ARUNDOCLAYTONIA, A NEW GENUS OF THE STEYERMARKOCHLOEAE (POACEAE: ARUNDINOIDEAE) FROM BRAZIL[1]

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ABSTRACT

Arundoclaytonia dissimilis Davidse & Ellis, gen. et sp. nov. is described from Amazonian campinas in Amazonas and Pará, Brazil. It represents the second genus of the tribe Steyermarkochloeae (Poaceae: Arundinoideae). Morphologically it is characterized by a caespitose growth habit, proliferation and lignification of the numerous basal culm internodes, normally developed leaves with spiral phyllotaxy, unisexual hemispherical inflorescences aggregated into a false panicle, 3–9-flowered male spikelets with 2 anthers per flower, 3-flowered female spikelets with only the middle floret fertile and its palea convolute and many-nerved, lack of lodicules, terminal exsertion of the stigmas and stamens, and fusiform caryopsis with an elliptic-punctate hilum. Anatomically this species is characterized by C_3 anatomy, including nonradiate, compact isodiametric chlorenchyma, and 2 bundle sheaths; abaxially by the absence of stomata and microhairs, reduction of silica bodies, thick epidermis, and hypodermal sclerenchyma; and adaxially by prominent ribs and furrows. Its classification in Steyermarkochloeae is based primarily on the morphology of the spikelets.

During 1974 an unusual grass was collected by William R. Anderson and associates in Pará, Brazil. Although it was recognized as an undescribed taxon, the inflorescences were too immature to show the exact morphology of the spikelets. In 1979 Cleofé E. Calderón and coworkers collected abundant mature material of the same taxon in Amazonas, Brazil. Our study of both these collections indicates that they represent the second genus of the recently described tribe Steyermarkochloeae (Davidse & Ellis, 1984). We are naming the genus in honor of Dr. W. D. Clayton, eminent agrostologist at the Royal Botanic Gardens, Kew, who has made and continues to make outstanding contributions to agrostology. The compound generic name at the same time refers to the arundinoid affinity of the genus. The specific epithet alludes to the strongly dissimilar male and female inflorescences and spikelets.

DESCRIPTION

Arundoclaytonia dissimilis Davidse & Ellis, gen. et sp. nov. TYPE: Brazil. Amazonas: Transamazon Highway, ca. 53 km W of the Aripuaña River, abundant dominant plant of the vegetation. Growing in a white sand soil "campina." This plant grows in large, open areas mixed with shrubs and alternating with narrow strips of islands of low tree forest. Most of the population reduced to burnt bases. These trunks look like big candelabra, some ca. 70 cm or less. From them come up solid stems with thickened bases formed by aerial roots. In many cases from the top of burnt trunks, bunches of leaves start coming again. Few plants still blooming. Plants ca. 2–3 m tall when flowering. 28 June 1979, *C. E. Calderón, O. P. Monteiro & J. Guedes 2706* [holotype, INPA; isotypes, CANB, K, LE, MO (mounted as 8 sheets), PRE, RB, SP, US (mounted as 11 sheets)]. Figures 1–7.

Gramen perenne; culmi internodiis numerosis inferioribus solidis lignosis superioribus cavis arundaceis; phyllotaxis spiralis; vagina cava marginibus liberis; ligula membranacea ciliata; lamina plana vel involuta; inflorescentiae unisexuali constans ex fasciculis hemisphaericis aggregatis in inflorescentiam falsam; spiculae unisexualis rotundatae dorsales infra glumis disarticulates; glumae 2; spiculae masculinae 3–

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[1] We extend our gratitude to the late Dr. Thomas R. Soderstrom, Smithsonian Institution, who made the ample Calderón et al. collections and photographs available to us and who encouraged us in our studies. We very much appreciate the very useful review comments by Dr. Steve Renvoize, but, pending additional data, still disagree with him on the tribal classification of Steyermarkochloeae. We thank John Myers for drawing Figure 7, and Dr. William R. Anderson, University of Michigan, for information about his collecting itinerary in the Serra do Cachimbo.

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9-florae palea 2-carinata; stamina 2; spiculae femineae 3-florae flosculo inferissimo sterili flosculo supererissimo rudimentali, palea flosculi mediani convoluta, 9–13-nervis lemmatibus longiorior; lodiculae 0; stylus 1, stigmate 2; caryopsis fusiformis-teres hilo punctato.

