

Morphological, Anatomical,
and Taxonomic Studies in
Anomochloa and *Streptochaeta*
(Poaceae: Bambusoideae)

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ABSTRACT

Judziewicz, Emmet J., and Thomas R. Soderstrom. Morphological, Anatomical, and Taxonomic Studies in *Anomochloa* and *Streptochoaeta* (Poaceae: Bambusoideae). *Smithsonian Contributions to Botany*, number 68, 52 pages, 24 figures, 1 table, 1989.—Although resembling the core group of the bambusoid grasses in many features of leaf anatomy, the Neotropical rainforest grass genera *Anomochloa* and *Streptochoaeta* share characters that are unusual in the subfamily: lack of ligules, exceptionally long microhairs with an unusual morphology, a distinctive leaf blade midrib structure, and 5-nerved coleoptiles. Both genera also possess inflorescences that are difficult to interpret in conventional agrostological terms. *Anomochloa* is monotypic, and *A. marantoidea*, described in 1851 by Adolphe Brongniart from cultivated material of uncertain provenance, was rediscovered in 1976 in the wet forests of coastal Bahia, Brazil. The inflorescence terminates in a spikelet and bears along its rachis several scorpioid cyme-like partial inflorescences. Each axis of a partial inflorescence is subtended by a keeled bract and bears as its first appendages two tiny, unvascularized bracteoles attached at slightly different levels. The spikelets are composed of an axis that bears two bracts and terminates in a flower. The lower, chlorophyllous, deciduous spikelet bract is separated from the coriaceous, persistent, corniculate upper bract by a cylindrical, indurate internode. The flower consists of a low membrane surmounted by a dense ring of brown cilia (perigonate annulus) surrounding the andrecium of four stamens, and an ovary bearing a single hispid stigma. Other peculiarities of *A. marantoidea* include its hollow leaf sheaths and long, hollow, bipulvinate pseudopetioles and chromosome number of $n = 18$. The caryopsis and embryo are large, but their structure is typically bambusoid. *Streptochoaeta* consists of three species and one subspecies (*S. spicata* subsp. *ecuatoriana*, newly described here) and conforms to the bambusoid core group in seedling morphology and leaf anatomy. *Streptochoaeta* and *Anomochloa* are quite divergent but may be more closely related to each other than to any other grass. They share features that indicate affinities with the Olyreae.

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Morphological, Anatomical, and Taxonomic Studies in *Anomochloa* and *Streptochoaeta* (Poaceae: Bambusoideae)

Emmet J. Judziewicz and Thomas R. Soderstrom

Introduction

The eight tribes of herbaceous bamboos have long interested the agrostologist concerned with tracing the evolution of the Poaceae. Although they appear to have their closest affinities with the woody bamboos (Bambuseae) of the Bambusoideae, the intertribal relationships of the herbaceous group have remained uncertain until recently because of a lack of suitable material for the study of such taxonomically critical characters as inflorescence, spikelet, lodicule, gynecium, fruit, and seedling morphology. Of the eight tribes the Olyreae, with about 20 genera and over 100 species, is native only to the New World and is dealt with in detail in the papers of Soderstrom and collaborators (Calderón and Soderstrom, 1973, 1980). In leaf anatomy this tribe appears to be closest to the woody bamboos (Bambuseae) (Soderstrom and Ellis, 1987). It may also be related to the poorly known Buergersiochloae, a monotypic tribe of northern New Guinea (Fijten, 1975). The other tribes of herbaceous bamboos are more isolated. For example, the Phareae, with inverted, obliquely veined leaves bearing distinctive fibrous epidermal bands, but lacking bicellular microhairs, is perhaps the most isolated tribe among the herbaceous bamboos. The Streptogyneae, with a unique seedling morphology for the subfamily (Soderstrom, 1981a), is nearly as isolated as the Phareae (Soderstrom et al., 1987). While the African *Puelia* (Puelieae) and *Guaduella* (Guaduelleae) bear many-flowered spikelets of a typical graminoid type, more material, including caryopses and seedlings, is required to understand their affinities.

The two remaining tribes, the monotypic Anomochloae and Streptochaeteae, are the subject of this paper. Above all others these Neotropical forest herbs have intrigued agrostologists because their inflorescence and spikelet structures are so different from those of other grasses. They have been called the most primitive grasses, and until recently some workers have questioned whether they were truly graminaceous (Campbell, 1985).

The present investigation was made possible because of the rediscovery of *Anomochloa*. Material gathered in 1976, 1978, 1982, 1983, and 1986 by various botanists is the basis of our studies of the inflorescence and spikelet structure and taxonomic affinities of *Anomochloa marantoidea*. T.R. Soderstrom wrote the section herein on the history and rediscovery of this taxon.

For purposes of comparison we have also studied *Streptochoaeta*. Inflorescences of both genera are unique within the grass family and the present study is intended to clarify the relationship of these peculiar bamboos.

MATERIALS AND METHODS

Herbarium specimens of *Anomochloa* and *Streptochoaeta* were examined from the following herbaria (acronyms follow Holmgren et al., 1981): AAU, B, BM, BR, CANB, CAY, CEPEC, DUKE, F, G, IBGE, INPA, ISC, K, L, LE, M, MO, NA, NY, P, PDA, QCA, R, RB, S, SI, UC, US, W, and WIS. Observations of living plants of *Streptochoaeta* were made by Soderstrom (Costa Rica, 1966; Brazil, 1972) and Judziewicz (Costa Rica, Panama, 1983), and of *Anomochloa* by Soderstrom (October 1983) and Judziewicz (February and March 1986). Some of these plants were preserved in FAA (90% ethanol, 5% acetic acid, 5% formalin) and later transferred to

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70% ethanol (see Appendix).

The culms, leaves, and reproductive structures of voucher specimens were studied using a Wild M5 dissecting microscope. These structures were also studied by serial cross-sections at thicknesses of 8–13 μm using a rotary microtome. Before dehydration with dimethoxypropanol (DMP), infiltration with tertiary butyl alcohol (TBA), and embedding in paraffin, leaves and spikelets were soaked for several days in hydrofluoric acid (HF) in order to remove silica. For the study of bicellular microhairs in *Anomochloa marantoidea* a preserved leaf was stained in Chlorazol Black E and areas with abundant microhairs were scraped with a razor blade. Formal descriptions of the leaf anatomy of *Anomochloa* and *Streptochaeta* follow the model of Soderstrom et al. (1987). Embryos of both genera were dissected out of the caryopses, rehydrated using Aerosol-OT, embedded in agar, then dehydrated and embedded in paraffin using the procedure described above. Sections were cut at widths of from 4–10 μm , and stained with Chlorazol Black E. Starch grains from caryopses were sectioned with a freezing microtome and then stained with I_2KI . Epidermal scrapes were prepared using the method of Tomlinson (1961). Photomicrographs were made using Zeiss microscopes with green filters and Kodak Panatomic X ASA 32 film.

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We also thank the curators of the herbaria from which we borrowed specimens.

Anomochloa Brongniart

Anomochloa Brongniart, 1850:57 [nomen nudum]; 1851:368.

HISTORY AND REDISCOVERY

by T.R. Soderstrom

When Adolphe Brongniart described *Anomochloa* (1850, 1851) he chose an apt name for this weird and remarkable, truly anomalous grass that reportedly had come from Brazil. One or more plants of the genus were in cultivation in the greenhouse of the Jardin des Plantes in Paris in the 1840s. When Brongniart, then director of the Muséum d'Histoire Naturelle, saw the plant he decided it was a grass and described it as *Anomochloa marantoidea*, because the clustered broad pseudopetiolate leaves gave it the appearance of a genus of Marantaceae.

A plant was later sent to Kew by Charles Decaisne, Professor of Culture at the Serres (greenhouses) du Jardin des Plantes and was cultivated there until at least 1866. Herbarium specimens made of the plants at Paris and Kew represented the only material available for study by later workers. The desire to rediscover this genus and have fresh material for further study was well expressed by Agnes Arber who made studies on herbarium material (1934:131-133):

It will be recognised even from this brief description, that *Anomochloa*, if a member of the Gramineae, is a most erratic one. Its rediscovery is much to be desired; a complete study of its structure and development would be of deepest interest.

Besides Arber, several other botanists studied the plant from dried specimens. Schuster (1909:30–32) examined the spikelet of *Anomochloa* as part of his dissertation on the morphology of grass flowers. Page (1947) noted the presence of large mesophyll cells in the leaf, based on an external study of the single leaf in the collections at the U.S. National Herbarium. Metcalfe (1960:28-29) was the first to give a description of the leaf cross-section anatomy and epidermis, stating that "this grass has obvious points in common with the bamboos."

My own early studies of herbaceous bamboos began during field work in Guyana in 1962 and Suriname in 1963 when I collected several genera of bambusoid grasses. This work led me to the literature on *Anomochloa* and a desire to relocate this grass in particular. Its rediscovery took many paths and I think the story interesting enough to relate here.

Brongniart (1851), in his beautiful paper on the new genus, did not mention anything about the plant in cultivation and gave as its provenance only the name of Morel and the province of Bahia, Brazil. The earliest mounted specimen at Paris has two labels, one a handwritten note signed "herb. Houillet, July 1890," stating: "This plant was given by Monsieur Morel who

received it from Brazil from Monsieur Pinelle from Morro Chemado, Province of Rio de Janeiro in 1842" [my translation from the French]. The other label, with a printed heading of the Paris Herbarium, has the following information [my translation]: "Brazil. Bahia. Monsieur Porte, given by Monsieur Morel. Paris Botanical Garden, August 1848." The U.S. National Herbarium has two herbarium collections, one with a piece of inflorescence from a sheet at Paris, the other with a floret from a sheet at Leiden (in turn from the Balansa Herbarium at Paris), in addition to a leaf from a cultivated specimen at Kew.

Both of the US sheets have annotations by Agnes Chase who wrote "Bahia in Porto," having misread "Bahia M[onsieur] Porto." She added a note, "Is 'Bahia' alleged locality for this 'bay,' meaning bay of Rio de Janeiro?" This was a logical conclusion since the word for bay in Portuguese is "bahia." Mrs. Chase, who collected for several months in Brazil in 1924 and 1925, was anxious to relocate this grass and thought that it grew around Rio de Janeiro where she spent several days. In the files of L.B. Smith (Smithsonian Institution) is a letter of 6 December 1927 to Dr. Smith (who was going to Brazil the following year) from Mrs. Chase, who wrote the following.

The grass I most wanted in Brazil and failed to find was *Anomochloa*. It occurs to me that you may like to read the original manuscript of the paper I had to reduce to 50 percent for the Smithsonian Report, so I shall send it. Please return it when you have read it. In this manuscript you will see that this grass was described from "the province of Bahia." In the Paris Museum last May I found a note on the specimen in that herbarium which shows that "bahia" (bay in Portuguese) referred to the bahia of Rio de Janeiro I can not find where Morro Chemado (if Chemado is a proper name) is ... *Anomochloa* is a broad-leaved grass obviously of shaded places. So Prov. Rio de Janeiro is a far more likely place for it than arid or semiarid Bahia.

The many steps that led to the eventual rediscovery of *Anomochloa* actually started with my first trip to Brazil in 1964 when I accompanied Dr. Howard S. Irwin, Jr., on his expedition to the cerrados of the central part of the country. In Brasília I made the acquaintance of a young botanist, Romeu Belém, who collected with us one day in a gallery forest near the city. There we found large clumps of a species of the herbaceous bamboo, *Olyra*, with beautifully purple-mottled culms (later described as *O. taquara* Swallen). I showed Belém how to make a collection of such a grass and encouraged him to look for these on his collecting trips. He was shortly to go to Bahia, where he was being sent by Dr. Joao Murca Pires, to start an herbarium at the CEPEC in Itabuna.

The first collections in that now-rich herbarium are those of Belém. His collections and those of others that followed are cited in a paper by Scott Mori and L.A. Silva (1979), the former of whom spent two years (1978–1980) collecting in the wet coastal forest region of Bahia and curating the CEPEC herbarium. Shortly after Belém's arrival in Itabuna we received a small package of bambusoid grasses, many unknown to me at the time and quite different from the others that I had so far studied. Among these was a collection that Belém made with C.M. Magalhães (no. 886) in 1965. I had provisionally dubbed

that collection "Raddiolyra" when I first saw it because it resembled both *Raddia* and *Olyra* but was certainly distinct from either of them. I later described this as a new genus, *Sucrea* (Soderstrom, 1981b).

In June 1967 in a forest near Maracay, Venezuela, I noticed that insects were always to be found around the inflorescences of the bambusoid genus, *Pariana*. Since this association seemed to be common I made collections of the plants and the insects, which in this case turned out to be a new genus of Diptera (Cecidomyiidae), described by Gagné (1969). The possibility of insect pollination in these herbaceous bambusoid grasses that grew in the rainforest was intriguing and deserved further investigation. Upon my return from Venezuela I discussed my observations with an Argentine colleague, Cleofé Calderón, who was working in my laboratory at the time. We decided to pursue the problem and made plans for her to visit a number of localities in Central and South America where she would collect bambusoid grasses and make observations on the insects that visited the inflorescences. Thus in late 1967 Calderón left for Panama and continued on to Colombia and Brazil, making collections in each of these localities. Most of the insect observations were made in the forests around Belém, Pará, Brazil, and the results of this work were published in Soderstrom and Calderón (1971).

However, the most interesting part of the trip, from the standpoint of new bamboo taxa, turned out to be Bahia, which was included in her itinerary because of the interesting collections that Romeu Belém had sent us. Calderón's further collections from Bahia showed the region's wet forest region, where Itabuna was located, to be rich indeed in bambusoid taxa.

Up to this point we still had no idea where *Anomochloa* might be found. However, based on Brongniart's statement (1851) and the other kinds of bambusoid grasses found by Belém and Calderón in Bahia, that locality was a good possibility. Mrs. Chase, who had discounted Bahia as a suitable habitat, felt it was too arid but she was referring to the part of the state where she had traveled, between Salvador and Juazeiro on the Rio Sao Francisco. She was not familiar with the narrow strip of tropical rainforest along the coast.

With funds from the National Geographic Society and Smithsonian Institution, Calderón and I traveled to Brazil in 1972 to explore various parts of the eastern coastal forest with the purpose of finding *Anomochloa*, along with another bambusoid grass, *Diandrolyra*, known only from cultivation at Kew. At that time we felt that *Anomochloa* could be found either in Bahia or in the mountains around Rio de Janeiro. Thus Calderón returned for further exploration in Bahia, where she collected with R.S. Pinheiro and Talmon S. dos Santos. I returned to the states of Rio de Janeiro and Espírito Santo, collecting with Dimitri Sucre of the Jardim Botânico in Rio de Janeiro. These concurrent trips yielded a fine collection of bamboos, including two species of *Diandrolyra*, new genera, and many new species. But *Anomochloa* still eluded us.

It was time now to see if information about those persons involved with the original collection might offer a clue as to

where the plant was first collected. Who were Morel, Pinel, and Porte—names associated with Brongniart in the beginning? One of the original labels stated “Bahia M. Porte” and “Dn par [given by] M. Morel.” Since I had seen these names in species of orchids, a search through the horticultural literature of the time was undertaken by an assistant, Stephen Cahir (SI), during the summer of 1973. Some leads came about through this effort and that fall I spent a few weeks in London and Paris continuing the search. This involved literature reviews at the Royal Horticultural Society library in London, the archives at Kew herbarium, of old manuscripts at the Paris herbarium, and a visit to the records in the town archives of St. Mandé where Morel had lived. Through all of this effort we were persuaded to return to Bahia, which we were now convinced was the home of *Anomochloa*.

Charles Morel had lived in a suburb of Paris called St. Mandé, which is now a part of the city itself. The town records show that he was born in Reims (Maxne) on 28 July 1793 and was listed as a proprietaire (property owner?). The horticultural literature speaks highly of this gentleman and his greenhouses with their large collection of rare orchids. Morel was active in horticultural societies and had several correspondents who sent him orchids from abroad. One of these correspondents was Monsieur Pinel, who sent material from Brazil. Morel must have received material of *Anomochloa*, which he gave to Brongniart for cultivation in the greenhouses of the Museum.

Morel was the author of a book on orchid culture (1855), which he dedicated to his friend, Prof. Brongniart. On page 9 he speaks of Pinel from Rio and Porte of Bahia: “This is the place to pay just tribute and give thanks to M. Pinel of Rio de Janeiro and to M. Porte of Bahia, for it is to their activity and their good taste that we owe the greater part of beautiful plants of these regions” [my translation from the French].

Monsieur (or Chevalier) Pinel, a merchant who resided in Bahia, appears in the literature with two spellings, Pinel and Pinelle. Pinel, whose first name I have not found, collected living plants, probably from the region of Rio de Janeiro and sent them to horticultural establishments in France and Belgium. Mulford Foster purportedly remarked that the bromeliad, *Aechmea pineliana*, was named possibly for Dr. Pinel, French consul in Rio de Janeiro at the time (1851), but I have not been able to confirm this. There are many plants named for Pinel and records of his sending material to Morel in Paris. The name of “Morro chemado” appears more than once in Pinel collections, one of which is for an orchid with locality “Station Sommite des Serra de Morro-queimado.” I collected on a Morro Queimado in Rio de Janeiro, which was within the boundaries of the Tijuca forest, but I do not know if this is the same locality. It is possible that Pinel lived in the area during the last century and that “M. Pinel, Morro chemado” referred to the man and where he lived rather than a locality for *Anomochloa* (which he may not have collected).

On the label of the type of the bromeliad, *Aechmea (Echinostachys) pineliana* Brongniart in the Houliet herbarium, which is part of the Paris herbarium, is a note: “This plant has

been sent to Mr. Morel by Mr. Pinel of Morro-chemado (near Rio de Janeiro) in 1846 and has been introduced into botanical culture by him [Morel?]” [translation from the French by E. Judziewicz]. This again suggests that the plant was sent by Pinel of Morro-chemado.

Marius Porte, whose name appears on one of the Paris labels as having sent a plant to Pinel, was a businessman in Bahia. Like Pinel he must have been interested in exotic plants for horticulture such as orchids. Only because of its great beauty and possibility for horticulture would Pinel have collected a grass such as *Anomochloa* and he most likely would have mistaken it for a member of the Marantaceae. I was hoping that Porte, in his correspondence in the Paris Museum archives, would have described some of his collecting localities. But I found only three letters, all from Manila to Prof. Brongniart in 1860, and remarking on the orchids of the Philippines where he had moved. Porte is said to have died shortly after arrival due to the results of a long and tedious journey to the Philippines from Brazil.

Adolphe Brongniart was Professor of Botany at the Paris Museum and at one time its director. He was an expert in many fields, including botany and paleobotany. His paper on *Anomochloa* is superb and his analysis and illustration of the original plant outstanding. At the Paris Herbarium, M. Jolinon led me to boxes of old manuscripts where I came upon the original handwritten manuscript of Brongniart on *Anomochloa*. He included sketches of his dissections (which were not published) and the spikelet he had studied was still attached to the paper in an envelope.

In 1975 Calderón and I again were granted funds from the National Geographic Society to return to Brazil and intensify our field efforts in Bahia. We spent January through March in the eastern coastal forests of the state, headquartered at CEPEC in Itabuna. We each made several separate trips of about two weeks each to different areas, and we returned to Itabuna for a few days in between each trip to prepare the herbarium specimens.

Our efforts were finally rewarded with the rediscovery of *Anomochloa* on 21 April 1976. Calderón was traveling along a small road with Sr. Talmon S. dos Santos near the city of Una, Bahia. Cleo felt a peculiar—or psychic, as she put it—urge to stop near a particular wooded area. Not far into the woods, which bordered a cultivated area of cacao on somewhat rocky slopes, they came upon a colony of the grass. Further observations of the colony were made by Victoria Hollowell (University of South Carolina) in 1982 and by myself in 1983. In 1986, another colony was found by dos Santos and Judziewicz who had gone to Brazil to make field observations for the present study.

The rich forested areas in the Bahian municipality of Una, where *Anomochloa* is native, are rapidly disappearing, a common story today in the Neotropics. The only populations of *Anomochloa* with which we are familiar occur on rocky slopes adjacent to cacao plantations; these may survive as long as the plantations are not expanded. Any opening in the canopy

with a concomitant increase in light intensity, however, could well cause these communities to succumb. A few plants are in cultivation at Rio de Janeiro and in the United States but they are not thriving and, like the plants of 19th century Paris greenhouses, they have never attained the robust size observed in the tall, densely shaded, and rocky rainforest in which they are native. Unless there are colonies still to be discovered we are probably facing the imminent demise of this unique grass.

TAXONOMY

1. *Anomochloa marantoidea* Brongniart

FIGURES 1-4

Anomochloa marantoidea Brongniart, 1851:368, pl. 23. [Type: Brazil, Bahia: "e provincia Bahiensi Brasiliae accepti clar. Morel, Morro Queimado," anno 1842, without collector [or collector Pinel?], cultivated in Paris, August 1848 (Holotype, P; photograph and fragment, US; isotype, P).]
A. macrantioidea Brongniart in Pritzl, 1866:74 [error for *A. marantoidea* Brongniart.]

DESCRIPTION.—Plants cespitose, to 1 m tall in many-stemmed loose clumps, prop roots not present; rhizomes sympodial, 0.5–5 cm long, to 7 mm in diameter, papery and weak.

Culms weak, up to 0.5 m tall, all but the uppermost leaves borne at the base of the plant; bladeless sheaths below, preceding 5–10 fully developed leaves, the lowest with ovate leaf blades, several mm long, finely puberulent, these grading above into longer linear ones, the uppermost bladeless sheath linear, up to 23 cm long; leaves with reduced, transitional blades not present.

Leaves 4–7 per culm, all clustered at the base of the culm except frequently for the uppermost one; the bases of the sheaths strongly two-ranked and divergent, the blades held at different heights above the ground; leaf sheaths erect, yellowish green, hollow, striate, open, 15–30 cm long and up to 1 cm wide (folded width), semicircular in cross-section, the margins extended into prominent membranous wings up to 5 mm wide near the base of sheath, these narrowing abruptly to a width of 1–2 mm near the apex, with one margin prolonged into a rounded, glabrous auricle 1–3 mm long; summit of sheath without lateral appendages and oral setae; inner ligule a dense, emarginate fringe of clear cilia 1–2 mm long, not membranous; outer ligule absent; pseudopetioles strongly divergent from summit of sheath, (5)13–18(23) cm long, hollow, grooved adaxially, bipulvinate, the lower pulvinus up to 3 mm long, the upper pulvinus up to 5 mm long, both pulvini solid, turgid, dark-colored, and covered with clear, appressed hairs up to 1.5 mm long, especially on the adaxial surface; expanded portion of blade (18)25–40 cm long, (4)6–10 cm wide, narrowly lanceolate to most commonly oblong-lanceolate, the margins parallel in the lower half of the blade, then gradually tapering to the apex in the upper portion; lamina thin, papery, glabrous above, scaberulous below, the venation almost strictly parallel, with nearly all of the nerves meeting

at the base; base truncate to slightly subcordate with the slightly auriculate portions on each side of the upper pulvinus slightly upturned; midrib raised on both surfaces, prominent and with slightly overhanging margins adaxially (0.8–1.2 mm wide near the base of the blade), low dome-shaped and not as prominent abaxially (where 0.4–0.5 mm wide); blade margins glabrous, or scaberulous near apex; primary lateral veins 4–6 on each side of the midrib; tertiary lateral veins spaced 0.8–1 mm apart, prominent only on the lower (abaxial) surface, transverse veinlets present, also prominent only abaxially; a vein intermediate in size between the primary and tertiary lateral veins often present midway between each pair of primary lateral veins; uppermost leaf of culm frequently small, with a slightly inflated leaf sheath about 10 cm long, a short pseudopetiole, and the expanded portion of the lamina ovate, 10–15 cm long.

Inflorescence borne on a subglabrous peduncle 5–7 cm long, terminal (but often inconspicuous because of the overtopping leaf blades on the same shoot), spike-like, often curved when developing but straight at maturity, laterally compressed and bilaterally symmetrical, 7–14 cm long, 1.3–2.5 cm wide (or up to 5 cm wide when bracts subtending partial inflorescences (main branches) fully spread at maturity), terminating in a fully developed spikelet; rachis zigzag, puberulent (especially below the nodes), alternately bearing 4–7 partial inflorescences, the lowest partial inflorescence often separated from the upper ones by an exposed portion of the rachis up to 5 cm long; general bracts subtending each partial inflorescence 4.5–9 cm long, folded width 0.7–1 cm, lanceolate, attenuate, rounded on the back but somewhat carinate near apex, prominently many-nerved and cross-veined, green, the general bract subtending the lowermost partial inflorescence always appressed-ascending and frequently bearing a small blade up to 5 cm long, the general bracts subtending the upper partial inflorescences always strongly overlapping, bladeless, gradually smaller and becoming divergent from the rachis with age.

