piptatherum*. Among shared features are coriaceous lemmas that envelop the paleas along the margin and florets with an obtuse callus that are dorsally compressed. *Milium* resembles *Piptatherum miliaceum* by having a short hilum (Freitag, 1975). Koch (1837, 1846) apparently started the tradition of including *Milium* in Stipeae, a misconception which although not widely accepted, repeatedly resurfaced in taxonomic literature until the second part of the 20th century (e.g., Freitag, 1975; Clayton & Renvoize, 1986).

Bentham & Hooker (1880) recognized *Piptatherum* as a section in an enlarged *Oryzopsis* of Old World species with equilateral lemmas and a subcentral awn. All New World short-spikeleted species (except *Eriocoma*) were placed in *O.* sect. *Euoryzopsis*. This work was followed by Spegazzini (1901, 1925) who employed *Oryzopsis* for a wide range of short-spikeleted South American species now placed in *Nassella* or *Piptochaetium*. Hackel (1887, 1890) followed Trinius (1834) by dividing *Oryzopsis* into two subgenera based on geographic distribution. The scheme of Hackel became very influential for the major part of 20th century (Roshevitz, 1934; Grigoriev, 1940; Hitchcock, 1951; Bor, 1970; Kam & Maze,

1974). *Piptatherum* was reinstated as a genus by Roshevitz (1951) who combined both the approaches of Hackel (1890) and Bentham & Hooker (1880), while maintaining *Nassella* and *Piptochaetium* as separate New World genera.

In a thorough revision of the Old World *Piptatherum*, Freitag (1975) made a detailed analysis of the floret revealing that characteristics such as transverse elliptic or linear disarticulation scars and basally unfused lemma margins occurred in all examined species except *P. miliacea* and *P. virescens*.

Evolutionary theories. — Evolutionary inferences for *Piptatherum* preceding molecular studies are scarce (Tzvelev, 1977; Barkworth & Everett, 1987; Barkworth, 1993). Tzvelev (1977) suggested that *Piptatherum* represented a specialized, derived branch of *Achnatherum* through *P.* sect. *Virescentia* Roshev. ex Freitag (*P. virescens*, *P. paradoxum*) and *Achnatherum chinense*.

There have been several attempts to infer the molecular phylogeny of Stipeae including several species of *Piptatherum* and *Oryzopsis* (Jacobs & al., 2000, 2007; Barkworth & al., 2008; Cialdella & al., 2010). These analyses all revealed scattered placements for the species currently residing in *Piptatherum*, casting doubt upon its monophyly. In the ITS analysis of Jacobs & al. (2007) some species of American *Piptatherum* (*P. canadense*, *P. shoshoneanum*, *P. micranthum*, *P. exiguum*) were aligned with *Piptochaetium*; *P. miliaceum* was isolated on a long branch; *P. pungens*, another member of American *Piptatherum*, was found embedded among species of *Jarava*; Eurasian *P. paradoxum* was aligned with *Anisopogon*; and Eurasian *P. laterale* and *P. songaricum* were found in the same clade with *Diarrhena*. The multigene analysis of Barkworth & al. (2008) presented a different pattern: *P. miliaceum* was loosely aligned with *Stipa parviflora* and *Austrostipa*; *P. canadense* and *P. micranthum* formed a basal unresolved lineage loosely aligned with *P. holciforme* and *P. microcarpum*; and *P. virescens* was loosely aligned with some species of Eurasian *Achnatherum*.

In our previous molecular analyses of the Stipeae (Romaschenko & al., 2008, 2010) we presented well-supported phylogenetic schemes with few ambiguities. Based on 10 plastid regions our phylogenetic tree (Romaschenko & al., in prep.) consisted of four major clades in the tribe, three retaining the plesiomorphic lemma epidermal pattern (LEP) condition of long and sinuate fundamental cells (saw-like pattern), while a fourth clade was supported by an LEP with short fundamental cells (maize- or ladder-like pattern). Old World and New World species were strongly separated with a single exception. In the first clade there was an Old World subclade comprising *Stipa*, *Ampelodesmos*, *Psammochloa*, *Oryzopsis asperifolia* (the New World exception), *Trikeriaia*, *Orthoraphium*, and *Ptilagrostis*. Its sister subclade was strictly New World, including *Aciachne*, *Anatherostipa*, *Hesperostipa*, *Lorenzochloa*, *Ortachne*, American *Piptatherum*, and *Piptochaetium*, along with *Pappostipa* (a polyploid genus of ambiguous, possibly reticulate origin, with a maize-like LEP). The second and third clades included *Piptatherum kuoi* and *Patis coreana* (= *Achnatherum coreanum* (Honda) Ohwi), and 10 species of Old World *Piptatherum*, respectively. The fourth clade included species with

short fundamental cells we tentatively called “achnatheroid grasses”. These were divided into: an Australian clade with *Anemanthele* and *Austrostipa*; three Eurasian clades: one with four species in the “*Timouria* group”; a second with two species of *Piptatherum* (*P. miliaceum*, *P. thomasi*); and a third with *Achnatherum* including *Piptatherum virescens* and *P. paradoxum* (both in *Piptatherum* sect. *Virescentia*); and a major American clade divided into an “*Eriocoma* group” subclade and a subclade with *Jarava*, a “*Pseudoeriacoma* group”, *Amelichloa*, and *Nassella*. Thus: *Oryzopsis asperifolia*, Old World *Piptatherum*, and New World *Piptatherum* are distantly related; species of *Piptatherum* sects. *Miliacea* and *Virescentia* belong to achnatheroid grasses rather than within the other Old World *Piptatherum* s.str.; and the taxonomic position of the *P. kuoi* needs to be reassessed (Romaschenko & al., in prep.).

In our present study we provide the latest estimates of the phylogeny for a large set of species that currently or formerly were included in the *Oryzopsis/Piptatherum* complex by analyzing four sequences from the plastid genome—*ndhF*, *rpl32-trnL*, *rps16-trnK*, and the *rps16* intron. We include 287 new sequences in our study. Twenty-two species of the Eurasian *Piptatherum* are surveyed (12 of these have never been used in a molecular analysis), and we include the complete set of American species of *Piptatherum*. Based on our phylogenetic and lemma micromorphological evidence we propose a new genus, *Piptatheropsis*, and resurrect *Patis*. In addition, we provide morphological descriptions, a key to the genera, and make the necessary nomenclatural changes.

■ MATERIALS AND METHODS

Taxon sampling. — The dataset of 87 accessions includes representatives of all known phylogenetic groups that contain short-spikeleted species of the Stipeae (Romaschenko & al., 2010), and a majority of the species with short spikelets attributed to *Oryzopsis* or *Piptatherum*. Sampling was intended to represent the taxonomic and geographical diversity of *Piptatherum* in its current sensu lato state. The major lineages of Stipeae species with elongated spikelets were also included in the analysis. All seven North American species of *Piptatherum* are represented in the analysis, along with *P. racemosum*, which was not in our previous analyses (Romaschenko & al., in prep.). Seven North American species of *Achnatherum* with short spikelets that sometimes have been attributed to *Oryzopsis* or *Piptatherum* were included in the study. Of these, four species (*A. contractum*, *A. bloomeri*, *A. swallenii*, and *A. webberi*) have never been phylogenetically analysed. Eurasian *Piptatherum* was represented by 22 species (approximately 80% of the Old World species) of which 18 are used in our molecular analysis for the first time. These 22 species represent most of the sections and/or subsections within *Piptatherum* described by Roshevitz (1951) and Freitag (1975). We were not able to obtain several species from *P.* sect. *Himalayana* Roshev. ex Freitag. We included *Piptatherum keniense* (Pilg.) Roshev. (currently treated as *Stipa keniensis* (Pilg.) Freitag) from the sub-Saharan in Tanzania to South Africa, to represent the southern border of

the distribution of *Piptatherum*. The voucher information and accessions for molecular data are presented in the Appendix. In determining the species of Eurasian *Piptatherum* we followed the narrow species concept of Roshevitz (1951), rather than the wider concept of Freitag (1975).

DNA extraction, amplification, and sequencing. — All procedures were performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution. DNA isolation, amplification, and sequencing of *ndhF*, *rpl32-trnL*, *rps16-trnK*, and *rps16* intron was accomplished following procedures outlined in Peterson & al. (2010a, b) and Romaschenko & al. (2010). We specifically targeted these four plastid regions that proved to be most informative in our previous studies on stipooid grasses (Romaschenko & al., 2010). Eighty-two percent (287) of the sequences used in our study are newly reported in GenBank and only 2.9% (10) are missing data.

Phylogenetic analyses. — Sequences of *ndhF*, *rpl32-trnL*, *rps16-trnK*, and the *rps16* intron were aligned using Muscle (Edgar, 2004) implemented in Geneious v.5.3.4 (Drummond & al., 2010) and then adjusted manually in BioEdit v.7.0.5 (Hall, 1999). We identified models of molecular evolution for the cpDNA regions using jModeltest (Posada, 2008). For three regions (*ndhF*, *rpl32-trnL*, *rps16-trnK*), the Akaike Information Criterion (AIC) indicated different models from the GTR family of which the model for *rps16-trnK* had equal among-site variation (Table 1). For the *rps16* intron the best-fit model was K80+G (Kimura, 1981), which distinguishes between transitions and transversions (ti/tv, ratio in Table 1) and assumes

equal base frequencies. The low gamma shape parameter (α) for this region also indicated strong rate heterogeneity in our data. To calculate bootstrap support for clades we tested both maximum parsimony (MP) and maximum likelihood (ML) approaches. jModeltest indicated a dissimilarity among substitution models with a substantial range of likelihood scores across the 88 models, and rate heterogeneity in the data (Table 1). These conditions favor the use of ML to infer bootstrap values rather than MP which may be biased because of high rate heterogeneity in the data. Therefore, only ML and Bayesian inference (BI) searches were used to calculate statistical support for the clades. The combined data set was partitioned into four region subsets and the ML parameters fixed according to AIC criteria.

