The Grasses (Poaceae): Robert Brown and now

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Abstract

Clark, Lynn G. (Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, Iowa 50011-1020, USA) 2004. The grasses (Poaceae): Robert Brown and now. Telopea *10(2): 505–514.* Robert Brown provided the first account of the Australian grasses in his 1810 *Prodomus*, in which he described a number of new grass genera and species and arranged the genera primarily according to floret number and floral sexuality. Implicit in his circumscription of the family was the recognition of the unique nature of the caryopsis and the specialised grass embryo. In the 1814 *Botany of Terra Australis*, Brown discussed the morphology of grasses and revised his general classification of the family. Brown divided the family into two 'tribes' (what we would today call subfamilies), the Paniceae and Poaceae, and he explicitly noted the trends toward basal reduction in the spikelets of Paniceae and apical reduction in the Poaceae. He described grass spikelets in detail and drew the general conclusions that these were branched structures, and that the lodicules represented perianth parts. Brown also noted that the Paniceae were more diverse in tropical latitudes, and the Poaceae in temperate latitudes. Brown's basic classification persisted without radical modification well into the 20th century. Recent phylogenetic analyses of the grass family demonstrate the paraphyly of Brown's Poaceae, which actually comprises 11 subfamilies, but his Paniceae is retained to a large extent in the modern Panicoideae.

Introduction

Robert Brown knew the grasses (family Poaceae) as an important component of both the monocots and the Australian flora, noting that grasses comprised about 25% of the known species diversity of both groups (Brown 1810, 1814). Grasses currently comprise approximately 15% of monocot species diversity, and, with about 1320 native and naturalised species in Australia (B. Simon, pers. comm.), no more than 10% of the Australian vascular flora, but an appreciation of the ecological and economic importance of grasses has only continued to grow (GPWG 2001 and references cited therein).

Although Robert Brown studied other plant families in more detail (e.g., Proteaceae, Apocynaceae), he nonetheless made significant contributions to grass morphology and classification. In this paper I will discuss Brown's work on grasses (both descriptive and morphological), the current state of grass systematics, and Brown's contributions to grass systematics.

Brown and the grasses

Brown (1810) described 32 genera (including one he elevated to generic status) and nearly 200 species of grasses, primarily from the Australian flora. The descriptions emphasised spikelet and floral characters, and were concise and largely parallel. Occasionally comments on distribution, affinities, and/or additional details of spikelet morphology also were included. Larger or more complex genera were often subdivided; for example, the species of *Eriachne* R. Br. were divided into two groups based on whether the lemma was awned or muticous. The description of the family was quite detailed and included both vegetative and reproductive characters, without emphasising one feature over another.

In addition to the purely descriptive aspect of his grass work, Brown (1810) provided an artificial classification of the family that he further refined in 1814. In the earlier work, Brown divided the genera of the family into three major, artificial groups, based primarily on the number of florets and whether the flowers were perfect or unisexual. The first two groups included a majority of the genera, with the third representing a small group of odd genera characterised by three-flowered spikelets, with one floret bisexual and the two 'lateral' florets masculine or neuter. In the later work, Brown focused on the first two groups (his two 'great tribes'), which he formally named the Poaceae and Paniceae, and did not discuss the disposition of the minor third group. He noted that the Poaceae had spikelets with one to many florets and a tendency toward apical reduction (what he called 'imperfection') in the spikelet (Fig. 1a), and that the Poaceae were prevalent in temperate climates. The Paniceae, on the other hand, had two-flowered spikelets, with the lower floret always masculine or neuter and frequently consisting of only a lemma (Fig. 1b), and were more diverse in tropical regions.

Brown made several cogent observations of grass morphology that can be inferred from his 1810 description of the family, and others that were explicitly discussed in the 1814 work. Brown (1810) listed the open leaf sheath, distichous florets within a spikelet, presence of lodicules, caryopsis (fruit with the pericarp adnate to the seed