Partial inflorescences bearing up to 5 spikelets in a second arrangement along a greatly twisted axis; main axis of partial inflorescence erect, terminating in a spikelet borne on a thickened and slightly obconic pedicel 7–15 mm long and 2–3 mm wide; main axis bearing near its base on the adaxial side 2 linear, membranous, nerveless, apically brown-ciliate, and unequal bracteoles, the smaller member linear, delicate, not keeled, up to 5 mm long, the larger attached slightly higher on the branch, typically lanceolate, strongly keeled, up to 10 mm long; main axis bearing above the bracteole pair on the side opposite the rachis a membranous to scarious, elliptic or ovate bract 7.5–15 mm long with a strong, often ciliate midnerve and several faint lateral nerves, often ciliate at the apex; this bract subtending a lateral branch, the latter continuous with the pedicel of the second spikelet, 5–13 mm long, often slightly exceeding the pedicel of the first spikelet, and bearing a rudimentary or fully developed spikelet in robust inflorescences; branching of partial inflorescences reiterating in a scorpioid cyme-like manner to produce up to 3 fully



FIGURE 1.—Field photographs of *Streptochaeta* and *Anomochloa*: *a*, fruiting clump of *S. spicata* subsp. *spicata* on Barro Colorado Island, Panama (note tangled, pendent masses of pseudospikelets); *b*, Habit of *A. marantoidea*, Bahia, Brazil (site of collection of Calderón *et al.* 2381), showing leaf blades borne at different heights and in different orientations due to varying lengths of the leaf sheaths and pseudopetioles. Photographs by Judziewicz.



FIGURE 2.—Field photographs of *Streptochaeta* and *Anomochloa*: *a*, upper leaves and inflorescence of *S. sodiroana*, La Selva, Costa Rica. *A. marantoidea*, Bahia, Brazil (site of collection of Calderón *et al.* 2381); *b*, inflorescence during late phase of flowering, showing exserted stamens (note the varying lengths of the leaf pseudopetioles and the cupped bases of the expanded portion of the leaf blades); *c*, inflorescence during early phase of flowering, showing solitary stigmas exserted from the corniculate upper spikelet bracts; *d*, inflorescence as it appears among the foliage as viewed from the “back” side (a few stigmas visible). Photographs by Judziewicz.

developed spikelets and 2 progressively smaller rudimentary spikelets, each successive lateral branch subtended by an ovate, keeled, scarious bract whose midrib nests with those of successive lower and higher subtending bracts, and the axis of each branch oriented so that the smaller (lower) member of the 2 bracteoles of a given branch is positioned directly behind (abaxial to) the keel of the bract subtending the branch of the next highest order.

Spikelets terminal, 1-flowered, bisexual, deciduous from pedicels at maturity, consisting of a deciduous lower bract separated by a cylindrical internode from a persistent upper bract that encloses the floret.

Lower spikelet bract 10–15 mm long, broadly lanceolate, rounded on the back below, somewhat carinate near the tip, green, 10–17-nerved, conspicuously cross-veined, the apex with hyaline, ciliate margins, at length deciduous, separated from the upper spikelet bract by an indurate, whitish, slightly obconic internode 3–4 mm long and 2.5–3.5 mm in diameter, this glabrous or with scattered cilia above, at length deciduous from lower spikelet bract and summit of pedicel along with the persistent upper spikelet bract and its enclosed caryopsis.

Upper spikelet bract on the opposite side of the cylindrical internode of the lower spikelet bract, consisting of an ovoid body surmounted by a linear horn-like appendage (corniculum); body of upper bract 9–13 mm long, coriaceous at maturity, whitish, densely pubescent with prickles and clear hairs about 1 mm long, the margins meeting and strongly overlapping and locking with one another (except near the summit at anthesis), the venation inconspicuous externally, consisting of 4–6 irregularly spaced principal nerves (including a midnerve only slightly more conspicuous than the main lateral nerves) and 5–8 minor nerves, the former not visible on the outer surface of the body but visible as ridges on the interior surface; corniculum 13–18 mm long, ~1–2 mm wide (often slightly wider near the summit), firmly membranous, finely pubescent, slightly grooved, slightly curved and protruding from the lower spikelet bract, at length deciduous.

Perigonate annulus closely surrounding base of andrecium, consisting of a continuous fringe of brown cilia 0.5–2 mm tall borne on the summit of a low membranous ring.

Andrecium of 4 stamens (occasionally the rudiment of a 5th present), these extruded from between the upper margins of the body of the upper spikelet bract at anthesis; filaments free, to 2 cm long, 2 mm wide, succulent, white, the anthers 3–5 mm long, white, elliptic-sagittate, attached to the filaments in such a way that the connective surrounds the summit of the filament without fusing to it for 0.4–0.7 mm; thecae introrse, facing the center of the andrecial circle.

Gynecium with ovary stout, ellipsoid, 3–4 mm long and 1–2 mm wide, oblong-pyramidal, obliquely tipped, glabrous; style and stigma 1, the latter papillose, white, exiting through the open tip of the corniculum and extending up to 1 cm beyond it, lax.

Caryopsis oblong-rectangular, laterally compressed, up to ~10 mm long, 2.5 mm wide, and 4 mm deep (in profile),

glabrous, the summit of the style persistent as a short, folded, oblique beak; hilum inconspicuous, a shallow groove extending nearly the full length of the grain; pericarp thin, yellowish brown; endosperm mealy; embryo oblique-basal, large, up to 2.7 mm tall and 1.8 mm wide.

DISTRIBUTION.—Known only from wet, lowland tropical forests in the Municipio of Una, Bahia, Brazil.

ADDITIONAL SPECIMENS SEEN.—(Because of the rarity of this species, the specimen labels are quoted in their entirety to avoid any future confusion.) BRAZIL. Specimens from the type plant (or descendents) were cultivated as late as 1866 (K!, fragment US ex L, W!). Municipio de Una: Primary forest on steep (45°) rocky slope bordering cacao plantation, altitude 180–200 m, old inflorescences, 21 Apr 1976, *C.E. Calderón, T.S. dos Santos, and L.B. de Oliveira 2381* (CEPEC, IBGE, K, LE, RB, US [3 sheets], WIS), 11 Jul 1978, old inflorescences, *T.S. dos Santos and L.A. Mattos da Silva 3236* (CEPEC, K, MO), 20 Jan 1982, sterile, only a few plants in old fruit, *V.C. Hollowell, T.S. dos Santos and A.M. de Carvalho 3000* (CEPEC, F, ISC, R, SI, UC, US, W), 3001 (B, P), 3002 (INPA), 3003 (SP), 3004 (G), 18 Oct 1983, in all stages of flowering and fruiting, *T.S. dos Santos, G. Martinelli, and T.R. Soderstrom 3880* (CANB, CEPEC, NY, RB, US), 21 Feb 1986, all sterile, *E.J. Judziewicz and T.S. dos Santos s.n.* (US), 12 Mar 1986, most plants sterile, *E.J. Judziewicz and T.S. dos Santos s.n.* (US); Municipio de Una, disturbed primary forest on 30° rocky slopes, altitude 160–180 m; 21 Feb 1986, all sterile, *T.S. dos Santos and E.J. Judziewicz 4111* (CEPEC), 12 Mar 1986, all sterile, *T.S. dos Santos and E.J. Judziewicz 4266* (CEPEC, US; living plants cultivated at CEPEC and US).

VOUCHER SPECIMENS FOR ANATOMICAL STUDIES.—Brazil: *Calderón, dos Santos, and Oliveira 2381* (US) (leaves); *dos Santos, Martinelli, and Soderstrom 3880* (US) (leaves, inflorescence, spikelets, starch grains, embryos).

DISCUSSION.—The two localities at which *Anomochloa marantoidea* grows are humid, tall forests on the steep, rocky (with granite boulders), lowermost slopes of the low mountains west of Una. At each site the area throughout which the plants grow consists of only a hectare or two, and only about 90 individual plants were counted at any one station. Individuals growing in treefall gaps, partial shade, or forest edges are much smaller than those growing in dense shade. Visits to the extant sites from January through April (1976, 1982, 1986) have revealed plants with mostly old infructescences and only a few in flower. The October 1983 visit by Talmon dos Santos et al. revealed the 1976 colony in all stages of flowering and fruiting, but dos Santos (pers. comm., 1986) indicates that the plants usually bloom during the height of the local rainy season during June and July.

Anomochloa marantoidea is the only species in its genus and tribe. Because of its rarity (and because the species is not well established in cultivation) we are not citing here the exact collection localities of the two known populations; this information is available in the files of the McClure Bamboo Library, Department of Botany, National Museum of Natural

History, Smithsonian Institution. Unfortunately most other potentially suitable sites for the species in the Una region have been destroyed in recent years through increased planting of

cacao. Because only about 30 herbarium sheets exist we urge that anyone visiting the sites refrain from making further gatherings.

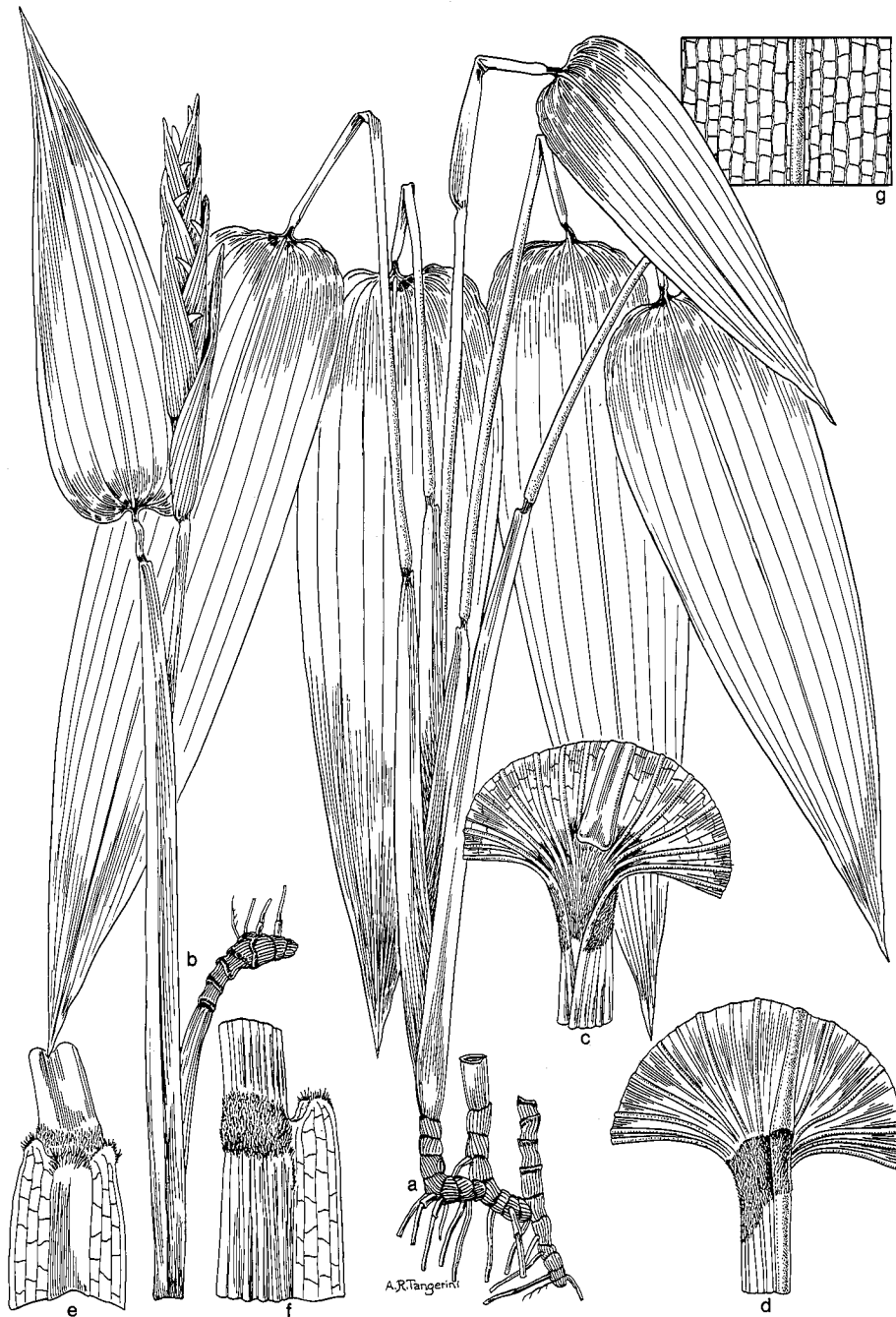


FIGURE 3.—*Anomochloa marantoidea*: a, habit, showing leaf blades borne on leaf sheaths and pseudopetioles of varying lengths ($\times 0.22$); b, inflorescence terminating culm with uppermost subtending leaf, the lowest leaves removed ($\times 0.22$); c, upper portion of pseudopetiole and base of leaf blade showing upper pulvinus, adaxial view ($\times 1.72$); d, upper portion of pseudopetiole and base of leaf blade showing upper pulvinus, abaxial view ($\times 1.72$); e, inner (adaxial) view and f, side view of summit of sheath and lower portion of pseudopetiole showing lower pulvinus and ciliate inner ligule ($\times 1.72$); g, portion of leaf blade, abaxial surface showing transverse veinlets ($\times 1.72$). (a and g based on Calderón *et al.* 2381, b–f on dos Santos *et al.* 3880, both from Brazil.) Illustration by Alice R. Tangerini.

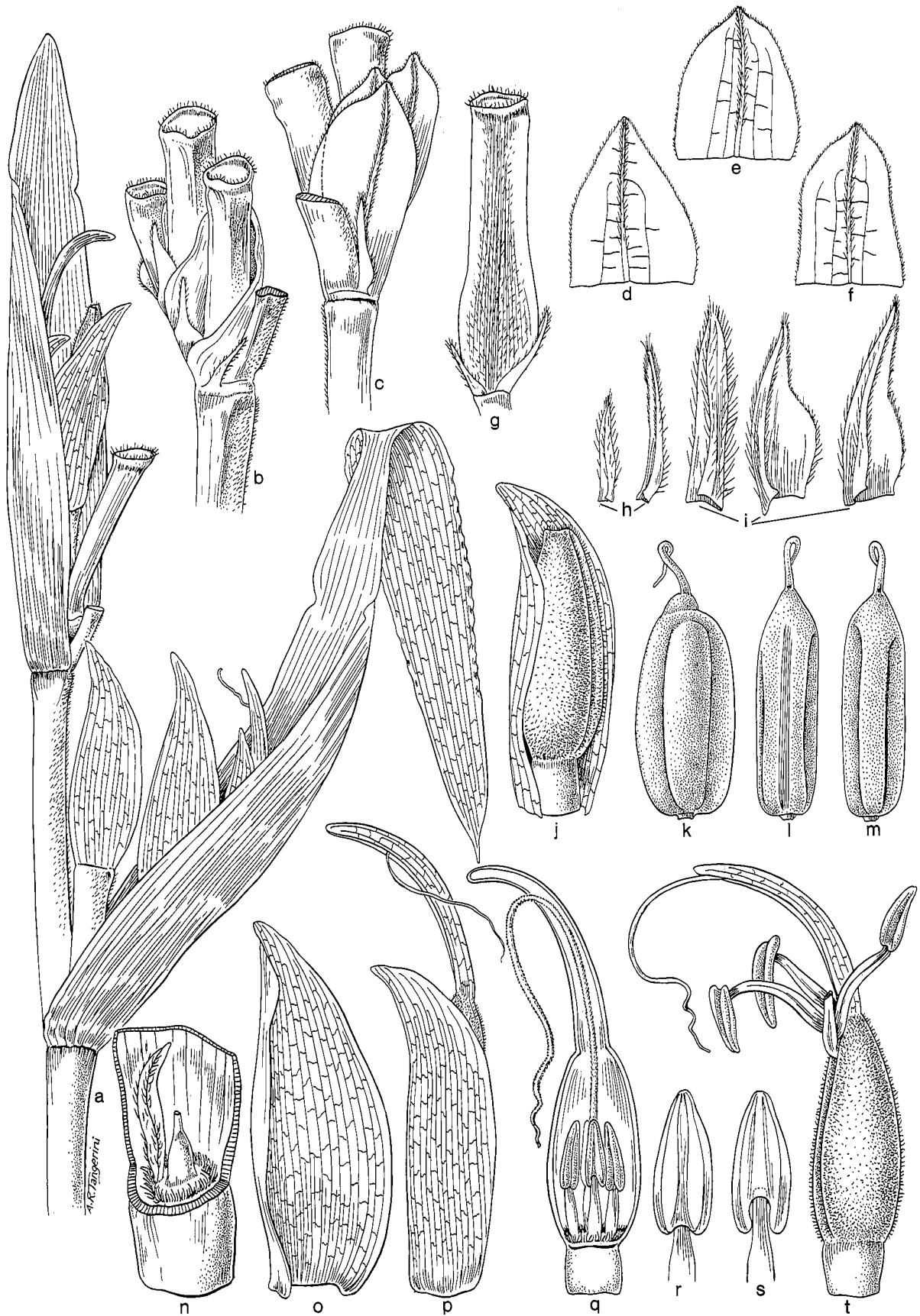


FIGURE 4 (left).—Details of partial inflorescences and spikelets of *Anomochloa marantoidea*: *a*, portion of inflorescence showing the lowest and next to lowest partial inflorescences (note reduced leaf blade on bract subtending lowest partial inflorescence) ($\times 1.59$). Base of partial inflorescence, the bract subtending the partial inflorescence removed ($\times 3.18$); *b*, ventral view; *c*, dorsal view, showing keeled, nested bracts that subtend each successive branch. *d-f*, Variation in bract that subtends each lateral branch ($\times 3.18$); *g*, basal portion of primary axis, showing pair of small, lower (left) and large, upper (right) bracteoles at base (subtending bract between bracteoles and axis removed) ($\times 3.18$); *h*, variation in the small bracteole found as the first appendage on each successive lateral branch ($\times 6.36$); *i*, variation in the large bracteole found as the second appendage of each successive lateral branch ($\times 6.36$); *j*, spikelet showing deciduous lower bract and pedicelled upper bract (the corniculum fallen from the latter) ($\times 3.18$). Caryopsis ($\times 4.77$): *k*, side view, showing oblique beak; *l*, ventral view, showing linear hilum; *m*, dorsal view. *n*, Portion of spikelet (upper bract partially dissected away) showing ovary surrounded by perigonate annulus and with anomalous bract found in one spikelet (stamens removed) ($\times 6.36$), *o*, lower spikelet bract, adaxial view ($\times 3.18$); *p*, spikelet, side view showing corniculate upper bract embraced by lower bract (note exerted stigma) ($\times 3.18$); *q*, longitudinal section of spikelet (lower bract removed), with thickened internode supporting upper bract, perigonate annulus, stamens, and gynecium ($\times 3.18$); *r*, anther, adaxial view ($\times 6.36$); *s*, anther, abaxial view ($\times 6.36$); *t*, spikelet (lower bract removed) at male flowering stage, showing the stamens emerging from between the margins of the summit of the body of the upper bract ($\times 3.18$). (Based on *dos Santos et al.* 3880, Brazil.) Illustration by Alice R. Tangerini.

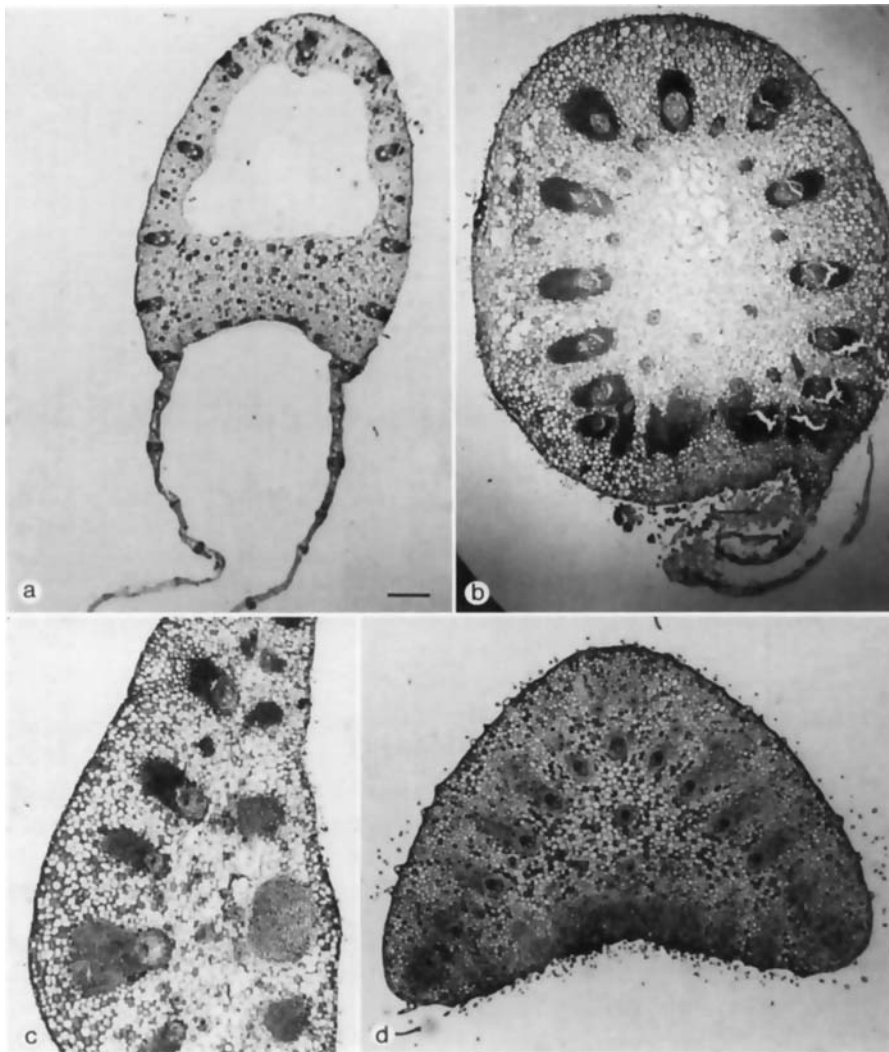


FIGURE 5.—Transverse sections of sheaths and pseudopetiolar regions of leaves of *Anomochloa* and *Streptochaeta*. *A. marantoidea* (*Calderón et al.* 2381): *a*, leaf sheath showing prominently winged margins and hollow body; *b*, lower pulvinus, showing smaller sheath margin wings and ciliate inner ligule (arrow); *c*, upper pulvinus as it expands into the blade, showing complex vasculature (adaxial epidermis on right). *d*, Pulvinus of *S. spicata* subsp. *spicata* (*Calderón* 2046, Brazil), showing complex vasculature and pubescent adaxial surface below. Scale bar: *a* = 400 μm ; *b-d* = 250 μm .

