

CALDERONELLA, A NEW GENUS OF GRASSES, AND ITS RELATIONSHIPS TO THE CENTOSTECOID GENERA¹

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ABSTRACT

A new genus and species, *Calderonella sylvatica* (Gramineae), is described from the rain forests of Panama. Features of its spikelet morphology and leaf anatomy reveal that the affinities of *Calderonella* are with the centostecoid group of grasses, of which *Zeugites* appears to be the most closely related genus. A brief characterization of the centostecoid group is presented, as well as a key to the genera included in it, with comments on each.

In the rain forests of tropical America occur some of the most ornamental members of the grass family. The new genus is no exception. Delicate plants which inhabit the densely shaded forests of Panama (Fig. 1) in the Province of Colón, the lanceolate blades and white spikelets borne on long filiform culms create the illusion of a liliaceous plant (Figs. 2-3). Plants of *Calderonella* are common in the forests of Santa Rita and were first discovered by Correa and Dressler in January 1968, when access to the previously undisturbed forests was made possible by a new lumber road. Large gatherings have since been made in the same location, with field observations carried out by Cleofé E. Calderón, after whom the genus is named. The specific name alludes to the forest habitat of the new grass.

Plants of the new genus also occur in the forests of Cerro Jefe, Provincia de Panamá. Living material was collected by Calderón in October 1971 and is now under greenhouse cultivation in Washington, D.C.

Calderonella sylvatica Soderstrom & Decker, gen. et sp. nov.—Fig. 5.

Gramen perennis usque ad 30 cm altis. Culmi erecti vel suberecti, filiforme, compresses. Foliorum vaginæ compressae, forte nervatae, tessellatae; ligula membranacea, brevis, fusca, chartacea; lamina lanceolata pagina abaxiali transverse nervata, petiolo basi solido, piloso, geniculato. Inflorescentia angusta, racemiformis, spiculis 6 vel 7. Spiculae flosculis 3-5, infimo femineo, supernis masculis, gluma inferiore 15- vel 16-nervata, tessellata, glume superiore 10- vel 11-nervata, tessellata. Flosculus femineus ad maturitatem gibbosus, lemmate 15-19-nervato, tessellato. Flosculi masculi non gibbosi, lemmate 5-9-nervato, tessellato. Lodiculæ 2, carnosae, multi-nervatae, irregulariter obtusae. Stamina 3. Ovarium globosum, stylo brevi, stigmatibus 2. Caryopsis lateraliter compressa. Embryon parvus. Hilum rotundatum basale.

Perennial to 30 cm high (excluding the inflorescences) in clumps of several shoots clustered together in cespitose-like arrangements, the shoots arising from approximate nodes of a rhizome with foreshortened internodes, or internodes absent, the internodes between the cespitose-like clusters elongated into stolons. Culms erect or suberect, filiform, compressed, glabrous, the elongated portion