The ML analysis of combined sequences was performed with the program GARLI v.0.951 (Zwickl, 2006) using the Metropolis-Hastings algorithm for analyzing heterogeneous datasets (Ronquist & Huelsenbeck, 2003). In addition to the ML analysis, we performed MP analyses of separate and combined datasets using PAUP* v.4.0b.10 (Swofford, 2000). Each heuristic search was conducted with 1000 replicates of random sample additions with tree bisection-reconnection branch swapping. The gaps were treated as missing data. The incongruence length difference (ILD) test (Farris & al., 1994) was implemented in the program WinClada v.1.00.08 (Nixon, 2002) to test for incongruence among the plastid datasets. Default parameters for 1000 replicates were executed. Bootstrap analyses (Felsenstein, 1985) were performed using GARLI with 1000 repetitions, and the

Table 1. Summary of the four plastid regions and parameters used in maximum likelihood and Bayesian searches indicated by Akaike Information Criterion (AIC).

	<i>ndhF</i>	<i>rpl32-trnL</i>	<i>rps16-trnK</i>	<i>rps16 intron</i>	Combined data
Total aligned characters	782	953	813	838	3386
Proportion of excluded characters [%]	–	20.9	0.8	6.7	28.5
Range of Likelihood scores across 88 models [–lnL]	3234.6472– 3010.1008	3011.0283– 2865.5759	2447.1615– 2303.9237	2140.6894– 2025.7810	–
Number of substitution types	6	6	6	2	–
Model for among-site rate variation	Gamma	Gamma	Equal	Gamma	–
Substitution rates of GTR model	1.0000 2.1294 0.6067 0.6067 2.1294	0.7922 1.3941 0.4217 0.8776 1.3941	1.0000 2.8105 0.9468 0.9468 2.8105	–	–
Character state frequencies	Equal	0.3720 0.1412 0.1291 0.3577	0.3002 0.1524 0.1508 0.3965	Equal	–
Kappa (ti/tv)	–	–	–	1.596 (0.798)	–
Proportion of invariable sites	0.6280	0.0	0.0	0.0	–
Substitution model	TPM1+I+G	TVM+G	TPM1uf	K80+G	–
Gamma shape parameter (α)	1.0650	0.8723	–	0.0550	–

program PAUP* v.4.0b10 (Swofford, 2000) was used to compute the bootstrap majority-rule consensus tree.

Bayesian posterior probabilities (PP) were estimated using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Initially, the analysis was set to run for two million generations with a sample frequency set for 100. The analysis was continued until the convergence diagnostic (standard deviation of split sequences) dropped below 0.01. The fraction of the sampled values discarded as burn-in was set at 0.25. Posterior probabilities of 0.95–1.00 were considered significant.

Two representatives of tribe Phaenospermateae Clayton (Clayton & Renvoize, 1986; Schneider & al., 2009), *Duthiea brachypodium* (P. Candargy) Keng & Keng f. and *Phaenosperma globosa* Munro ex Benth. were chosen as the outgroup since this tribe was shown to be sister to the Meliceae–Stipeae–Diarrheneae lineage (Romaschenko & al., 2008, 2010; Davis & Soreng, 2010).

Scanning electron microscopy. — All studies of lemma ultrastructure were performed at varying magnifications on a Jeol (JSM35C, Japan) scanning electron microscope (SEM) housed at the M.G. Kholodny Institute of Botany. Dry mature florets from one to four herbarium specimens per species were selected for study. The epicuticular wax on the lemmas was removed by soaking florets in xylene for four hours. Samples were mounted on stubs and then covered with gold from a vacuum spray gun (JII-4X, Japan) before viewing.

■ RESULTS

Analysis of plastid sequences. — The MP analysis of the combined datasets yielded 20 most parsimonious trees of the length of 867 steps. The phylogenetic indices were as follows: consistency index = 0.79, retention index = 0.93, rescaled consistency index = 0.74, and homoplasy index = 0.29. All analyses using MP, ML, and BI yielded phylogenetic trees with the same topology for each region and for the combined dataset. The ILD test ($P = 0.3054–0.9182$; 95% confidence level) failed to reject the null hypothesis of congruence among the ML plastid datasets; therefore, we combined them.

The ML tree from the combined analysis of the four plastid regions (*ndhF*, *rpl32-trnL*, *rps16-trnK*, *rps16* intron) is well resolved with high support for many nodes (Fig. 1). The species currently placed in *Piptatherum* do not align in a single clade and are found in five principal clades. The division of species among principal lineages is as follows: clade A (BS = 100, PP = 1.00) includes most representatives of the American branch of the genus *Piptatherum* (“Piptatheropsis group” sensu Romaschenko & al., 2010), clade B (BS = 100, PP = 1.00) includes *P. racemosum*, Asian *P. kuoi*, and *Patis coreana* (“*Patis* group” sensu Romaschenko & al., 2010); clade C (BS = 100, PP = 1.00) includes 22 Eurasian species of *Piptatherum*; clade D (BS = 100, PP = 1.00) includes Eurasian *Piptatherum* from sect. *Miliaceae* Roshev. ex Freitag (*P. miliacea*, *P. thomasi*); and clade E (BS = 95, PP = 1.00) includes two Eurasian *Piptatherum* sect. *Virescentia* (*P. virescens*, *P. paradoxa*). All species displayed in

boldface in Fig. 1 at one time have been referred in the literature to either *Piptatherum* or *Oryzopsis*.

The relationship of *Oryzopsis asperifolia* within the larger clade including *Stipa* s.str. (represented by *S. eriocaulis* and *S. pennata*) is poorly supported. *Oryzopsis asperifolia* is sister (PP = 0.86) to *Trikeria hookeri–Ptilagrostis dichotoma–P. mongolica*. The separation of a New World clade of species in the upper portion of the tree (bounded by *Ptilagrostis kingii* and *Anatherostipa obtusa*) is only weakly supported (BS = 56; PP = 0.93). *Ptilagrostis kingii* as sister to the American *Piptatherum* is weakly supported (BS = 68; PP = 0.87). Within American *Piptatherum* (clade A in Fig. 1), *P. exiguum* and *P. shoshoneanum* form a clade (BS = 99, PP = 1.00) and are sister to *P. micranthum–P. canadense–P. pungens* (BS = 99, PP = 1.00). *Aciachne* (two species) and *Anatherostipa* (five species, three of which used to be included in *Oryzopsis*) form a strongly supported clade (BS = 96, PP = 1.00), and together they are sister (BS = 99, PP = 1.00) to *Piptochaetium* (four species: two were formally ascribed to *Oryzopsis*). A monophyletic *Hesperostipa* (*H. comata* and *H. spartea*) is strongly supported as sister (BS = 94, PP = 1.00) to the *Piptochaetium–Aciachne–Anatherostipa* clade.

A strongly supported *Patis* clade (BS = 100; PP = 1.00; clade B in Fig. 1) consists of the Asian *Piptatherum kuoi* as sister to a strongly supported clade (BS = 100, PP = 1.00) of Asian *Patis coreana* and North American *Piptatherum racemosum*. *Patis* is moderately supported (BS = 73, PP = 0.98) as sister to the strongly supported clade of *Piptatherum* s.str. plus the achnatheroid clade (C+AC; BS = 95, PP = 1.00).

The remaining Eurasian *Piptatherum* species are divided in two sister clades, clade C (*Piptatherum* s.str.) and the AC clade, both of which have strong support (BS = 95; PP = 1.00; clade C in Fig. 1). Clade C encompasses Mediterranean–Eurasian *P. coerulescens* (type) as sister to the remaining mostly Asian species of the genus (BS = 100, PP = 1.00). The relationship of *P. munroi* with other members of *Piptatherum* clade C (except *P. coerulescens*) is not well resolved, but the other species form two multi-species clades primarily with poor internal structure. The clade supported only by high posterior probability values (BS = 69, PP = 1.00) includes *P. holciforme*, *P. aequiglume*, *P. alpestre*, *P. kokanicum*, *P. ferganense*, *P. songoricum*, and *P. latifolium*, while the other strongly supported clade (BS = 94, PP = 1.00) includes a well-supported clade (BS = 93, PP = 1.00) of *Oryzopsis kopetdagensis* and *Oryzopsis brachyclada* as sister to another clade of 11 species with strong support (BS = 98, PP = 1.00). Relationships among these 11 species were weakly resolved in a trichotomy of *P. molinioides* (un-supported), a *P. fasciculatum–P. sphacellatum* clade (BS = 67, PP = 0.99), and an eight-species clade (BS = 66, PP = 0.99) including *P. laterale*, *P. hilariae*, *P. fedtschenkoi*, *P. microcarpum*, *P. angustifolium*, *P. badachschanicum*, *P. sogdianum*, and *P. vicarium*.