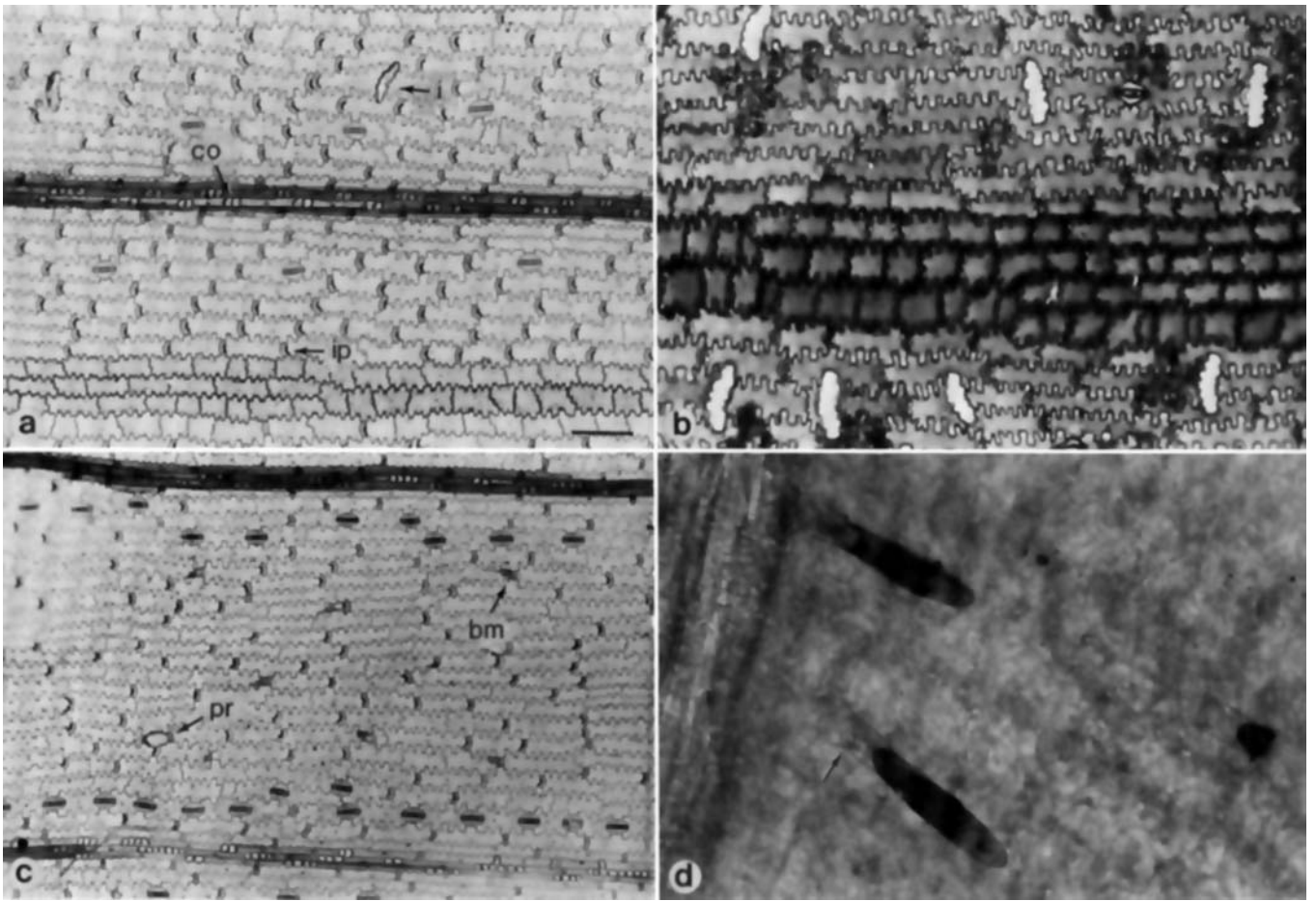


FIGURE 6.—Leaf epidermides of *Anomochloa marantoidea*: *a,b*, adaxial epidermis, showing bulliform cells, crescentic silica/cork cell pairs, and isolated vertical-crenate silica cells; *c*, abaxial epidermis (note scattered prickles and bicellular microhairs; basal cell only intact); *d*, bicellular microhairs from abaxial epidermis (note constricted basal cell, arrow). Abbreviations: bm = bicellular microhair; co = costal silica cell; is = intercostal isolated silica cell; ip = intercostal paired silica cell; pr = prickle. Scale bar: *a,c* = 100 μm ; *b* = 25 μm ; *d* = 30 μm . (Based on Calderón *et al.* 2381, Brazil.)

MORPHOLOGY-ANATOMY

Culm and Leaf Sheath

The culm of *Anomochloa marantoidea* is solid. The leaf sheaths are hollow with a large lacuna and prominent winged margins (Figure 5*a*), which embrace successive leaf sheath bodies. The marginal wings have about five vascular bundles and are often inrolled in a scroll-like fashion. The adaxial side of the leaf sheath is thicker and has several superposed tiers of small vascular bundles.

Toward the summit of the sheath its marginal wings narrow and approach each other, and the summit of the sheath and lower pulvinus are nearly elliptical (Figure 5*b*). The sheath becomes solid in the area of the lower pulvinus for a few millimeters, but the vascular bundles still consist of a circle of approximately 10 to 12 large bundles with a roughly

alternating circle of small vascular bundles just interior to them. Continuing acropetally through the lower pulvinus, these smaller vascular bundles and some of the larger ones contribute to a complex plexus in the center of the sheath.

Ligule and Pseudopetiole

No external ligule is present; the internal ligule is present as a fringe of ciliate hairs. At the summit of the lower pulvinus the pseudopetiole begins; again there is a lacuna in its center, but not so large as in the leaf sheath. The body of the pseudopetiole is V-shaped in cross-section.

Pulvini

In cross-section the upper pulvinus is slightly V-shaped, with the trough of the V on the adaxial surface. The ground

tissue consists of large parenchyma cells. The epidermis is sparsely papillate and pubescent. The main vascularization consists of a V-shape arch of bundles near the abaxial epidermis. These bundles are connected, or nearly so, to that epidermis by sclerenchyma caps. Subjacent to the adaxial surface are 5 to 8 sclerenchymatous areas that lack vascular bundles. The area between the adaxial epidermis and the main arch of vascular bundles consists of parenchyma cells in which are embedded about 10 small vascular bundles in a complex pattern.

At its base the pulvinus encloses a large block of sclerenchyma buried a few cells beneath the adaxial epidermis (Figure 5c). Farther up, this block of cells approaches the epidermis and is contiguous with a broad, shallow, sclerenchyma plate covering the top of the adaxial midrib (Figure 7d). Toward the base of the lamina the adaxial midrib appears abruptly and soon takes on its characteristic square or anvil shape.

Leaf-blade Anatomy

TRANSVERSE SECTION (Figure 7d-g).—*Outline*: blade flat, expanded (except near cup-like base), the epidermides nearly straight, the margins rounded to slightly acute. *Midrib outline*: distinctive, projecting both adaxially and abaxially; adaxial projection in lower $2/3$ of the blade anvil- or keystone-shaped, narrowed at the base and with a broad, flat, top with margins that slightly overhang the lamina (this keel reduced to merely an inverted U-shape in the uppermost $1/3$ of the lamina); abaxial projection less prominent, low dome-shaped. *Midrib vasculature*: complex in well-developed blades, with at least two tiers of vascular bundles; one large, median, first-order bundle with a lysigenous cavity and a pair of metaxylem vessels always present subjacent to the abaxial epidermis, this not flanked by any smaller bundles; several third-order vascular bundles present in adaxial half of the midrib, characteristically in a crude T- or Y-shaped pattern, with the base of the Y or T in about the center of the midrib. *Midrib sclerenchyma*: in two plates, one on the adaxial keel, relatively shallow (5–8 cells wide), and unconnected to any of the subjacent minor vascular bundles; the other on the abaxial keel deeper (–8–12 cells wide), more well developed, and partially surrounding the median vascular bundle, with the sclerenchyma continuous with the bundle sheath. *Vascular bundle arrangement in the lamina*: all bundles closer to the abaxial than adaxial epidermis. *Primary vascular bundles*: ovate in outline; double sheath present, the outer sheath of large, thin-walled, inflated cells with few plastids, complete on the adaxial side and often with a small extension to the adaxial sclerenchyma cap, but interrupted on the abaxial side, where interrupted by the sclerenchyma of the abaxial bundle cap; inner sheath of two complete rows of narrow, achlorophyllous, thick-walled cells; lysigenous cavity and two metaxylem vessels present; adaxial sclerenchyma cap squarish or inverted triangular, 10–17-celled, abaxial sclerenchyma cap narrow, horizontal, about 15–20-

celled. *Third-order vascular bundles*: somewhat rectangular in outline; double sheath present, similar to that of the first-order vascular bundles, but adaxial outer bundle sheath extension never developed and abaxial sclerenchymatous interruption of the outer sheath only one cell wide; inner bundle sheath one or two cell-layers thick; adaxial sclerenchyma cap small, usually inverted-triangular, consisting of (2-) 5–12 cells, the abaxial cap of 8–14 cells. *Intercostal sclerenchyma*: absent. *Mesophyll*: chlorenchyma not radiate, consisting of one layer of cells immediately subjacent to each epidermis on either side of inflated fusoid cells, each one cell-layer thick, and separated by inflated fusoid cells; adaxial chlorenchyma rectangular, horizontal, the cells with several moderately developed arms projecting inward towards the fusoid cells; abaxial chlorenchyma cells less conspicuous than adaxial layer, narrowly rectangular and lacking any projections; fusoid cells well developed, rectangular, adjacent fusoid cells separated by a well-developed chlorenchymatous column 1–3 cells wide.

ABAXIAL EPIDERMIS (Figure 6c,d).—Costal and intercostal zones well differentiated. *Intercostal long cells*: homogeneous, rectangular (length:width, 4–6:1), with strongly sinuous walls; in well-developed cells the sinuations themselves undulating. *Stomata*: in 1–3 short, interrupted rows along each side of the costal zones, each short row staggered so that it continues where the last row terminated; subsidiary cells low dome-shaped to slightly triangular; stomates separated by 1(–3) long cells. *Bulliform cells*: absent. *Papillae*: absent. *Prickle hairs*: fairly common in intercostal zones; base greatly inflated, tip small, narrow, sharp; usually paired with a cork cell. *Macrohairs*: absent. *Microhairs*: scattered throughout intercostal zone between the stomatal regions; apparently bicellular; basal cell 40–50 μm long, cylindrical, relatively thick-walled, with an apparent constriction near the base; apical cell narrowly ellipsoid, 45–65 μm long, tapering to a blunt tip, thin-walled and easily deflated; total length of microhair 90–115 μm . *Short cells*: abundant, typically in pairs (silica/cork), these alternating with the long cells; cork cells crescent- or kidney-shaped, embracing a similarly shaped but slightly smaller silica cell; occasionally, solitary short cells (apparently cork cells) alternating with the long cells in the stomatal region. *Costal cells*: in rows of 2–4, consisting of modified, long-rectangular (length:width, –10:1) long cells separated by short to long (2–8 individual cells) rows of squarish silica cells; cork cells rare or absent.

ADAXIAL EPIDERMIS (Figure 6a).—Basically similar to the abaxial epidermis. *Bulliform cells*: in 3 or 4 rows, covering about $1/4$ of the intercostal zones, well developed and distinct from typical long cells, square to rectangular (length:width, 1–3:1), with moderately sinuous walls; not alternating with any other cell type. *Intercostal long cells*: rectangular (length:width 3–4:1), strongly sinuous, alternating with short cell pairs. *Papillae*: absent. *Prickles*: not seen. *Macrohairs*: absent. *Microhairs*: extremely rare, only one seen. *Short cells*: similar to those of abaxial epidermis. *Silica cells*: occasional to fairly common in intercostal zones, interpolated between adjacent

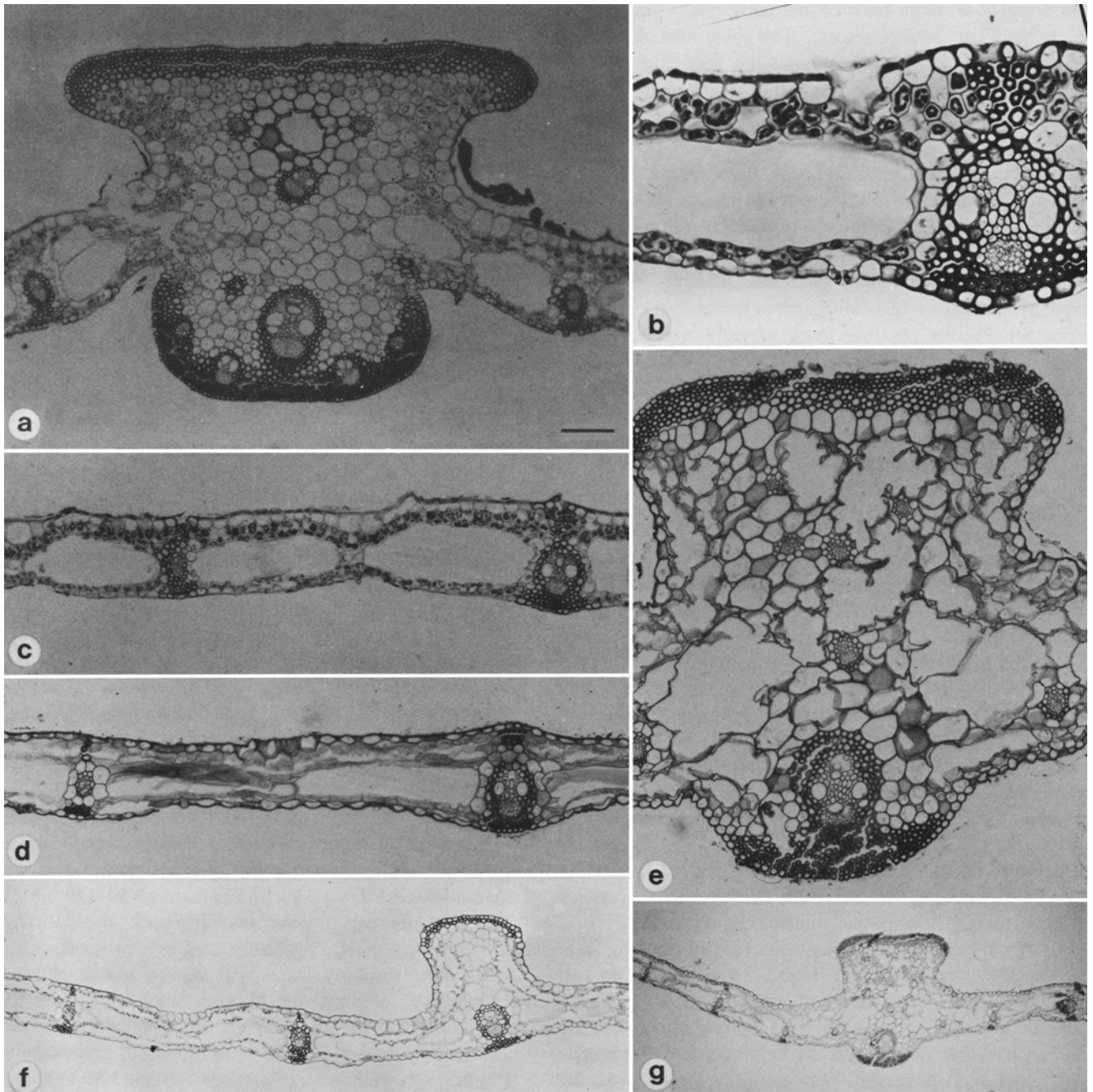


FIGURE 7.—Transverse sections of leaf blades of *Streptochaeta sodiroana* (a–c) and *Anomochloa marantoidea* (d–g) (in all cases the adaxial epidermis faces upwards): *S. sodiroana* (Soderstrom 1205): a, characteristic midrib with its complex vasculature; b, detail of fusoid cell and primary vascular bundle in the lamina; c, detail of lamina showing minor vascular bundle, fusoid cells, and primary vascular bundle. *A. marantoidea* (Calderón et al. 2381, Brazil): d, section of lamina showing minor vascular bundle, fusoid cells, and primary vascular bundle; e, g, midrib section from a robust leaf, showing characteristic shape and complex vasculature; f, section of lamina including midrib, cut from a small leaf. Scale bar: a, c–e = 100 μ m; b = 50 μ m; f = 200; g = 250 μ m.

long cells in the same row, and protruding above and below that row halfway into the rows of long cells above and below it; consisting of a vertical, elliptic cell enclosing a crenate silica body. *Stomata*: occasional near veins, in short irregular rows;

subsidiary cells generally more triangular than those of abaxial epidermis. *Costal cells*: similar to those of the abaxial epidermis, but silica cells tending to be rounder.

Inflorescence

In the above description of the inflorescence and spikelets of *Anomochloa marantoidea* we have chosen not to give any formal morphological interpretations of the components of the partial inflorescences, spikelet bracts, and perigonate annulus at this point. We do wish to elaborate on the complex patterns of branching and bract disposition in the inflorescence, features that do not lend themselves well to a formal taxonomic description (Figures 4, 8, 9, 15). The structure of the partial inflorescence in the following robust individual is typical of all other individual partial inflorescences examined in the species.

The rachis of the inflorescence always terminates in a fully developed spikelet (Figure 15), which is not associated with any rudimentary spikelets or prolongation of the rachis. Below the terminal spikelet are a series of 4–7 alternating lanceolate, chlorophyllous, foliaceous bracts spaced along the rachis. The lowest of these bracts, which, unlike the upper ones, often bears a reduced, pseudopetiolate leaf blade (Figure 4a), is frequently separated from the second lowest by an exposed portion of the rachis several centimeters long. Each of these prominent subtending bracts, which we shall refer to as “general bracts” (after the designation “bractées générales” of Brongniart), subtends a partial inflorescence bearing from 1 to 3 fully developed and 1 or 2 rudimentary spikelets (Figure 4a). Figure 4 illustrates a partial inflorescence taken from a robust inflorescence. The general bract subtends the primary axis of the lateral branch, which terminates in a fully developed spikelet. Near the base of the primary axis, on the side nearest the rachis, is usually borne a pair of delicate unequal bracteoles, with the smaller bracteole borne on a slightly lower level (Figure 4g) than the larger bracteole. The bracteoles are separated by about 120° with respect to the center of the axis that bears them.

The lower bracteole of this pair is narrowly linear (Figure 4h) while the other is broadly lanceolate and strongly keeled (Figure 4i). Both bracteoles lack any vascularization and are hyaline and covered, especially in the upper portion, with brown cilia. Slightly above them on the primary axis of the branching system is a bract (Figure 4d–f) that subtends a secondary axis. The smaller of the two bracteoles just discussed is positioned near the keel of this bract (Figure 4c), which is ovate, hyaline, and has a well-developed midrib containing a vascular bundle. Its keel is positioned at right angles with respect to a line drawn from the center of the rachis through the center of the successive axes of the lateral inflorescence. As in the primary axis, the secondary axis subtended by the bract terminates in a fully developed spikelet and bears a pair of delicate, unequal bracteoles from near its base on the side facing the rachis. The smaller member is borne on a slightly lower level than the larger. Again, the members of the bracteole pair are separated by about 120° and tipped with a fringe of brown cilia. Above these bracteoles on the secondary axis is situated an ovate, keeled bract subtending the tertiary axis of

the partial inflorescence. Like the preceding branch-subtending bract, this subtending bract is rotated about 90° with respect to a line connecting the rachis and successive lateral branches. Because of this its keel appears to be nested within the keel of the preceding branch-subtending bract (Figure 4c).

In the specimen examined (*dos Santos et al.* 3880) the tertiary axis emanating from the axil of this subtending bract also terminates in a fully developed spikelet, bears near its base a pair of unequal bracteoles with the smaller bracteole arising on a slightly lower level, and above these bracteoles bears a keeled bract (whose keel nests with the keels of the bracts subtending the secondary and tertiary axes) that subtends a fourth-degree axis. The fourth-degree axis of the partial inflorescence terminates in a small spikelet containing a rudimentary gynecium and four stamens and bears a pair of tiny unequal bracteoles attached at nearly the same level near its base, and above these bracteoles a small keeled bract that subtends an axis bearing two tiny bracteoles as its first appendages and terminating in a tiny, rudimentary fifth spikelet.

Each axis in the branching system terminates in a spikelet and bears near its base on the adaxial side a pair of delicate bracteoles. The smaller member of the pair is borne on a slightly lower level and is positioned near the keel of the bract subtending the next axis of the branching system (Figure 4). The larger bracteole is lanceolate, keeled, and is separated from the smaller bracteole by about 120° with respect to the axis that bears it. The bracteole pair members are tipped with a fringe of brown cilia and lack any vascular bundles. The bracts actually subtending each successive lateral axis of the branching system are much larger than the bracteoles and are ovate, scarious, and keeled (Figure 4d–f). In a robust partial inflorescence the keels of successive subtending bracts are nested at an angle of 90° with respect to a line drawn from the center of the rachis through the centers of successive lateral axes. The bracteole pair members of successive axes are also nested to the extent that all large bracteole pair members are aligned on one side of the partial inflorescence (Figure 4b) while all small bracteoles are aligned on nearly the opposite side of the partial inflorescence. The smaller member of the bracteole pair arises slightly lower on the axis than the larger member, and the pair members are always completely separate from each other, even at their bases.

The inflorescence of *Anomochloa marantoidea*, then, is topped with a spikelet and bears on its axis alternating partial inflorescences, each of these subtended by a prominent general bract that gives the inflorescence its marantaceous aspect. The inflorescence is laterally compressed and has a quite different appearance depending on which side is viewed. From one side all that is seen are the overlapping general bracts subtending each partial inflorescence (Figure 3b). But viewed from the opposite side many features are observed (Figure 2b,c): the general bracts subtending each successive partial inflorescence are visible but so are the upper portions of one or two of the spikelets in each partial inflorescence. Typically the upper

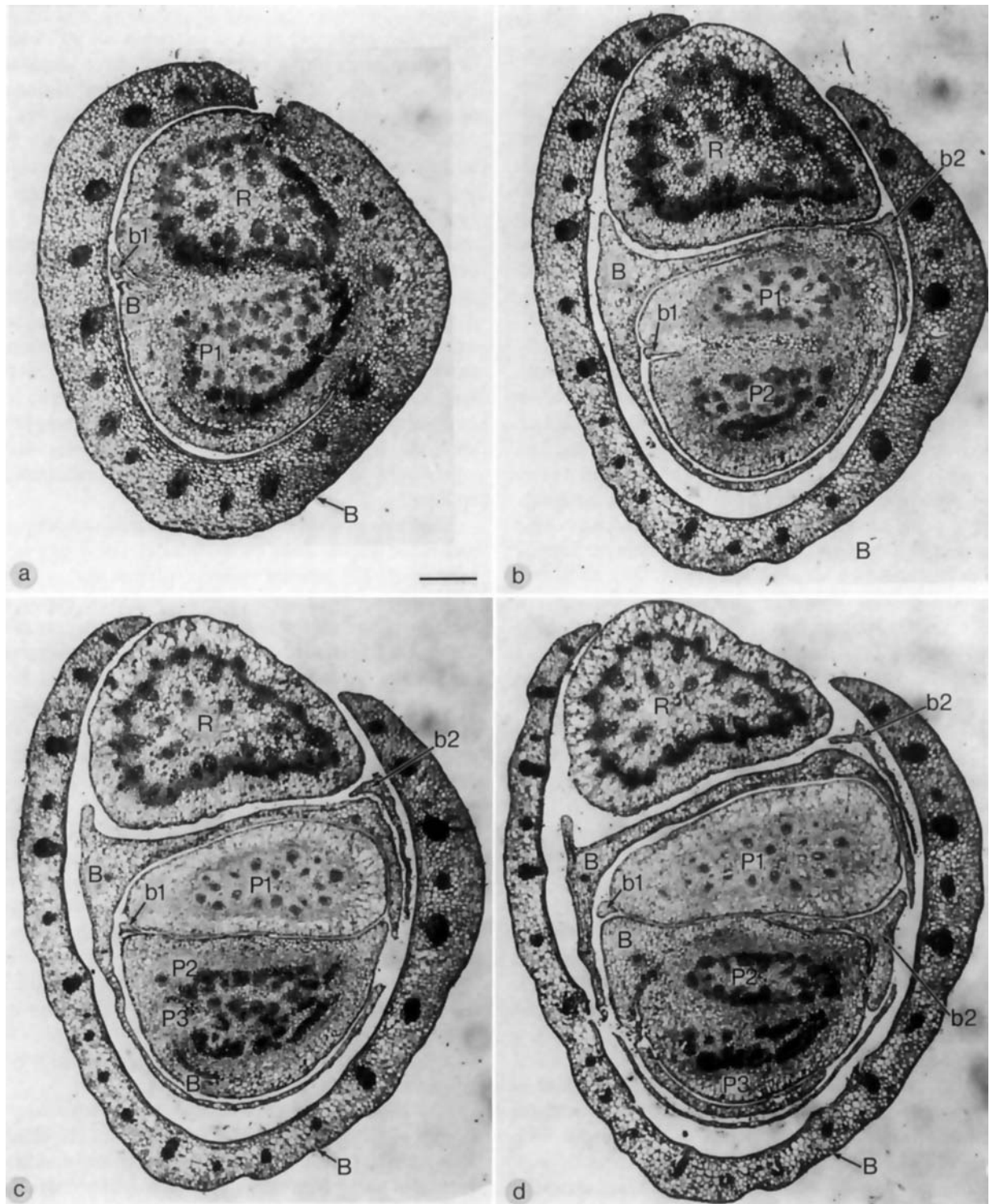


FIGURE 8.—Acropetal serial transverse sections through a partial inflorescence of *Anomochloa marantoidea*: *a*, rachis (above) and pedicel of first spikelet (below) enclosed by the “general bract” (B); *b*, emergence of pedicel of second spikelet (below); *c*, pedicel of second spikelet completely free from pedicel of first spikelet; *d*, beginning of emergence of pedicel of third spikelet. Abbreviations: B = bracts subtending successive branches of the partial inflorescence; b(1,2) = first or second bracteoles on each successive lateral branch; P(1–3) = successive lateral branches, terminating in a spikelet pedicel; R = rachis. (Based on *dos Santos et al.* 3880, Brazil). Scale bar: 500 μ m for all sections.