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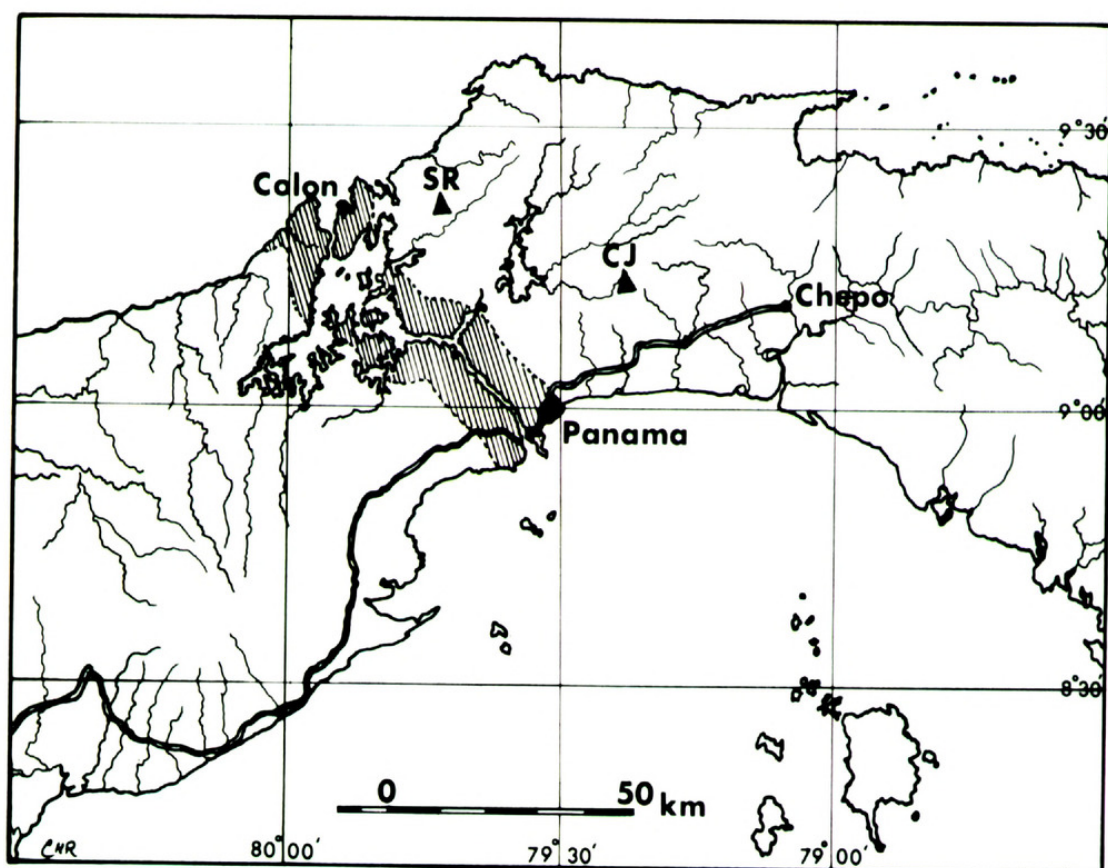


FIGURE 1. Map of Panama showing localities in which *Calderonella sylvatica* has been collected. SR, Santa Rita; CJ, Cerro Jefe. The cross-hatched area is the Canal Zone.

which terminates in the inflorescence with a single node at which is borne a sheath 7–8 cm long bearing a reduced blade. Flowering culm at maturity geniculating at the node and assuming a more or less horizontal position at time of spikelet abscission. Leaf sheaths compressed and strongly nerved with transverse veinlets, especially in the upper part, green over the back, golden-brown on the thinner margins, glabrous; ligule a brown chartaceous membrane 0.1–0.2 mm long, pilose abaxially; blades attenuate basally into a petiole 2–8 cm long, the lowermost 1–2 mm of which is thickened, solid, densely pilose, geniculate, the upper expanded portion of the blade lanceolate, tapering evenly at both ends, 8–20 cm long, 1–1.5 cm wide, flat, glabrous on the abaxial surface, sparsely papillose-strigose on the adaxial surface (at least when young), the midvein white, forming a prominent ridge on the abaxial surface, the veins connected by numerous transverse veinlets manifest on the abaxial surface only. Inflorescence a raceme 3–5 cm long consisting of 6 or 7 evenly spaced spikelets with thick pedicels 1–2 mm long, on the terminal portion of a weak, filiform peduncle

FIGURE 2. Photographs of *Calderonella sylvatica* in the field (Santa Rita forest, Panama, Calderón 2141).—A. Mature plant growing at base of tree.—B. Close-up of basal part of plant.