The achnatheroid clade (AC; BS = 100, PP = 1.00) consists of *Celtica gigantea* as sister to the core achnatheroid clade (CAC) with weak support (BS = 65, PP = 0.93), and *Achnatherum chinense–Timouria saposhnikovii–A. caragana* (“*Timouria* group” sensu Romaschenko & al., 2010) with strong

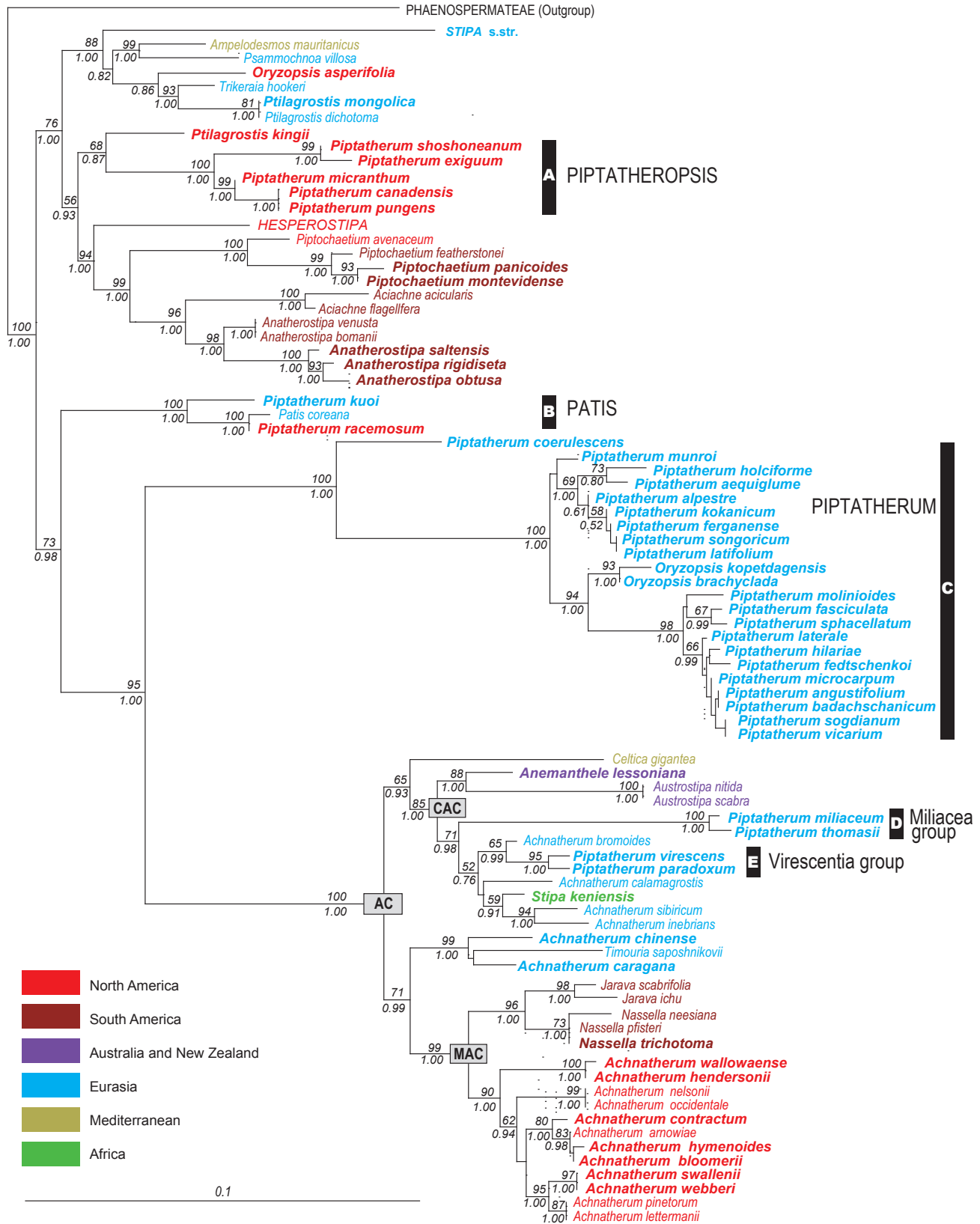


Fig. 1. Phylogram of the ML tree from the analysis of combined *ndhF*, *rpl32-trnL*, *rps16-trnK*, and *rps16* intron plastid sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; taxon color indicates native distribution; species names in bold and larger type have at one time been included in the *Oryzopsis/Piptatherum* complex. **A**, *Piptatheropsis* clade; **B**, *Patis* clade; **C**, *Piptatherum* clade; **D**, Miliacea group; **E**, Virescentia group; **AC**, achnatheroid clade; **CAC**, core achnatheroid clade; and **MAC**, major American clade.

support (BS = 99, PP = 1.00) as sister to the major American clade (MAC) also having strong support (BS = 99, PP = 1.00). The phylogenetic relationships of the species currently or formerly included in *Piptatherum* or *Oryzopsis* within CAC (BS = 85, PP = 1.00) are *Anemanthele lessoniana* as sister to two species of *Austrostipa* (BS = 88, PP = 1.00), a strongly supported clade of *Piptatherum miliaceum* and *P. thomasi* (“Miliacea group”; BS = 100, PP = 1.00), and a strongly supported clade of *Piptatherum virescens* and *P. paradoxum* (“Virescentia group”; BS = 95, PP = 1.00). However, clades D and E are not sister, and clade E is nested within an *Achnatherum* s.str. clade that also includes *Stipa keniensis*.

Within MAC, the short-spikeleted species formerly included in *Oryzopsis* were placed into two strongly supported sister clades. The South American clade (BS = 96, PP = 1.00) includes *Nassella trichotoma* (type)–*N. neesiana*–*N. pfisteri* (BS = 73, PP = 1.00) as sister to *Jarava scabrifolia*–*J. ichu* (BS = 98, PP = 1.00). The North American clade with strong support (BS = 90, PP = 1.00) represents 12 species of *Achnatherum* (“Eriocoma group” sensu Romaschenko & al., 2010). There is strong support for three terminal clades within these 12 species of *Achnatherum* (sensu Barkworth, 1993, 2007) as follows: *A. wallowaense*–*A. hendersonii* (BS = 100, PP = 1.00), *A. nelsonii*–*A. occidentale* (BS = 99, PP = 1.00), and *A. swallenii*–*A. webberi* (BS = 97, PP = 1.00).

Morphological characters.—The Eurasian species of *Piptatherum* share the following morphological features: dorsally compressed florets with a truncate, flat callus and transverse elliptic to linear disarticulation scars; coriaceous lemmas with separate (unfused) borders (Fig. 2A, H) and the lemma marginally enveloping the palea; short styles that exert laterally at anthesis (Fig. 2A). All the other short-spikeleted Stipeae have lemma borders basally fused and distally open or often subadjacent or overlapping (Fig. 2B–G, I), and longitudinally elliptic to circular disarticulation scars that are often grooved (Fig. 2B–G, I). Of the North American species of *Piptatherum*, *P. micranthum* most closely resembles the Eurasian species (Fig. 2B), although it has lemmas that do not envelop the paleas, a rounded callus, circular disarticulation scars (not grooved), and basally fused lemma borders. *Piptatherum* sects. *Miliacea* and *Virescentia* have circular disarticulation scars and basally fused lemma borders (Fig. 2G), which distinguish them from Eurasian *Piptatherum* of clade C.

The lemma epidermal pattern (LEP) of Eurasian *Piptatherum* (Fig. 1C; excluding sects. *Miliacea* and *Virescentia*) and American *Piptatherum* is similar since both have the “saw-like” type and elongated fundamental cells with sinuate walls, and irregularly placed silica body/cork cell pairs (Fig. 2K–N). However, some species of American *Piptatherum* (*P. canadensis*, *P. pungens*) have a “saw-like” LEP with abundant and prominent prickles, somewhat shortened fundamental cells, and rare silica/cork cell pairs. This feature distinguishes American species from Eurasian *Piptatherum* which possesses a lemma surface normally devoid of prickles (Fig. 2J).

Stipa keniensis has a typical achnatheroid “maize-like” LEP with extremely short fundamental cells and regularly placed quadrate silica bodies often lacking cork cells (Fig. 2O).