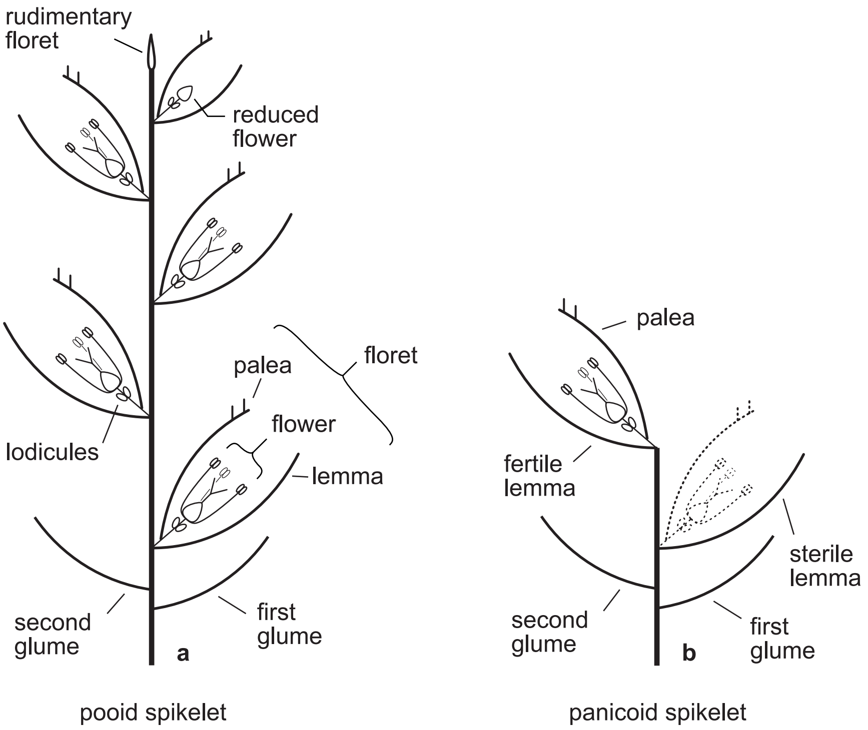

Fig. 1. Diagrammatic grass spikelets. **a,** multiflowered pooid (Pooideae) spikelet with apical reduction; **b,** two-flowered panicoid (Panicoideae) spikelets with basal reduction. Dotted lines indicate structures that are usually absent.

coat), specialised embryo in a basal and lateral position, and starchy endosperm among the characters that define the family. With respect to the embryo, Brown referred to the scutellum (which he interpreted as a fleshy, shield-shaped cotyledon), and he also noted the presence of a well-developed shoot with primary leaves. Brown (1814) recognised that the grass spikelet is a branched structure (Fig. 1); he noted that the outer envelope (i.e., the pair of glumes) contained "several flowers with distinct and often distant insertions on a common receptacle." Brown was also interested in the origin of the two valves of the inner envelope (i.e., the lemma and the palea), for which he proposed two alternate hypotheses. According to the floral hypothesis, the lemma and palea were regarded as a modified calyx and corolla (with bilateral symmetry and fusion of parts as seen in other groups of flowering plants), but the origin of the lodicules was unexplained. In the foliar hypothesis, the lemma and palea were considered to be bracts subtending the flower, and thus the lodicules represented the true perianth. He finally settled on an intermediate explanation, in which the lemma and palea represented the calyx, and the lodicules the corolla.

Current state of grass systematics

A detailed discussion of the history of grass systematics is given in GPWG (2001), but a brief summary is provided here. Subsequent to Brown's work on grasses, various classifications of the family, based on spikelet and inflorescence morphology, appeared in the 19th century. Usually nine or ten tribes (equivalent to modern usage of this term) were recognised. Bentham (1878) formalised Brown's division of the family into two great groups. By the end of the 19th century, some workers were beginning to analyze spikelet structure using an evolutionary perspective (e.g., Čelakovský 1889; Goebel 1895), and additional data sets were accumulating (e.g., leaf anatomical, Duval-Jouve 1875 and embryological, van Tiegham 1897), leading to a broad reassessment of evolutionary relationships. Classification systems based on presumed evolutionary relationships and recognizing three or more subfamilies began to appear as early as the 1930s (e.g., Roshevits 1937; Table 1, GPWG 2001), but Brown's two group system persisted into the 1950s (e.g., Hitchcock & Chase 1950). By the 1980s, usually five to seven subfamilies were recognised, based either on phenetic analyses or presumed evolutionary relationships. A more explicit approach to grass classification and evolution began in the late 1980s with the application of cladistic methodology and the use of molecular data, including both RFLPs (restriction fragment length polymorphisms) and DNA sequences. In recent years, phylogenies derived from DNA sequence data, RFLPs and morphology began to converge, showing in particular that 1) the traditionally recognised bamboos were polyphyletic and included the earliest-diverging lineages of the family, and 2) a group now called the PACCAD clade was strongly supported as having originated from a single common ancestor.