to 30 cm long. The uppermost spikelet developing first, at maturity ca. 8 mm long, stramineous when young, testaceous at maturity, with 3–5 dimorphous florets, the lowermost pistillate (and maturing first), the remaining staminate (or the one succeeding the pistillate with a pistil in addition to the stamens but not producing fruit?), at first lanceolate and parallel to the rachis, at maturity the lowermost floret becoming gibbous and causing the whole spikelet to bend at right angles to the rachis and become triangular in appearance. Disarticulation of the spikelets below the glumes. Lower glume ca. 6.5 mm long, lanceolate with thick pronounced veins, sparsely papillose-pilose between the nerves (evident especially at maturity), ciliolate on the upper margin, 15- or 16-nerved (1 or 2 of which may be faint and manifest only at the base) with numerous transverse veinlets (especially in the upper two-thirds), the basal margins encircling the rachilla and enclosing the base of the upper glume; upper glume ca. 4.5–5 mm long, parabolical (from side view), with the thick pronounced veins, sparsely papillose-pilose between the veins (evident especially at maturity), ciliolate on the upper margin, 10- or 11-nerved (of which one nerve may be faint and visible only at the base), with a few transverse veinlets on the upper half, the margins fuse at the very base and encircling the rachilla. Lower floret pistillate (with three staminodes present), at first erect and lanceolate, at length becoming gibbous and turned 90° from the rachilla; lemma ca. 5 mm long, bowed out at the base, sparsely papillose-pilose between the thickened nerves (evident especially at maturity), 15–19-nerved (many nerves manifest only at the base), with several transverse veinlets on the upper half of the margins encircling the rachilla at the base and fused on the lower one-eighth of the length; palea shorter than the lemma, with two keels, each keel with a nerve and wing extending from each keel, the two nerves connected at the summit by a transverse veinlet, narrowed abruptly above the truncate ciliolate apex, otherwise glabrous. Upper florets staminate, ca. 2.2–3.5 mm long; lemma 2.7 mm long, lanceolate, glabrous, membranous, 5–9-nerved with the nerves near the midvein connected toward the summit by a transverse veinlet, the margins at the base encircling the rachilla; palea with 2 keels, each containing a single nerve, winged. Lodicles of the lowermost floret 2, opposite the palea, 0.5–1.2 mm long, cuneate, broad, fleshy throughout with the outer margin a little higher than the inner, and with 3 or 4 vascular traces extending almost to the apex, the inner edges somewhat overlapping in front of the ovary at its base and partially fused below. Androecium consisting of 3 stamens, the filaments attached to the connective toward the base of the anther. Mature gynoecium consisting of a roundish ovary which narrows apically into a short style about 0.2 mm long, bifurcating to produce two branches, each ca. 6 mm long, the lower two-thirds glabrous, the upper third covered with short stigmatic processes. Caryopsis 2.3 mm long, compressed laterally, ventrally,

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FIGURE 3. Photographs of *Calderonella sylvatica* in the field (Santa Rita forest, Panama, Calderón 2141).—A. Mature plant with many inflorescences.—B. Young inflorescence.—C. Inflorescence at a later stage showing the stigmas exerted from the uppermost spikelets, which develop first.



and at the base, with the base of the style persistent; embryo small; hilum basal, round.

Holotype: PANAMA. PROVINCIA DE COLÓN: Santa Rita lumber road, 24 May 1968, R. L. Dressler 3511 (Holotype, US; isotypes, BAA, K, MO, P).

Additional specimens examined: PANAMA. PROVINCIA DE COLÓN: Santa Rita lumber road ca. 25 km before Colón on the Transisthmus highway, 5 March 1968, *Calderón* 2079a (BAA, K, P, US). Santa Rita, 12–20 km from the Transisthmus highway, elevation ca. 300 m, latitude 9°21' N, longitude 79° 42' W, shady forest, abundant, 31 October 1971, *Calderón & Dressler* 2141 (B, BAA, CORD, F, K, MO, NY, OWU, P, RB, RM, S, TNS, US). East Santa Rita lumber road, 16 January 1968, *Correa & Dressler* 643 (US). Santa Rita lumber road, ca. 15 km east of Colón forest, 5 October 1969, *Dressler & Lewis* 3729 (MO).

LEAF ANATOMY

The mesophyll of *Calderonella* consists of a rather distinct *palisade layer*, 1 or 2 cells in height, while the remainder of the mesophyll consists of rather large, irregularly shaped chlorenchyma cells. The *bulliform* cells are arranged in prominent, often wide fans of 3–5 cells each on the adaxial side of the leaf. The bulliform cells are large, inflated, projecting on the adaxial epidermis and frequently extending to about half the width of the mesophyll. The vascular bundles are surrounded by a large-celled outer bundle sheath and an inner bundle sheath composed of much smaller cells widely thickened on their inner surfaces. The outer bundle sheath is complete and conspicuous on vascular bundles of all sizes except on the midvein, where it is obscure and grades into the parenchyma cells making up the enlarged portion of the midrib. Frequently the outer bundle sheath cells on the lateral sides of the vascular bundle are more prominent and extend into the mesophyll. The vascular bundles occur in approximately 2 sizes: small bundles and first order bundles in ratios varying from 5 to 8 small bundles to 1 first order bundle. The *sclerenchyma* is confined to small patches or girders immediately beneath the epidermis and above and below each vascular bundle. On first order bundles in particular, the sclerenchyma frequently extends from the epidermis to the outer bundle sheath but does not interrupt it. Wider, thicker plates of sclerenchyma occur in the midrib.