Perennial 2–3 m tall, erect. *Vegetative culms* usually densely covered for 2–70 cm to a thickness of 1.5–6 cm by aerial roots tightly appressed to the culm and by remnants of leaf sheath bases; internodes numerous, 2–15 mm long, 1–1.5 cm diam., solid, lignified; nodes bearing one prominent prophyllate bud; phyllotaxy 2/5; branching intravaginal near the basal cluster of leaves. *Flowering culms* to 1 cm diam., consisting of many, often elongated internodes; internodes 1–16 cm long, glabrous, densely waxy when young, green in the exposed portions when older, hollow, gradually becoming solid toward the base of the plant; nodes glabrous; branching primarily intravaginal, profuse in the upper ⅓ of the culm to form a false inflorescence. *Leaves* primarily clustered toward the base, those of the flowering culms fewer and gradually reduced in size toward the tip of the culm. *Basal leaves* with the sheaths densely overlapping, much longer than the internodes, stramineous, long persistent, turning brown and eventually reduced to fibers in age, rounded and glabrous abaxially, without a differentiated midrib, the margins glabrous, free to the base, the base pilose at the point of insertion and between the veins or glabrescent, the apex ciliate with hairs 2–4 mm long, wider than the base of the blade, rounded, a collar not clearly differentiated; ligule a ciliate membrane 0.9–2.1 mm long, the membrane 0.3–0.9 mm long, the cilia 0.5–1.2 mm long; blades 45–80 cm long, 8–16 mm wide, flat with involute margins or entirely involute, the upper portion always involute and the apex pungent, the abaxial surface green, glabrous and smooth, the adaxial surface grayish green, densely and minutely scabrous, grooved between the veins, the veins approximately the same size, a midrib not differentiated, the margins ciliate with hairs 2–3 mm long in the lower ⅓, scaberulous in the upper ⅔. *Cauline leaves* similar to the basal leaves but smaller, the uppermost much reduced with the blade shorter than the sheath and entirely involute. *Inflorescences* numerous, borne on axillary, exserted peduncles, aggregated into a false panicle, unisexual, consisting of hemispherical clusters of 7–20 spikelets, each cluster surrounded by 1 or 2 series of bracts and/or rudimentary spikelets; male inflorescences produced before the female, 9–13 mm wide, 6–11 mm high; female inflorescences 20–36 mm wide, 15–23 mm high; peduncles geniculate and pilose at the base with hairs 0.5–1.5 mm long, sometimes with a line of pubescence or with a scarious bract 1–3 mm below the cluster of spikelets, always subtended by a sheath, the sheath terminating in a sharp point; peduncles of the male inflorescences usually longer than those of the female inflorescences. *Female spikelets* 7–19 mm long at anthesis, sessile or short-pedicellate with pedicels to 0.5 mm long, lanceoloid, rounded on the back, disarticulating below the glumes, falling as a unit, slightly curved, 3-flowered; glumes 2, unequal, herbaceous, shorter than the lemmas, ovate, broadly acute, pilose at the base, otherwise scaberulous, the nerves free or connected by cross-veinlets, the lower 1.5–2.0 mm long, 1–3-nerved, the upper 2.2–3.5 mm long, 3–5-nerved; lower floret without a flower, the lemma 3.0–5.1 mm long, 7–9-nerved, ovate, broadly acute, pilose at the base, otherwise scaberulous, cross-veinlets few, the palea absent or rudimentary, 0.7–1.5 mm long and hyaline when present; middle floret unisexual, the lemma 5.7–8 mm long, 9–11-nerved with conspicuous cross-veinlets, ovate, acute, pilose at the base and between the nerves just above the base with hairs 1–1.5 mm long, otherwise scaberulous, the palea conspicuously longer than the lemma, 7.5–17 mm long, 9–13-nerved, slightly curved in the upper half, convolute, shallowly grooved on the back, spongy-thickened, smooth and shiny in the lower ½–⅔, herbaceous and scaberulous in the upper ⅓–½, ciliate on the overlapping margin at the base with hairs 1–1.5 mm long; upper floret rudimentary or consisting of a single 3-nerved bract, 0.1–4 mm long, ciliate at the base, borne on a prominent rachilla 3.5–10.5 mm long, the floret and rachilla fitting into the palea groove of the middle floret; lodicules absent; staminodia absent or present as an anterior pair of rudiments to 0.2 mm long; gynoecium cylindrical, the ovary wall free from the ovule, the style one, dividing into 2 inconspicuously plumose stigmas slightly below the tip of the middle palea, the stigmas 2.5–4 mm long, terminally exserted through an apical, tubular orifice formed by the convolute palea; caryopsis fusiform-terete, narrowing apically, 6–7 mm long, 0.8–1.2 mm diam., glabrous, the embryo $\frac{3}{10}$–$\frac{4}{10}$ as long as the caryopsis, the hilum elliptic-punctate. *Male spikelets* 3.5–7.5 mm long, sessile or short-pedicellate with pedicels to 0.5 mm long, rounded on the back, disarticulating below the glumes, 3–9-flowered, the florets (except the uppermost) bearing flowers, the middle florets slightly larger than those above or below, the uppermost usually rudimentary; glumes 2, unequal, shorter than the lemmas, membranous, ovate, erose, truncate or obtuse, pilose at the base, usually with cross-veinlets, the lower 1.3–2.1 mm long, 1–3-nerved, the upper 1.8–2.5 mm long, 3-nerved; lemmas similar to the glumes in pubescence, shape and texture, 2.6–4.1 mm long, shorter than the paleas, 3–9-nerved; paleas 3.2–5.8 mm long, broadly obtriangular, truncate, sometimes erose, 2-keeled (each keel with a nerve), the base with hairs 1–1.5 mm long, the back sulcate, the keels ciliolate, the margins overlapping; lodicules absent; stamens 2, one situated on each side of the sulcate palea, terminally exserted through an opening formed by the overlapping palea margins, the filaments separate, basifixed, the anthers 2.2–2.9 mm long.

Paratypes. BRAZIL. PARA: Alto Tapajós, Rio Cururú, northwest edge of Serra do Cachimbo, 25 km by foot NE of Missão Velha on Rio Cururú, elev. ca. 400 m?, 7° ca. 30′S, 57° ca. 15′W, outcrop of blocky sandstone, with shrubs on rocks and smaller cover on wet sand between rocks, 2 m tall, among rocks, 14 Feb. 1974, *W. R. Anderson, S. G. da Fonsêca, R. Reis dos Santos & R. Souza 10950* (MO, NY, UB).

MORPHOLOGICAL OBSERVATIONS

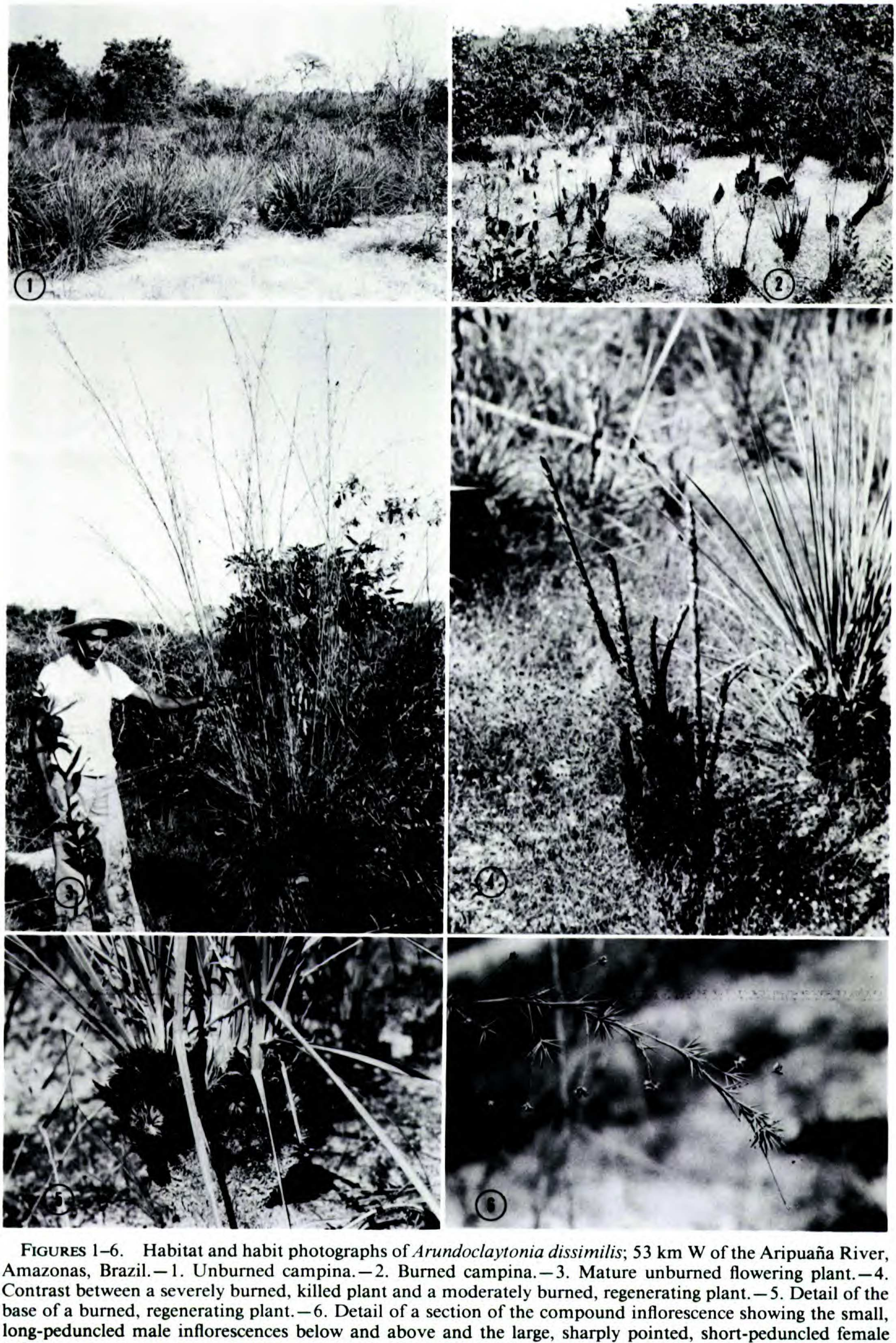
Arundoclaytonia dissimilis when fully mature and undisturbed by fire has an unusual appearance caused by the thick accumulation of leaf sheath bases and adventitious aerial roots (Figs. 1, 3). Such plants in the aspect of their basal parts are more reminiscent of certain species of *Vellozia.* This unusual appearance is accentuated after the plants have been moderately or severely burned (Figs. 2, 4, 5).