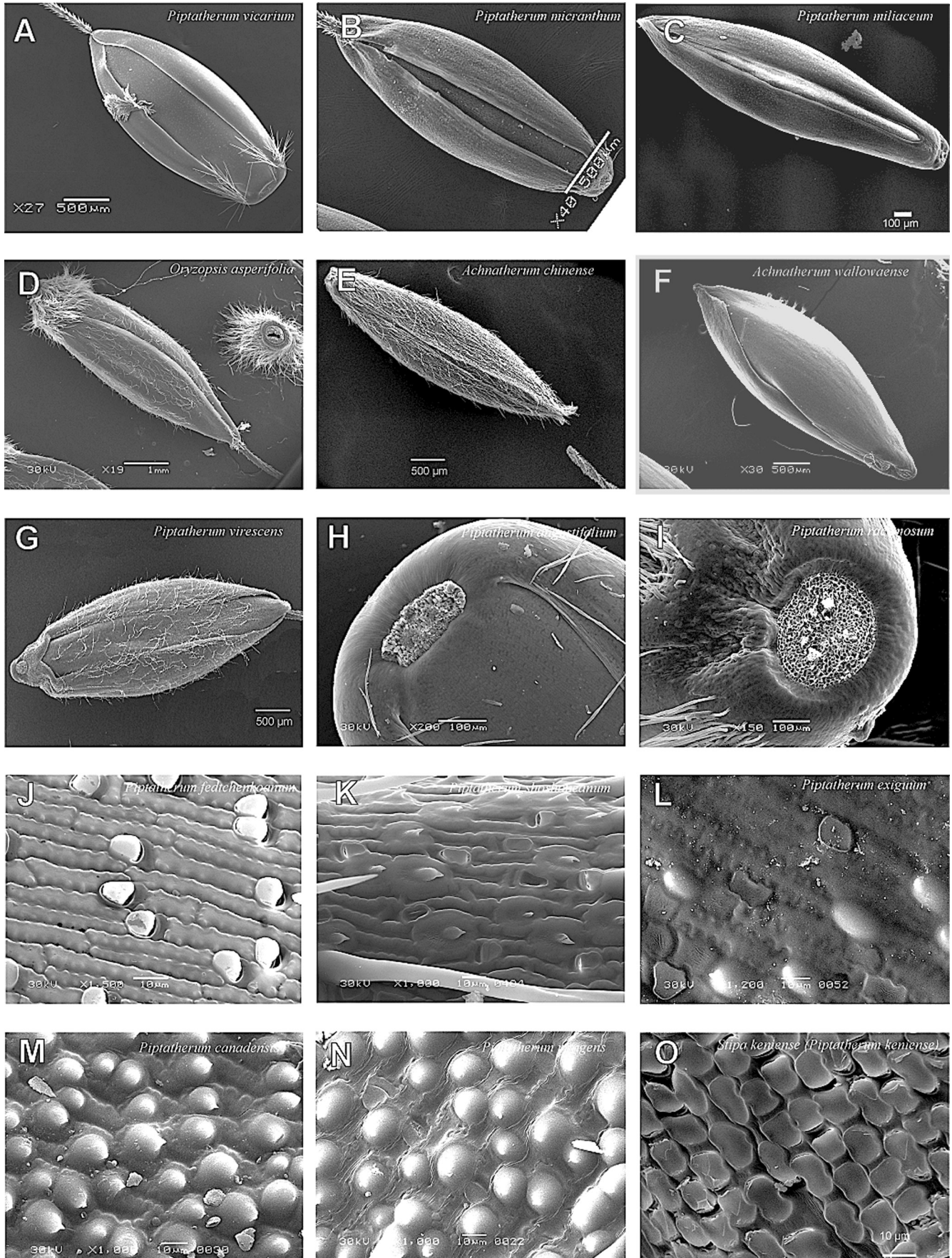
DISCUSSION

The taxonomic history of the *Oryzopsis/Piptatherum* complex represents a concerted attempt by taxonomists to attach phylogenetic meaning to prominent characteristics, i.e., short-spikeleted species with coriaceous to cartilaginous and caducous-awned lemmas, and florets with a blunt callus (Trinius & Ruprecht, 1842; Roshevitz, 1951; Freitag, 1975). The gradual accumulation of new species with a different combination of morphological features made it difficult to maintain this concept of attributing all short-spikeleted Stipeae to either *Piptatherum* or *Oryzopsis*. Our current molecular analysis based on four plastid markers has shown that *Piptatherum*, in its current form (Freitag, 1975; Tzvelev, 1976; Barkworth, 1993, 2007; Dorn, 2001), is polyphyletic and does not represent a natural entity. The misleading placement of *Piptatherum miliaceum* and *P. virescens* in a single genus with *P. coerulescens* by Palisot de Beauvois (1812) was never questioned until our molecular data became available (Romaschenko & al., 2010). Obviously, short-spikeleted species of Stipeae arose multiple times within separate evolutionary lineages. The most striking examples of independent origin of short-spikeleted species are found in *Piptochaetium* (normally with elongated spikelets), Eurasian *Achnatherum* (where short-spikeleted forms are shown to be related to *Achnatherum* sects. *Aristella* (Trin.) Tzvelev and *Achnatheropsis* (Tzvelev) Prob.—both with elongated, fusiform spikelets), and American *Achnatherum* and *Nassella* (Fig. 1).

The type species of *Piptatherum*, as lectotypified by Hitchcock (1920), is *P. coerulescens*. Appropriately, the generic name must be reserved only for the monophyletic group of Eurasian species that have florets with transverse disarticulation scars and non-fused basal borders, including *P. coerulescens*. This circumscription excludes species of *Piptatherum* sect. *Miliacea* (*P. miliaceum*, *P. thomasi*) and sect. *Virescentia* (*P. virescens*, *P. paradoxum*) which represent specialized forms of core achnatheroid grasses. This conclusion is confirmed by our DNA data and the “maize-like” LEP they share. However, taxonomic realignment of these species within the CAC clade, within *Achnatherum*, is problematical and will be assessed in subsequent analyses.

Based on our analysis we are erecting a new genus, *Piptatheropsis*, to accommodate five North American species of *Piptatherum*. The sister to *Piptatheropsis*, *Ptilagrostis kingii*, is only weakly supported with clade A in our current phylogenetic analysis and morphologically the gap between these taxa appears substantial (Barkworth, 1983). In the future we intend to investigate *Ptilagrostis kingii* with a more thorough set of molecular markers in hopes of elucidating its true affinities.

Piptatherum racemosum was included in early taxonomic treatments of North American species of *Oryzopsis*. It was reported as the only polyploid ($2n = 46$; Johnson, 1945) species in this group, and was characterized by having wide and long cauline leaves and underdeveloped basal leaves. Our analysis provides strong evidence for its close relationship with two Asian species, *Patis coreana* and *Piptatherum kuoi*. Both of these species were somewhat anomalous in their respective genera as *Patis coreana* was often attributed to *Achnatherum*



(Ohwi, 1941; Wu & Phillips, 2006), but there was no suspicion that they might share a most recent common ancestor. *Patis coreana* and *Piptatherum kuo* have prominent transverse veinlets between the longitudinal veins of the glumes (these are visible but faint in *P. racemosum*), and all three species have wide, long flag-leaf blades and underdeveloped or absent basal leaf-blades (i.e., they have cataphylls). In addition, *Patis coreana* shares the same chromosome number ($2n = 46$) as *Piptatherum racemosum* (Tateoka, 1986) and has a similar “saw-like” LEP with some minor variations (Romaschenko & al., in prep.). Therefore, we emend the concept of *Patis* to accommodate several newly identified features shared among these three species.

■ TAXONOMIC TREATMENT

Key to the genera of short-spikeleted Stipeae currently placed in *Oryzopsis* or *Piptatherum*

- 1. Disarticulation scar transverse-elliptic or linear, never grooved; callus flattened, never protruding; palea exposed except for the apex; lemma margins free..... *Piptatherum* s.str.
- 1. Disarticulation scar circular or elliptic, often grooved; callus often protruding and conical; palea distally exposed to completely concealed by the margins of the lemma; lemma margins basally fused, sometimes forming small fleshy warts at the junction..... **2**
- 2. Basal leaf blades absent (leaves cataphyllous) or up to 2 cm long; cauline leaves up to 35 cm long and 2 cm wide; glumes 5–9-veined, with faint or prominent transverse veinlets..... **Patis**
- 2. Basal leaf blades well developed (leaves not cataphyllous), 4–90 cm long; cauline leaves similar to basal leaves,

- sometimes shorter or rudimentary; glumes 1–5-veined, transverse veinlets rarely present, never prominent..... **3**
- 3. Callus barbed with a dense ring of long flexuous hairs, hairs 1.0–1.5 mm long; style 1; lodicules 2; awn subcentral; cauline leaves much reduced, only 0.8–1.8 cm long; LEP “saw-like”..... **Oryzopsis**
- 3. Callus glabrous or with short straight hairs not forming a ring, hairs 0.1–0.5 mm long; styles 2; lodicules 3; awn central; cauline leaves well developed, similar to basal leaves or somewhat shorter but not strongly reduced; LEP “saw-like” or “maize-like”..... **4**
- 4. Central vein of the lemma not prominent; anther apices glabrous; LEP “saw-like”; awns caducous and straight, basally slightly twisted or persistent and geniculate with a strongly twisted first segment..... **Piptatheropsis**
- 4. Central vein of the lemma prominent; anther apices minutely bearded; LEP “maize-like”; awns persistent or caducous, straight, never twisted..... **5**
- 5. Lemmas hairy, the white hairs 0.3–0.5 mm long; central vein of lemma grooved; lower glumes 5-veined, with faint transverse veinlets..... **Virescentia group** (*Piptatherum paradoxum*, *P. virescens*)
- 5. Lemmas glabrous; central vein of lemma not grooved; lower glumes 3-veined, without transverse veinlets..... **Miliacea group** (*Piptatherum miliaceum*, *P. thomasi*)

Piptatherum P. Beauv., Ess. Agrostogr.: 17, 173. 1812, emend. Romasch., P.M. Peterson & Soreng – Type: *Piptatherum coerulescens* (Desf.) P. Beauv., Ess. Agrostogr.: 18. 1812, lectotype designated by Hitchcock in Bull. U.S.D.A. 772: 156. 1920.