In the abaxial *leaf epidermis* dumbbell-shaped silica bodies are frequently in a single row over the veins. The silica bodies in the intercostal regions are cross-shaped and modified cross-shaped. The filiform bicellular microhairs are approximately 30 microns long with both the basal and distal cells approximately equal in length. The stomata are ovoid with low dome-shaped, sometimes triangular subsidiary cells, and are confined to 1 or 2 rows on each side of the veins. The fundamental cells of the epidermis have relatively thick, sinuous walls, are elongate, and are more or less 6-sided. The fundamental cells are separated by cross-shaped siliceous cells or microhairs.

HISTORICAL CONSIDERATIONS

Features of spikelet morphology and leaf anatomy reveal that the affinities of *Calderonella* are with the centostecoid ("centothecoid") group of grasses. Since various genera have been assigned to this group by different authors, and the history of the group indicates a number of changes in its disposition, we feel

that the following account is necessary before we define the group as we now understand it. The historical considerations will be followed by a brief characterization of the gross morphology of the group and its differentiation from the bambusoid group of grasses. We will then present a key to the genera included in the centostecoid group with brief comments on each genus.

Centosteca (Fig. 4a, b) and genera related to it have been recognized variously as a tribe (Centotheceae), subtribe (Centothecinae), or group (centostecoid). The genus *Centosteca* was described by Desvaux (1810: 189) based on *Cenchrus lappaceus* of Linnaeus. Two years later Palisot de Beauvois (1812: 69) published the name of *Centotheca*. Desvaux in the following year (1813: 70) employed Beauvois' spelling giving the source of derivation as Greek "χεῖτων, piquant, et $\theta\eta\chi\eta$, enveloppe." Sharp (piquant) covering (enveloppe) is doubtless in allusion to the uppermost lemma which is covered with reflexed bristles in the type species. In the 1810 publication Desvaux published two other generic names ending in "steca," namely *Heterosteca* (page 188) and *Calosteca* (page 189). In the 1813 publication he retained the name *Heterosteca* but changed *Calosteca* to *Calotheca* and *Centosteca* to *Centotheca*. Interestingly, for the derivation of *Centotheca* (1813: 70) he gives $\theta\eta\chi\eta$ as "enveloppe"; for *Calotheca* (1813: 71) he gives $\theta\eta\chi\eta$ "couverture"; and for *Heterosteca* (1813: 68) he also gives $\sigma\tau\epsilon\chi\eta$ as "couverture." It is apparent that Desvaux considered both words "theca" and "steca" to be equivalent to "couverture" or covering, and this must have been his original thinking when he formulated the name *Centosteca*. Even though Palisot de Beauvois changed the spelling of *Centosteca* and Desvaux himself accepted this change, the original spelling must be retained as it was neither an orthographic nor typographic error (see Article 73, *International Code of Botanical Nomenclature*). In a recent note on the genus, Monod de Froideville (1971: 57) remarks that "the spelling [*Centotheca*] has been used by all authors . . . and it is obvious that it should be retained, although according to the *Code of International Botanical Nomenclature*, the original spelling should be used." The name *Centotheca* could be used only if conserved, but since the original spelling appears to be correct, representing neither an orthographic nor typographic error, we see no reason for its conservation.

The history of *Centosteca* and genera considered allied to it is interesting to recount, as the earlier authors were well aware of the relationships of many of these genera from their observations of gross morphology. Nees von Esenbeck (1829), in his work on Brazilian grasses, placed *Orthoclada* (Fig. 4c) in his tenth "family" of the order "Gramineae"—Gramineae Bambuseae. He considered it to be related to such bamboos as *Arundinaria* and *Merostachys*, placing these three apart from the true bamboos, "Bambuseae verae." But Steudel (1855: 116) considered *Centotheca* to be related to *Panicum* and placed it in Tribe III, Paniceae. However, most authors since his time have considered the genus to be a member of the Festuceae. In his magnificent treatise on grasses, Bentham (1881) recognized the Centotheceae as the seventh subtribe of the Festuceae, remarking that the tribe is formed of small tropical grasses, several of which had been referred to Bambuseae but rejected from that group by specialists. He mentioned that even though the spikelets resemble some Eu-Festuceae or Meli-



ceae, the foliage is unusual in the broad flat lamina which has cross venation, a feature which is not found elsewhere in the order except in a few Bambuseae. Benthham included five genera in the subtribe Centotheceae: *Centotheca* (mentioning here also *Poa mucronata* [= *Megastachya*]), *Orthoclada*, *Lophatherum*, *Streptogyne* [*Streptogyna*], adding that this genus is quite isolated in habit and in a number of characters, and *Zeugites*. The same treatment was given by Benthham and Hooker in *Genera Plantarum* (1883: 1092) and also by Hackel, in Engler and Prantl, *Die natürlichen Pflanzenfamilien* (1887: 71) except for the addition of *Poecilostachys* Hackel.