Although the plant is fundamentally a tussock plant, the dense cluster of leaves, which is normally basal in a tussock grass, is raised up to 70 cm above ground level in older plants of *Arundoclaytonia* (Figs. 2–5). These small "trunks" result from the proliferation of numerous, short internodes in the basal portion of the culms. Short basal internodes are typical of grass culms. What is unusual in *Arundoclaytonia* is their large number, thickness, woodiness, and perennial duration. Annual culms characterize most grasses.

In typical caespitose perennial grasses the short basal internodes perennate and bear the buds from which new tillers are produced for the new growing season. It is this region of the culm that is much elongated by the proliferation of internodes and gives *Arundoclaytonia* its trunklike appearance. The internodes of this region are solid in most grasses, and this is also true in *Arundoclaytonia.* In contrast, the elongated internodes of the flowering culm produced above the cluster of basal leaves gradually become hollow, as is common among grasses.

When the sheath bases and mass of aerial roots have been removed from the lower portion of the culm (as may happen after severe burning and the subsequent wearing off of the root and sheath remains), it becomes apparent from the position of the axillary buds that the leaf arrangement is not distichous. Every sixth node bears a solitary, prophyllate, dormant bud (Fig. 7A) that occurs in the same relative position as the buds five nodes above and below it. Since two complete turns around the culms must be made to attain the same position, phyllotaxy is 2/5. The arrangement of the spikelet bracts appears to be nearly distichous; however, the relative position of the bracts is much more difficult to observe because the very short internodes of the spikelet and the broad bases of the glumes and lemmas obscure the exact point of insertion of these spikelet parts. Distichous phyllotaxy is characteristic of the Poaceae (Arber, 1934: 282; Barnard, 1964: 47). Only one other exception has been reported: spiral phyllotaxis in *Micraira subulifolia* F. Muell., a mosslike plant from Queensland (Watson & Dallwitz, 1980: 89).

Branching occurs near the base of the plant to form the main culms that constitute the bulk of the tussock (Figs. 4, 5). These branches originate from the buds illustrated in Figure 7A. Branching is very infrequent in the middle portion of the culms but profuse in the upper portion. At each upper node, a smaller axillary branch is produced which itself is rebranched several times (Fig. 8) into branchlets terminating in inflorescences. The branching pattern is the relatively simple one that characterizes most nonbambusoid grass genera. A prophyllum is the first foliar organ produced at the lowest node of each branch (Fig. 8). Each prophyllum is many-nerved and prominently two-keeled with narrow wings on the keels. Buds at subsequent nodes on the branch are subtended by leaves with blades reduced and generally smaller than the sheaths. These leaves are gradually reduced upward along the branches. Just below the inflorescences they are reduced to scarious bracts, presumably representing reduced sheaths only.



FIGURES 1–6. Habitat and habit photographs of *Arundoclaytonia dissimilis*; 53 km W of the Aripuaña River, Amazonas, Brazil.—1. Unburned campina.—2. Burned campina.—3. Mature unburned flowering plant.—4. Contrast between a severely burned, killed plant and a moderately burned, regenerating plant.—5. Detail of the base of a burned, regenerating plant.—6. Detail of a section of the compound inflorescence showing the small, long-peduncled male inflorescences below and above and the large, sharply pointed, short-peduncled female inflorescences in the center. Photographs by Dr. Cleofé E. Calderón.