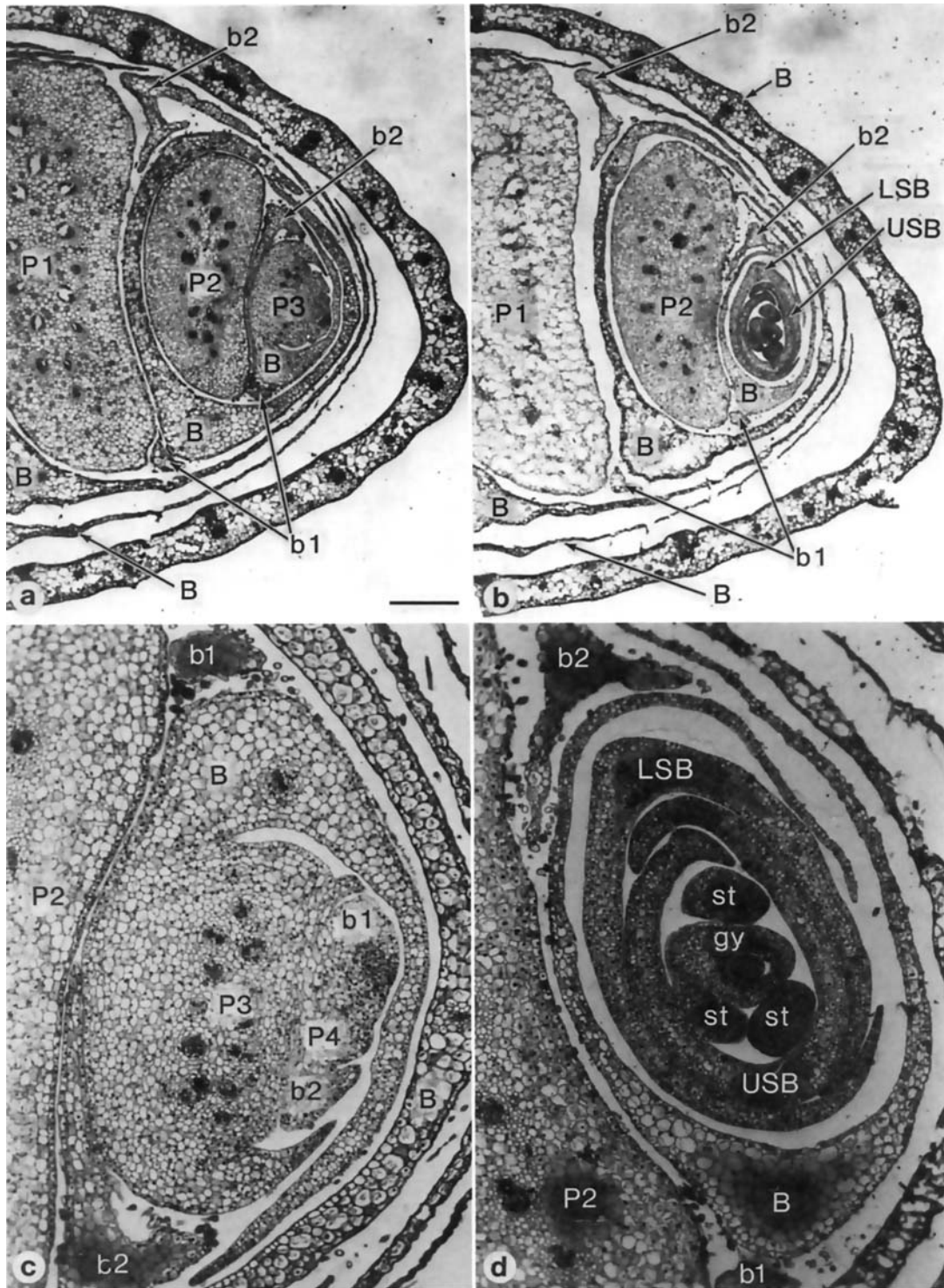


FIGURE 9.—Acropetal serial transverse sections through a partial inflorescence of *Anomochloa marantoidea*: *a*, pedicels of first three spikelets with pedicel of rudimentary fourth spikelet emerging; *b*, rudimentary third spikelet; *c*, detail of *a*; *d*, detail of *b*, showing rudimentary third spikelet with three rudimentary stamens surrounding the rudimentary gynecium. Abbreviations: B = bracts subtending successive branches of the partial inflorescence; b(1,2) = first or second bracteoles on each successive lateral branch; gy = gynecium; LSB = lower spikelet bract; P(1-4) = successive lateral branches terminating in a spikelet pedicel; st = stamen; USB = upper spikelet bract. (Based on dos Santos *et al.* 3880, Brazil.) Scale bar: *a, b* = 500 μ m; *c, d* = 150 μ m.

portion of the bodies and the cornicula of the upper spikelet bracts are visible, as well as the the upper portion of the lower spikelet bracts that sheath the upper bract (Figure 4a). In robust partial inflorescences the cornicula of the upper spikelet bracts of the second and third spikelets are also visible. In any case the cornicula of the upper spikelet bracts have a characteristic curvature, arching towards the partial inflorescences on the opposite side of the rachis. The stigmas are exerted through these cornicula (Figure 4q,t), face the same direction as that to which the cornicula point, and are held close to the inflorescence. Thus at anthesis (see following discussion; Figure 2c) the stigmas are conspicuous against the green background of the general bracts and lower spikelet bracts. In contrast the stamens, when extruded from between the margins of the body of the upper spikelet bract, are held almost horizontally away from the body of the inflorescence at a distance of a 1 or 2 cm (Figure 2b).

Spikelet

LOWER SPIKELET BRACT.—This appendage bears a strong resemblance to the general bracts that subtend each partial inflorescence. It is chlorophyllous and strongly nerved, with many transverse veinlets. This bract does not possess fusoid cells as would a typical lamina, nor does it possess the laminated structure typical of the upper bract (see "Upper Spikelet Bract").

THICKENED INTERNODE.—The internal anatomy of this structure is difficult to interpret because the cells were highly distorted in preparation. In cleared spikelets and longitudinal sections (Figure 12b) a complex floret stele or vascular plexus is found in the uppermost $\frac{1}{5}$ of the internode. The epidermis of the internode is smooth or may bear scattered brown or clear cilia.

UPPER SPIKELET BRACT.—The upper bract is complex, and for convenience it may be divided into two parts: the lower, ellipsoid body and an apical, deciduous horn or corniculum. The abaxial epidermis of the body is covered with a dense, fine indumentum of clear, 1-celled ciliate macrohairs, intermixed with prickles and rounded, silicified papillae (Figure 10a-c). Subjacent to this is a similar layer of undifferentiated parenchyma cells. Just below this are transversely elongated cells (length:width, ~10:1) with moderately thickened walls; this stratum is 6-8 cells thick. In some sections single transverse veinlets, consisting of only a single xylem vessel, are apparent. This transverse stratum gives the organ a distinctive "laminated" appearance, especially well displayed in paradermal sections (Figure 12d). This laminated structure continues for a millimeter or more into the summit of the thickened internode below the bract. Subjacent (adaxial) to the transversely elongated layer are the vascular bundles and 4-7 layers of roundish, thin-walled, vertically elongated parenchyma cells, these subjacent to the adaxial epidermis. There are 5 or 6 principal vascular bundles in the upper bracts of the

spikelets examined, each containing well-developed metaxylem vessels and a protoxylem lacuna, and associated with a slight rib on the adaxial surface of the bract. The median vascular bundle is slightly more prominent than the others. Alternating with these major bundles are from 8-12 minor bundles, these located close to the adaxial boundary of the transverse cell layer. Many of these minor bundles consist of but a single xylem vessel. One, occasionally 2, or rarely 3 minor bundles are situated between successive major bundles. The bract margins overlap strongly so that one margin retains a spiral- or sickle-like aspect and curls over and interlocks with the other, which resembles the head of a hammer (Figure 11a). This tight interlocking is maintained throughout the lower two-thirds of the bract, but becomes looser in the upper portion of the body. The corniculum of the upper bract is covered externally with the same type of ciliate, transparent macrohairs that cover the body; internally the corniculum is 5-8-nerved.

PERIGONATE ANNULUS (Figures 10a-c, 11a-b, 12c).—The basal membranous part of this circular structure is only a few cells high and wide, and is appressed to the base of the filaments. The ring is complete; in acropetal serial cross-sections of the spikelet it is not evident which side of the ring appears first; it appears to arise, along with the andrecium and gynecium, from the summit of the cylindrical internode separating the lower and upper spikelet bracts. No vascular bundles were detected entering or even approaching the perigonate ring. The dense fringe of hairs surmounting the ring consists of tapering, brown (less commonly transparent), thin-walled, apparently 1-celled cilia. These hairs vary in length from 0.5-2 mm. When cross-sectioned, these hairs often appear to break up into, or release, round brown globules. The hairs appear to be identical in structure to the cilia found in the ligular and pulvinal areas of the leaf and also on the surface of the upper spikelet bract.

ANDRECIUM.—In cross-sections made just below the bases of the filaments (Figures 10, 11), we found two large gaps on either side of the vascular bundle leading into the posterior stamen opposite the single, anterior stigma bundle (i.e., on the side of the upper spikelet bract in which the margins overlap; Figure 10a).

Several unusual structures were found in some spikelets: in one andrecium the base of the filament of the anterior stamen had a distinct lateral appendage (Figure 11b) that appeared to represent the rudiment of a fifth stamen; this rudiment was less than 50 μ m long and bore no anther. In another spikelet the gap between the anterior and one of the posterior lateral stamens was occupied by a hyaline, unvascularized linear (U-shaped in cross-section) appendage 5 mm long with strongly brown-ciliate margins (Figure 4n). The connective of the anthers completely encircles but does not fuse with the summit of the filaments for a short distance (0.4-0.7 mm) near the base of the anthers (Figures 11d, 12a). In cross-sections through their lower and middle portions, the anthers have an introrse aspect because their thecae are rotated forward slightly

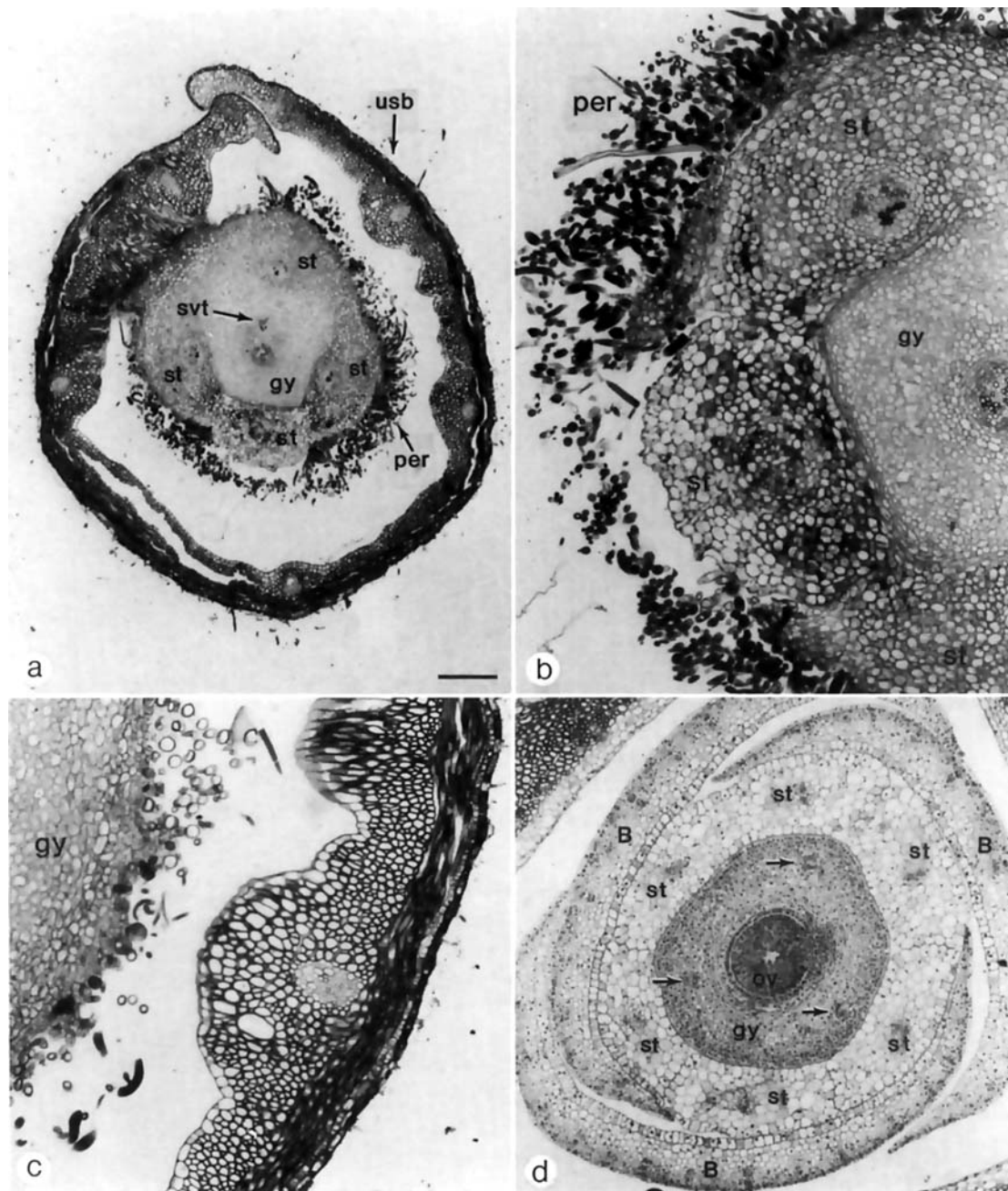


FIGURE 10.—Transverse sections of spikelet of *Anomochloa* and pseudospikelet of *Streptochaeta*. *A. marantoides* (lower spikelet bract not sectioned) (dos Santos *et al.* 3880., Brazil): *a*, near base, showing flower still partially attached to base of upper spikelet bract, and perigonate annulus and filaments starting to separate from the ovary; *b*, detail of spikelet showing perigonate annulus, three posterior filaments, and portion of ovary; *c*, detail of spikelet showing laminated anatomy of upper spikelet bract (right), with perigonate annulus and part of ovary (left). *d*, Pseudospikelet of *S. spicata* subsp. *spicata* (Soderstrom and Calderón 1861, Brazil), showing overlapping bracts X through XII surrounding the flower; flower composed of six stamens surrounding an ovary with three stigmatic vascular bundles (arrows); note attachment of ovule on right side of ovary. Abbreviations: B = pseudospikelet bracts X–XII; gy = gynecium; per = perigonate annulus; st = stamen; svt = stigmatic vascular trace; usb = upper spikelet bract. Scale bar: *a* = 300 μ m; *b–d* = 100 μ m.

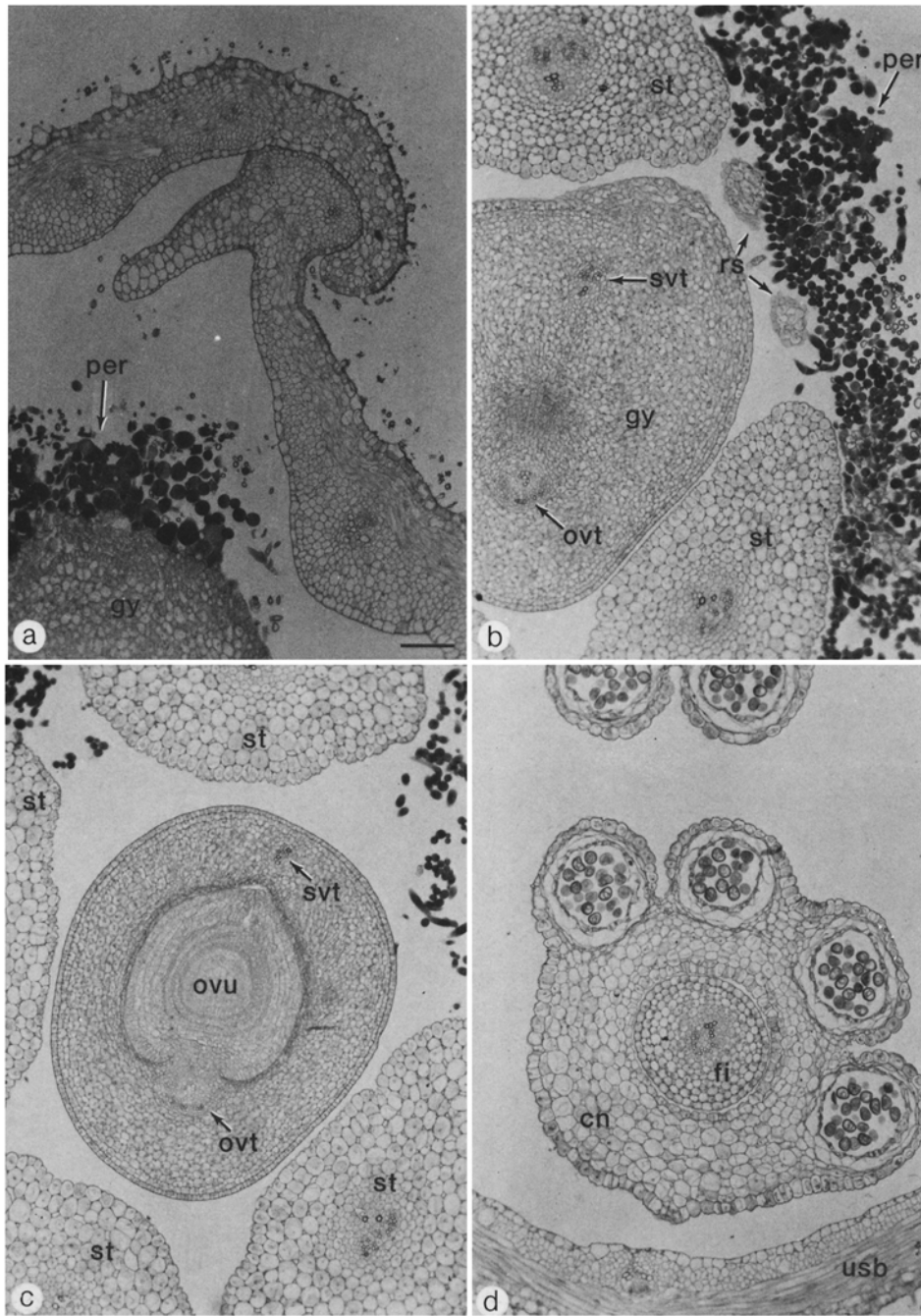


FIGURE 11.—Transverse sections of spikelet of *Anomochloa marantoidea*: *a*, characteristic interlocking margins of the upper spikelet bract; *b*, rudimentary 5th stamen located between anterior stamen (upper) and one of the posterior lateral stamens (lower); *c*, detail of ovary showing absence of posterior lateral stigmatic vascular traces; anterior stamen at top, posterior at lower left; *d*, detail of stamen showing filament unfused to connective and the pollen sacs rotated towards the adaxial side of the stamen (upper right in this section); note also the laminated structure of the upper spikelet bract (lower). Abbreviations: cn = connective; fi = filament; gy = gynecium; ovt = ovular (posterior) vascular trace; ovu = ovule; per = perigonate annulus; rs = rudimentary stamen; st = stamen; svt = stigmatic (anterior) vascular trace; usb = upper spikelet bract. (Based on *dos Santos et al.* 3880, Brazil.) Scale bar: 100 μ m for all sections.

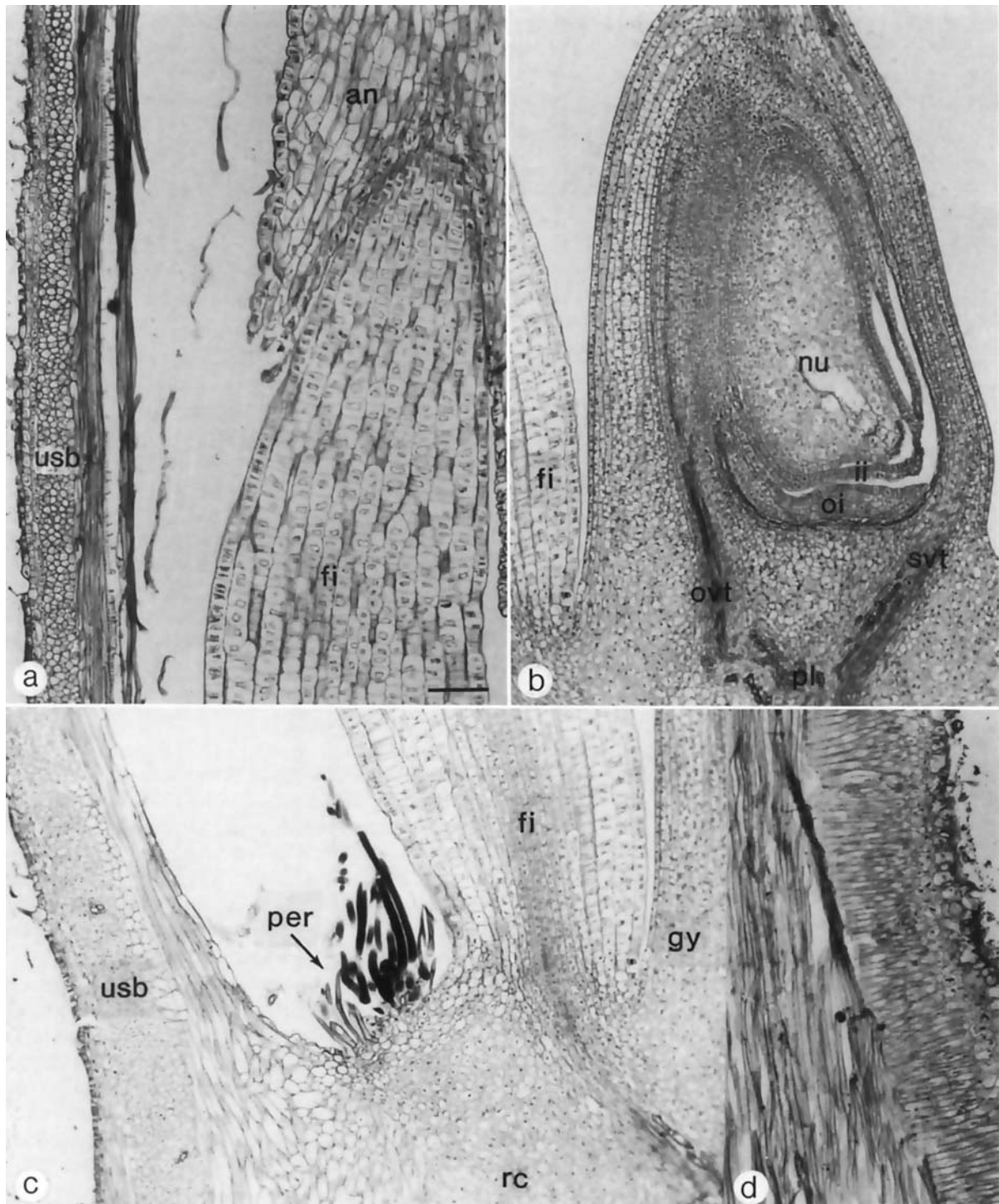


FIGURE 12.—Longitudinal sections of spikelet of *Anomochloa marantoidea*: *a*, laminated structure of upper spikelet bract (left) and filament attached to anther (right); *b*, detail of gynecium (note the vascular plexus at summit of internode below); *c*, detail of upper spikelet bract, perigonate annulus, and filament; *d*, oblique paradermal section of upper spikelet bract showing laminated structure. Abbreviations: an = anther; fi = filament; gy = gynecium; ii = inner integument; nu = nucellus; oi = outer integument; ovt = ovular vascular trace; per = perigonate annulus; pl = vascular plexus at base of flower; rc = internode between lower and upper spikelet bracts; svt = stigmatic vascular trace; usb = upper spikelet bract. (All based on *dos Santos et al.* 3880, Brazil.) Scale bar: *a*–*c* = 100 μ m; *d* = 25 μ m.

and face the center of the andrecial circle (Figure 11*d*). In the upper portion of the anther, however, the thecae have a more lateral arrangement on both sides of the connective.

GYNECIUM.—Cross-sections of the gynecium revealed the presence of two vascular bundles, one located on the posterior side (i.e., on that side at which the ovule is attached) of the ovary and leading into the ovule (ovular strand) and one located on the anterior side of the ovary and leading into the style (Figures 10*a*, 11*b,c*). Longitudinal sections of the ovary revealed the presence of two integuments surrounding the megasporangium (Figure 12*b*), which is attached to the ovary wall near the apex of the ovular cavity. The style with its single vascular bundle tapers apically into a single papillose stigma.

Fruit

CARYOPSIS.—The caryopsis, which is tightly invested by the upper spikelet bract at maturity, is elongate-prismatic with a slightly oblique beak and a shallow, inconspicuous linear hilum. The embryo is oblique-basal and is hidden by the papery, light brown pericarp.

STARCH GRAINS.—The endosperm of the mature caryopsis is mealy, and the starch grains are highly compound. Approximately 50–100 ellipsoidal grains occur in each cell and each grain ranges in size from 10–20 μm in diameter. Each grain is composed of 20–50 sharply angular granules and the granules range in size from 2.5–4.5 μm in diameter.