The Grass Phylogeny Working Group (GPWG) was formed in 1996 to combine a series of these existing data sets to produce a comprehensive phylogeny for the grasses, to focus taxon sampling in the development of grass data sets, and to test the existing subfamilial classifications of the grass family based on the results of its phylogenetic analyses. Analysis of eight data sets (four plastid, three nuclear, and one structural) produced a single most parsimonious tree (Fig. 2; GPWG 2000, 2001), and a revised classification recognizing 12 subfamilies was proposed based explicitly on the phylogeny (Fig. 2; GPWG 2001).

This phylogenetic hypothesis and available fossil evidence allow us to explore the evolutionary history of the grasses with greater clarity (GPWG 2001 and references cited therein), although many intriguing questions remain. The oldest known fossils indicate that the family most probably originated some time between 55 and 70 million years ago (mya) in the southern hemisphere. The earliest grasses inhabited

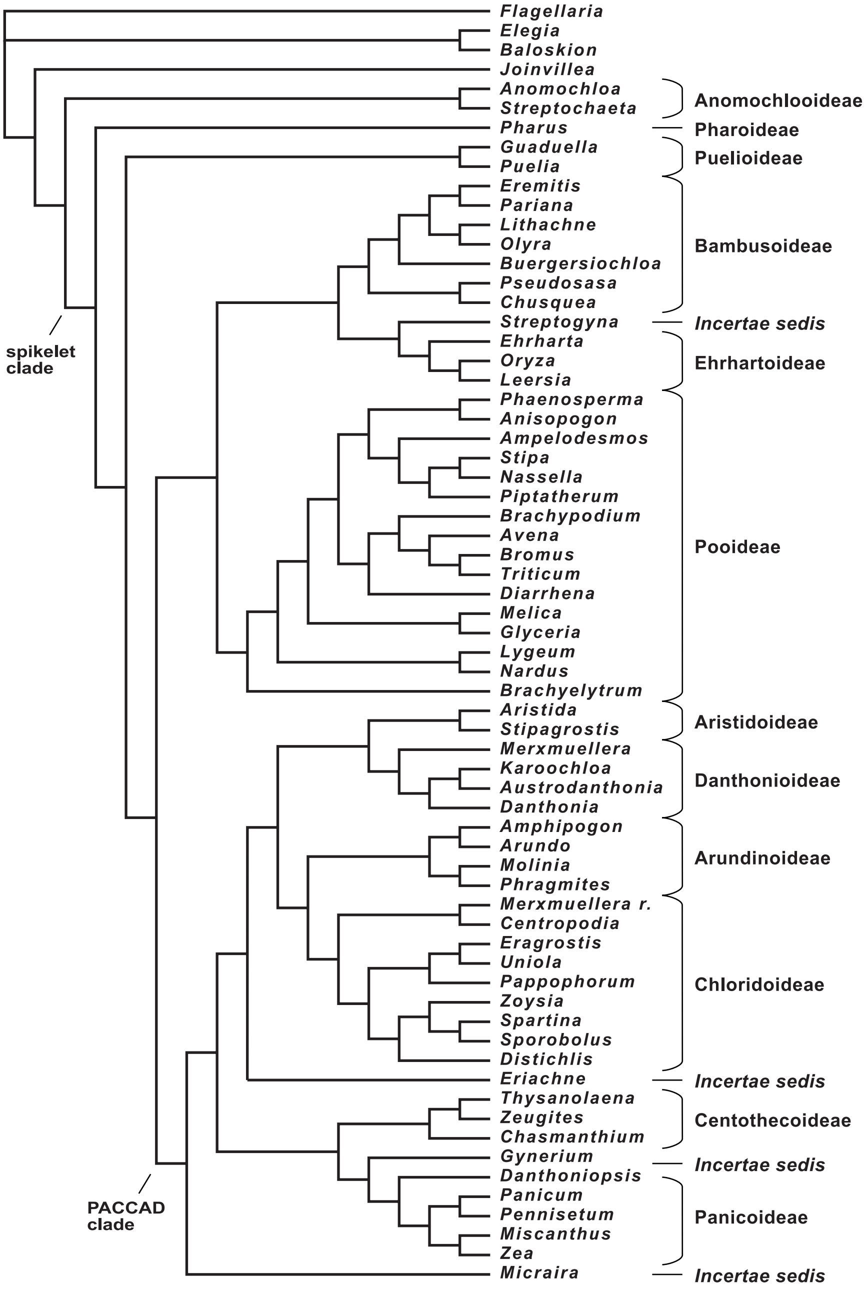

Fig. 2. Single most parsimonious tree for the grasses (*Anomochloa* through *Micraira*) and relatives (*Flagellaria* through *Joinvillea)* obtained in the GPWG (2001) analysis, showing the revised subfamilial classification for the grass family.

tropical forests and shared a number of characteristics, including (but not limited to) a rhizomatous, herbaceous, perennial habit; relatively broad, pseudopetiolate leaf blades with fusoid cells in the chlorenchyma; leaves with an open sheath and an adaxial ligule; a bracteate inflorescence and a reduced perianth; spikelets (or spikelet equivalents) with one flower; flowers with six stamens in two whorls; a uniloculate, uniovulate gynoecium with three stigmas; a basic (dry) caryopsis; a specialised, laterally positioned embryo; and C_3 photosynthesis. By the mid-Tertiary, as the continental interiors became drier and more open, the grasses began their radiation into more open habitats. At about this time, the number of stamens was reduced to three. All of the major lineages of the grasses were present by the close of the Miocene (about 5 mya); grass-dominated ecosystems also appeared at about that time. The PACCAD clade, which includes all of the C_4 lineages, arose no later than 15 mya. One major lineage, the Bambusoideae, either never left the forest habitat or went back to it, and another major lineage, the Pooideae, diversified extensively in cooler climates. Features such as intercalary meristems, drought tolerance, vegetative reproduction, and dispersal mechanisms likely played important roles in the great Tertiary diversification of the grasses, but the evolution of these features is still not well understood.