Plants perennial, tightly to loosely caespitose or shortly rhizomatous. *Culms* 10–100 cm tall, erect, glabrous. *Sheaths* open, glabrous, smooth or scabrous, shorter than internodes. *Ligules* 1–10 mm long, hyaline, acute to obtuse or truncate, often

Fig. 2. Lemma micromorphology of *Piptatherum* s.l. and relatives. **A**, *Piptatherum vicarium* (Fedtschenko 247, LE; Russia) with non-grooved transverse, narrow elliptic scar with basally separated lemma borders, two basal tufts of hair, and laterally exerted styles; **B**, *Piptatherum micranthum* (Peterson 18437, Saarela & Smith, US; Canada) with basally fused lemma borders, non-grooved circular disarticulation scar and exposed palea; **C**, *Piptatherum miliaceum* (Gillett 16094, US; Jordan) with narrow open lemma borders that are fused basally, non-grooved circular scar; **D**, *Oryzopsis asperifolia* (Saarela 384, UBC; Canada) with prominent basal ring of hairs, circular scars, and closed lemma borders; **E**, *Achnatherum chinense* (Petrov s.n., LE; China) with densely hairy lemma with borders joined and basally fused, circular callus, and caducous awn; **F**, *Achnatherum wallowaense* (Maze 1006, Robson & Henn, US; U.S.A.) with circular, slightly grooved scar, overlapping lemma borders that are fused basally, caducous awn; **G**, *Piptatherum virescens* (Romaschenko 445 & Didukh, KW; Ukraine) with open lemma borders that are basally fused, circular scar that is slightly grooved, and hairy lemma; **H**, *Piptatherum angustifolium* (Nepli 144, LE; Tajikistan) with lower part of the floret with lemma borders widely open, transverse narrow elliptic disarticulation scar that is not grooved; **I**, *Piptatherum racemosum* (Dugal 1260, BRY; Canada), lower part of the floret with basally fused lemma borders forming a small flashy wart, circular disarticulation scar that is grooved; **J**, *Piptatherum fedtschenkoi* (Botschantzev 1559, LE; Tajikistan) showing “saw-like” lemma epidermal pattern (LEP) with long and sinuous fundamental cells, silica body/cork cell (SN/CC) pairs abundant, silica bodies rounded, regularly paired with crescent-shaped cork cells, prickles absent; **K**, *Piptatherum shoshoneanum* (Eno 13, US; U.S.A.) showing “saw-like” LEP, with long and sinuate fundamental cells, SB/CC pairs abundant, silica bodies rounded to slightly elongated not regularly paired with crescent- to squared-shaped cork cells, prickles small; **L**, *Piptatherum exiguum* (Reveal 1073, KW; U.S.A.) showing “saw-like” LEP, long and sinuous fundamental cells, SB/CC pairs not abundant, silica bodies rounded to slightly elongated sometimes with shallow contraction, not regularly paired with crescent- to square-shaped cork cells, prickles small; **M**, *Piptatherum canadense* (Raymond s.n., US; Canada, confirmation of Thomasson, 1980) showing “saw-like” LEP, long and sinuous fundamental cells, SB/CC pairs not observed, prickles abundant, prominent; **N**, *Piptatherum pungens* (Hermann 13407, US; U.S.A.) showing “saw-like” LEP, long and sinuate fundamental cells, SB/CC pairs scarce, silica bodies rounded with crescent-shaped cork cells, prickles abundant, prominent; **O**, *Stipa keniensis* (Hansen 6254 & Heemstra, C; Somalia) showing “maize-like” LEP, extremely short fundamental cells, square to slightly elongated silica bodies, cork cells not observed.

lacerated. *Basal leaf blades* 10–30 cm long, 0.7–15.0 mm wide, flat, involute or convolute; abaxial surface glabrous, scabrous; adaxial surface glabrous, scaberulous, pilose to pubescent. *Cauline leaves* 15–31 cm long, 1–12 mm wide; flat to involute; abaxial surface glabrous to scabrous; adaxial surface pilose, scaberulous, glabrous sometimes papillose or tuberculate. *Panicles* 5–37 cm long, lax or contracted. *Branches* 3–15 cm long, ascending to spreading, paired or solitary, rarely up to 4, straight to flexuous, usually scabrous. *Spikelets* 5–14 mm long, ovate to broadly lanceolate, yellowish or pale green often with anthocyanic coloration. *Glumes* subequal, exceeding the floret, purplish, pale green or variegated with purplish back and yellowish, straw-coloured or hyaline margins, sometimes with green back and purple margins and tips; glumes 3–9-veined; apices acute. *Florets* dorsally compressed, linear-lanceolate, lanceolate, ovate, elliptic to broadly elliptic. *Callus* 0.1–0.5 mm long, blunt, flattened, glabrous. *Disarticulation scar* transverse-elliptic or linear, never grooved, peripheral ring not developed. *Lemmas* 2.6–6.5 mm long, coriaceous, hairy or glabrous, sometimes with two tufts of hairs near the base, dark brown to black, shiny at maturity; margins not overlapping, basally free leaving the palea exposed except for the tip; lemma apex obtuse to acute, awned; awn insertion apical, occasionally subapical; lemma lobes rarely developed, small. *Lemma epidermal pattern* “saw-like” (long fundamental cells with sinuous sidewalls); silica bodies often rounded, rarely slightly elongated; cork cells frequent, regularly paired with silica bodies, crescent-shaped, sometimes slightly squared; prickles not developed. *Awns* 1–15 mm long, caducous, rarely subsistent, straight, not twisted. *Paleas* similar to the lemmas in length, texture, and indumentum. *Lodicules* 3. *Anthers* 1.5–3.6 mm long; apex barbate or glabrous. *Styles* 2, sometimes 2 or 3 branched, short, at anthesis, exerted laterally. *Caryopsis* glabrous, ellipsoid. *Hilum* linear, slightly shorter than caryopsis. $2n = 24$.

Note. – Twenty-two species (excluding *Piptatherum* sects. *Miliacea* and *Virescentia*, and *Stipa keniensis*). Eurasia, temperate forests, shrublands, and openings.

Piptatherum brachycladum (Pilg.) Romasch., **comb. nov.** ≡ *Oryzopsis brachyclada* Pilg. in Notizbl. Bot. Gart. Berlin-Dahlem 14: 345–346. 1939 – Type: Kashmir: Nanga-Parbat-Gebiet, Oberes Rakhiot-Tal: Moränen des Ganalo-Gletschers, nach Süden exponierte Hochgras-Matten, 4000 m, 9 Jul 1937, C. Troll 7774 (holotype: B, destroyed?).

Piptatherum kopetdagense (Roshev.) Romasch., **comb. nov.** ≡ *Oryzopsis kopetdagensis* Roshev. in Komarov, Fl. URSS 2: 117, 743, t. 5, f. 17. 1934. – Type: Asia Media. Turcomania in rupestribus montium Kopetdagh, inter St. Kurt-Su et Gaudan, 29 Apr 1912, W. Lipsky 2418 (holotype: LE!).

Piptatheropsis Romasch., P.M. Peterson & Soreng, **gen. nov.** – Type: *Piptatheropsis canadense* (Poir.) Romasch., P.M. Peterson & Soreng.

Gramen perenne, caespitosum. *Culmi* 10–85 cm alti, erecti, scaberuli vel glabri. *Vaginae foliorum* glabrae, laeves

vel scabrae. *Ligulae* 1.0–5.5 mm longae, hyalinae; apice acutae vel truncatae. *Folia basalia* 4–45 cm longa, 0.5–2.5 mm lata, convoluta, involuta aut plana; subtus et supra laevia vel scabra. *Folia caulinarum* 3–11 cm longa. *Paniculae* 3.5–22.0 cm longae, laxae vel contractae. *Rami* 1–12 cm longi, recti vel flexuosi, fere scabri. *Spiculae* 2.5–5.3 mm longae, ovatae, ellipticae, flavidae vel fulvae; saepe absque colore anthocyanae (dilutae in *P. shoshoneano*). *Glumae* subaequalae, longitudine flosculis aequales vel paulo longiores; 1–3(–5) nervia cum apice acuto saepe rotundato. *Flosculi* dorso compressi aut teretes, lanceolati, elliptici vel obovati. *Callus* obtusus, 0.1–0.5 mm longus, fere protrudens, glabrus vel pilosus. *Cicatrix* elliptica vel circularis. *Lemmata* 1.5–6.0 mm longa, pubescentia interdum glabra fulva usque brunnea, 3–5 nervia; marginibus non superpositis, basi connatis, apice plana, rarius emarginata lobis duobus, aristata. *Lemmarum epidermalis typus* “serra-similis”: cellulae fundamentae longae cum parietibus sinuosis; corpora silicea rectangularia vel rotunda, interdum 1–3 contracta; cellulae suberosae quadratae; saepe aculeolatae. *Paleae* lemmati similes longitudinis et indumenti texture. *Lodiculae* 3. *Aristatae* 1–15 mm longae, persistentes, geniculatae tortiliaeque ad segmente primo aut caducae et rectae. *Antherae* 0.6–3.0 mm, interdum penicillatae. *Styli* 2, ramosi (2 vel 3) vel haud ramosi, saepe coniuncti base coni simile, elongati, sub anthesi ab apice flosculorum exserti. *Caryopsis* glabra, ovoidea. *Hilum* lineare, paulo caryopsidis brevius.