EMBRYO.—In median sagittal section (Figure 13*c,d*) the embryo exhibits a massive scutellum, an epiblast, and a fairly inconspicuous cleft between the lower part of the scutellum and the coleorhiza. Due to the prominence of the scutellum and the relative inconspicuousness of the coleoptile and coleorhiza this cleft appears not basal but is situated about $\frac{1}{3}$ of the way up the abaxial side of the embryo. The coleoptilar-coleorhizal axis is rotated about 60° from the vertical, and no internode (mesocotyl) is present between the divergence of the vascular traces to the scutellar and coleoptilar nodes. In acropetal series of transverse sections through the embryo (Figure 14) near the base of the coleoptile 5 nerves are evident, 2 being submarginal, 2 submedian, and 1 median. The median nerve is soon lost distally, appearing to merge with one of the submedian nerves. Sections made nearer the middle of the coleoptile reveal the structure of the first embryonic leaf; it is 3-nerved, has margins that meet but do not overlap, and encloses a small second embryonic leaf. In sections made still further up the coleoptile, a distinct cleft begins to appear on the side of the coleoptile opposite the scutellum. This cleft broadens until a distinct, oblique slit is observed in the coleoptile near its summit (Figure 14*a*, arrow). It is difficult to interpret the free margins of the coleoptile as either meeting without overlapping or as actually overlapping. Until near its apex, all four remaining nerves are still apparent in cross-sections of the coleoptile.

CHROMOSOMES

The only count was made by Juan H. Hunziker (pers. comm.), who found $n = 18$, based on the following collection: *dos Santos, Martinelli, and Soderstrom 3880*.

DISCUSSION

Habit

In the dense shade of the forest *Anomochloa marantoidea* is a robust, clumped plant reaching up to a meter in height (Figure 1*b*). In cultivation or in treefall gaps individuals are much smaller; Brongniart (1851) used the adjective "humile" in his original description of greenhouse material. Plants of *Anomochloa* present an unusual aspect in that the heights and orientations of successive leaf blades are regulated by several adaptations involving the leaf sheaths, pseudopetioles, and possibly the pulvini, and not by their disposition at the successive nodes of an elongated culm as in most grasses. The leaf sheaths have a nearly vertical orientation, but diverging from their summits by 45° or more are long pseudopetioles of varying lengths, with those of the upper leaves much longer than those of the lower. The variable lengths of the leaf sheaths and pseudopetioles may ensure that the blades are held at differing heights above the soil. The leaf sheaths are unusual in that they are consistently hollow. The base of the expanded portion of the lamina is slightly cordate and cupped upwards (Figures 2*b*, 3), a trait *Anomochloa* shares with other large-leaved umbrophilic herbaceous bamboos, such as the Bahian endemic *Sucrea monophylla* (Bambusoideae: Olyreae) and the African *Puelia schumanniana* (Bambusoideae: Puelieae), as well as the broad-leaved *Ichnanthus grandifolius* (Panicoideae: Paniceae). Although Brongniart (1851) described the leaf blades as subarticulating we found no evidence that they are deciduous. The hollow leaf sheaths and pseudopetioles of *Anomochloa* may be unique in the family.

Diurnal sleep movements of the leaf blades of the type observed in certain olyroid herbaceous bamboos (*Arberella*, *Cryptochloa*, *Lithachne*, *Raddia*; cf. Soderstrom, 1980) have not been seen in *Anomochloa*. However, in mature plants the blades have quite different orientations on the same shoot: some are held horizontally, while others are distinctly descending or ascending, and the blades of successive leaves are not placed in a strictly opposite orientation with respect to one another. It may be that the pulvini, although not involved in diurnal movements of the blades, help determine the mature orientation of the lamina. Bipulvinate pseudopetioles, although not common in the Poaceae, are known from large-leaved species of the centothecoid genus *Zeugites*.

Leaves

Two features are prominent in a transverse section of a leaf blade (Figure 7) of *Anomochloa marantoidea*. First, the fusoid

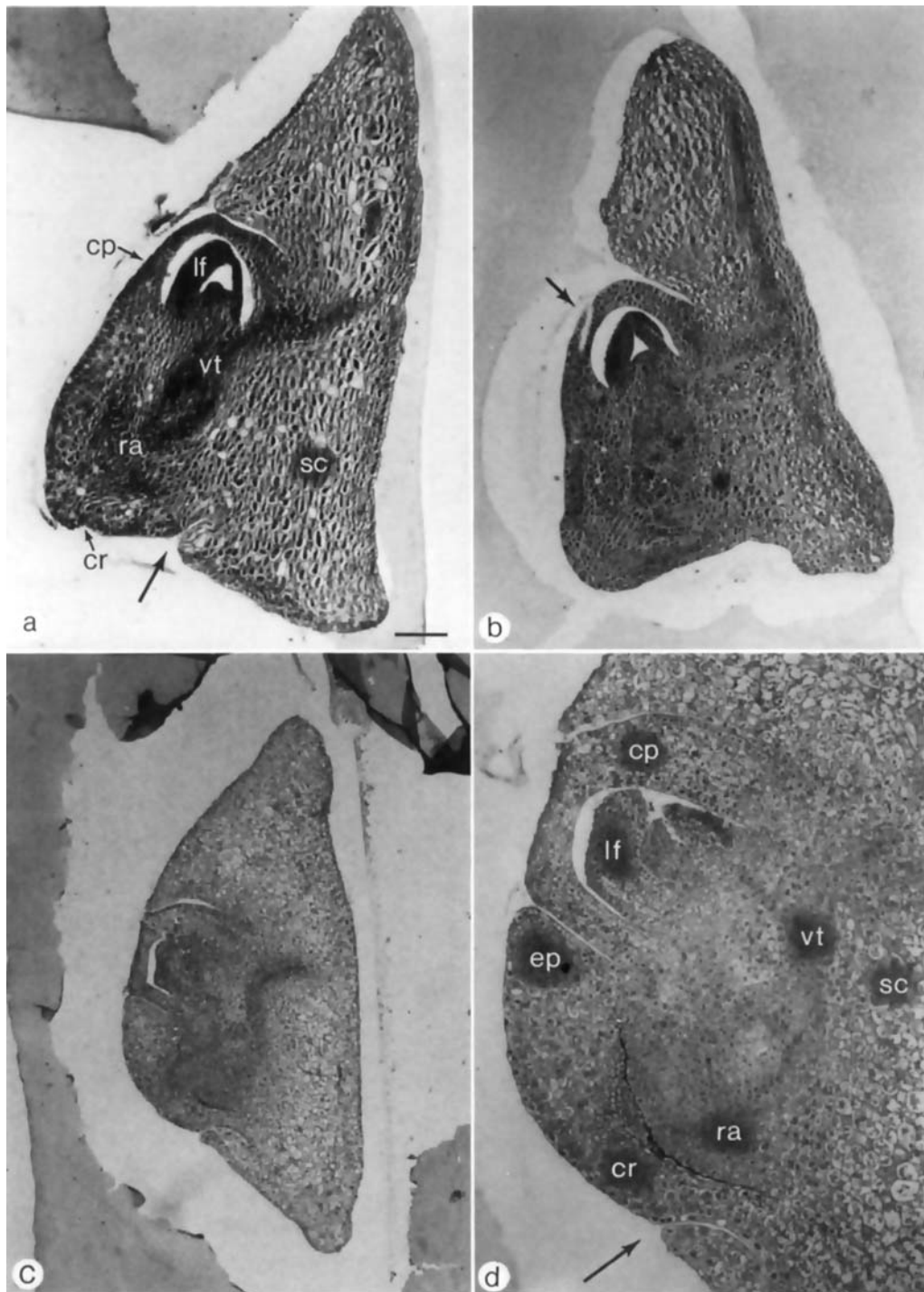


FIGURE 13.—Median sagittal sections, embryos of *Streptochaeta* and *Anomochloa*: a, *S. spicata* subsp. *spicata* (Soderstrom and Sucre 1896, Brazil), showing poorly developed cleft between scutellum and coleorhiza (arrow); b, *S. sodiroana* (Calderón 2096, Panama), showing overlapping margins of coleoptile (arrow); c, *A. marantoidea* (dos Santos et al. 3880, Brazil), showing massive scutellum; d, detail of c showing abaxial position of cleft between coleorhiza and scutellum (arrow). Abbreviations: cp = coleoptile; cr = coleorhiza; ep = epiblast; lf = first embryonic leaf; ra = radicle; sc = scutellum; vt = vascular trace. Scale bar: a,b,d = 100 μ m; c = 25 μ m.

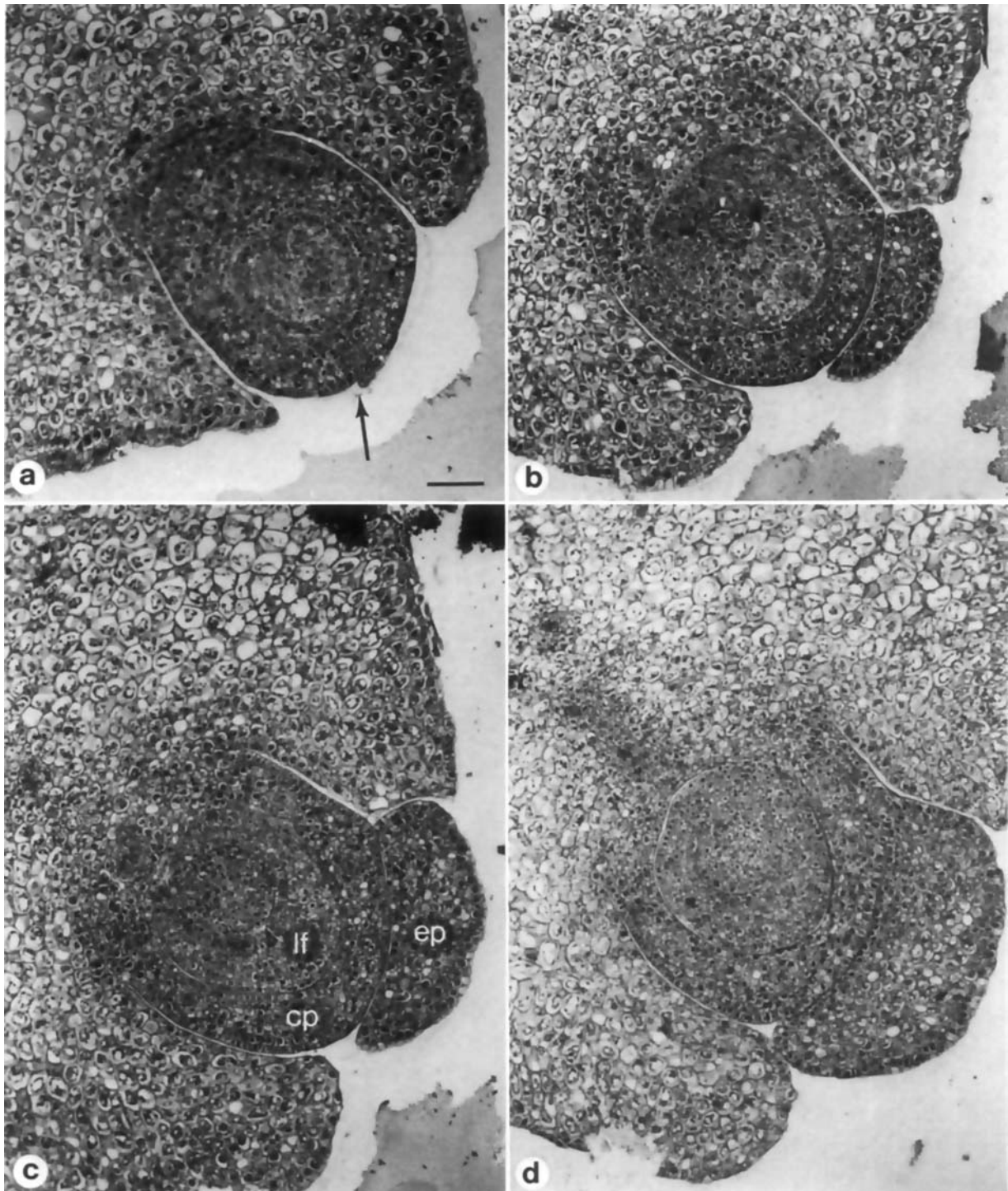


FIGURE 14.—Transverse sections through plumule of embryo of *Anomochloa marantoidea* (dos Santos *et al.* 3880, Brazil) (*a* through *d* proceeding in a downward (basipetal) direction with respect to the embryonic axis): *a*, unfused, obliquely meeting margins of coleoptile (arrow); *b, c*, margins of first embryonic leaf; *d*, entrance of vascular trace from scutellum, which becomes the midnerve of the coleoptile. Abbreviations: cp = coleoptile; ep = epiblast; lf = first embryonic leaf. Scale bar: 100 μ m in all sections.

cells are large, occupying about one-half of the volume of the lamina (Figure 7e). And secondly, the midrib possesses two projecting keels. The adaxial keel is more prominent and has a strongly flattened top with edges that overhang the base slightly. The abaxial keel is low, dome-shaped and is associated with the median vascular bundle, which lies just below the epidermis. Small blades have merely a dome-like adaxial keel, no abaxial keel, and a simple vasculature with but a single median vascular bundle lying close to the abaxial epidermis (Figure 7f).

The vascular bundles of the leaf blades of *Anomochloa* have typically bambusoid sheaths, with an outer sheath of large, thin-walled cells with few plastids, and an inner sheath of one or two layers of small, thick-walled, fibrous cells. Arm cells are not well developed in the mesophyll subjacent to the adaxial epidermis, and bulliform cells on the adaxial epidermis are only moderately well developed.

The epidermides of *Anomochloa* exhibit typically bambusoid sinuous long cells. Leaf epidermal papillae, common in most bambusoids, are lacking in *Anomochloa*. The silica-cork cell pairs are unusual in that both members are vertically crescent-shaped with the larger cork cell embracing the much smaller silica cell. The costal silica cells contain silica bodies that vary from round to squarish to slightly cross-shaped. A third type of silica cell is found on the adaxial epidermis, present as large, solitary, vertically elliptical cells enclosing ovoid crenate silica bodies.

The microhairs of *A. marantoidea* are found almost exclusively on the abaxial epidermis and are large, some attaining 115 μm in length (Figure 6b). Metcalfe (1960:28) first reported their presence and noted that it was difficult to find examples in which the distal cell had not collapsed and, thus, many of the hairs appeared to be unicellular. Renvoize (1985), using the same material as ours (*Calderón et al.* 2381), reported and illustrated anomalous short bicellular microhairs in which the distal cell was globose, not long and pointed as we found them in undamaged hairs. We have been unable to find this hair type in our preparations. The basal cell (40–50 μm long) is cylindrical but has an apparent constriction or invagination approximately one-third of the way up from the base; that part of the cell below the constriction is conical in shape and might be mistaken for a separate cell. The delicate upper cell of the microhair (45–65 μm long) is narrowly ellipsoidal and tapers to a slightly pointed apex. It is rare in the bamboos for the upper cell to be distinctly longer than the lower one (Metcalfe, 1960, fig. 16). This character is frequent in the panicoid grasses, which, however, have much smaller microhairs.

Inflorescence

The principal difficulty in interpretation of the inflorescence of *Anomochloa* is the highly contorted and bracteate nature of the partial inflorescences. If we take as a generalized ancestor the typical graminaceous branching pattern, we should expect

to find a bract subtending each successive branch of the inflorescence; and secondly, a bikeeled bract (prophyllum) would be the first appendage borne on each lateral branch. In grasses with complex branching systems, such as many bamboos, this organ can be a useful "marker" in interpreting branching patterns. Instead of bicarinate bracts as the first appendage of each successive lateral branch, *Anomochloa* has a pair of tiny bracteoles. Brongniart, as revealed in his unpublished notes in the Paris Herbarium on the inflorescence of *Anomochloa*, did note the presence of these bracteoles, but he did not figure them in his published schematic diagram of a partial inflorescence (1851). Doell (1871:24) also detected the bracteoles ("squamulae") and he suggested that they result from the separation of a single organ. He correctly placed them about 120° apart between the areas of contact of the rachis and axis of the primary lateral branch. He also noted that they appear to be the result of the splitting of a single organ by the compression of the rachis against this lateral branch. He suggested that the two organs might be the result of a prophyllum that had been split by the pressure of the two axes just mentioned. Doell did not, however, observe the smaller bracteole pairs that were almost certainly present in the higher orders of branching in his partial inflorescence. While the position and consistent morphology of these bracteole pairs does suggest the possibility that they are the remnants of a prophyllum that has split into two portions, it should be noted that the bracteoles are never in actual contact, even at their bases, and that in dissections and in acropetal serial sections they appear to arise at different levels on the lateral branch. Also, split prophylls are not known from any other grass.

The interpretation of the partial inflorescence of *Anomochloa* depends on how one interprets the nature of these bracteole pair members, which are the first appendages of each successive branch of the partial inflorescence. Since the smaller member of each bracteole pair arises slightly below the upper member, the former appendage is best interpreted as a prophyll and the upper bracteole as the second appendage on the lateral branch, that is, simply an empty bract lacking a bud in its axil. The third appendage on the axis is the prominent keeled bract that subtends the next lateral branch.

If this interpretation is correct, then in formal morphological terms each partial inflorescence could be labeled a scorpioid cyme (Figure 15). This was the interpretation of Brongniart (1851) although he did not give a detailed explanation for his designation.

Spikelet

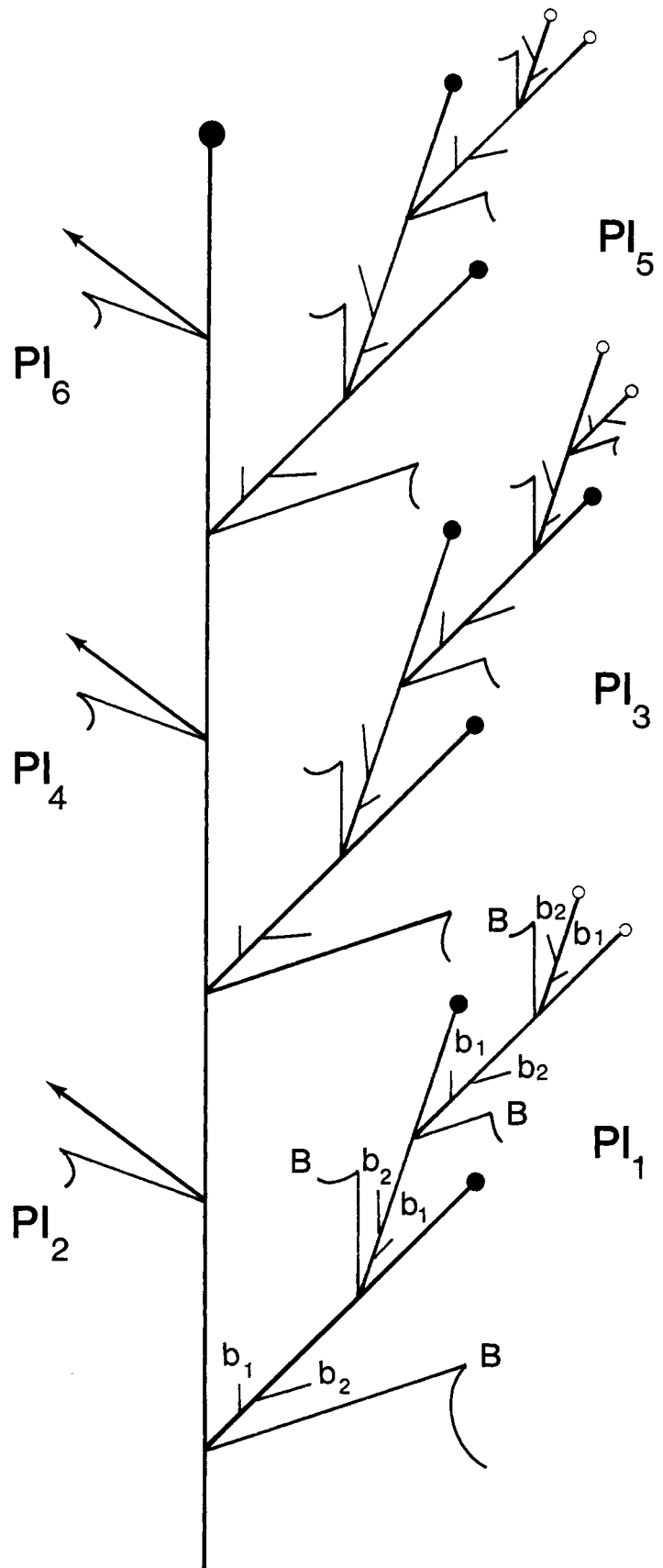
Perhaps the best way to understand the structure of the spikelet of *Anomochloa* is to begin examination at the apex of the branch bearing the flower and to proceed downward along this axis. For the purposes of the following discussion we will assume that the primitive grass had 6 stamens (arranged in alternating whorls of 3) and a 3-styled ovary with the vascular

FIGURE 15.—Schematic of the inflorescence of *Anomochloa marantoidea* showing partial inflorescences (PI) (only those on right side fully diagrammed) alternating on a rachis that terminates in a spikelet. Solid dots represent fully developed spikelets, open dots represent rudimentary spikelets. Abbreviations: B = bracts subtending lateral branches; b₁(2) = first or second bracteole of a lateral branch.

bundles leading to the stigmas placed alternate to the three stamens of the inner whorl. However, it is by no means certain that this supposition is correct. There is evidence, for example, that in grasses the stamens do not arise in whorls of 3, and that the lodicules do not all arise from a single whorl (see Clifford, 1987, for a review of this subject). Lacking developing inflorescences of *Anomochloa* for study we will draw our conclusions using conventional assumptions on the interpretation of the parts of the grass flower.

GYNECIUM.—Our observation that the ovary of *Anomochloa marantoidea* retains but a single anterior stigmatic vascular bundle is in accordance with the observation of Arber (1929) but not that of Schuster (1909), who figured three stigmatic bundles in the gynecium. The lateral posterior pair of stigmatic bundles present, for example, in species of *Sireptochaeta* (Figure 10*d*) is not present in *Anomochloa*.

ANDRECIUM.—The flowers of *Anomochloa marantoidea* consistently bear four stamens. Based on comparison with other Bambusoideae we assume that the primitive state in the subfamily is six and that two have been lost. This idea was first suggested by Brongniart (1851), who stated that the stamens are arranged in a homogeneous cycle such that it is impossible to determine which pair had been lost. The schematic figure of Schuster (1909, fig. 22) of a spikelet cross-section shows two gaps in the andrecial ring that might pertain to the lost stamen pair. His figure is otherwise misleading, however, in that three stigma bundles are figured and the position of the interlocking margins of the upper spikelet bract with respect to the andrecium and gynecium is incorrect. In transverse sections made just below the bases of the filaments (Figure 10*a*), we found two large gaps on either side of the vascular bundle leading into the posterior stamen opposite the single stigma bundle. If it is assumed that the ancestor of *Anomochloa* indeed had six stamens and three stigmas, and that the three stamens of the inner whorl were placed alternately with the three stigmatic bundles of the ovary (of which only the anterior remains), then it seems reasonable to conclude that these two gaps in the andrecium correspond to positions of the lateral anterior pair of stamens from the inner whorl, which have been lost. Arber (1929) arrived at this same hypothesis by a different line of reasoning. Based on her studies of the flowers of woody bamboos she noted that the inner whorl of stamens was more liable to reduction than the outer whorl and that the posterior stamen of the inner whorl was less liable to reduction than the anterior lateral pair. Although not observing gaps in the andrecium base of *Anomochloa* she did note that the posterior stamen was slightly smaller than the other three and thus might correspond to a stamen of the inner whorl, in which case the



two lateral anterior members of the whorl have been lost. An additional fact in support of the hypothesis that it is the anterior lateral pair of stamens that have been lost is the observation that in several sections of one spikelet the base of the filament of the anterior (outer whorl) stamen had a distinct lateral appendage (Figure 11*b*) that may represent the rudiment of a fifth stamen (one of the anterior lateral pair of the inner whorl). In the specimen examined this rudiment is less than 50 μm long and bears no anther. Arber (1929) also pointed out that the stamens of *Anomochloa* resemble those of no other grass in that the bases of the anthers completely encircle but do not fuse with the filament for a short distance near the base of the former. We also found this to be the case (Figure 11*d*). In cross-sections through their middle portions the anthers have an introrse aspect because their thecae are rotated forward slightly and face the center of the andrecial circle. In the upper portion of the anther, however, the thecae have a more lateral arrangement on both sides of the connective.