Evidently the first to consider the group as a tribe was Ridley (1907), who included *Centotheca* and *Lophatherum* in the Centotheceae in his treatment of Malaysian grasses. Bews (1929) in his treatment of the world's grasses included *Centotheca* (which he considered the most primitive of the group), *Zeugites*, *Lophatherum*, and *Streptogyna* in the subtribe Centothecinae of the Festuceae. Hubbard (1934) followed Bews in recognizing the Centothecinae as a subtribe of the Festuceae, and included *Centotheca*, *Orthoclada*, *Lophatherum*, and *Zeugites*. He did not include *Streptogyna* nor did he make mention of the genus elsewhere in his treatment of the Gramineae. Prat (1935), basing his conclusions on studies of the leaf epidermis and other microcharacters, pointed out that *Centotheca* and allies were quite unlike *Festuca* and related genera, i.e. not "festucoid." He stated that the tribes "Pappophorinées" and "Centothecinées" are quite different from festucoid grasses and further remarked that the worldwide distribution of the genera of the latter favored an ancient distribution. In the tribe he recognized *Centotheca*, *Zeugites*, *Lophatherum*, and *Streptogyna*. Roshevitz (1937) recognized the same tribe in his series Phragmitiformes and to the genera listed by Prat added *Bromuniola* and *Pseudostreptogyne*. Hubbard (1940), in his description of a new species of *Orthoclada* from Africa, recognized the tribe Centotheceae as had Ridley and Prat before him.

On the basis of morphological studies the above authors, at one time or another, indicated a close relationship among the following genera: *Bromuniola*, *Centosteca*, *Lophatherum*, *Megastachya*, *Orthoclada*, *Poecilostachys*, *Pseudostreptogyne*, *Streptogyna*, and *Zeugites*. One of these, *Poecilostachys*, a genus of Madagascar, has spikelets which are panicoid and is most closely related to the panicoid genus *Oplismenus*, according to Stapf (1916). The systematic position of another Malagasy genus, *Pseudostreptogyne*, has been discussed by Hubbard (1936). The type of the genus, *P. richardii* A. Camus, was found to be synonymous with *Streblochaete longiaristum* (A. Rich.) Pilger, a grass whose relationship is with *Danthonia* and *Phaenanthoecium*. The systematic position of *Streblochaete* has been discussed by Tateoka (1969), who also noted (1958) that the leaf anatomy of *Streptogyna* agrees with that of bamboos; he further indicated that the three lodicules of *Streptogyna* were similar to those of bamboos.

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FIGURE 4. Field photographs of Old and New World genera of the centostecoid group.—A.—B. *Centosteca lappacea* (Purwodadi, Java, Indonesia, T. R. Soderstrom & Soejatmi Sunarko 1360).—C. *Orthoclada laxa* (Madre de Dios, Costa Rica, C. E. Calderón 2110).



FIGURE 5. Habit sketch and spikelet dissection of *Calderonella sylvatica*.—A. Spikelet, $\times 6$.—B. Pistil of young flower, $\times 12.5$.—C. Lower glume, $\times 6$.—D. Upper glume, $\times 6$.—E. Male florets, $\times 6$.—F. Stamens, with lodicules at the base, $\times 12.5$.—G. Lemma of female floret, $\times 6$.—H—I. Lodicules, $\times 25$.—J. Caryopsis, side view, $\times 6$.—K. Caryopsis, front view, $\times 6$.—L. Habit of the plant, $\times 0.5$.—M. Section of leaf to show cross veins, greatly enlarged. —N. Juncture of leaf sheath and blade, $\times 1$. (Drawing *b* based on *Calderón & Dressler 2141*, all others on *Dressler 3511*.)