Plants perennial, caespitose. *Culms* 10–85 cm tall, erect, glabrous or scabridulous. *Sheaths* open, glabrous, smooth or scabrous. *Ligules* 1.0–5.5 mm long, hyaline, acute or truncate. *Basal leaf blades* 4–45 cm long, 0.5–2.5 mm wide, flat, convolute or involute; abaxial and adaxial surfaces smooth to scabrous. *Cauline leaves* 3–11 cm long. *Panicles* 3.5–22.0 cm long, open or contracted. *Branches* 1–12 cm long, straight to flexuous, usually scabrous. *Spikelets* 2.5–5.3 mm long, oval to elliptic, green-yellowish to tawny; anthocyanic coloration often absent (weak in *P. shoshoneanum*). *Glumes* subequal, of the same length or slightly exceeding the floret; 1–3(–5)-veined with apices acute, rarely rounded, transverse veinlets absent. *Florets* dorsally compressed to terete, lanceolate, elliptic or obovoid. *Callus* 0.1–0.5 mm long, blunt, often protruding, glabrous or hairy. *Disarticulation scar* circular or elliptic, slightly grooved, peripheral ring often developed. *Lemmas* 1.5–6.0 mm long, coriaceous, pubescent, sometimes glabrous, tawny to brownish, 3–5-veined, central vein not prominent; margins not overlapping at maturity, flat, basally fused; lemma apex flat, rarely emarginate with two lobes, glabrous or hairy, awned. *Lemma epidermal pattern* (Fig. 2K–N) “saw-like”; silica bodies rectangular or square-rounded, sometimes with 1–3 shallow contractions, cork cells square, prickles often present. *Awns* 1–15 mm long, central, persistent, geniculate and twisted at the first segment or caducous and straight. *Paleas* similar to the lemmas in length, texture and indumentum, partially exposed. *Lodicules* 3. *Anthers* 0.6–3.0 mm long, sometimes penicillate. *Styles* 2, branched (2 or 3) or unbranched, often attached to cone-like bases, elongated, at anthesis exerted from the apex of the floret. *Caryopsis* glabrous, ovoid. *Hilum* linear, slightly shorter than caryopsis. $2n = 20, 22, 24$.

Note. – The name *Piptatheropsis* comes from adding Greek $\omega\pi\tau\iota\varsigma$ – “aspect” to “*Piptatherum*” and refers to its supposed resemblance to this genus. Five species. North America (Canada, United States), cool temperate and boreal forest and openings.

Key to the species of *Piptatheropsis*

1. Awns caducous, straight, 1–8 mm long 2
1. Awns persistent, geniculate, first segment twisted, 3–15 mm long 4
2. Lemmas glabrous, rarely sparsely pubescent; callus not protruding, 0.1 mm long; awns 2–3 times longer than the lemma *Piptatheropsis micrantha*
2. Lemmas hairy; callus protruding, 0.2–0.3 mm long; awns 1/2 to as long as the lemma 3
3. Glumes obtuse, middle vein not reaching the apex *Piptatheropsis pungens*
3. Glumes acute, middle vein reaching the apex *Piptatheropsis shoshoneana*
4. Lemma apex entire, apical lobes not developed; panicles open, 9–15 cm long, branches up to 6 cm long, ascending to divergent *Piptatheropsis canadensis*
4. Lemma apex emarginate, apical lobes 0.3–0.4 mm long; panicles contracted, 3.5–9.0 cm long, branches 1–2 cm long, appressed to the rachis *Piptatheropsis exigua*

Piptatheropsis canadensis (Poir.) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Stipa canadensis* Poir. in Lamarck, *Encycl.* 7: 452. 1806 = *Stipa juncea* Michx., *Fl. Bor.-Amer.* 1: 54. 1803 (non L., 1753) = *Urachne canadensis* (Poir.) Torr. in Gray, *N. Amer. Gram.* 2: 114. 1835 = *Oryzopsis canadensis* (Poir.) Torr., *Fl. New York* 2: 433. 1843 = *Oryzopsis juncea* Britton, Sterns & Poggenb., *Prelim. Cat.*: 67. 1888 = *Piptatherum canadense* (Poir.) Dorn, *Vasc. Pl. Wyoming*, ed. 3: 377. 2001 – Type: Montagnes streril. a la hauteurs du Terres, *Michaux s.n.* (lectotype: P, designated by Hitchcock in *Contr. U.S. Natl. Herb.* 12: 150 1908)

= *Stipa macounii* Scribn. in Macoun, *Cat. Canad. Pl.* 5: 390. 1890 = *Oryzopsis macounii* (Scribn.) Beal, *Grass. N. Amer.* 2: 229. 1896.

Piptatheropsis exigua (Thurb.) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Oryzopsis exigua* Thurb. in Torrey in Wilkes, *U.S. Expl. Exped.* 17(2): 481. 1874 = *Piptatherum exiguum* (Thurb.) Dorn, *Vasc. Pl. Wyoming*, ed. 3: 377. 2001 = *Stipa exigua* (Thurb.) Columbus & J.P. Sm. in *Aliso* 28: 66–67. 2010 – Type: U.S.A., Oregon: Cascade Mts., *Wilkes Expl. Exped. s.n.*

Piptatheropsis micrantha (Trin. & Rupr.) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Urachne micrantha* Trin. & Rupr., *Sp. Gram. Stipac.*: 16. 1842 = *Oryzopsis micrantha* (Trin. & Rupr.) Thurb. in *Proc. Acad. Nat. Sci. Philadelphia* 1863: 78. 1864 = *Piptatherum micranthum* (Trin. & Rupr.) Barkworth in *Phytologia* 74(1): 19. 1993 = *Stipa divaricata*

Columbus & J.P. Smith in *Aliso* 28: 66. 2010 – Type: Hooker misit. Ticket 219 p.p. (holotype: LE-TRIN-1467.01!).

Piptatheropsis pungens (Torr.) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Milium pungens* Torr. in Sprengel, *Neue Entdeck. Pflanzenk.* 2: 102. 1821 = *Panicum firmum* Kunth, Révis. *Gramin.* 1: 37. 1829 = *Oryzopsis pungens* (Torr.) Hitchc. in *Contr. U.S. Natl. Herb.* 12(3): 151. 1908 = *Piptatherum pungens* (Torr.) Dorn, *Vasc. Pl. Wyoming*, ed. 3: 377. 2001 – Type: U.S.A., Schenectady in Massachusetana, *Milium* no. 3 Muhlenberg gram. p. 78 [Descr. *Gram.* 1817]

= *Oryzopsis parviflora* Nutt. in *J. Acad. Nat. Sci. Philadelphia* 3: 126. 1823

= *Urachne brevicaudata* Trin. in *Mem. Acad. Imp. Sci. Saint-Petersbourg*, Ser. 6, *Sci. Math.*, Seconde Pt. *Sci. Nat.* 3: 127. 1834.

Piptatheropsis shoshoneana (Curto & Douglass M. Hend.) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Stipa shoshoneana* Curto & Douglass M. Hend. in *Madroño* 45(1): 59, f. 1. 1999 = *Piptatherum shoshoneanum* (Curto & Douglass M. Hend.) P.M. Peterson & Soreng in *Contr. U.S. Natl. Herb.* 48: 495. 2003 – Type: U.S.A., Idaho: Salmon River Mts., ca. 15 km NW of Challis, Morgan Creek Canyon, ca. 7 km NW of US Hwy 93, *L. Eno 17* (holotype: CAS; isotypes: BRY, ID!, K, MIN, MO!, NY!, RM, UC, US!, UTC, WTU!).

Patis Ohwi in *Acta Phytotax. Geobot.* 11: 181. 1942, emend. Romasch., P.M. Peterson & Soreng – Type: *Patis coreana* (Honda) Ohwi.

Plants loosely caespitose to shortly rhizomatous. *Culms* 50–100 cm tall, erect, scabrous to pubescent, 2–3 mm in diameter; with 2–8 nodes. *Sheaths* open, glabrous, smooth or scabrous, sometimes pubescent near the margins or pilose at collar. *Ligules* 0.3–3.0 mm long, obtuse or truncate. *Basal leaf blades* underdeveloped, up to 2 cm long or absent (cataphyllous). *Cauline leaf-blades* 10–35 cm long, 5–20 mm wide, flat, broadly linear or linear-lanceolate, scaberulous or puberulous especially on abaxial surface, apex acuminate. *Panicles* 12–35 cm long, lax or contracted. *Branches* 1.0–9.5 cm long, straight to flexuous, scabrid or puberulous, suberect, ascending to divergent, single or paired, with 1–5 spikelets. *Spikelets* yellowish green, gray-green or dark-green, without anthocyanic coloration; oval, elliptic or elongated, often dorsally compressed. *Glumes* 4–15 mm long, subequal, slightly shorter to exceeding the floret by 1/3 of its length, ovate, elliptic-obovate or lanceolate; 5–9-veined with transverse veinlets (weak in *P. racemosa*), each vein flanked with two lines of regularly placed prominent prickles; apices acute or rounded. *Florets* dorsally slightly compressed or terete. *Callus* 0.31 mm long, obtuse, sometimes knob-like. *Disarticulation scar* circular or elliptic. *Lemmas* 4.5–10.2 mm long, shiny dark brown or gray yellow, glabrous, sparsely or evenly pubescent; lemma margins partially overlapping at maturity, joined or open, fused at the base; lemma apex entire or shortly lobed; lemma lobes when present acute and minutely hairy. *Lemma epidermal pattern* “saw-like”; silica bodies rounded to

oval, sometimes with a single shallow to deep contraction, cork cells square, scarce, prickles present or absent. *Awns* 10–35 mm long, persistent, straight, sometimes with prominent grooves on the basal, dorsal part of the awn; upper part flexuous. *Paleas* similar to the lemmas in length, texture and indumentum, often exposed except for basal parts and tips. *Lodicules* 3, central lodicule somewhat shorter, often rounded. *Anthems* 3.5–7.0 mm long, not penicillate, apex glabrous. *Styles* 2; sometimes ovary hairy below the styles. $2n = 46, 48$.