Brown's contributions to grass systematics

Brown provided the first significant treatment of Australian grasses, and this publication is still a major reference for anyone working on Australian grass diversity. Twenty-eight (or 87.5 %) of his genera are still accepted (Watson & Dallwitz 1992). Brown's artificial but useful classification of the grasses into two great groups (i.e., subfamilies) persisted until the 1950's without radical modification. Brown's Poaceae is now recognised as paraphyletic, and comprises 11 subfamilies under the most recent proposed classification (GPWG 2001). Brown's Paniceae, however, remains more or less as he circumscribed it and is now recognised as the Panicoideae. The presence of a basal female-sterile floret appears to be a synapomorphy for this subfamily (GPWG 2001). *Holcus* L., which Brown included his Paniceae, shares apical reduction with the Pooideae and as presently circumscribed is classified within that subfamily. The confusion arose because *Holcus*, as understood by Brown, included many andropogonoid genera (e.g., *Sorghum* Moench) and thus his interpretation was consistent; he could not have known that priority was to be made retrospective.

With regard to grass morphology, Brown was correct in his recognition of the caryopsis, the specialised structure of the embryo, and its basal and lateral position as characters that define the grass family. All of these characters are today regarded as synapomorphies for the Poaceae (Fig. 3; GPWG 2001). Brown was the first to recognize that the spikelet is a branched structure, but the implications of this insight for interpretation of the grass inflorescence were largely ignored by subsequent workers. The spikelet, as an aggregation of flowers, is arguably equivalent to an inflorescence (Stapleton, 1997; Judziewicz et al., 1999), but in any case continues to be equated inaccurately to a flower, as seen in the description of grass inflorescences as panicles, racemes, or spikes (e.g., floristic works, Clark & Pohl 1996) at least in part as a means of maintaining consistent usage of terminology. The grass-type spikelet is present in all but the earliest-diverging lineage of the family (the spikelet clade, Fig. 4; GPWG 2001); lemmas are universal within this clade. Brown presciently framed the current debate over the origin of the lemma, the palea, and the lodicules nearly 200 years ago. Currently, the lemma and palea are most commonly regarded as foliar in origin (with the lemma homologous to a subtending bract and the palea homologous to a prophyll) but there is some support for these structures as perianth-like (GWPG 2001). Molecular genetic studies do, however, support the lodicules as petaloid in origin