PERIGONATE ANNULUS.—Completely surrounding and closely appressed to the base of the stamen ring is a low membrane bearing at its summit a dense fringe of brown cilia. Brongniart (1851) called this circular structure simply a “discus annulus” and, although he offered no formal interpretation of it, he did note that lodicules (“squamulae”) are lacking in *Anomochloa*, thus implying that the ring could not represent a highly modified set of lodicules. Hooker (1862), Doell (1871), Schuster (1909), and Pilger (1954) all appear to agree with this interpretation although Doell (1871:24) does add in his description of the feature the query “perigonio?” [perianth]. Arber (1929) offered two suggestions as to the nature of the ring: it could indeed represent a reduced and fused ring of lodicules (the “ciliate perigon” of her figure 52) or that it could represent a greatly reduced lemma. The latter interpretation was suggested to Arber by the condition in the pooid genus *Lygeum* in which lemmas from adjacent florets are fused into a tube whose summit bears a dense fringe of hairs. Hubbard (1934:219) apparently was influenced by Arber’s first interpretation as he describes the ring as “lodicules?” We shall call this structure the perigonate annulus, a term that is descriptive of its morphology and position in the spikelet but that lacks the interpretive implications of “perigon.” Because the annulus does have a membranous portion it might represent a ring of reduced, fused lodicules as hinted by Doell. Grasses (e.g., *Melica*) are known that have partially to totally fused lodicules. These lodicules, however, retain discrete sets of vascular bundles indicating the individual nature of these organs. Because the perigonate annulus of *Anomochloa* is a homogeneous ring and does not have any vascular bundles entering it or even leading to it, the structure is of little use in interpreting the nature of the upper spikelet bract that surrounds it. We are unable to find convincing evidence that it is either a reduced lemma, palea, ring of lodicules, or outgrowth of the base of the andrecium.

UPPER SPIKELET BRACT.—Outside of the perigonate annulus, and enclosing it and the floret, is the upper spikelet bract.

Its tightly interlocked margins (Figure 11*a*) meet on the side of the flower (with respect to the position of the attachment of the ovule to the wall of the ovary) that would correspond to the position of a palea in a conventional grass spikelet, and indeed Brongniart interpreted it as a palea. However its laminated structure, deciduous apical appendage, many nerves, and lack of an associated prolongation of the rachilla is not characteristic of a palea.

THICKENED INTERNODE.—Below the upper bract is a thickened, barrel-like indurate internode that separates the lower from the upper spikelet bracts.

LOWER SPIKELET BRACT.—The base of the thickened internode bears the lower spikelet bract, a many-nerved, tessellate structure that is placed alternate to the upper bract and alternate to the bract that subtends the branch that terminates in the flower.

Brongniart (1851) mainly based his interpretation of the *Anomochloa* spikelet on the terminal position of the flower and the position of the upper spikelet bract with respect to the stamens. He pointed out that despite the fact that the upper spikelet bract lacked two keels, paleas were known in the oryzoid grasses (e.g., *Oryza*) that were 3-nerved and lacked well-defined bicarinate keels. Given this “marker,” the lower bract, he argued, must represent a lemma. The oryzoid grasses often have reduced or absent glumes. But teratological evidence suggests that the so-called palea of *Oryza* is actually a lemma and that the true paleas in the spikelet have been lost (Nuñez, 1968:95). Schuster (1909, fig. 23) was impressed with the peculiar hammer-and-sickle fit of the upper bract margins of *Anomochloa*, and turning, like Brongniart, to *Oryza*, he noted (1909:32) that the lemmas in that genus have at least superficially similar interlocking margins; in his interpretation, then, the lower bract represented a glume. Unfortunately Schuster’s (1909, fig. 22) schematic drawing of a cross-section of a spikelet *Anomochloa* is misleading on several counts. First, as already noted he figures three vascular bundles in the gynecium; and secondly, his floret is rotated 180° with respect to its true orientation within the upper spikelet bract, so that the missing stamen pair would appear to be the lateral posterior pair of the outer whorl. Still, his hypothesis that the upper bract represents a lemma is a reasonable one. One fact lending support to this idea is that the female lemmas of all genera of the Phareae, another tribe of herbaceous bamboos, possess a “laminated” internal structure quite similar to that found in the upper bract of *Anomochloa* (figured by Schuster (1909, fig. 23) but first noted by Arber (1934, fig. 52); see Figures 11*d*, 12*a,b-d*). Although it is difficult to imagine that this striking feature was independently derived in the two groups, it may be noted that in the pharoids the transversely elongated cell layer is subjacent to the adaxial epidermis, while in *Anomochloa* the similar cell layer is subjacent to the abaxial epidermis. We have also observed a laminated structure in the culm-leaf sheaths of some woody bamboos.

Arber (1929, fig. 52) labeled the lower and upper spikelet bracts and the perigonate annulus in her drawing of a

cross-section of an *Anomochloa* spikelet as the flowering glume (lemma), palea, and ciliate perigon, respectively. Yet she was also impressed by the similarity of the perigonate annulus of *Anomochloa* to the reduced, hairy lemma found in the anomalous genus *Lygeum*. Although not claiming that the two groups were particularly closely related, Arber suggested that if the reduction of the grass lemma could definitely proceed so far in *Lygeum*, it was not impossible for it to have proceeded farther yet in *Anomochloa*. Clayton and Renvoize (1986:58) apparently find this suggestion attractive as well.

None of the three extant hypotheses has an overwhelming weight of evidence behind it. The suggestion of Schuster (1909:32) that the two spikelet bracts be interpreted as just bracts appears to be the most reasonable at this point. Developmental studies of abundant material of initiating and developing inflorescences of *Anomochloa* will be required to elucidate further the problem of how to interpret the spikelet structures more satisfactorily. For now we must tentatively interpret the spikelet bracts as two lateral appendages on an axis that terminates in the flower. The terminal position of the flower on the branch indicates that, as in *Stipa* (Clifford, 1987), the uppermost spikelet bract cannot always be correctly designated as a palea.

Fruit

The caryopsis of *Anomochloa marantoidea* is remarkable for its large size (Figure 4k-m). Although many woody bamboos have larger caryopses, among the herbaceous bamboos only the fruits of *Olyra caudata* approach those of *Anomochloa* in volume. The three available caryopses that we examined were roughly cylindrical in shape and tightly invested by the upper spikelet bract at maturity. The oblique-basal embryo, although relatively small (as is typical for bambusoid grasses) when compared with the size of the caryopsis, is in absolute terms the largest known for any herbaceous bamboo. The embryo has a Reeder (1957) formula F+PF (Figures 13c,d, 14): there is no internode between the divergence of the coleoptilar and scutellar traces (F, a pooid [festucoid] feature); an epiblast is present (+, a pooid feature); there is a cleft between the lower part of the scutellum and the coleorhiza (P, a panicoid feature), and the margins of the embryonic first leaf meet but do not overlap (F, pooid). Thus, except for the non-overlapping embryonic leaf margins, *Anomochloa* has a typically bambusoid embryo formula (Reeder, 1962). Other bambusoid grasses are known that have a formula of F+PF, that is, with non-overlapping first leaf margins, for example *Pharus mezii* and *P. lappulaceus* (see Judziewicz, 1987) and the woody bamboo *Alvimia* (Soderstrom and Londoño, 1988).

Reproductive Biology

Depending on whether or not the stigmas or stamens are visible the aspect of the inflorescence of *Anomochloa marantoidea* is quite different. The following preliminary

description of anthesis is based on observations of two small flowering plants followed daily in Bahia, Brazil, for several weeks in February and March 1986. The entire flowering episode took approximately two weeks in these plants, which bloomed out of season and exhibited small inflorescences with only one functional spikelet in each partial inflorescence.

The stigmas appear before the stamens, and in both plants the terminal spikelet (the only spikelet not borne in a partial inflorescence) was the first to exert its stigma through the corniculum of its upper spikelet bract. A day or two later the stigmas of the spikelet of the lowest partial inflorescence (PI₁ in Figure 15) were exerted. A few days later those of the spikelets of the subapical partial inflorescences appeared in acropetal sequence (PI₂-PI₆). Several days after the last stigmas had been exerted, that is, about a week after the appearance of the first stigma, the stamens began to be extruded from between the margins of the upper part of the body of the upper spikelet bracts. The terminal spikelet extruded its stamens first. On the next day, the spikelet of the lowermost partial inflorescence extruded its stamens, and male flowering then proceeded upward, with the spikelet of the subapical partial inflorescence the last to extrude its stamens.

Based on our field observations *Anomochloa* is protogynous, as noted by Brongniart (1851), whose figure of an inflorescence "au commencement de la floraison" shows all of its stigmas exerted but no stamens visible. This type of flowering pattern is frequent in the herbaceous bamboos. Several species of *Pharus* (Judziewicz, pers. obs.) and *Leptaspis* (collectors' notes), *Streptochaeta sodiroana* (Judziewicz, pers. obs.) and *S. spicata* (Soderstrom, pers. obs.) all exhibit this pattern. This pattern was also observed by Soderstrom in the woody bamboo, *Dendrocalamus membranaceus* (Soderstrom 2660, US) in plants cultivated in India.

What is the dispersal mechanism for the caryopsis of *Anomochloa marantoidea*? Unlike the Phareae, Streptochaeteae, and Streptogyneae, the spikelets and inflorescences of *Anomochloa* show no adaptations for external animal dispersal (Ridley, 1930:598ff; Van Der Pijl, 1982:78ff), a dispersal strategy that may have enabled these tribes to survive as widespread taxa to the present day (Soderstrom and Calderón, 1974; Soderstrom, 1981a). The diaspore of *Anomochloa* consists of the thickened, cylindrical internode between the lower and upper spikelet bracts, above which is attached the persistent, indurate upper spikelet bract, this enclosing the large caryopsis (Figure 4j). Davidse (1987) has shown that the superficially similar internodes between the glumes and floret of the olyroid *Cryptochloa* (all species) and *Olyra* (some species) are elaiosomes that at maturity contain oils that attract foraging ants. Davidse notes that although similar-appearing thickened internodes in the olyroids *Arberella* and *Lithachne* produce no oils, *Anomochloa* should be investigated for this feature. Unfortunately, all of the mature spikelets available for this study were preserved in FAA, which destroys oils. Our sections of the central part of the internode showed either poor cell preservation or lack of cellular structure.

Streptochoeta* Schrader ex Nees von EsenbeckStreptochoeta* Schrader ex Nees von Esenbeck, 1829:536.

HISTORY

Streptochoeta is widely distributed in Neotropical forests and thus material has long been available for its study. The papers of Nees von Esenbeck (1829, 1835, 1836), Doell (1877), Čelakovský (1889), Hackel (1890), Arber (1929), Page (1951), Dobrotvorskaya (1962), and Soderstrom (1981a) all represent contributions to the understanding of the inflorescence of this grass, long thought to be the most primitive genus in the family. The embryo of *Streptochoeta* has also been the subject of studies by Yakovlev (1950) and Reeder (1953); starch grains by Yakovlev (1950) and Tateoka (1962); and leaf anatomy by Page (1947), Metcalfe (1960), and Renvoize (1985). Because the genus shares certain features of the microhair, leaf midrib, starch grain, and embryo structure with *Anomochloa* we are presenting here a formal study of its leaf anatomy and taxonomy.

TAXONOMY

DIAGNOSIS.—Perennial forest grasses. *Culms* hollow, erect, branched or not above; lowermost leaves consisting of bladeless sheaths; prophylls many-nerved, not bicarinate. *Leaves* lacking both inner and outer ligules, but with lateral appendages and oral setae present at the summit of the sheath; pseudopetiole short, terminating in a stout, appressed-hispid, dark-colored pulvinus at the base of the expanded portion of the blade; lamina usually broad, the midrib raised on both surfaces (more prominently so above), the secondary lateral veins and transverse veinlets prominent below (abaxially) only, both surfaces glabrous or rarely the abaxial surface hirtellous; venation pattern slightly oblique, at least one primary lateral

vein joining the midrib a few centimeters above the base of the lamina; uppermost leaf (or two) below the inflorescence a bladeless sheath(s) surrounding the developing inflorescence. *Inflorescence* a terminal spike or contracted raceme of spirally arranged, appressed pseudospikelets, these borne on short cupulate pedicels; peduncle absent to well developed; occasionally a second inflorescence produced from a bud in the axil of the uppermost leaf. *Pseudospikelets* lacking glumes, lemmas, paleas, and lodicules, terete, falling entire, composed of 11 or 12 spirally arranged bracts on 4 different axes; first 5 bracts short, membranous, greenish stramineous, irregularly truncate, lobed, or dentate at the summit, strongly several-nerved, bracts I–III facing the rachis of the inflorescence and smaller than bracts IV and V; bract VI separated from bracts I–V by a curved, glabrous internode; bract VI large, indurate, slightly saccate-based (gymnostegial flap), obscurely many-nerved, bearing a long terminal awn, this straight in the lower portion, strongly coiled in the upper part and at maturity becoming entangled with the awns of other pseudospikelets, all pseudospikelets in the inflorescence frequently shed as a unit; bracts VII and VIII similar, appearing to be placed opposite bract VI, sometimes fused at the base, triangular-lanceolate, indurate, their summits spreading away from each other; bract IX usually present only as a minute flange of tissue above and opposite the attachment of bracts VII and VIII; bracts X–XII subequal, coriaceous, lanceolate, unawned, strongly nerved, forming a trimerous whorl around the floret, but with overlapping margins. *Andrecium*: Stamens 6, exerted from the pseudospikelet but not pendent, the filaments attached to the anthers a short distance above their bases, the filaments free to fused into a stamen tube; ovary glabrous. *Gynecium*: Stigmas 3, hispid; fruit a linear-lanceolate caryopsis, the hilum linear (or broadening in center of caryopsis), extending only about $\frac{2}{3}$ of the length of the grain; embryo small, basal, lacking an epiblast.

Key to the Species of *Streptochoeta*

1. Pseudospikelets (42)70–100 per inflorescence; leaf blades large, 17–30 cm long, 5–9.5 cm wide [moist to more commonly wet forests, Mexico to Panama; Venezuela (rare); Pacific Ecuador; Amazonian Peru (rare)] 1. *S. sodiroana*
1. Pseudospikelets 5–19 per inflorescence; leaf blades various, in the common species usually less than 17 cm long and 5 cm wide.
 2. Leaf blades 5–18 mm wide, hirtellous below; pseudospikelet bracts X–XII 12–14.5 mm long [rare endemic of Espírito Santo, Brazil] . 3. *S. angustifolia*
 2. Leaf blades 30–73 mm wide, glabrous or rarely hirtellous below; pseudospikelet bracts X–XII 16–23(30) mm long 2. *S. spicata*
 3. Pseudospikelets 5–11 per inflorescence; leaf blades 11–16(20) cm long, 3–5(6) cm wide; widespread; Mexico and Trinidad to Paraguay and Rio Grande do Sul, Brazil 2a. *S. spicata* subsp. *spicata*
 3. Pseudospikelets 13–19 per inflorescence; leaf blades 19–29 cm long, 4.8–7.3 cm wide; endemic to Pacific Ecuador 2b. *S. spicata* subsp. *ecuatoriana*, new subspecies

1. *Streptochaeta sodiroana* Hackel

FIGURES 16, 17

Streptochaeta sodiroana Hackel, 1890:111. [Type: Ecuador. Pichincha: "San Miguel, in silv. trop. flumen Peripa," anno 1883, *L. Sodiro 9/1 [or 9/1?]* (Holotype, W; isotypes, W (2 sheets), fragment at US.)

DESCRIPTION.—Plants caespitose in clumps of a few culms, mature culms sometimes becoming decumbent and rooting at the lower nodes. Culms 50–100 cm tall, unbranched above the base, frequently stout, 3–9 mm in diameter, glabrous, with a small central lumen; lower nodes exposed, short-hispid. Leaves: Leaf sheaths glabrous below, the margins fringed near summit with papillose cilia; sheath auricles absent or uncommonly present and up to 5 mm long; lateral appendages inconspicuous, rarely to 3 mm long, if present fringed with oral setae 1–2.5 mm long; pseudopetiole 4–10(13) mm long, terminating in a stout pulvinus; pulvinus dark, turgid, covered with fine appressed hairs; expanded portion of blade oval to less commonly lanceolate, 17–30 cm long, 5–9.5 cm wide, glabrous or with the margins fringed with a few cilia at the base; secondary lateral veins and transverse veinlets conspicuous below, 1° nerves 6–8 on each side of the midrib, 3° lateral veins spaced 0.6–0.9 mm apart; well-developed blades 3–6 per culm. Inflorescence 17–27 cm long, 0.9–1.3 cm wide, erect at first but becoming pendent with age, its base included in the uppermost bladeless sheath or exerted on a peduncle up to 20 cm long; rachis finely papillose to appressed-pubescent, with a conspicuous tuft of cilia up to 4 mm long on the pedicel of each pseudospikelet. Pseudospikelets (42)70–100, crowded; bracts I–V 2–4.5 mm long; body of bract VI 12–18 mm long, 9–13-nerved, the terminal awn 4–9 cm long, scabrous; bracts VII–VIII 8–12 mm long; bracts X–XII 10–17 mm long; anthers yellow, ~5 mm long, the filaments apparently not fused; caryopsis 9–12 mm long, 1.5–2 mm wide, the hilum a narrow groove in the lower third of the grain, terminating in a broad, shallow depression in the central third; embryo 1–1.2 mm long.

DISTRIBUTION.—Occurring from sea level to 250 meters (occasionally to 830 meters) in the shaded understory of moist to more commonly wet lowland rainforests of Central America (Caribbean slope from Chiapas, Mexico, and southern Belize south to the canal area of Panama; Pacific slope from near Quepos, Costa Rica, south to Darién, Panama), Venezuela (Caribbean slope south of Lake Maracaibo), Pacific slope of Ecuador (common); Amazonian Peru (rare); not known from Colombia (Figure 18). At La Selva, Costa Rica, it is most often found at the base of slopes near small streams.

ADDITIONAL SPECIMENS SEEN.—BELIZE. Toledo, *Peck 652* (K, NY); Temash River, *Schipp S-961* (US).

COSTA RICA. ALAJUELA: 1 mi (1.6 km) S of Río Penas Blancas bridge of CR-142, *Hammel et al. 14052* (MO); 4 km W of Muelle San Carlos, 10°28' N, 84°30' W, *Liesner 14111* (MO); 2 km N of Santa Rosa, 10°38' N, 84°31' W, *Liesner et al. 15017* (MO, WIS); 1 km W of Jabillos, 10°23' N, 84°33' W, *Liesner et al. 15162* (MO, WIS); Llanura de San Carlos, near

Los Angeles, *Molina et al. 17684* (BM, F, MO, NY); between Upala and San Antonio de Upala, *Pohl and Gabel 13563* (F, MO); El Fósforo, 3 km N of Upala, *Pohl and Gabel 13707* (F); 12.6 km N of Bijagua by road, *Pohl and Pinette 13231* (F, MO, NY). GUANACASTE: Frontera Norte, anno 1910, *Brenes s.n.* (F). HEREDIA: Finca La Selva, 3 km S of Puerto Viejo, *Hammel 8056* (DUKE), *8429* (DUKE). LIMÓN: Río Catarata (Río Sand Box), Bribri, 9°37' N, 82°49' W, *Burger et al. 10305* (F, MO); Finca Theobroma, Río Hondo, near Río Cimarrones Viejo, *Calderón 2108* (US); Bandeco Farm #3, 3 km E of El Carmen, *Lent 2435* (F, MO); base of Cerro Tortugero, *Pohl and Lucas 13046* (F); Laguna Alova [sic, for Jalaba], 55 km NW of Moín, *Pohl and Lucas 13048* (F); La Columbiana farm, *Standley 36809* (US); Collines de Sikurbeta, Talamanca, *Tonduz 9201* (BR, US). PUNTARENAS: hills above Palmar Norte, trail to Buenos Aires, *Allen 5913* (BM, F, US), *Croat 35131* (MO), *Schubert 1161* (US); 1 km SE of Río Claro along NE side of Carretera Interamericana, 8°39' N, 83°04' W, *Burger and Matta 4818* (F, NY); 5 km W of Rincón de Osa, *Burger and Liesner 7214* (F, MO, NY); Finca El Edén, km 183, Route 2, near Santa Marta, *Gómez 22950* (MO); Rincón airstrip, *Kennedy 1929* (MO); 2 miles (3.2 km) W of Golfito, *Lathrop 5581* (S, US); Osa forest camp, *Lathrop 5585* (US); Rincón de Osa, *Liesner 1783* (MO), *Pohl and Davidse 10749* (F); Sirena, 8°29' N, 83°36' W, *Liesner 2941* (MO); 2 km S of Hatillo, 9 Oct 1968, *Pohl and Davidse* (F); 5 km W of Palmar Norte on road to Puerto Cortez, *Pohl and Davidse 11584* (F, K); 3 km NE of Quepos, *Pohl and Davidse 11691* (F); valley of Río Terraba, S of crossing of Río Ceibo and Carretera Interamericana, *Pohl and Davidse 11773* (F); between Golfo Dulce and Río Terraba, *Skutch 5291* (F, US); ~10 km S of Palmar Sur on the Carretera Interamericana, Finca 18, *Soderstrom and Calderón 1205* (US, WIS); Playa Blanca, Golfo Dulce, *Valerio 425* (BR, F).

ECUADOR. Without locality, *Lehmann 4400* (US fragment ex K). ESMERALDAS: km 170–175, via Santo Domingo–Quinindé, *Acosta-Solis 13644* (F); Rosa Zarate, Quinindé, *Asplund 16302* (B, G, NY, S); E of Río Blanco and S of Quinindé, *Fagerlind and Wibom 2553* (S); via Esmeraldas–Tanaty–Cuchilla de Timbre, *Jaramillo 57* (AAU, QCA); Río Cayapas, *Kvist s.n.* (AAU); Coronel C. Concha, ~30 km S of Esmeraldas, *Maas et al. 2925* (K, MO). LOS RÍOS: Río Palenque Biological Station, km 56 highway Quevedo–Santo Domingo, *Croat 38964* (MO), *Dodson 5021* (US), *Gentry 9866* (MO), *Lojman and Molau s.n.*, Fl. Ecuador 15752 (AAU); Hacienda Ana María, Cantón Vices, *Mexia 6648* (BM, US); Hacienda Monica, 12 km E of San Carlos, *Sparre 19388* (S). PICHINCHA: 20 km W of Santo Domingo de los Colorados, *Cazalet and Pennington 5109* (NY, US); 37 km S of Santo Domingo de los Colorados, *Pennington 49 S.D.* (K, NY); Rancho Brahman, ~10 km NW of Santo Domingo de los Colorados on road to Esmeraldas, *Sparre 15208* (S).

GUATEMALA. IZABAL: Los Amates, *Deam 97* (F, MO, NY, W). PETÉN: between Finca Yalpamech along Río San Diego and San Diego on Río Cancún, *Steyermark 45355* (F); between



FIGURE 16.—*Streptochaeta sodiroana*: a, habit, showing pseudospikelets disarticulating from rachis ($\times 0.29$); b, junction of leaf sheath with blade, showing prominent pulvinus ($\times 1.42$); c, portion of rachis ($\times 2.29$); d, pseudospikelet ($\times 2.29$). (a, c, d based on *Schubert 1161*, Costa Rica (US), b based on *Standley 54180*, Honduras (US). Illustration by Gesina B. Threlkeld.