Note. – Three species. East Asia (China, Japan, Korea), and eastern North America (Canada, United States), subtropical and temperate forest and openings.

Key to the species of *Patis*

1. Panicles open or lax; lemma margins separated, exposing the palea *Patis racemosa*
1. Panicles contracted; lemma margins overlapping and concealing the palea 2
2. Lemmas cylindrical, 10–12 mm long, 1/3 as long as the glumes, yellowish or tawny at maturity; glumes lanceolate, apices acuminate *Patis coreana*
2. Lemmas elliptic, 4–5 mm long, shortly exerted from glumes, dark brown at maturity; glumes obovate, apices rounded *Patis obtusa*

Patis coreana (Honda) Ohwi in Acta Phytotax. Geobot. 11(3): 181. 1942 = *Stipa coreana* Honda in Tozawa & Nakai, Koryo Shikenrin Ippan: 80. 1932 = *Achnatherum coreanum* (Honda) Ohwi in J. Jap. Bot. 17: 404. 1941 = *Orthoraphium coreanum* (Honda) Ohwi, Bull. Natl. Sci. Mus. 33: 66. 1953 – Type: Korea, in silvis Koryo, Sep, *T. Nakai 13211* (holotype: TI).

Patis obtusa (Stapf) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Oryzopsis obtusa* Stapf in Hooker's Icon. Pl. 24(4): pl. 2393. 1895 = *Piptatherum obtusum* (Stapf) Roshev. in Bot. Mater. Gerb. Bot. Inst. Komarova Acad. Nauk S.S.S.R. 14: 102. 1951 (non Nees & Meyen, 1841) = *Piptatherum kuoi* S.M. Phillips & Z.L. Wu in Novon 15(3): 474–475. 2005 – Type: China, Hubei: Ichang and immediate neighbourhood, *A. Henry 3507* (lectotype: K, designated by Phillips & Wu in Novon 15(3): 474–475. 2005).

Patis racemosa (Sm.) Romasch., P.M. Peterson & Soreng, **comb. nov.** = *Milium racemosum* Sm., Cycl. 23: *Milium* No. 15. 1813 = *Urachne racemosa* (Sm.) Trin., Gram. Unifl. Sesquifl.: 174. 1824 = *Oryzopsis racemosa* (Sm.) Ricker ex Hitchc. in Rhodora 8(95): 210. 1906 = *Piptatherum racemosum* (Sm.) Barkworth in Phytologia 74(1): 19. 1993 – Type: U.S.A., Pennsylvania: Lancaster, 1793, *Muhlenberg 30* [holotype: LINN-Smith herb. (K illustr.; US sketch of K illustr.)].

= *Oryzopsis melanocarpa* Muhl., Descr. Gram.: 79. 1817 = *Urachne melanosperma* Link, Hort. Berol. 1: 94. 1827 = *Piptatherum nigrum* Torr., Fl. N. Middle United States 1: 79. 1823.

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Appendix. List of specimens sampled, voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accessions for DNA sequences in the order of *rps16-trnK*, *rps16* intron, *rpl32-trnL*, and *ndhF*. An asterisk (*) indicates sequences generated by this study; a dash (–) indicates missing data.