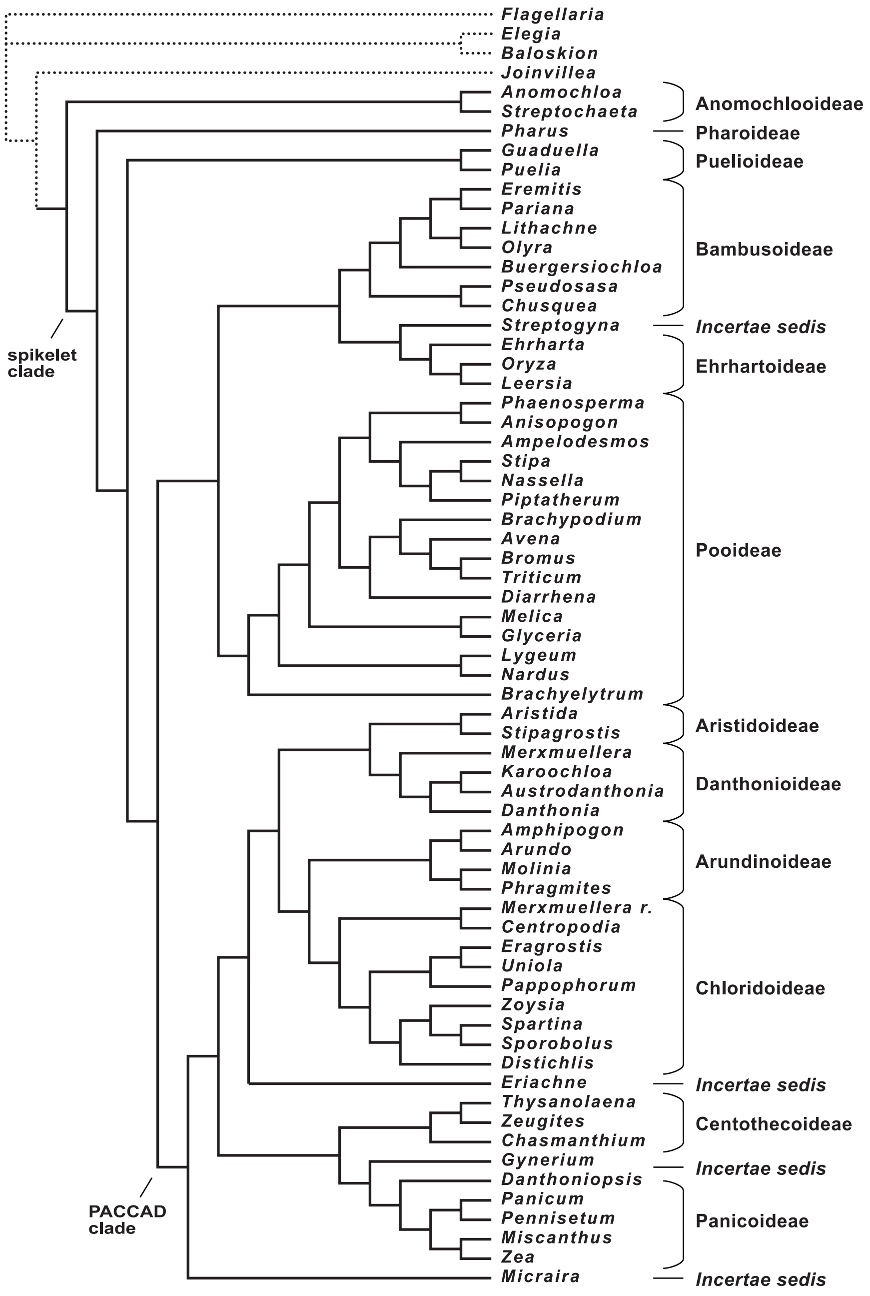

Fig. 3. Distribution of the grass-type embryo in the grass family, as optimized on the GPWG (2001) tree. Solid lines = presence of the character.