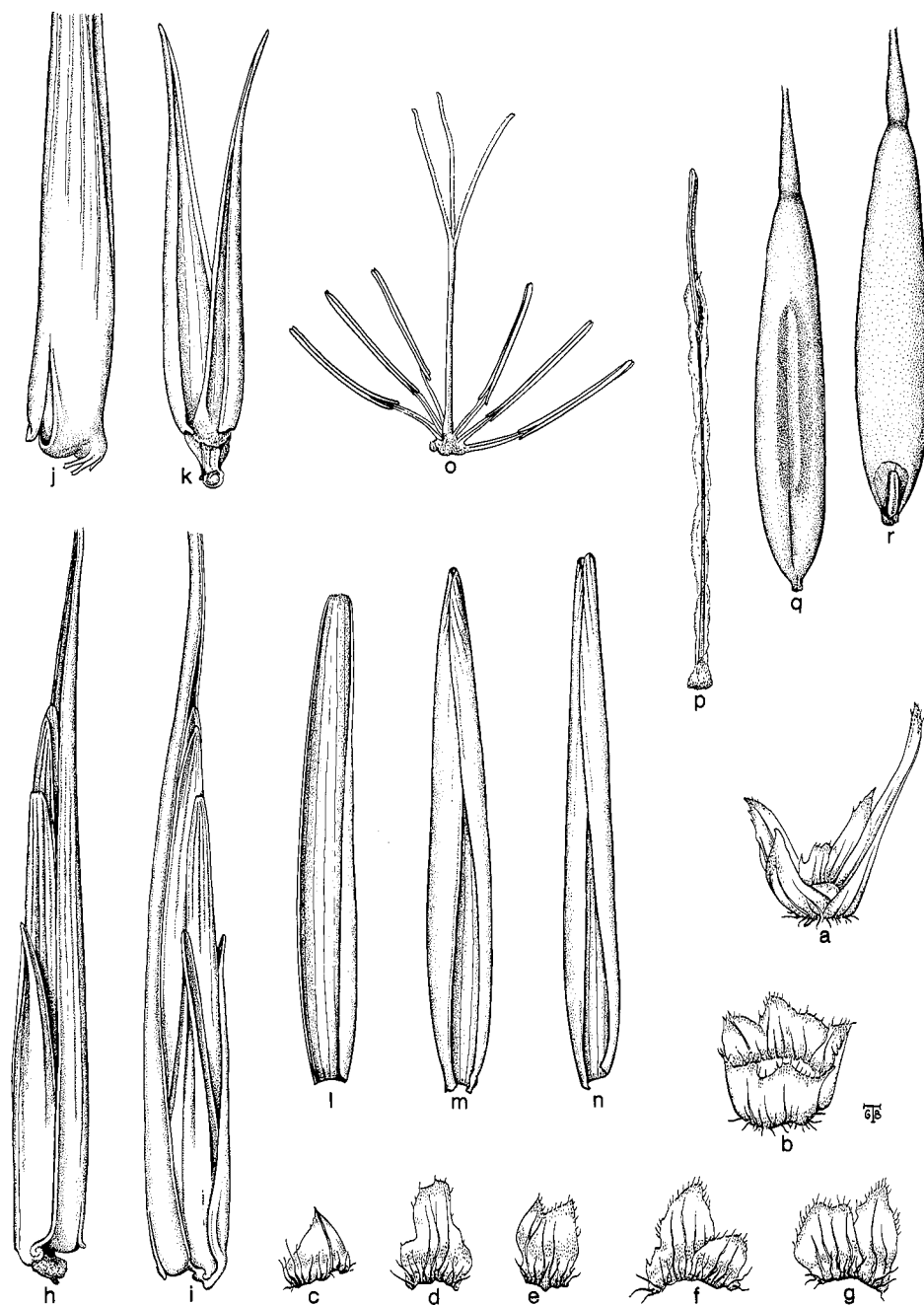


FIGURE 17.—*Streptochaeta sodiroana*, showing detail of the pseudospikelet: *a, b*, two views of the complex of bracts I–V from the base of the pseudospikelet ($\times 5.75$); *c–g*, bracts I–V ($\times 5.75$); *h, i*, two views of a pseudospikelet (bracts I–V removed) ($\times 2.88$); *j*, bract VI, showing gynostegium near base ($\times 2.88$); *k*, bracts VII–VIII; *l–n*, bracts X–XII, which envelop the flower ($\times 2.88$); *o*, flower in early stage of anthesis, showing six stamens and gynecium with three stigmas ($\times 2.88$); *p*, pistil surrounded by delicate staminal tube, late stage of anthesis ($\times 2.88$); *q*, caryopsis, ventral face showing hilum terminating in a broad, central depression ($\times 2.40$); *r*, caryopsis, dorsal face showing persistent beak and small, basal embryo ($\times 2.40$). (*a, b, h–j, l–n, q, r* based on *Schubert 1161*, Costa Rica (US); *c–g, k, o, p* based on *Standley 54180*, Honduras (US).) Illustration by Gesina B. Threlkeld.

Finca Yalpamech and Chinaja, *Steyermark 45425* (F, K).

HONDURAS. ATLANTIDA: Lancetilla Botanical Garden, S of Tela; rainforest on way to Tela water supply dam, *Pohl and Gabel 13813* (F, ISC), *Standley 52876* (F, US), *53139* (F, US), *54180* (F, US), *55416* (F, US); Puerto Sierra, Lippmann's plantation, Río Esperanza, *Wilson 548* (NY).

NICARAGUA. ZELAYA: region of Braggman's Bluff, *Englesing 184-B* (F); Cerro Waylawás, 13°38-39'N, 84°48-49'W, *Pipoly 4193* (MO); montañas de Esquipulas y Alemán, drenaje Río Alemán, *Shank and Molina 4829* (F); drenajes de los Ríos Punta Gorda, Alemán, y Zapote, *Shank and Molina 4974* (F); trail Cerro Saslaya to San José del Hormiguero, between Caño

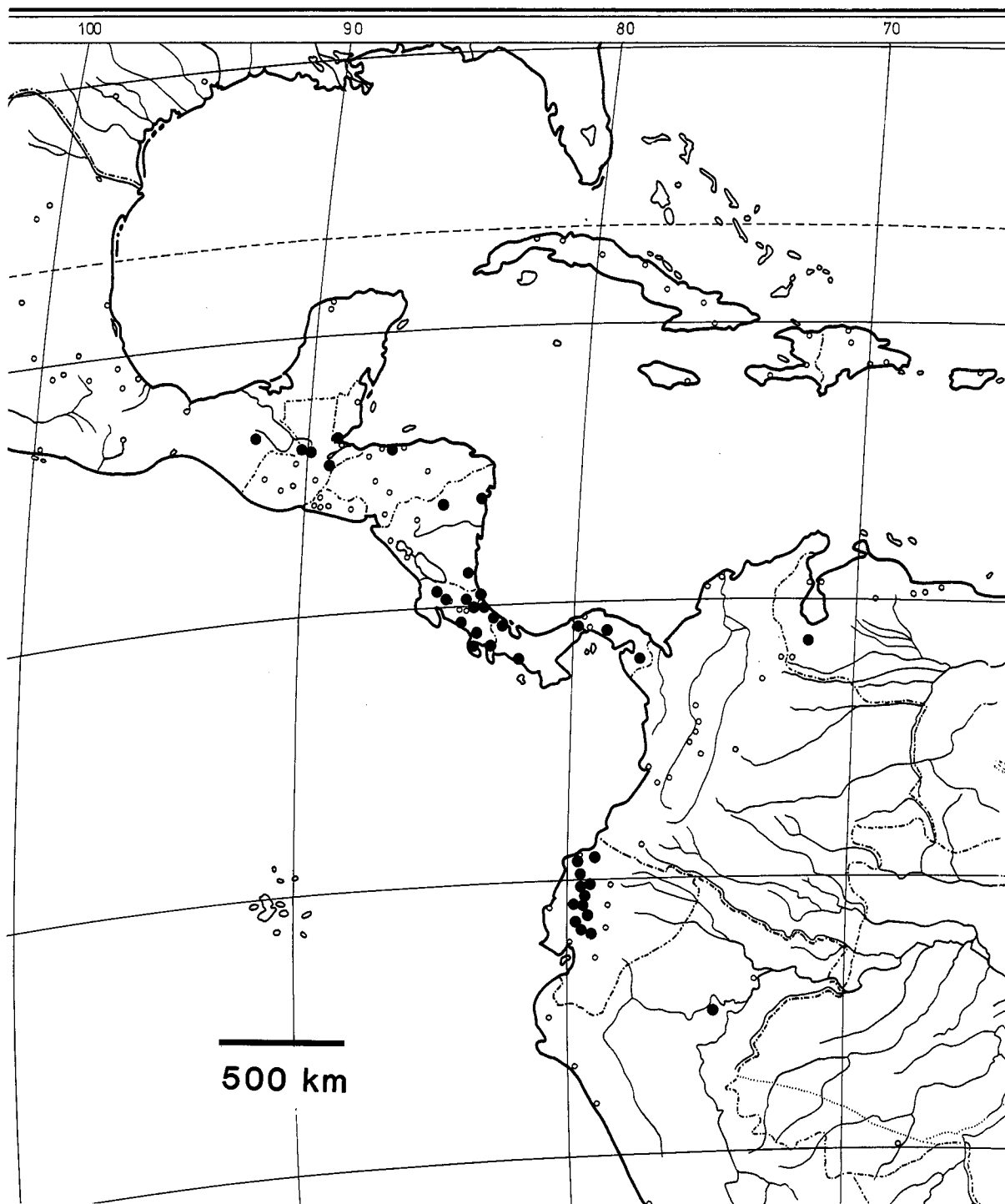


FIGURE 18.—Distribution of *Streptochaeta sodiroana*.

Majagua and Caño Sucio, approximately 13°45'N, 85°00'W, *Stevens 6852* (ISC); along Río Waspuk, ~1 km upstream from confluence of Río Pis Pis, 14°15'N, 84°36'W, *Stevens 13084* (MO); ~1.5 km NE of La Esperanza de Las Quebradas, 13°38'N, 85°02'W, *Stevens 19341* (MO).

PANAMA. BOCAS DEL TORO: Filo Almirante, trail to Riscó Abajo, 3 km SW of Almirante, *Nee and Hansen 14104* (F, MO, WIS). CANAL AREA: Barro Colorado Island, *Áviles 23-B* (MO), *Busey and Croat 246* (MO), *Calderón 2096* (US), *Croat 5313* (F, MO), *6325* (MO), *7092* (F, MO), *7380-A* (MO), *8816* (F, MO), *12930* (MO), *13226* (MO), *Foster 1764* (F), *Judziewicz 4435* (MO, WIS), *Kenoyer 103* (US), *Maxon et al. 6824* (NY, US), *Shattuck 755* (F, MO), *Standley 31374* (US), *41084* (US); Juan Mina, Salvador Hill, *Bartlett and Lasser 16790* (MO); Pipeline Road, 9°15'N, 79°45'W, *Hamilton et al. 3242* (MO); headwaters of Río Chinilla, above Nuevo León, *Maxon 6896* (US). CHIRIQUÍ: road from Puerto Armuelles to San Bartolo Limite, 7 km W of Puerto Armuelles, *Croat 35066* (MO); Rabo de Puerco, 8 km W of Puerto Armuelles, *Liesner 26* (MO); Cerro de la Plata, near San Felix, *Pittier 5164* (US). COCLÉ: Cerro Moreno between Molejón and Coclecito, 8°46'44"N, 80°31'54"W, *Davidse and Hamilton 23707* (MO); road from La Pintada to Coclecito, 8°45'N, 80°30'W, *Hamilton and Davidse 2871* (MO). COLÓN: Río Escandaloso, near abandoned manganese mine, *Hammel 2666* (MO). DARIÉN: Río Aruza, *Bristan 1364* (US?), upper Río Tuquesa, *le Clezio 45* (MO); Río San José, *Duke and Bristan 415* (MO); Cerro Sapó, *Hammel 1217* (MO); 2–3 mi (3–4.8 km) SE of Pijibasal on Río Paraseneco, ~9–10 mi (14.5–16 km) S of El Real, *Hartman 12056* (MO); Río Pirre, trail up river from house of Bartolo, *Kennedy 2900* (MO, US). PANAMÁ: 3 km from Cañitas towards Bayano Dam, *Calderón and Dressler 2153* (US); Serranía de Majé, trail between headwaters Río Ipetú Grande and Charco Rico, 8°53'N, 78°32'W, *Churchill and de Nevers 4408* (MO); 4–5 hours walk upriver from Torti Arriba, *Folsom et al. 6836* (MO); 9 km N of Margarita on road to Madroño, *Hammel 6036* (MO); Serranías de Majé, ridges S of Chocó village of Ipetú, 8°47'N, 78°27'W, *Knapp and Sysma 2366* (MO); Chimán, *Lewis et al. 3252* (MO).

PERU. LORETO: Prov. Nauta, Río Samiria, puesto vigilancia Santa Elena, 115 m, *Encarnacion 25321* (USM, not seen; fragment and photocopy, WIS).

VENEZUELA. MÉRIDA: El Vigía–Panamericana–Caño Amarillo, 100–200 m, selva pluvial, abundante en cierta zona del bosque, *Bernardi 1891* (NY, US).

VOUCHER SPECIMENS FOR ANATOMICAL STUDIES.—Costa Rica: *Calderón 2108* (US) (starch grains, embryos), *Liesner, Judziewicz, and García 15162* (MO) (starch grains, embryos), *Soderstrom and Calderón 1205* (US) (leaves, starch grains, embryos). Ecuador: *Mexia 6648* (US) (starch grains, embryos). Panama: *Calderón 2096* (US) (starch grains, embryos).

DISCUSSION.—*Streptochoaeta sodiroana* flowers principally during the dry season, from December through March. Lars P. Kvist (AAU, pers. comm.) indicates that both the Cayapas

and Colorado tribes of Pacific Ecuador use the immature inflorescences to remove facial hair, a process he has witnessed several times.

2a. *Streptochoaeta spicata* subsp. *spicata* Schrader ex Nees von Esenbeck

FIGURES 19, 20

Streptochoaeta spicata Schrader ex Nees von Esenbeck, 1829:537. [Type: Brazil. Bahia: "Im urwald an der Estrada de Minas [illegible] Capitain Filisberto" [Fazenda of Felisberto Caldeira Brant, Marques de Barbacena, near Ilhéus], anno 1816, *Prince Maximilian A.F. de Neuwied s.n.* [or 120?]] (Holotype, B, fragment US; isotype, BR).]

Lepideilema lancifolium Trinius, 1830:93. [Type: Brazil, no collector or exact locality given.]

DESCRIPTION.—Plants cespitose in clumps of a few culms, sometimes becoming decumbent and rooting at the nodes. Culms 35–105 cm tall, 2–4 mm in diameter, unbranched above the base or rather frequently rebranched 1–3 times in scorpioid fashion, successive branches borne on one side of the plant, each branch bearing a terminal inflorescence; lower nodes exposed, glabrous to finely appressed-hispid. Leaves when fully developed (3)5–7(10) per culm, the leaf sheaths 4–6(7) cm long, glabrous except sometimes puberulent on the back and ciliate on the margins near the summit; sheath auricles absent to frequently prominent, up to 9 mm long; lateral appendages usually inconspicuous, up to 2 mm long, fringed with oral setae 1–2.5 mm long; pseudopetiole 2–7 mm long, the terminal pulvinus dark, turgid, pubescent; expanded portion of blades elliptic-lanceolate, less commonly oval or narrowly lanceolate, 11–16(20) cm long, 3–5(6) cm wide, shiny, dark green, and glabrous above, glabrous or (rarely) hirtellous below, especially near the apex, the margins smooth to scabrous, the 1° lateral veins 4–6 on each side of the midrib, the 3° lateral veins spaced 0.45–0.65 mm apart, the transverse veinlets inconspicuous on both surfaces. Inflorescence 9–16 cm long, included in uppermost bladeless sheath or exerted on a peduncle up to 16 cm long; rachis pubescent with rusty-colored, curling cilia, especially on the pseudospikelet pedicels near the summit. Pseudospikelets 5–11, separated by internodes 10–23 mm long, borne on pedicels 0.9–1.3 mm long; bracts I–V up to 3–6 mm long; body of bract VI 17–28 mm long, 7–13-nerved, the terminal awn 3–9 cm long, glabrous to slightly scabrous; bracts VII–VIII 11–15 mm long; bracts X–XII 14–23(30) mm long; stamens in 2 groups of 3 each, the filaments of each group apparently fused for a short distance at the base; caryopsis 12–16 mm long, 1.5–2 mm wide, lanceolate, tapering to apex, the ovary persistent at the summit as a small, glabrous beak, the hilum a narrow groove extending through the lower two-thirds of the grain; embryo 1–1.2 mm long.

DISTRIBUTION.—Moist or wet forests below 500 meters (occasionally to 1000 meters), often in old treefall gaps or on steep rocky slopes, from Veracruz, Mexico, and Trinidad to



FIGURE 19.—*Streptochaeta spicata* subsp. *spicata*: *a*, habit, showing disarticulated pseudospikelets pendent by awns from the apex of the rachis (note lateral branch of culm terminating in a second inflorescence) ($\times 0.26$); *b*, base of plant showing stout sympodial rhizomes ($\times 0.52$); *c*, summit of leaf sheath and base of blade showing prominent sheath auricle tipped oral setae ($\times 1.57$); *d*, view of opposite side of summit of leaf sheath and base of blade showing smaller sheath auricle and turgid pulvinus ($\times 1.57$). (*a* based on *Bailey and Bailey 723*, Brazil (US); *b, d* based on *Chase 11011*, Brazil (US); *c* based on *Garnier 4459*, Nicaragua (US).) Illustration by Gesina B. Threlkeld.

the Pacific slope of Ecuador (rare), Amazonian Peru (rare), Paraguay, and Rio Grande do Sul, Brazil; scattered throughout its range; most common in Atlantic and southern Brazil (Figure 21).

BOLIVIA. SANTA CRUZ: Estancia La Dolorida, 500 m, 16°15'S, 62°15'W, Killeen 1968 (ISC).

ADDITIONAL SPECIMENS SEEN.—BRAZIL. Without locality, Riedel *s.n.* (G, P). BAHIA: km 5, rodovía Lages-Ubaitaba,

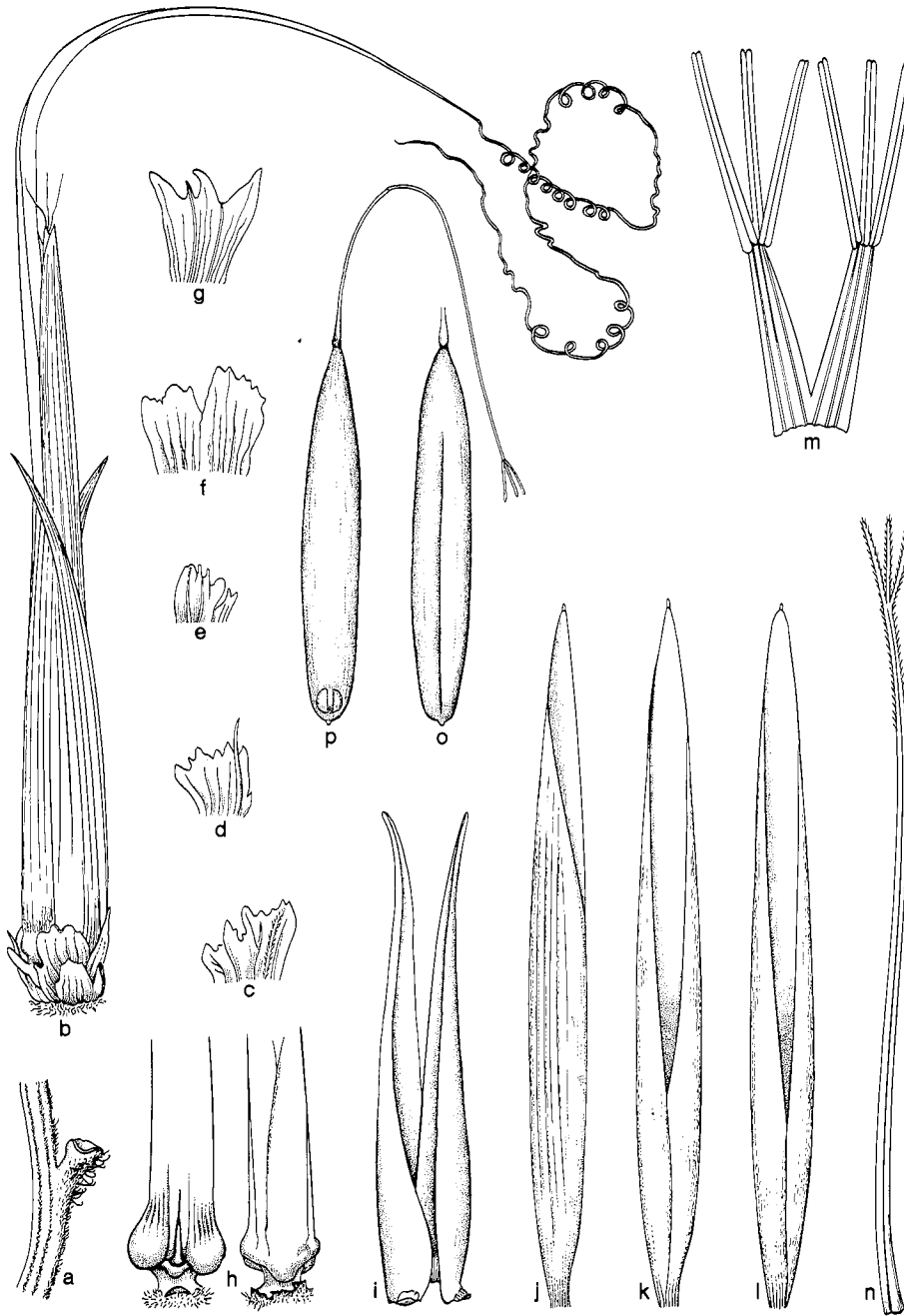


FIGURE 20.—*Streptochaeta spicata* subsp. *spicata*, showing details of pseudospikelet: *a*, portion of rachis showing pseudospikelet pedicel covered with hooked hairs ($\times 2.35$); *b*, pseudospikelet, showing long awn on bract VI ($\times 2.35$); *c-g*, series of bracts I-V at the base of a pseudospikelet, showing their variable venation and shape ($\times 2.35$); *h*, views of base of bract VI, showing the gymnostegial area and the internode between bract V and bract VI ($\times 2.35$); *i*, bracts VII and VIII ($\times 2.35$); *j-l*, bracts X-XII ($\times 2.35$); *m*, andrecium showing short, elongating stamen tube ($\times 2.35$); *n*, gynecium ($\times 2.35$); *o*, caryopsis, ventral view, showing linear hilum ($\times 2.35$); *p*, caryopsis, dorsal view showing persistent style and small, basal, embryo ($\times 2.35$). (All based on *Bailey and Bailey 723*, Brazil (US).) Illustration by Gesina B. Threlkeld.

approximately 14°18'33"S, 39°19'30"W, *Calderón 2041* (US); km 5 camino hacia Santa Cruz Cabralia, approximately 16°15'06"S, 39°00'18"W, *Calderón 2046* (US); Ferradas, Fazenda Aberta Grande, 14 km SW of Itabuna, approximately 14°51'S, 39°20'W, *Calderón and Pinheiro 2162* (US); Reserva Biologica Pau Brasil, 16 km W of Pôrto Seguro, approximately 16°23'S, 39°11'W, *Calderón and Pinheiro 2193* (US); 6 km E of Ubaira City, Rio Jequiriçá, approximately 13°16'S, 39°37'W, *Calderón and Pinheiro 2246* (US); rodovia BA-265, trecho Caatiba–Barra do Choçá, 6 km W de Caatiba, *Mori and dos Santos 11577* (MO, NY, US); CEPEC, Municipio Ilhéus, *dos Santos 3419* (RB); Fazenda Uruguayana, 8 km S of Santa

Cruz de Vitória, *Soderstrom et al. 2118* (US); Reserva Gregorio Bondar, experimental station of CEPEC, Municipio Belmonte, *Soderstrom et al. 2139* (US). CEARÁ: Serra de Baturité, *Ule 8991* (G, K). ESPÍRITO SANTO: Canto Grande, Reserva Florestal de Linhares, 19°24'S, 40°04'W, *Soderstrom and Sucre 1881* (US), 1896 (US), *Zuloaga et al. 2437* (US); Flecheira, Municipio Aflilio Vivacqua, *Soderstrom and Sucre 1911* (US); road from Cachoeiro de Itapemirín to Itabira, 20°51' S, 41°05'W, *Soderstrom and Sucre 1963* (RB, US). MATO GROSSO DO SUL: vicinity of Dourados, *Chase 11011* (F, MO, RB, US), *Swallen 9403* (US). PARÁ: range of hills ~20 km W of Rendenção, near Córrego São João and Troncamento



FIGURE 21.—Distribution of *Streptochaeta spicata* subsp. *spicata* (dots) and *S. s.* subsp. *ecuatoriana* (asterisks). Inset shows distribution of *Streptochaeta angustifolia* (triangle) and *Anomochloa marantoidea* (circled star).

Santa Teresa, approximately 8°03'S, 50°10'W, *Plowman et al.* 8646 (MO, NY, US). PARANÁ: Rio Ivai, Municipio Terra Bôa, *Hatschbach* 15727 (F, MO); 7 km E of Londrina, *Swallen* 8743 (US); Rio Vermelho, 18 km NE de Bela Vista, *Tessmann* 3830 (US). RIO DE JANEIRO: Mun. Macãe, Lagoa Comprida, *Araujo* 4984 (K); Corcovado range, *Bailey and Bailey* 723 (US), *Glaziou* 13327 (BM, K, P, W), *Hoehne* 17226 (NY, US); Camino dos Macacos, Jardim Botânica to Alto Boa Vista, *Chase* 8430 (F, MO, NY, US, W); Rio Comprido, Rio de Janeiro, *Glaziou* 5438 (US fragment), 5439 (P, W), 5449 (S), 17925 (K, W); Palmeiras, *Hemmenhorff* 303 (S); Parque Estadual de Desengano, Fazenda Agulha do Imbé, 21°56'S, 41°52'W, *Plowman and de Lima* 12929 (F); Morro Novo Mundo, *Soderstrom and Calderón* 1861 (B, US); Reserva de Tinguá, Municipio Nova Iguaçu, *Soderstrom* 2632 (US). RIO GRANDE DO SUL: estrada BR-101, Colônia São Pedro, Municipio Torres, *Valls* 1095 (US); Três Cachoeiras, 6 km from ocean, 29°27'S, 49°56'W, *Soderstrom et al.* 1989 (US). RONDÔNIA: Igara-pé, Miolo, affl. do Gy-Paraná, *Kuhlmann* 1834 (US). RORAIMA: Colônia Fernando Costa, Rio Mucajá, *Black and Magalhães* 51-12891 (K, P, US). SANTA CATARINA: Blumenau, anno 1887, *Müller s.n.* (MO, RB), *Schwacke* 5749 (RB), *Ule* 980 (P); Municipio Içara, km 376 da BR-101, no trecho de Tubarão a Criciúma, *Valls et al.* 2736 (US). SÃO PAULO: 1 km W Rio São Mateus, Municipio Paraguaçu Paulista, 22°32'S, 50°48'W, *Clayton* 4581 (K); beira de mata de Planalto, Municipio Adamantina, *Taroda s.n.* (F).