Achnatherum arnowiae (S.L. Welsh & N.D. Atwood) Barkworth, *Franklin 7682* (BRY), U.S.A., JF754681*, JF754735*, JF754716*, JF754698*; *Achnatherum bloomeri* (Bol.) Barkworth, *Fertig 22632* (BRY), U.S.A., JF754682*, JF754736*, JF754717*, JF754699*; *Achnatherum bromoides* (L.) P. Beauv., *Romaschenko 439* & *Didukh* (KW), Ukraine, JF698367*, JF698213*, JF697915*, GU254734; *Achnatherum calamagrostis* (L.) P. Beauv., *Pyke 164* (US), Spain, JF698368*, JF698214*, JF697916*, GU254743; *Achnatherum caragana* (Trin.) Nevski, *Goloskokov s.n.* (US), Kazakhstan, JF698369*, JF698215*, JF697917*, GU254732; *Achnatherum chinense* (Hitche.) Tzvelev, *Petrov s.n.* (LE), China, JF698370*, JF698216*, JF754718*, GU254735; *Achnatherum contractum* (B.L. Johnson) Barkworth, *Refsdal 4718* (BRY), U.S.A., JF754683*, JF754737*, JF754719*, –; *Achnatherum hendersonii* (Vasey) Barkworth, *Maze 1000* & *Robson* (US), U.S.A., JF698377*, JF698223*, JF697924*, JF697854*; *Achnatherum hymenoides* (Roem. & Schult.) Barkworth, *Saarela 205* (UBC), U.S.A., JF698378*, JF698224*, JF697925*, GU254733; *Achnatherum inebrians* (Hance) Keng ex Tzvelev, *Soreng 5393*, *Peterson & Sun Hang* (US), China, JF698379*, JF698225*, JF697926*, GU254750; *Achnatherum lettermanii* (Vasey) Barkworth, *Hartman 72830* (US), U.S.A., JF698383*, JF698229*, JF697930*, JF697858*; *Achnatherum nelsonii* (Scribn.) Barkworth, *Saarela 593* (UBC), Canada, *JF698386**, *JF698232**, *JF697933**, *GU254761*; *Achnatherum occidentale* (Thurb. ex S. Watson) Barkworth, *Saarela 594*, *Sears & Maze* (UBC), Canada, *JF698388**, *JF698234**, *JF697935**, *GU254740*; *Achnatherum pinetorum* (M.E. Jones) Barkworth, *Bostick 4875* (US), U.S.A., *JF698392**, *JF698237**, *JF697939**, *JF697863**; *Achnatherum sibiricum* (L.) Keng ex Tzvelev, *Soreng 5104*, *Peterson, Wang & Zhu* (US), China, *JF698397**, *JF698242**, *JF697944**, *GU254741*; *Achnatherum swallenii* (C.L. Hitchc. & Spellenh.) Barkworth, *Rosentreter 3841* (BRY), U.S.A., *JF754684**, *JF754738**, *JF754720**, *JF754700**; *Achnatherum wallowaense* J. Maze & K.A. Robson, *Maze 1006*, *Robson & Henn* (US), U.S.A., *JF698400**, *JF698246**, *JF697947**, *JF697868**; *Achnatherum webberii* (Thurb.) Barkworth, *Tiehm 12416* & *Nachlinger* (BRY), U.S.A., *JF754685**, *JF754739**, *JF754721**, *JF754701**; *Aciachne acicularis* Laegaard, *Peterson 13931* & *Refugio Rodriguez* (US), Peru, *JF698401**, *JF698247**, *JF697948**, *GU254806*; *Aciachne flagellifera* Laegaard, *Laegaard 19436* (AAU), Ecuador, *JF698402**, *JF698248**, *JF697949**, *GU254805*; *Ampelodesmos mauritanicus* (Poir.) T. Durand & Schinz, *Pyke 702* (BC), Spain, *JF698405**, *JF698250**, *JF697951**, *GU254797*; *Anatherostipa mucronata* (Griseb.) F. Rojas, *Peterson 19551*, *Soreng, Salariato & Panizza* (US), Argentina, *JF698407**, *JF698252**, *JF697953**, *GU254803*; *Anatherostipa obtusa* (Nees & Meyen) Peñailillo, *Peterson 13811* & *Refugio Rodriguez* (US), Peru, *JF698408**, *JF698253**, *JF697954**, *JF697869**; *Anatherostipa rigidiseti* (Pilg.) Peñailillo, *Beck s.n.* (LPB), Bolivia, *JF698409**, *JF698254**, *JF697955**, *GU254809*; *Anatherostipa venusta* (Phil.) Peñailillo, *Pfister 9394* (US), Chile, *JF698411**, *JF698256**, *JF697957**, *GU254801*; *Ane-mathele lessoniana* (Steud.) Veldkamp, *Mez 13236* (US), New Zealand, *JF698412**, *JF698257**, *JF697958**, *JF697870**; *Austrostipa nitida* (Summerh. & C.E. Hubb.) S.W.L. Jacobs & J. Everett, *Canty 2164* (US), Australia, *JF698418**, *JF698265**, *JF697965**, *JF697875**; *Austrostipa scabra* (Lindl.) S.W.L. Jacobs & J. Everett, *Peterson 14442*, *Soreng & Rosenberg* (US), Australia, *JF698421**, *JF698268**, *JF697967**, *GU254738*; *Celtica gigantea* (Link) F.M. Vázquez & Barkworth, *Pyke 705* (BC), Spain, *JF698427**, *JF698274**, *JF697973**, *GU254775*; *Duthiea brachypodium* (P. Candargi) Keng & Keng f., *Soreng 5358*, *Peterson & Sun Hang* (US), China, *JF698433**, *JF698280**, *JF697978**, *GU254793*; *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Saarela 595*, *Sears & Maze* (UBC), Canada, *JF698434**, *JF698281**, *JF697979**, *GU254812*; *Hesperostipa spartea* (Trin.) Barkworth, *Holmes 214* (US), U.S.A., *JF698436**, *JF698283**, *JF697981**, *GU254745*; *Jarava ichu* Ruiz & Pav., *Peterson 20745*, *Soreng & Romaschenko* (US), Peru, *JF698439**, *JF698286**, *JF697984**, *GU254763*; *Jarava scabrifolia* (Torres) Peñailillo, *Peterson 11712* & *Annable* (US), Argentina, *JF698443**, *JF698290**, *JF697988**, *GU254760*; *Nassella neesiana* (Trin. & Rupr.) Barkworth, *Peterson 10258* & *Annable* (US), Argentina, *JF698450**, *JF698298**, *JF697996**, *GU254767*; *Nassella pfisteri* (Matthai) Barkworth, *Soreng 7017a* & *Soreng* (US), Chile, *JF698451**, *JF698299**, *JF697997**, *JF697885**; *Nassella trichotoma* (Nees) Hack. ex Arechav., *Peterson 11506* & *Annable* (US), Argentina, *JF698452**, *JF698300**, *JF697998**, *GU254742*; *Oryzopsis asperifolia* Michx., *Saarela 384* (UBC), Canada, *JF698456**, *JF698304**, *JF698002**, *GU254788*; *Oryzopsis brachyclada* Pilg., *Rechinger 37233* (US), Afghanistan, *JF754688**, *JF754742**, *JF754724**, *JF754705**; *Oryzopsis kopetdagensis* Roshev., *Botschantzev s.n.* (LE), Turkmenistan, –, –, *JF754722**, *JF754702**; *Patis coreana* (Honda) Ohwi, *Liou 1085* (US), China, *JF698373**, *JF698219**, *JF697921**, *JF697850**; *Phaenospesma globosa* Munro ex Benth., *Soreng 5325*, *Peterson & Sun Hang* (US), China, *JF698462**, *JF698310**, *JF698008**, *GU254792*; *Piptatherum aequiglume* (Duthie ex J.D. Hooker) Roshev., *Koelz 1389* (US), India, *JF698463**, *JF698311**, *JF698009**, *JF697887**; *Piptatherum alpestre* (Gris.) Roshev., *Grigoriev 72* (LE), Tajikistan, *JF754686**, *JF754740**, –, *JF754703**; *Piptatherum angustifolium* (Munro ex Regel) Roshev., *Nepli 144* (LE), Tajikistan, *JF698464**, *JF698312**, *JF698010**, *GU254811*; *Piptatherum badachschanicum* (Tzvelev) Ikonn., *Darvaziev s.n.* (LE), Tajikistan, *JF754687**, *JF754741**, *JF754723**, *JF754704**; *Piptatherum canadense* (Poir.) Dorn, *Raymond s.n.* (US), Canada, *JF698465**, *JF698313**, *JF698011**, *JF697888**; *Piptatherum coerulescens* (Desf.) P. Beauv., *Soreng 3765* (US), Greece, *JF698466**, *JF698314**, *JF698012**, *GU254789*; *Piptatherum exiguum* (Thurb.) Dorn, *Reveal 1073* (KW), U.S.A., *JF698467**, *JF698315**, *JF698013**, *GU254752*; *Piptatherum fasciculatum* (Hack.) Roshev., *Stewart 19525* (US), India, *JF754689**, –, *JF754725**, *JF754706**; *Piptatherum fedtschenkoii* Roshev., *Botschantzev 1559* (LE), Tajikistan, *JF698468**, *JF698316**, *JF698014**, *JF697889**; *Piptatherum ferganense* (Littw.) Roshev., *Kamelin 100* (LE), Tajikistan, *JF698469**, *JF698317**, *JF698015**, *JF697890**; *Piptatherum hilariae* Pajiz, *Potaliev 343* (LE), Tajikistan, *JF698470**, *JF698318**, *JF698016**, *GU254807*; *Piptatherum holciforme* (M. Bieb.) Roemer & Schultes, *Didukh 1203* (KW), Ukraine, *JF698471**, *JF698319**, *JF698017**, *GU254817*; *Piptatherum kokanicum* (Regel) Roshev., *Ismatova 148* (LE), Tajikistan, *JF754691**, *JF754744**, *JF754727**, *JF754708**; *Piptatherum kuoi* S.M. Phillips & Z.L. Wu, *Soreng 4531* & *Kelly* (US), China, *JF698472**, *JF698320**, *JF698018**, *JF697891**; *Piptatherum laterale* Munro ex Regel, *Smolianinov s.n.* (LE), Tajikistan, *JF754692**, *JF754745**, *JF754728**, *JF754709**; *Piptatherum latifolium* (Roshev.) Nevski, *Goloskokov s.n.* (LE), Kazakhstan, –, *JF754746**, *JF754729**, *JF754710**; *Piptatherum micranthum* (Trin. & Rupr.) Barkworth, *Peterson 18437*, *Saarela & Smith* (US), Canada, *JF698473**, *JF698321**, *JF698019**, *GU254815*; *Piptatherum microcarpum* (Pilg.) Tzvelev, *Rechinger 35997* (US), Afghanistan, *JF754693**, *JF754747**, *JF754730**, *JF754711**; *Piptatherum miliaceum* (L.) Coss., *Gillet 16094* (US), Jordan, *JF698474**, *JF698322**, *JF698020**, *GU254776*; *Piptatherum miliaceum* subsp. *thomasi* (Duby) Freitag, *Pyke 833* (BC), Spain, *JF698475**, *JF698323**, *JF698021**, *JF697892**; *Piptatherum molinioides* Boiss., *Koelz 8421* (US), India, –, *JF754748**, *JF754731**, *JF754712**; *Piptatherum munroi* (Stapf) Mez, *Soreng 5686*, *Peterson & Sun Hang* (US), China, *JF698476**, *JF698324**, *JF698022**, *JF697893**; *Piptatherum paradoxum* (L.) P. Beauv., *Pyke 831* (BC), Spain, *JF698477**, *JF698325**, *JF698023**, *GU254744*; *Piptatherum pungens* (Torr.) Dorn, *Hermann 13407* (US), U.S.A., *JF698478**, *JF698024**, *JF697894**; *Piptatherum racemosum* (Sm.) Eaton, *Dugal 1260* (BRY), Canada, *JF754694**, *JF754749**, *JF754732**, *JF754713**; *Piptatherum shoshoneanum* (Curto & Douglass M. Hend.) P.M. Peterson & Soreng, *Eno 13* (US), U.S.A., *JF698479**, *JF698327**, *JF698025**, *GU254814*; *Piptatherum sogdianum* (Grig.) Roshev., *Konkov 1637* (LE), Tajikistan, *JF698480**, *JF698328**, –, *JF697895**; *Piptatherum songaricum* (Trin. & Rupr.) Roshev., *Goloskokov s.n.* (LE), Kazakhstan, *JF698481**, *JF698329**, *JF698026**, *JF697896**; *Piptatherum sphacelatum* (Boiss. & Buhse) Hack., *Rechinger 30627a* (US), Pakistan, *JF754695**, *JF754750**, –, *JF754714**; *Piptatherum vicarium* (Griz.) Roshev., *Fedtschenko 247* (LE), Russia, *JF754696**, *JF754751**, *JF754733**, *JF754715**; *Piptatherum virescens* (Trin.) Boiss., *Romaschenko 445* & *Didukh* (KW), Ukraine, *JF698482**, *JF698330**, *JF698027**, *GU254777*; *Piptochaetium avenaceum* (L.) Parodi, *Soreng 7739* & *Romaschenko* (US), U.S.A., *JF698483**, *JF698331**, *JF698028**, *GU254799*; *Piptochaetium featherstonei* (Hitche.) Tovar, *Peterson 10314* & *Annable* (US), Argentina, *JF698485**, *JF698333**, *JF698030**, *GU254796*; *Piptochaetium montevidense* (Spreng.) Parodi, *Peterson 20486*, *Soreng & Romaschenko* (US), Peru, *JF698486**, *JF698334**, –, *JF697897**; *Piptochaetium panicoides* (Lam.) E. Desv., *Soreng 7011* & *Soreng* (US), Chile, *JF698487**, *JF698335**, *JF698031**, *GU254794*; *Psammochloa villosa* (Trin.) Bor, *Safranovia 952* (LE), Mongolia, *JF698488**, *JF698336**, *JF698032**, *GU254786*; *Ptilagrostis dichotoma* Keng ex Tzvelev, *Soreng 5647*, *Peterson & Sun Hang* (US), China, *JF698489**, *JF698337**, *JF698033**, *GU254749*; *Ptilagrostis kingii* (Bol.) Barkworth, *Peirson 10819* (US), U.S.A., *JF698491**, *JF698339**, *JF698035**, *GU254813*; *Ptilagrostis mongholica* (Turcz. ex Trin.) Griseb., *Koloskov s.n.* (LE), Kyrgyzstan, *JF698494**, *JF698342**, *JF698037**, *GU254746*; *Stipa eriocalis* Borbás, *Romaschenko 314*, *Romo & Hidalgo* (BC), France, *JF754697**, *JF754752**, *JF754734**, *GU254751*; *Stipa keniensis* (Pilg.) Freitag, *Hansen 6254* & *Heemstra* (C), Somalia, *JF754690**, *JF754743**, *JF754726**, *JF754707**; *Stipa pennata* L., *Romaschenko 466* (BC), Ukraine, *JF698508**, *JF698356**, *JF698051**, *GU254759*; *Timouria saposhnikovii* Roshev., *Soreng 5475*, *Peterson & Sun Hang* (US), China, *JF698512**, *JF698360**, *JF698055**, *GU254731*; *Trikeria hookeri* (Stapf) Bor, *Koelz 2328* (US), India, *JF698513**, *JF698361**, *JF698056**, *GU254785*.