Metcalf (1960) also pointed out that the leaf anatomy of *Streptogyna* is like that of the bamboos, and recently Calderón and Soderstrom (1973) included the genus in the subfamily Bambusoideae.

Investigations made from standpoints other than gross morphology have shed light on the relationships of several of these grass genera and have also indicated that the following three belong to the *Centosteca* line: *Chasmanthium*, *Chevalierella*, and *Ramosia* (which we consider to be synonymous with *Centosteca*).

THE CENTOSTECOID GROUP

The following characterization of the group covers only features of the gross morphology. A comparative study of the leaf anatomy of all centostecoid genera is obviously needed before a complete delimitation of the group can be made.

Rhizomatous and/or stoloniferous annuals or perennials found in moist habitats of tropical and subtropical woodlands, ravines, or lake margins, or in warm temperate woodlands. *Leaves* typically petiolate with relatively broad blades and usually with manifest transverse veinlets; ligules membranous or ciliate or membranous with ciliate margins. *Spikelets* compressed laterally, 2-many-flowered with reduction either below or above the fertile florets, the florets perfect or unisexual; lodicules 2, more or less cuneate, many-nerved; stamens 1-3; stigmas 2; caryopsis flattened laterally; hilum basal, punctiform.

Genera included: *Bromuniola*, *Calderonella*, *Centosteca*, *Chasmanthium*, *Chevalierella*, *Lophatherum*, *Megastachya*, *Orthoclada*, and *Zeugites*.

CENTOSTECOID AND BAMBUSOID GRASSES

Most of the grasses—in number of taxa and individuals—which are found in the shaded habitat of the tropical American forests are related to bamboos. Because they are herbaceous, unlike their woody relatives, they have been referred to as herbaceous bambusoid grasses (Soderstrom & Calderón, 1971).

The herbaceous bambusoid grasses which are found at Santa Rita, along with *Calderonella*, are such genera as *Cryptochola* and *Maclurolyra*, members of the tribe Olyreae (Calderón & Soderstrom, 1967, 1973). The petiolate blades with tessellate venation and shaded habitat might lead one to assume that the new genus is also an herbaceous bambusoid grass. Indeed, the historical account given above shows that centostecoid genera have more than once been assigned a relationship with bamboos. Although superficial resemblance may be responsible for this, the characters presented in Figure 6 can be used to distinguish grasses of the two groups.

In the centostecoid genera the cells of the outer bundle sheath are large and inflated; the bulliform cells are large, prominent, and fan-shaped; and the mesophyll is composed of a well-marked palisade layer and spongy parenchyma with fairly large intercellular spaces. In the bambusoid genera the cells of the outer sheath are not so prominent nor are the bulliform cells. The mesophyll, furthermore, consists of fusoid cells and arm cells, the latter arranged in layers parallel to the epidermis. Lodicules of centostecoid grasses are two in number, more or less truncate, and glabrous, while those of bambusoid grasses are three in number, usually pointed, and often with hairs. The caryopsis of centostecoid