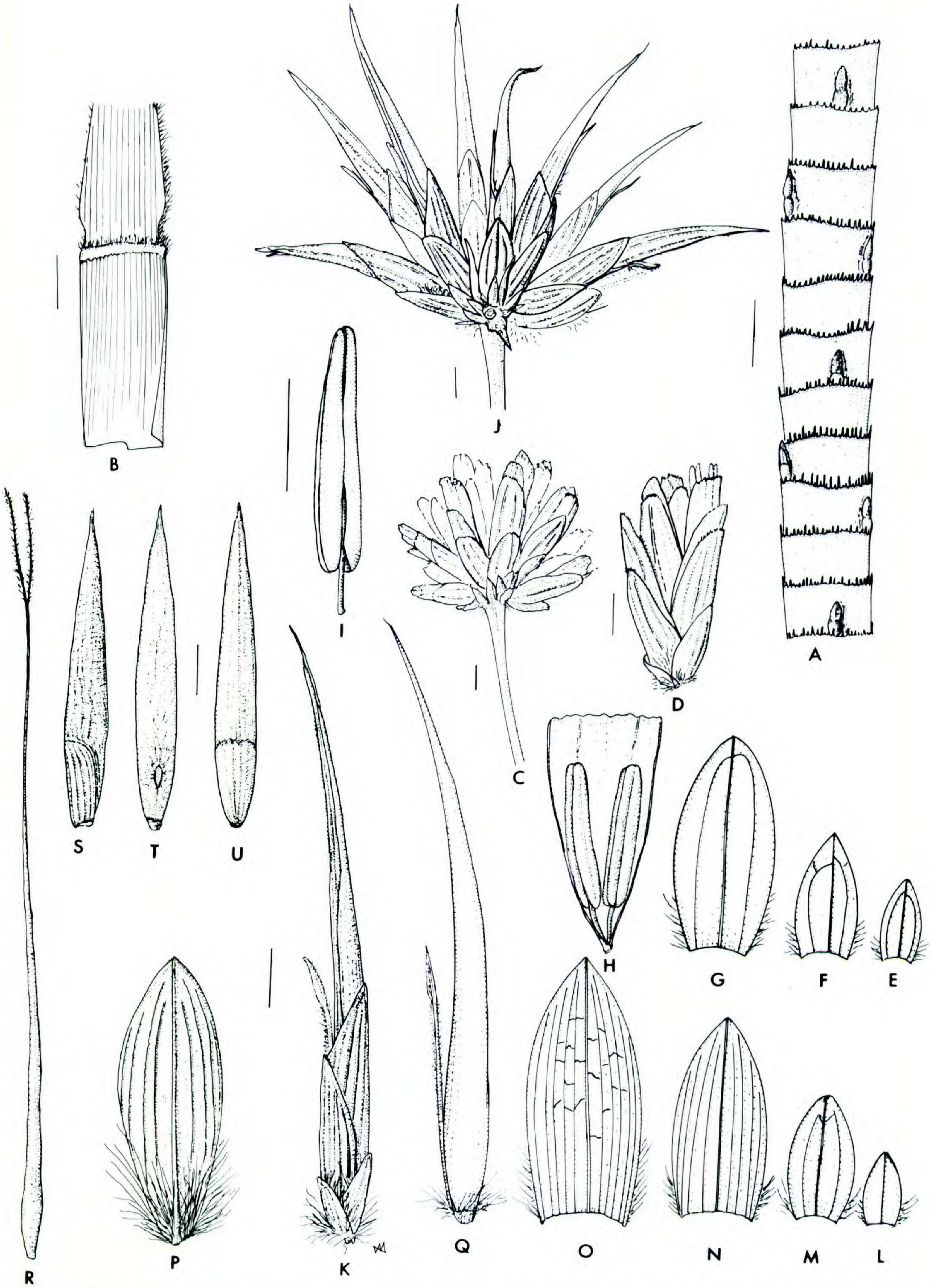


FIGURE 7. Morphology of *Arundoclaytonia dissimilis.*—A. Basal portion of culm with the sheath bases worn off and showing the approximately identical position of the buds every sixth node.—B. Portion of a leaf with ligule.—C. Male inflorescence.—D. Male spikelet. E–I. Components of male spikelet.—E. Lower glume.—F. Upper glume.—G. Lemma.—H. Inner view of palea with the two stamens composing the male flower.—I. Stamen.—J. Female inflorescence.—K. Female spikelets. L–R. Components of female spikelet.—L. Lower glume.—M. Upper glume.—N. Lower lemma.—O. Middle lemma, ventral view.—P. Middle lemma, dorsal view.—Q. Middle palea and rachilla extension with the rudimentary upper floret.—R. Gynoecium, probably pollinated and slightly expanded. S–U. Caryopsis in three different views.—S. Lateral view.—T. Hilum view.—U. Embryo view. Scales: A, B = 1 cm; C, D, I–K, U = 1 mm; magnification for E–H, K–R, and S–U the same.

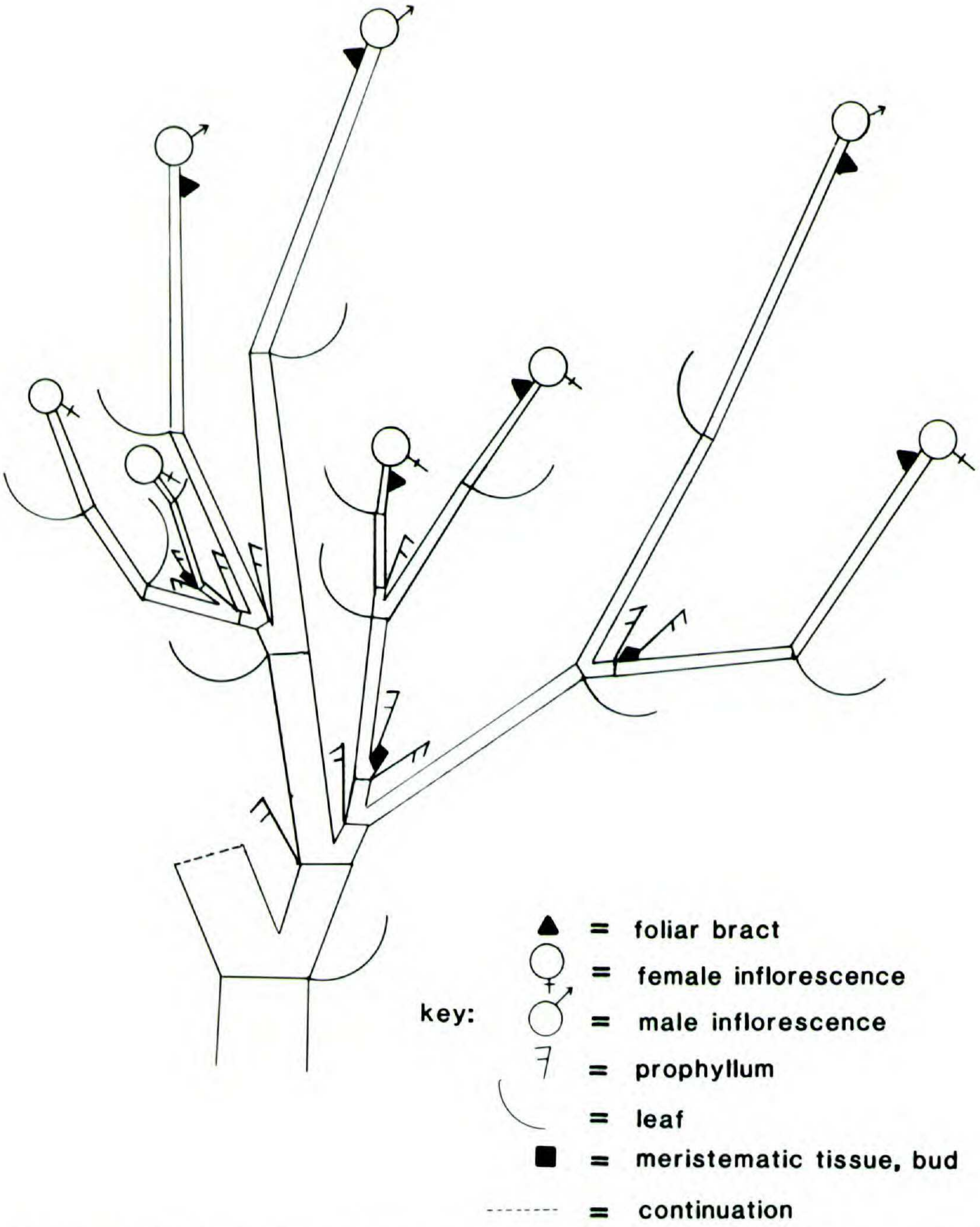


FIGURE 8. Diagrammatic illustration of a portion of the inflorescence of *Arundoclaytonia dissimilis* showing the relationship of the internodes, leaves, prophylla, and inflorescences. The proportions of the structures have been altered for clarity and are shown in two dimensions.