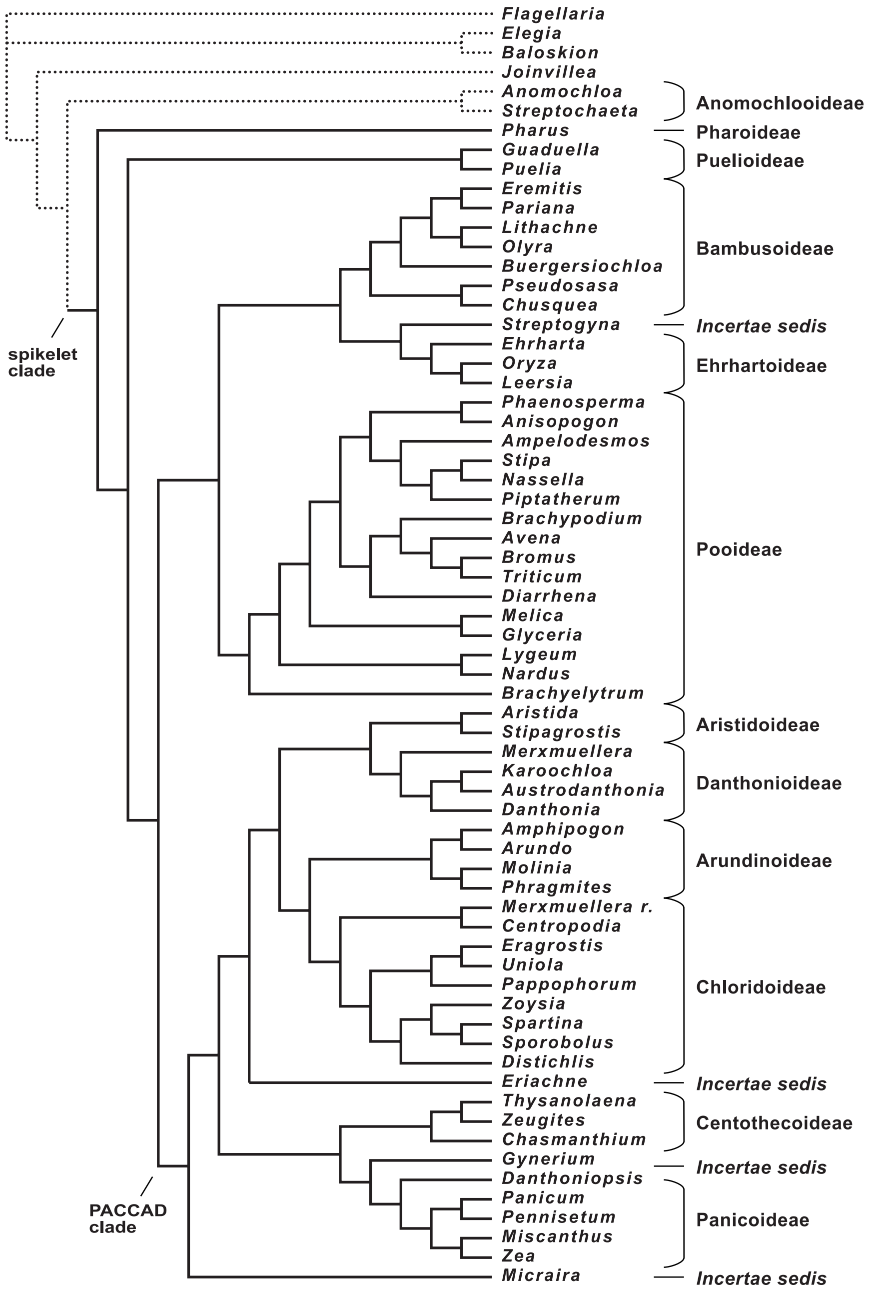

Fig. 4. Distribution of the grass-type spikelet in the grass family, as optimized on the GPWG (2001) tree. Solid lines = presence of the character.