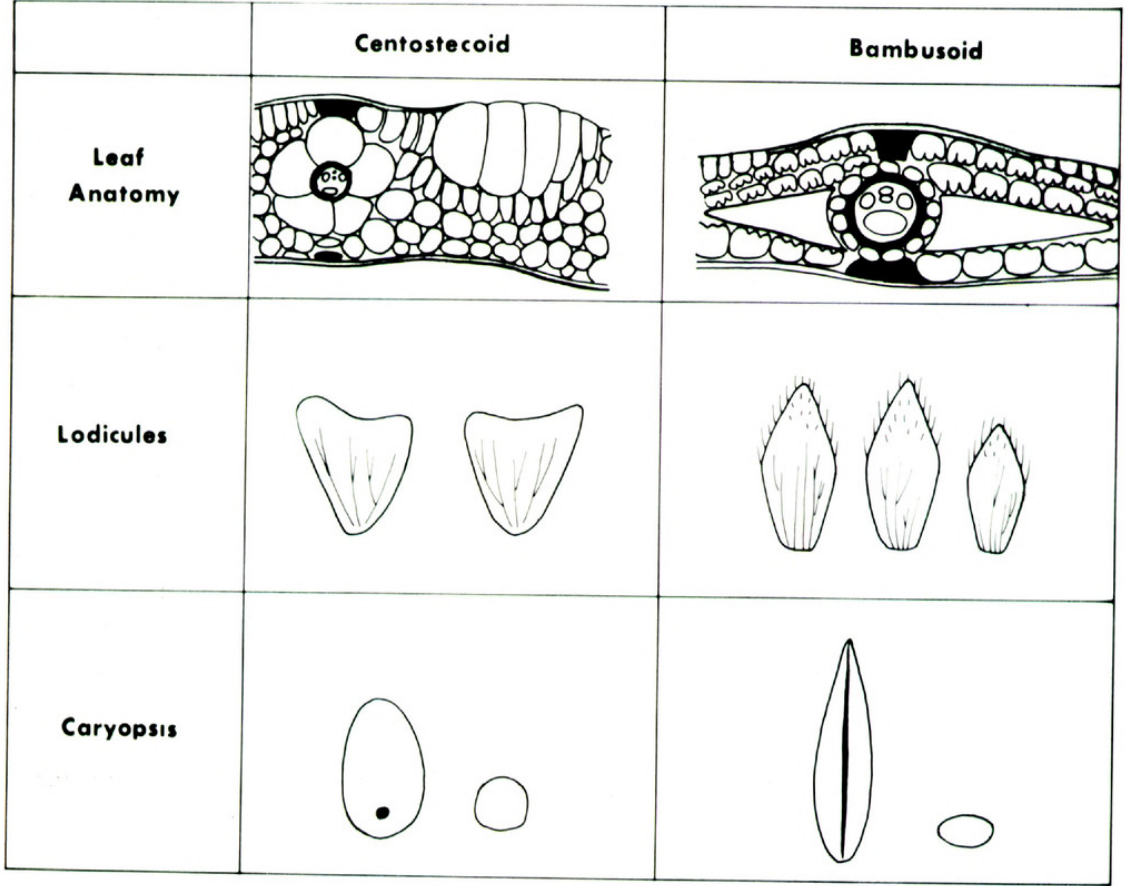


FIGURE 6. Schematic comparisons of the leaf anatomy, lodicules, and caryopses of the centostecoid and bambusoid groups of grasses.

grasses is compressed laterally and has a punctiform hilum, while in bambusoid grasses the caryopsis is usually round or dorsally compressed and has a linear hilum which extends almost the entire length of the caryopsis.

PROVISIONAL KEY TO THE GENERA OF THE CENTOSTECOID GRASSES

1. All florets within the same spikelet unisexual, the lowermost larger, ♀, becoming gibbous at maturity, upper florets ♂ 2
1. Florets, at least some, within the same spikelet bisexual; reduced florets also generally present 3
2. Inflorescence a panicle; fertile lemma less than 10-nerved; stigmatic processes long, thin (tropical America from Mexico and West Indies to Bolivia) *Zeugites*
2. Inflorescence a raceme; fertile lemma more than 10-nerved; stigmatic processes short, thick (Panama) *Calderonella*
3. Blades not manifestly tessellate (eastern and southern U.S.A. and northern Mexico) *Chasmanthium*
3. Blades manifestly tessellate 4
4. Rachilla of uppermost (usually rudimentary) floret adnate (on the lower part) to the palea of the preceding floret (tropical America and Africa) *Orthoclada*
4. Rachilla of uppermost floret free 5
5. Lemmas awnless or mucronate 6
5. Lemmas awned 7
6. Spikelets many (10-16)-flowered (Africa) *Megastachya*
6. Spikelets few (1-3)-flowered, the terminal floret rudimentary, club-shaped (tropical Asia) *Centosteca* (including *Ramosia*)

7. Basal floret sterile, represented by lemma only; fertile lemmas bowed out at the base (Africa: Angola, Northern Rhodesia, Kasai and Katanga) *Bromuniola*
7. Basal floret fertile; fertile lemmas not bowed out at the base 8
8. Awns curved, antrorsely scabrous; spikelets 2–3-flowered; nerves of glumes and lemmas weakly developed (Congo) *Chevalierella*
8. Awns straight, rigid, retrorsely scabrous; nerves of glumes and lemmas strongly developed (tropical Asia) *Lophatherum*

Bromuniola Stapf & Hubbard, Bull. Misc. Inform. 1926: 366. 1926.