At any node along the flowering portion of a main culm, male inflorescences are produced before the female inflorescences, and the male inflorescences are borne on longer branches than those of the female inflorescences. Each branch complement along the main culm ultimately terminates in a male inflorescence. The proportion of male to female inflorescences varies from 2 male : 1 female in the lowest portion, gradually changing to 1 male : 3 female in the uppermost portion. However, since the male spikelets are functionally 2–8-flowered compared with the functionally one-flowered female spikelets, the total number of male flowers is greater than female flowers. Although the plant is fundamentally protandrous, the large number of inflorescences produced by any mature plant ensures a significant overlap between the flowering of male and female spikelets. No information is available about self-incompatibility or frequency of flowering.

The male and female spikelets are strongly dimorphic and, besides the difference in flowers and number of anthoecia, differ significantly in the anthoecial morphology. Both the lemma and especially the palea of the functional floret of the female spikelets are convolute and thicker in texture, and the palea is greatly elongated and 9–13-nerved (Fig. 7K, O–Q). In contrast, the lemmas and paleas of the male spikelets are membranous, the lemmas are 3–9-nerved and rounded on the back, and the paleas are 2-keeled and

2-nerved (Fig. 7D, G, H). The relative lengths of lemmas and paleas in the two kinds of spikelets are similar, the paleas being longer in both kinds, although those of the female spikelets tend to be somewhat longer than those of the male spikelets.

In both kinds of inflorescences the outer whorl of spikelets is surrounded by a ring of small sterile bracts that we interpret to represent rudimentary spikelets (Fig. 7C, J). In some cases these rudimentary spikelets may reach 4 mm in length in the female inflorescence and consist of four or five bracts in the same positions as the normal female spikelet parts. From such rudimentary spikelets there is a gradual diminution and simplification to small solitary bracts. Occasionally one of the normally sized female spikelets on the outside of the inflorescence has an extra bract. However, those on the inside of the inflorescence uniformly have the two glumes and three florets. In the several cases where a small extra bract was observed in the inner part of the inflorescence, it clearly originated below the very short pedicel and presumably also represented a rudimentary spikelet.

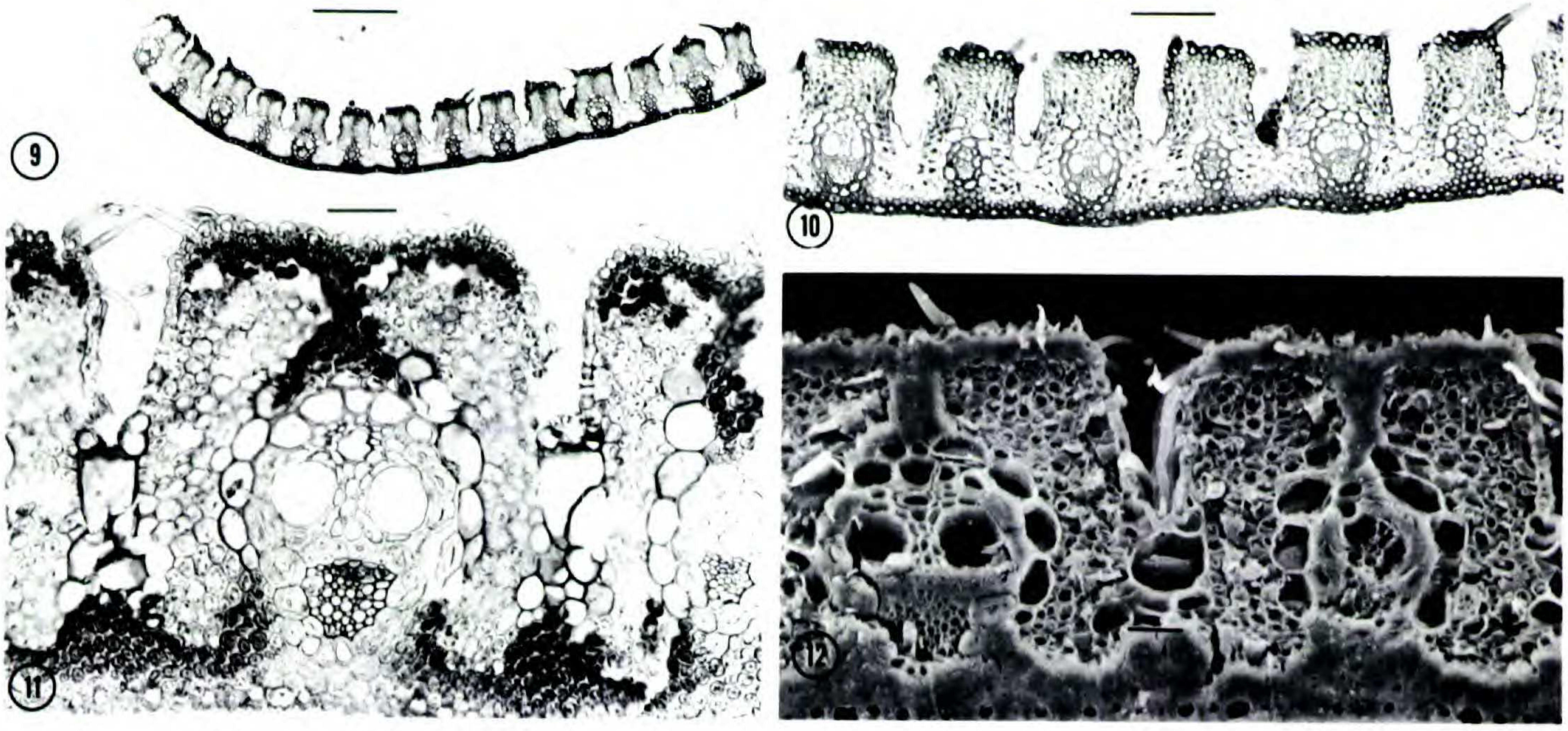
LEAF BLADE ANATOMY

ANATOMICAL TECHNIQUES

Anatomical studies were carried out on leaves from herbarium specimens and those fixed in the field in FAA. Preparation of the sections followed the methods outlined by Ellis (1984). The very fibrous nature of the leaf blades frequently caused the sections to tear as they were cut, making it difficult to obtain completely undamaged sections.