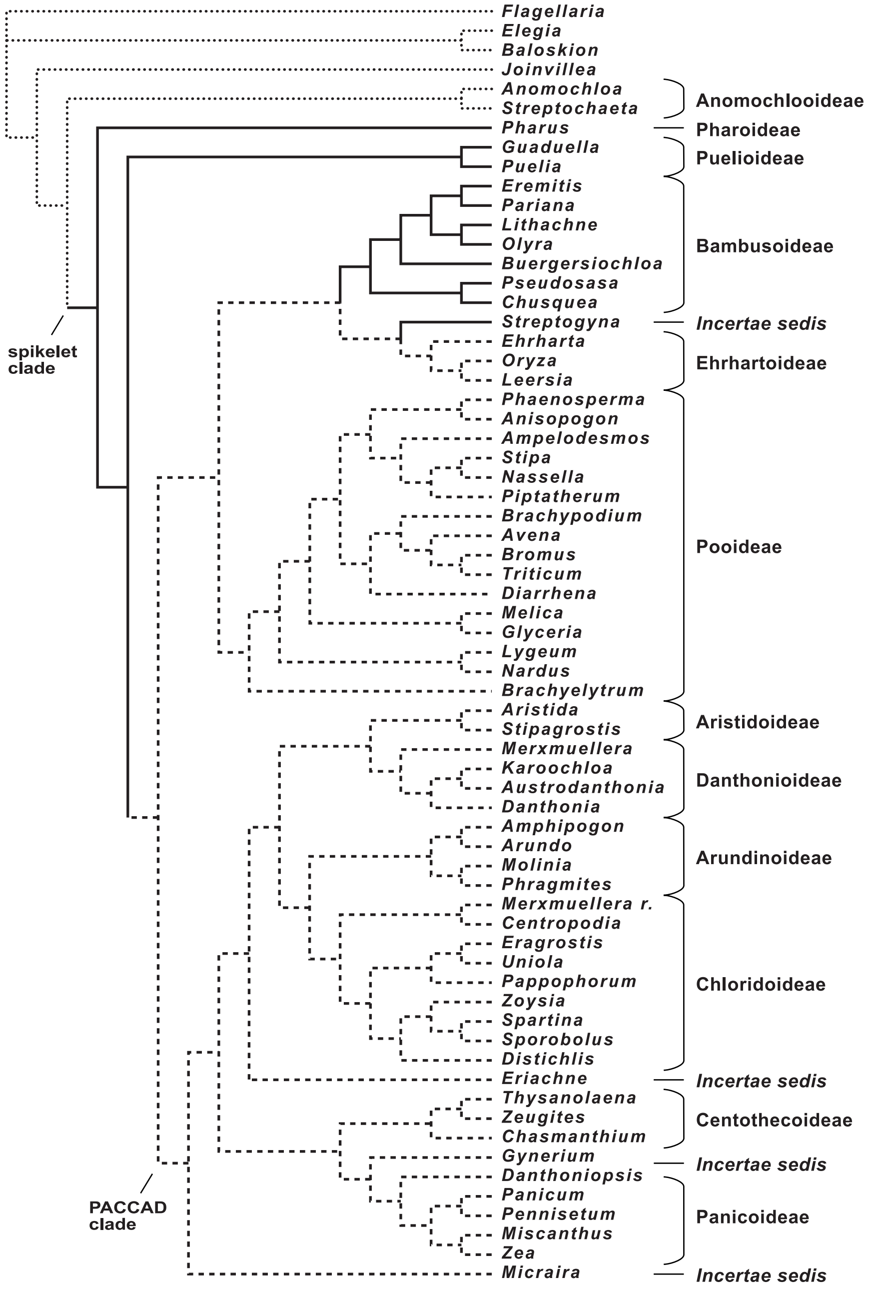

Fig. 5. Distribution of lodicule number in the grass family, as optimized on the GPWG (2001) tree. Dotted lines = lodicules absent; solid lines = three lodicules present; dashed lines = two lodicules present.

(Irish, 1998; Schmidt & Ambrose 1998; Ambrose et al. 2000). At their origin above the earliest-diverging lineage in the grasses (the spikelet clade), there are three lodicules, but above the Puelioideae there are only two, with a reversion to three in the Bambusoideae + Ehrhartoideae lineage (Fig. 5).

When Brown distinguished between the 'tropical' Paniceae and the 'temperate' Poaceae, he was observing the footprint of the evolution of the C_4 photosynthetic pathway in the grasses. We now know that all C_4 lineages of grasses evolved within the PACCAD clade (Fig. 2), and that the situation is far more complex than Brown could have realised (Sinha & Kellogg 1996; GPWG 2001), but he deserves credit for first recognizing this broad pattern.

Concluding thoughts

Robert Brown's two published works on grasses amply demonstrate that he was a keen observer of detail who incisively analyzed those observations. It is remarkable that Brown, who spent a comparatively small amount of time on this complex family, could have distilled such accurate morphological patterns from his study of its diversity, but that is exactly what he did. Brown was asking the right questions, especially regarding the origins of the lemma, palea, and lodicules. Perhaps we can now approach more definitive answers using our recently improved understanding of grass evolutionary history (GPWG 2001).

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