The type species, *B. gossweileri* Stapf & Hubbard, is the only representative of this West African genus. Stapf and Hubbard, in the original publication (p. 368), state that in general habit the genus resembles *Uniola latifolia* (*Chasmanthium latifolium*) and that it “also recalls some of the Centotheceae, but it differs from these in the presence of a third glume and in the awned valves.” Jacques-Félix (1962: 141) reported the distribution as Angola, Northern Rhodesia, Kasai, and Katanga.

Centosteca Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 189. 1810.

A small but widely distributed tropical genus, it is found in southeast Asia, China, Philippines, Japan, Polynesia, northeastern Australia, and tropical Africa. It prefers warm places in semi-shade, has compressed spikelets with 1–3 florets in which the rachilla extends beyond the uppermost floret as a club-shaped rudiment.

The genus *Ramosia* Merrill (Philipp. Jour. Sci. 11: 2. 1916) was based on material collected at the edge of Lake Polog in Sorsogon Province, Philippines. Merrill compared it with *Glyceria* in his discussion of the new genus, but at the same time he expressed dissatisfaction with the alignment. The genus has recently been transferred to *Centosteca* by Monod de Froideville (1971), a disposition with which we concur. In his paper, Monod de Froideville presents a key to the species of the genus.

Chasmanthium Link, Hort. Berol. 1: 159. 1827.

This is a woodland genus of five species, confined mostly to the southeastern and southern regions of the United States except for one species which has also been collected in northern Mexico. For years these species had been placed in *Uniola* and the position of the latter genus remained uncertain until Yates (1966a, 1966b) reinstated *Chasmanthium* as a genus. The leaves are not clearly tessellate in species of this genus, a feature which departs from the other centostecoid members. Plants of *C. latifolium* occur as far north as Massachusetts, U.S.A., and are thus adapted to cold conditions, unlike most centostecoid grasses which occur in the tropics and subtropics.

Chevalierella A. Camus, Rev. Int. Bot. Appl. Agric. Trop. 13: 421. 1933.

The type species, *C. congoensis* A. Camus, is the only representative of this genus and is known only from the Congo forests. Camus, in her description of the genus, while she did remark that it resembled *Centotheca* and *Lophatherum*, assigned it instead to the tribe Chlorideae and indicated that its affinities were with *Leptocorydion*. Pilger (1954) placed it in the Eragrosteae, Jacques-Félix (1962) in the Centotheceae.

Lophatherum Brongniart in Duperrey, Bot. Voy. Coquille 2: 49. 1831.—Type species: *L. gracile* Brongniart.

This is a small genus of forest grasses in tropical Asia with sterile lemmas that project from the top of the spikelet as a tuft of short, stiff awns. Bor (1960) placed the grass with *Centotheca* in the tribe Centotheceae.

Megastachya Palisot de Beauvois, Agrost. 74 (as *Magastachya*), 167 (as *Megastachya*). 1812.—Lectotype: *M. owariensis* P. Beauv., *op. cit.*, Atlas, pl. 15, fig. 5. [See Niles & Chase, Contr. U.S. Natl. Herb. 24: 182. 1925.]

This is a monotypic genus from tropical Africa with many-flowered spikelets on long slender pedicels arranged in an open panicle. Chippindall (1955) listed this grass as the sole representative of the Centotheceae in South Africa.

Orthoclada Palisot de Beauvois, Agrost. 69. 1812.—Type species: *O. rariflora* (Lam.) P. Beauv.

A ditypic genus of tropical America and tropical Africa, its members have broad petiolate leaves and compressed spikelets borne in a diffuse panicle. The American species, *O. laxa* (Rich.) P. Beauv., is not rhizomatous like the African one, *O. africana* C. E. Hubbard. In both, the rachilla of the uppermost reduced floret is adnate at its base to the palea of the preceding floret.

Zeugites P. Browne, Civ. Nat. Hist. Jamaica 341. 1756, *nom. cons.*—Type species: *Z. americanus* Willdenow, Sp. Pl. 4: 204. 1805.

This is a genus of about 10 species distributed from Mexico and the West Indies to Andean South America. The plants prefer shaded spots such as ravines, arroyos, and moist pockets on mountainsides, but in spite of their widespread distribution throughout the Americas they seem never to be a common element of the flora. The peculiar spikelet structure of *Zeugites*—with the upper florets male and lowermost one female, becoming gibbous at maturity—is similar to that of *Calderonella* and suggests a close relationship between the two genera. They are easily separated, however, on a number of characters as indicated in the above key to the genera of centostecoid grasses.

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