LEAF IN TRANSVERSE SECTION

Outline: open, expanded with the margins slightly recurved (Fig. 9). Leaf thickness 30 μm laterally to 40 μm centrally. *Ribs and furrows:* prominent, flat-topped adaxial ribs with straight, vertical sides present over all the vascular bundles (Fig. 10); ribs associated with first-order and third-order vascular bundles of identical size and shape; furrows narrow, cleftlike, penetrating at least half the leaf thickness. Abaxial ribs or furrows absent. *Median vascular bundle:* no midrib or keel developed; median vascular bundle structurally indistinguishable from lateral first-order bundles. *Vascular bundle arrangement:* more than 25 first-order bundles with metaxylem vessels per leaf section; one third-order bundle without metaxylem vessels between consecutive first-order bundles, this alternating pattern occurring across the full width of the blade (Figs. 9, 10). All vascular bundles located slightly closer to the abaxial surface. *Vascular bundle structure:* first-order bundles round to elliptical in outline (Figs. 9–12); phloem tissue adjoining the inner bundle sheath; protoxylem lacunae present; metaxylem vessel elements wide (±5 μm) with a diameter double that of the parenchyma sheath cells, thin-walled and slightly angular (Fig. 12). Third-order bundles elliptical with xylem and phloem tissue distinguishable. *Vascular bundle sheaths:* first- and third-order bundles completely surrounded by an inner bundle sheath (Fig. 11); mestome sheath cells relatively large, of the same diameter as the parenchyma sheath cells; secondary walls heavily but uniformly thickened, almost excluding the lumen (Figs. 11, 12). Outer bundle sheath round, adaxially and abaxially interrupted by sclerenchyma girders (Figs. 11, 12); bundle sheath extensions absent; cells elliptic, variable in size, thin-walled and lacking chloroplasts. *Sclerenchyma:* adaxial girders inversely anchor-shaped, following the shape of the adaxial ribs (Figs. 11, 12); abaxial sclerenchyma forming a continuous hypodermal band with projections toward the vascular bundles as well as the bulliform cell groups (Fig. 11). Fibers very thick-walled with lumens almost completely filled; lignified, except those projecting toward the bulliform cells which may have cellulose secondary walls (Fig. 10). *Mesophyll:* chlorenchyma not radiately arranged; cells small, isodiametric and tightly packed without visible intercellular air spaces (Fig. 11); occupying the sides of the ribs but divided abaxially by the bulliform cells, colorless cells, and abaxial hypodermal sclerenchyma; arm or fusoid cells absent. Colorless, inflated, thin-walled parenchyma cells linking the bulliform cells to the hypodermal sclerenchyma. *Adaxial epidermal cells:* bulliform cells at the base of all furrows and occurring in restricted, fan-shaped groups with an inflated central cell. Epidermal cells with a very thick cuticle, even on the sides of the furrows; papillae or macrohairs absent; interlocking prickles common on the sides of the furrows (Figs. 11, 12). *Abaxial epidermal cells:* bulliform cells absent; epidermal cells small, with an extremely thick, continuous cuticle equal in thickness to the diameter of the epidermal cells; hairs, papillae, and stomata absent; costal and intercostal zones not differentiated.



FIGURES 9–12. Leaf blade anatomy of *Arundoclaytonia dissimilis* in transverse section.—9. Outline showing the absence of a keel.—10. Alternating first- and third-order vascular bundles and prominent adaxial ribs and cleftlike furrows.—11. Anatomical detail showing double bundle sheath, compact mesophyll, inversely anchor-shaped adaxial sclerenchyma girder, abaxial hypodermal band and bulliform cells with associated colorless cells.—12. Scanning electron photomicrograph showing interlocking prickles in the adaxial furrows and structure of the metaxylem vessel elements. Scales: 9 = 50 μm; 10 = 20 μm; 11, 12 = 10 μm. Based on *Anderson et al. 10950* (Figs. 9, 10) and *Calderón et al. 2706* (Figs. 11, 12).

ABAXIAL EPIDERMIS

Zonation: costal and intercostal zones indistinguishable; entire epidermis composed of uniform long and short cells (Figs. 13–15). *Long cells:* elongate rectangular, length 3× the width, anticlinal walls parallel, end walls vertical (Fig. 14); horizontal and vertical anticlinal walls heavily thickened, pitted and deeply sinuous. Long cells usually adjoining one anther but infrequently separated by cork-silica cell pairs. *Stomata:* lacking on the abaxial surface (Fig. 13). *Short cells:* tall, with irregular outline; associated with silica cell of similar shape (Fig. 14); occurrence irregular. *Papillae:* absent. *Microhairs:* absent. *Silica bodies:* tall and narrow, irregular in outline; scattered throughout the epidermis.

ADAXIAL EPIDERMIS

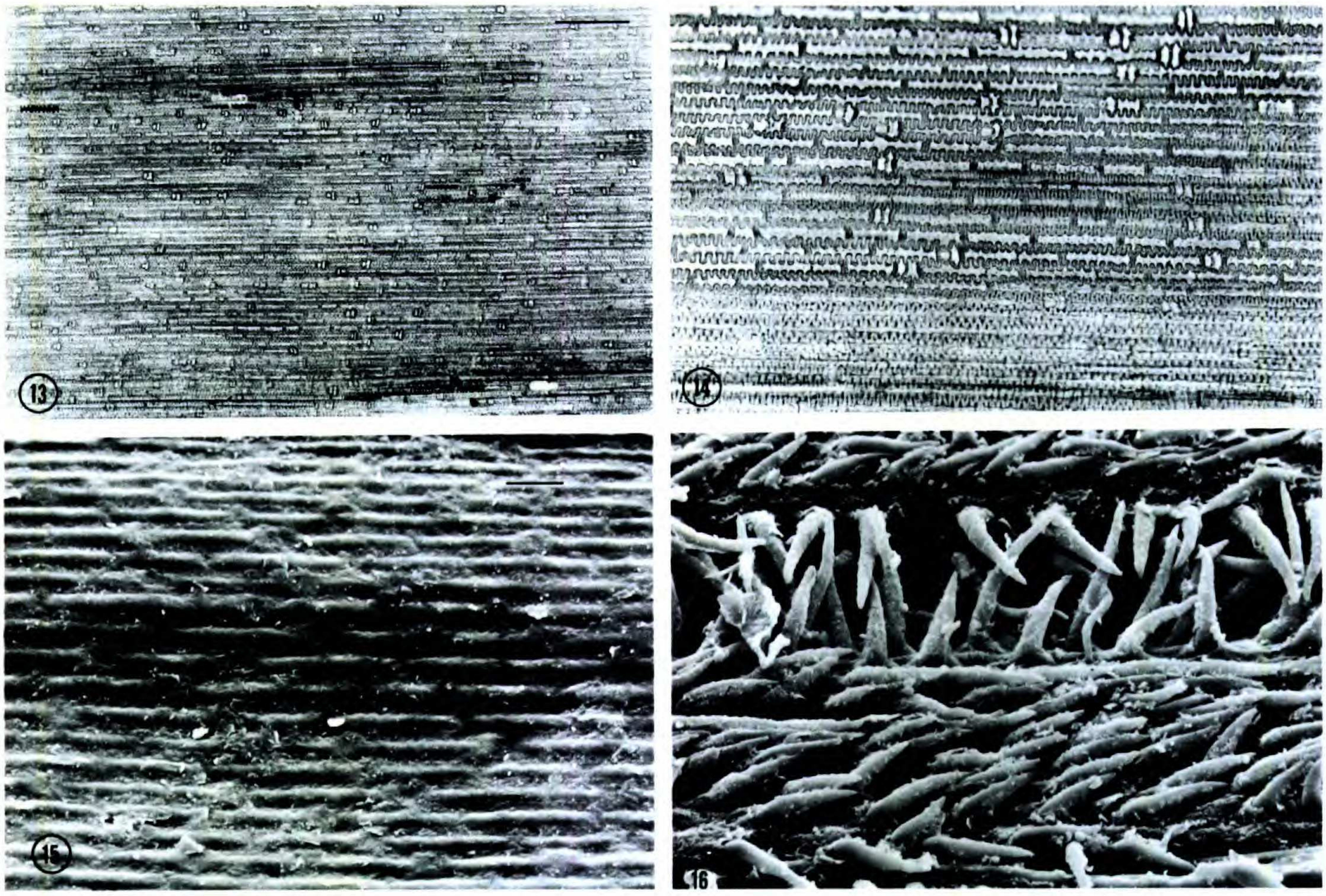
Sides and tops of the ribs covered with prickle hairs interlocking with hairs from the adjacent rib; barbs elongated, stiff and sharply pointed; prickles obscuring all other epidermal details of this surface (Fig. 16).

ANATOMICAL OBSERVATIONS

The anatomy of the leaf blade of *Arundoclaytonia* is highly modified and exhibits many xerophytic adaptations. This is demonstrated most clearly by the well-developed abaxial hypodermal sclerenchyma, extremely thickened abaxial epidermis, and strongly ribbed and furrowed adaxial surface. These xerophytic modifications appear to have led to the consequent loss or reduction of many epidermal features commonly well developed in most other grasses. The most important reductions are the lack of distinction between the abaxial costal and intercostal zones, the absence of abaxial stomata and microhairs, and the reduction of silica bodies. These xerophytic features undoubtedly allow a rapid inrolling of the leaves and may be responsible for the involute margins or completely involute leaves observed on the herbarium specimens.

CLASSIFICATION AND DISCUSSION

As mentioned in the introduction, we consider *Arundoclaytonia* to belong in the now bigeneric Steyermarkochloeae despite the fact that *Arundoclaytonia* differs markedly from *Steyermarkochloa* in growth habit, leaf morphology, and inflorescence morphology. When the morphology of the spikelets is compared, however, a remarkable resemblance between the genera becomes evident. Ignoring for the moment a low percentage of bisexual spikelets in *Steyermarko-*



FIGURES 13–16. Epidermal structure of the leaf of *Arundoclaytonia dissimilis.*—13. Abaxial epidermis showing uniform structure and absence of costal and intercostal zones.—14. Detail of the abaxial epidermis with heavily thickened, sinuous-walled long cells and infrequent cork-silica cell pairs.—15. Scanning electron photomicrograph of the abaxial epidermis illustrating the absence of both stomata and hairs.—16. Scanning electron photomicrograph of the adaxial epidermis showing interlocking prickles with long barbs. Scales: 13 = 30 μm; 15 = 10 μm; magnification for 14–16 = 10 μm. Based on *Anderson et al. 10950* (Figs. 13, 14) and *Calderón et al. 2706* (Figs. 15, 16).

chloa, the fundamental structure of the unisexual spikelets is identical in the two genera. The male spikelets have two stamens, are multiflowered, and lack lodicules in both genera. The major difference in the male spikelets is that those of *Arundoclaytonia* have more florets. This kind of variation is analogous to that between species of *Eragrostis, Bromus,* and *Bambusa,* to name just three of the many genera in which this kind of variation is well known. The female spikelets are identical in the number, arrangement, and shape of the florets. The only important differences are in the size and pubescence of the spikelets. These striking and fundamental spikelet similarities are almost certainly not due to convergent evolution but indicate a fundamental phylogenetic relationship which is reflected in our classification of *Arundoclaytonia* in the Steyermarkochloeae.

The generic status of *Arundoclaytonia* is justified by the following major differences from *Steyermarkochloa:* monomorphic vs. dimorphic culms; typical vegetative leaves with open sheath, many-ribbed blade, and ligule vs. highly modified vegetative leaves with stemlike, solid sheath, two-ribbed blade, and ligule absent; many small, hemispherical male and female inflorescences aggregated into a false panicle vs. single, large, terminal, spicate inflorescences bearing male, female, and bisexual spikelets; and in leaf anatomy—vascular bundles at one level vs. different levels; absence vs. presence of lacunae; absence vs. presence of abaxial stomata; and adaxial furrows and ribs associated with all vascular bundles vs. associated only with the median vascular bundle.

Our decision to place *Arundoclaytonia* in the Steyermarkochloeae necessitates a modification of the description of the tribe (Davidse & Ellis, 1984). Because the leaves of *Steyermarkochloa* are unique in the family, leaf characters were believed very important in characterizing the tribe and in differentiating it from others. This is now shown to be true only when *Steyermarkochloa* was known. In fact, at the macroscopic level, the tribe now encompasses both "normal" and highly modified leaves. In this light the unusual features of the leaves of *Steyermarkochloa*, both at the macro- and microscopic levels, must be seen as adaptations to its seasonally inundated habitat, just as the strongly xerophytic features of *Arundoclaytonia* are presumably adaptations that allow it to cope with the nutrient deficiencies, frequent moisture stress, and intense solar radiation of the white-sand soils of its campina habitat (Ab'Sáber, 1982; Anderson, 1981). Such white-sand soils are considered to be the most nutrient-deficient soils in South America (Eiten, 1978). Although the campinas are located in high rainfall regions, they dry out rapidly near the surface during periods of low rainfall and never experience the long-sustained inundation of the sabaneta or morichal habitats of *Steyermarkochloa* (Ab'Sáber, 1982; Eiten, 1978; Anderson, 1981).

The formal, emended tribal description is the following:

Steyermarkochloeae Davidse & Ellis, Ann. Missouri Bot. Gard. 71: 994. 1985.

Perennial grasses with mono- or dimorphic culms and leaves; leaves solitary or numerous per culm, consisting of a flattened sheath, blade, and ligule, or a solid, cylindrical sheath and flattened blade without a ligule, or reduced to bladeless flattened sheaths. Inflorescence spicate, elongate and cylindrical or a hemispherical cluster of spikelets, bearing male or female spikelets only, or bearing female spikelets above male and bisexual spikelets. Spikelets solitary, usually unisexual, dorsally compressed, disarticulation below the glumes; glumes 2; lodicules 0; uppermost floret rudimentary or reduced; stamens 2; stigmas 2, the style 1; caryopsis fusiform; male spikelets 2–9-flowered, the paleas 2-keeled; female spikelets 3-flowered, the lowest floret sterile, the middle floret fertile, the upper floret rudimentary and borne on a prominent rachilla segment; palea of the functional female floret spongy, curved, (5–)7–13-nerved, longer than the lemma.

When describing the Steyermarkochloeae and including it in the admittedly heterogenous Arundinoideae, Davidse & Ellis (1984) relied primarily on anatomical characters. At the same time, they recognized its uniqueness in the subfamily on the basis of the gross morphology of the leaves, inflorescence, spikelets, and flowers. Much of that detailed discussion is applicable to *Arundoclaytonia* as well.

The discovery of "normal" leaves in the Steyermarkochloeae lessens the importance of the unique leaves of *Steyermarkochloa* vis-à-vis the other genera of the Arundinoideae. In leaf morphology we now consider such leaves to be basic in the Steyermarkochloeae and thus well within the norm of the Arundinoideae, and we consider the leaves of *Steyermarkochloa* to be a later specialization that evolved in its own lineage.

In contrast, the inflorescences and flowers of *Arundoclaytonia* are derived and more specialized than those of *Steyermarkochloa*. Bisexual flowers are universally considered more primitive than unisexual flowers among grasses. Their occurrence, along with the more specialized unisexual flowers, in *Steyermarkochloa* and their absence in *Arundoclaytonia* indicates that the latter is more specialized in this respect. Similarly, we consider the occurrence of bisexual and unisexual spikelets in one inflorescence in *Steyermarkochloa* to be less specialized than the segregation of the spikelets into strictly male and female inflorescences in *Arundoclaytonia*. This strict separation of male and female flowers may be considered the ultimate step in the Charlesworth & Charlesworth (1978) model of the evolution of monoecism through a gynomonoecious pathway discussed by Davidse & Ellis (1984) for *Steyermarkochloa*.

Only in one respect of spikelet morphology might *Arundoclaytonia* be considered less specialized than *Steyermarkochloa*, and this is in the number of florets of the male spikelets. The occurrence of two sterile florets in the female spikelets of both genera suggests a reduction in number of fertile florets. This interpretation is supported by the occurrence of bisexual spikelets in *Steyermarkochloa* with two bisexual florets and others with a male floret below the bisexual floret. Against this background, the larger number of florets in the male spikelets of *Arundoclaytonia* might be less specialized. This interpretation must be tempered with the fact that floret number may easily change up or down, as is evident in the Arundinoideae, Pooideae, Chloridoideae, and Bambusoideae in general, although reduction seems to be prevalent in the family.

The number of florets in the Arundinoideae varies from one to many, but the predominant trend and probably the primitive condition in the subfamily is spikelets with many florets and with apical reduction. *Arundoclaytonia* displays this trend well in the male spikelets. In the female spikelets both apical and basal reduction are evident. In reduction of the lowest floret to a sterile lemma, *Steyermarkochloa* and *Arundoclaytonia* resemble the Panicoideae. However, the terminal rudimentary floret plus the numerous florets of the male spikelets of *Arundoclaytonia* suggest that this similarity is convergent. The rather rounded female spikelets of *Arundoclaytonia* and *Steyermarkochloa* are presumably due to reduction of the number of fertile florets to one.

One interesting aspect of the inflorescence morphology of these two genera is the reduction of the number of spikelets per inflorescence in *Arundoclaytonia*, but, at the same time, the aggregation of the many small unisexual inflorescences into a large false panicle. This exactly parallels a trend in other tribes in the family, for example, *Saccharum* vs. *Hyparrhenia* in the Andropogoneae (Clayton, 1969) and *Panicum ligulare* Nees vs. *P. rudgei* Roem. & Schult. in the Paniceae.

Anatomically, the absence of abaxial stomata and microhairs and the reduction of silica bodies in *Arundoclaytonia* complicates the phylogenetic interpretation of the anatomical structure of the leaf blade as many of these features are generally recognized as being diagnostic of the five subfamilies of the Poaceae (Renvoize, 1981). *Arundoclaytonia*, therefore, does not exhibit the complete set of diagnostic anatomical characters used to assign grasses to a given subfamily, thus limiting our ability to use these characters for determining the affinities of this unusual grass. However, by a process of elimination certain possibilities can be discarded.

Arundoclaytonia does not possess arm or fusoid cells and, therefore, cannot be accommodated in the Bambusoideae. The Chloridoideae is entirely Kranz with only one possible exception (Ellis, 1984), and the Panicoideae is predominantly C_4. Non-Kranz members of the panicoid group all have a semiradiate type of mesophyll and do not have the compact, isodiametric chlorenchyma of *Arundoclaytonia*. *Arundoclaytonia* is undoubtedly also C_3 but shows no anatomical resemblance with the panicoid grasses, and phylogenetic relationships with this subfamily appear most unlikely. The type of chlorenchyma found in *Arundoclaytonia* does, however, occur in many arundinoid grasses. Some members of the Pooideae also have this type of chlorenchyma, but the pooid grasses typically do not have sinuous long cells or tall, vertical silica bodies as does *Arundoclaytonia*. The leaf anatomical evidence, although somewhat limited, does suggest arundinoid affinities for *Arundoclaytonia*, and its systematic position does appear to lie with the Arundinoideae.

The tribes of the Arundinoideae cannot be separated on anatomical criteria and the decision to classify *Arundoclaytonia* in the Steyermarkochloeae is based on morphological evidence, mainly that of the spikelets. This decision is neither confirmed nor refuted by the anatomical evidence. The leaf anatomy of *Steyermarkochloa* and *Arundoclaytonia* differs substantially and both appear to have highly advanced and derived leaf anatomy. Because of these great anatomical differences, they undoubtedly cannot be accommodated in the same genus.

Clayton & Renvoize (1986) considered the Steyermarkochloeae to be a tribe in the Panicoideae, noting "an obvious resemblance to *Hymenachne*" in features that are not unique. They furthermore believe *Steyermarkochloa* to fundamentally differ from C_3 panicoids only in the lack of microhairs (Renvoize, in litt.). We believe that the additional evidence presented by us for *Arundoclaytonia* gives further support for our classification of the tribe, although we certainly recognize the isolated position of the Steyermarkochloeae in the Arundinoideae, and recognize that we are adding one more relatively discordant element to the traditional "dumping ground" of the family. Except for the lacunae and stellate cells in the leaves and the gross form of the inflorescence, but not its branching pattern, we find it difficult to observe any obvious resemblances between *Steyermarkochloa* and *Hymenachne*.

We do agree with Clayton & Renvoize (1986) that embryo characters would provide important new information for clarifying the taxonomic position of the tribe. Chromosome information could also be potentially useful. Unfortunately, we were unable to satisfactorily section caryopses obtained from an herbarium specimen of *Arundoclaytonia*. In the case of *Steyermarkochloa* all our meiotic cytological samples were too young. Unlike the typical situation in grasses, inflorescences of *Steyermarkochloa* must apparently be well exserted from the sheath before meiosis takes place.

The distribution of *Steyermarkochloa* in the northern Amazon basin and *Arundoclaytonia* in southcentral Amazonia suggests that other taxa of this alliance may eventually be discovered, since large areas of this region are botanically very poorly known. Obviously, the area between the ranges of these two genera would seem to be the most promising in this respect. Any relatively open vegetation on white-sand soils (campinas or Amazonian caatingas) might harbor further taxa of this tribe. These vegetation types are found in greatest abundance in the drainages of the Rio Negro and the Rio Branco (Eiten, 1978; Anderson, 1981).

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