COLOMBIA. META: Río Gúejar, ~10 km below junction with Río Zanza, N end of Cordillera Macarena, *Smith and Idrobo* 1530 (US).

COSTA RICA. GUANACASTE: Hacienda Guachipelín, Parque Nacional Volcán Rincón de la Vieja, *Pohl and Davidse* 11672 (K); 1 km W of headquarters, Santa Rosa National Park, *Pohl and Erickson* 12631 (ISC), *Janzen* 12213 (MO), *Judziewicz* 4279 (F, WIS).

ECUADOR. LOS RÍOS: Hacienda Clementina on Río Pita, *Asplund* 5562 (S, US).

GUATEMALA. IZABAL: El Estor, *Contreras* 11538-A (LL); Montaña del Mico, trail between Dartmouth and Morales, towards Lago Izabal, *Steyermark* 39029 (F, US); N slope of ridge N of Quirigua, *Weatherwax* 105 (US). PETÉN: Ceibal, *Molina* 15864 (F, NY).

HONDURAS. OLANCHO: Río Talgua, near the Escuela Granja Demonstrativa de Caticamas, *Molina* 8328 (US); along Hwy. 3, 12 km SW of Dulce Nombre de Culmí, *Pohl and Davidse* 12447 (ISC).

MEXICO. CHIAPAS: near junction of Río Perlas and Río Jatate at San Quintín, near Laguna Miramar, *Sohns* 1725 (US). OAXACA: Cerro de Nacimiento, E of Cosolapa, 17-20 km NE of Campo Experimental de Hule, *Santos* 2438 (US). VERACRUZ: Atoyac, *Düll* 125a (B); Cordova, *Finck s.n.*, Feb 1893 (K, NY); 7 km E of Sarabia, San Juan Guichicobi, *Vázquez* 1399 (BM, MO, WIS); Ejido de Manzanares, 1-4 km NW of Campo Experimental de Hule, *Santos* 2301 (US).

NICARAGUA. Without locality, *Garnier* 4459 (US). ZELAYA:

between Waspám and Ulwas, *Pohl and Davidse* 12296 (ISC); Miguel Bikan, ~52 km SE of Waspám, *Pohl and Davidse* 12311 (F, ISC); crossing of Río Lekus on road to Puerto Cabezas, *Pohl and Davidse* 12319 (F, ISC).

PANAMA. CANAL AREA: Barro Colorado Island, *Calderón* 2095 (US), *Calderón and Dressler* 2145 (US), *Croat* 4243 (F, MO, NY), 11832 (MO), *Foster* 2038 (F), 2316 (F), *Knight s.n.* (WIS), *Shattuck* 724 (F, MO); hills N of Frijoles, *Standley* 27489 (BM, MO, US). CHIRIQUÍ: Cerro de la Plata, near San Felix, *Pittier* 5164^{1/2} (US). DARIÉN: trail between Pinogana and Yavisa, *Allen* 245 (MO, US); Río Chico, 1 hour by boat from Yaviza at junction of Río Chucunaque (MO, US), *Duke and Bristan* 451 (MO); trail from Pucuro to Cerro Mali, Quebrada Pobre to La Laguna, *Gentry and Mori* 13549 (MO, NY); Río Chico, 10 km upstream from Narazeth, 8°20'N, 77°25'W, *Hahn* 113 (MO); 0.5-2.5 mi (0.8-4 km) NE of Manené, *Hartman* 12173 (MO); trail from Canglón-Yaviza road to Río Chucunaque, 7.7 mi (12 km) E of Canglón, 8°20'N, 77°50'W, *Knapp and Mallet* 3962 (MO); junction Río Canglón and Río Chucunaque, 15 km N of Yaviza, *Mori* 374 (WIS). PANAMÁ: ~2 mi (3 km) up Río La Maestra, *Kennedy* 1186 (US); Chimán, 3-4 mi (4.8-6.4 km) up Río Pasiga, *Kennedy* 1209 (MO, US), *Lewis et al.* 3237 (MO); edge of mangrove swamp S of Ft. Kobbe and Ft. Howard, E of Río Venado, 8°54'N, 79°35'W, *Knapp* 1893 (MO).

PARAGUAY. Plaine de Pirayu-bí, *Balansa* 179-A (G, also fragment US); Cordillera de Peribebuy, forêt de Naranjón, *Balansa* 4373 (BM, G, K, P), *Hassler* 1317 (G); Puerto Bertoni, *Bertoni* 5825 (W); Prov. Amambay, Parque Nacional Cerro Coro, *Soloman et al.* 6869 (MO).

PERU. AMAZONAS: Prov. Bagua, Quebrada Miraná (above km 277 of Marañón Road), valley of Río Marañón above Cascadas de Mayasí, *Wurdack* 1895 (F, NY, US).

TRINIDAD. Caparo forests, *Broadway* 4929 (US).

VENEZUELA. ANZOÁTEGUI: Cerro La Danta, bordering tributary of Río León, NE of Bergantín, *Steyermark* 61087 (F, US). APURE: Selva de Cutufí, 7°09-11'N, 71°56-58'W, *Davidse and González* 21723 (MO, NY, US). BARINAS: SW of Barinitas, *Bunting* 2265 (MO). ZULIA: cuenca del Embalse Burro Negro (Pueblo Viejo), sector between Quiros-El Pensado and the foot of Cerro Socopo, ~10 km E of Churugarita, *Bunting* 9448 (MO); Cerro Las Manantiales, E of Río Guasare, 12 km W of Corpozulia Campamento Carichuano, 11°01'N, 72°20'W, *Steyermark et al.* 123241 (MO, NY, US).

VOUCHER SPECIMENS FOR ANATOMICAL STUDIES.—Brazil: *Calderón* 2046 (US) (leaves), *Chase* 8430 (US) (starch grains, embryos), *Soderstrom and Calderón* 1861 (US) (spikelet), *Soderstrom and Sucre* 1896 (US) (starch grains, embryos). Panama: *Allen* 245 (MO) (embryos), *Calderón and Dressler* 2145 (US) (culm, leaves).

DISCUSSION.—Leaf blade number, size, and shape are variable in *Streptochaeta spicata*. While most populations have lanceolate blades, those from near Río de Janeiro, Brazil and near Lake Maracaibo in Venezuela have ovate blades,

which are, however, no longer than those of most populations of the species. Bahian populations of *S. spicata* also exhibit vegetative variability: some individuals have only 3 fully developed ovate blades per culm, while others possess up to 10 narrowly lanceolate blades, and some narrow-leaved populations (Mori and Santos 11577; Soderstrom et al. 2118) have abaxial surfaces bearing an indumentum of scattered pilose hairs with distinctive swollen bases, a feature that is otherwise well developed only in *S. angustifolia* (Figure 24c,d). However, these unusual specimens of *S. spicata* have overall blade surface areas that are much closer to that of characteristic specimens of *S. spicata* subsp. *spicata* (Figure 22) and their pseudospikelets are not as small as those of *S. angustifolia*.

In Central America *S. spicata* subsp. *spicata* exhibits a flowering peak during November and December, and possibly also July and August. Nearly all Atlantic Brazil collections have been made during the period from February through April.

2b. *Streptochoaeta spicata* subsp. *ecuatoriana*, new subspecies

TYPE SPECIMEN.—Ecuador, Los Ríos: Jauneche forest, Cantón Vinces, km 70 on road from Quevedo to Palenque, N of Mocachi on Estero Penafiel, 100 m, 23 Mar 1980, C.H. Dodson and A.H. Gentry 9832 (Holotype, MO).

DESCRIPTION.—Differt a *Streptochoaeta spicata* subspecies *spicata* laminae longiore (19–29 cm) latioreque (4.8–7.3 cm), inflorescentia longiore (18–30 cm), et spiculis 13–19.

Plants apparently cespitose. Culms 70–100 cm tall, apparently unbranched above the base, 3–5 mm in diameter, the lower nodes exposed. Leaves 4–6 per culm, the leaf sheaths glabrous except along margins near the summit; sheath auricles inconspicuous, to 1.5 mm long; lateral appendages inconspicuous, to 1 mm long; oral setae 1–2 mm long; pseudopetiole 2–10 mm long, the expanded portion of the blade 19–29 cm long, 4.8–7.3 cm wide, glabrous except occasionally for a few scattered hairs on the lower surface near the margins, the 3° lateral veins and transverse veinlets not particularly conspicuous on either surface. Inflorescence 18–30 cm long, ~0.8 cm wide, exerted on a peduncle 1–14 cm long; rachis pubescent. Pseudospikelets 13–19, not crowded; bracts I–V up to 4–7 mm long; body of bract VI 20–25 mm long, 12-nerved, the awn ~6 cm long; bracts VII–VIII 12–15 mm long; bracts X–XII 17–22 mm long; stamens not seen; immature caryopsis 8 mm long, linear-lanceolate.

DISTRIBUTION.—Endemic to moist, lowland forests on the Pacific slope of Ecuador (Figure 21).

PARATYPES.—ECUADOR. GUAYAS: between Las Americas and Palme, 28 Sep 1952, Fagerlind and Wibom 374 (MO, S); Río Daule below Pichincha, Hacienda Santa Barbarita, 18–26 Apr 1959, Harling 4798 (S). LOS RÍOS: Jauneche forest [topotypes], 15 Aug 1978, Dodson et al. 7067 (MO, US), 1 Apr 1980, Dodson and Gentry 10126 (MO), 20 Feb 1982, Dodson and Gentry 12706 (MO), 14 Jan 1981, Gentry et al.

30709 (MO). MANABI: El Recreo, 22 Aug 1893, Eggers 14863 (F, M, US).

VOUCHER SPECIMENS FOR ANATOMICAL STUDIES.—Ecuador: Dodson et al. 7067 (US) (leaves).

COMMENTS.—Four of the five populations of *S. spicata* known from Ecuador are robust plants with blades twice as large (as measured in surface area) and with twice as many pseudospikelets than is average for subspecies *spicata* (Figure 22). We have chosen to recognize these plants as the new subspecies *S. spicata* subsp. *ecuatoriana*. The single specimen of subspecies *ecuatoriana* examined anatomically had extremely long bicellular microhairs on the leaf blades.

The herbaceous bamboo flora of western Ecuador is impoverished by the apparent absence of common olyroid genera such as *Pariana*, *Arberella*, and *Piresia*, but non-olyroid tribes are well represented by *Pharus* (5 species, including a new endemic) and *Streptochoaeta*.

3. *Streptochoaeta angustifolia* Soderstrom

Streptochoaeta angustifolia Soderstrom, 1981a:30. [Type: Brazil. Espírito Santo: Município Cachoeiro de Itapemirim, 10 km from Cachoeiro toward Alegre, 20°47'S, 41°09'W, low forest dominated by Rutaceae with open understory, soil sandy clay, about 35 plants seen growing in several rhizomatous clumps, in fruit, 26 Apr 1972, T.R. Soderstrom and D. Sucre 1969 (Holotype, RB; isotypes, CEPEC, F, INPA, K, LE, MO, NY, P, US).]

DESCRIPTION.—Plants cespitose from a knotty, short-rhizomatous base, but also spreading by decumbent and rooting culms to form large clones. Culms 40–70 cm tall, hollow, glabrous except pubescent in a line below the nodes; nodes finely appressed-pubescent; unbranched or sparingly branched above, 2–2.5 mm in diameter. Leaves 4–8, evenly distributed on culms or in some sterile shoots the internodes shortened near the summit, forming a crowded fascicle of leaves with strongly overlapping sheaths; leaf sheaths glabrous except for ciliate margins in upper portion; sheath auricles, lateral appendages, and oral setae inconspicuous; pseudopetiole poorly differentiated from expanded portion of blade; blades narrowly lanceolate, 12–15 cm long, 1.3–1.7(2) cm wide, scaberulous on the upper surface, hirtellous or less commonly glabrous on the lower, the margins smooth at the base, scabrous near the apex; primary nerves 3 or 4 on each side of midrib; 3° lateral veins spaced about 0.4 mm apart; transverse veinlets inconspicuous on both surfaces. Inflorescence 8–11 cm long, borne on a subglabrous peduncle 10–13 cm long, the rachis flocculose. Pseudospikelets 6–9, not crowded, borne on ciliate-uncinate pedicels about 0.7 mm long; bracts I–V up to 3 mm long; bract VI 10–14 mm long, 12-nerved, with an awn 3–5 cm long, scabrous; bracts VII–VIII 8.5–10.5 mm long, 8- or 9-nerved; bracts X–XII 12–14.5 mm long, 12–15-nerved; filaments fused, forming a delicate tube surrounding the gynecium, the anthers yellow, 5.4 mm long, the free part of the filaments above ~2 mm long; ovary fusiform, ~4 mm long, the style to 3 mm long; stigmas ~5 mm long.

DISTRIBUTION.—Known only from a single moist lowland

forest (~90 meters elevation) in Espírito Santo, Brazil (Figure 21).

ADDITIONAL SPECIMENS SEEN.—BRAZIL. BAHIA: Plants from type population cultivated at Sucre property, Vargem Grande, Jacarepaguá, Rio de Janeiro, 15 Mar 1986, *Judziwicz s.n.* (WIS).

VOUCHER SPECIMENS FOR ANATOMICAL STUDIES.—Brazil: *Soderstrom and Sucre 1969* (US) (leaves).

DISCUSSION.—See comments under *Streptochaeta spicata* subsp. *spicata*. As noted by Soderstrom (1981a, fig. 6h) the filaments of this species are fused into a delicate stamen tube, a feature also present in the herbaceous bamboos *Froesiochloa*

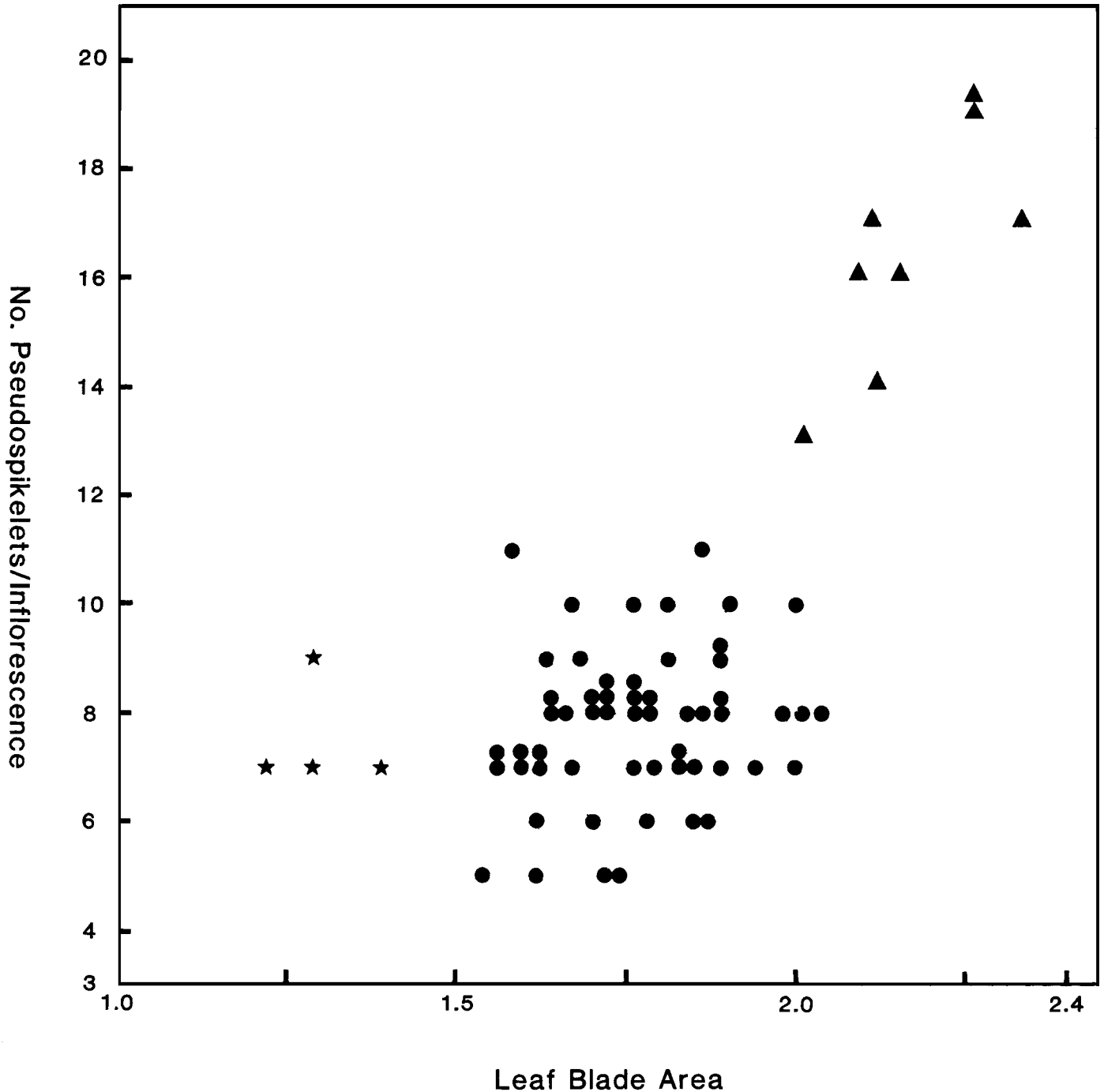


FIGURE 22.—Plot of pseudospikelet number versus leaf-blade size for MO and US collections of *Streptochaeta spicata* subsp. *spicata* (solid circles); *S. s. subsp. ecuatoriana* (triangles), and *S. angustifolia* (stars). The index for leaf-blade size (area) was computed by taking the logarithm of the product of leaf-blade length times width (both measured in centimeters).

(Olyreae), *Puelia* spp. (Puelieae), and *Buergersiochloa* (Buergersiochloae), as well as in several genera of woody bamboos such as *Gigantochloa* (Soderstrom, 1981a).

As is evident to anyone flying from Salvador to Rio de Janeiro, the forests of the Brazilian state of Espírito Santo, except for a few small reserves, have been destroyed. The olyroid herbaceous bamboo *Sucrea sampaiana* (two collections, 1924 and 1929), which grew here, is probably extinct, and it is likely that *Streptochaeta angustifolia*, collected only in a tiny remnant forest patch in 1972, is by now also extinct in the wild. However, the species has survived for 14 years in cultivation near Rio de Janeiro due to the care of Sr. Dimitri Sucre, who recently donated a plant from his thriving population to the Smithsonian Institution greenhouse in Washington, D.C., where it bloomed in August 1986.

MORPHOLOGY-ANATOMY

Culm, Leaf Sheath, and Pulvinus

The culms of all species of *Streptochaeta* are hollow, with the lumen ranging from about $\frac{1}{3}$ to over $\frac{1}{2}$ of the diameter of the culm. In a culm sectioned for this study (*S. sodiroana*, Soderstrom 1205) a circle of 42 alternating large and small vascular bundles, partially embedded in sclerenchyma, was noted subjacent to the epidermis and separated from it by a few rows of parenchyma. Interior to this ring was a ground tissue of parenchyma cells that extended all the way to the central lacunae, within which were embedded numerous scattered vascular bundles. The parenchyma cells were largest in the region midway between the epidermis and the lacunae, with the cells immediately adjacent to the lacunae noticeably smaller and with slightly thicker walls.

The leaf sheaths of *Streptochaeta* species are solid and crescent-shape in cross-section and do not have membranous, winged margins. In acropetal serial sections of *S. sodiroana* and *S. spicata* subsp. *spicata* the shape changes from concave to triangular, as the pulvinar area is approached, with the adaxial side slightly concave and the corners of the triangle rounded (Figure 5d). The epidermis has abundant rounded, silicified papillae and long, ciliate macrohairs, the latter particularly abundant on the adaxial epidermis. The main vascular bundles are disposed in a V-shape arc of about 20 bundles situated closer to the abaxial epidermis than to the center of the pulvinus; the peripheral bundles each have an irregular sclerenchymatous cap proceeding to the adaxial epidermis. Several arcs of minor vascular bundles are also present: an arc of about five tiny bundles is present abaxial to the main arc; an irregular arc of about ten small bundles is present subjacent to the adaxial epidermis; and there is an isolated medium-size vascular bundle present in nearly the exact center of the pulvinus, between the main arc and the adaxial arc of small bundles.

Leaf-blade Anatomy

TRANSVERSE SECTION (Figure 7a-c).—*Outline*: blade flat, the epidermides straight or with only slight undulations on the abaxial surface, with the blade thickest near the vascular bundles and thinnest near the bulliform cells. *Midrib outline*: distinctive, projecting both adaxially and abaxially; adaxial projection anvil- or keystone-like, slightly narrowed at the base and with a broad, flat top and overhanging corners; abaxial projection low-domed or low-rectangular. *Midrib vasculature*: complex, with several tiers of vascular bundles; one large median bundle always present subjacent to the abaxial epidermis, this flanked or not with minor bundles, and one to several vascular bundles usually present subjacent to the abaxial epidermis. *Midrib sclerenchyma*: a broad, shallow plate always present on the adaxial keel but unconnected to vascular bundles; a deeper, irregular plate present on the abaxial keel and often with minor bundles wholly embedded in it and the median bundle barely or not embedded in it. *Lacunae*: apparently present near the abaxial surface in the ground parenchyma in at least one species. *Vascular bundle arrangement in the lamina*: bundles of the first and third orders present, noticeably closer to the abaxial surface. *Vascular bundle description*: first-order bundles ovate; lysigenous cavity present; third-order vascular bundles small. *Vascular bundle sheaths of primary bundles*: double sheath present; outer sheath of large, thin-walled cells containing few plastids; usually incomplete both above and below because of interruptions by the sclerenchyma caps, no bundle sheath extensions present; inner sheath of two rows of small, achlorophyllous cells with uniformly thickened walls, complete. *Vascular bundle sheaths of third-order bundles*: double sheath present, the outer sheath of thin-walled cells, interrupted abaxially but usually not adaxially by sclerenchyma caps. *Sclerenchyma*: present as strands or caps above and below each vascular bundle; adaxial cap few-celled, abaxial cap larger, of cells with thicker walls; intercostal sclerenchyma not present. *Mesophyll*: chlorenchyma not radiate, consisting of two layers of cells located immediately subjacent to the adaxial epidermis and one layer subjacent to the abaxial epidermis, these two layers separated by fusoid cells; chlorenchyma cells vertically rectangular in basic outline, lacking arm-like extensions but lobed in most directions with much intercellular air space; fusoid cells well developed; uniseriate columns of chlorenchyma connecting adaxial and abaxial chlorenchyma layers and separating adjacent fusoid cells.

ABAXIAL EPIDERMIS (Figure 23).—Costal and intercostal zones well differentiated. *Intercostal long cells*: variable; strongly sinuous and rectangular to long, straight-walled, and fiber-like. *Stomata*: typically in rows flanking the veins; subsidiary cells low dome-shape or subhexagonal, separated by one to several thin-walled interstomatal cells. *Bulliform cells*: absent. *Papillae*: absent. *Prickle hairs*: typically absent. *Microhairs*: long, slender, 2-celled, typically found in the intercostal regions; basal cell curving, often silicified, distinctly

shorter than the pointed distal cell and with an apparent constriction about one-third of the way up from the base. *Macrohairs*: absent or present, if present commonest along the margins of the row of bulliform cells and borne on a prominent inflated base. *Silica cells*: uncommon intercostally, if present saddle-shape and projecting above and below the row in which developed; common costally, these solitary, paired with cork cells, or in short rows, and tending to be more square in outline and less saddle-shape. *Costal cells* in several rows, consisting of elongate, slightly sinuous long cells alternating with solitary or short rows of silica and cork cells.

ADAXIAL EPIDERMIS (Figure 24).—Basically similar to the abaxial epidermis. *Bulliform cells*: well developed in center of intercostal zone; walls sinuous. *Intercostal long cells*: consistently sinuous, never strongly tapering. *Stomata*: uncommon or absent. *Papillae*: absent. *Prickle hairs*: often present in intercostal and/or costal regions; consisting of a prominent,

inflated base and a relatively slender, short prickle. *Microhairs*: present, commonest near margins of the zone of bulliform cells. *Macrohairs*: absent. *Silica cells*: common, and larger than those on the adaxial surface; those in costal regions tending to be square rather than saddle-shape. *Costal cells*: similar to those of the abaxial epidermis.

Inflorescence and Pseudospikelets

The inflorescence, treated in detail most recently by Soderstrom (1981a), is spicate and consists of few to numerous (in *S. sodiroana*) short-pedicelled pseudospikelets arranged spirally along the rachis. Each pseudospikelet consists of 12, or more commonly 11, bracts arranged spirally on a curving axis. The bracts I–V are small, scale-like, and irregular in shape, while the upper bracts (except the ninth, which is only rarely present) are larger and elongate. Bract VI bears a long,

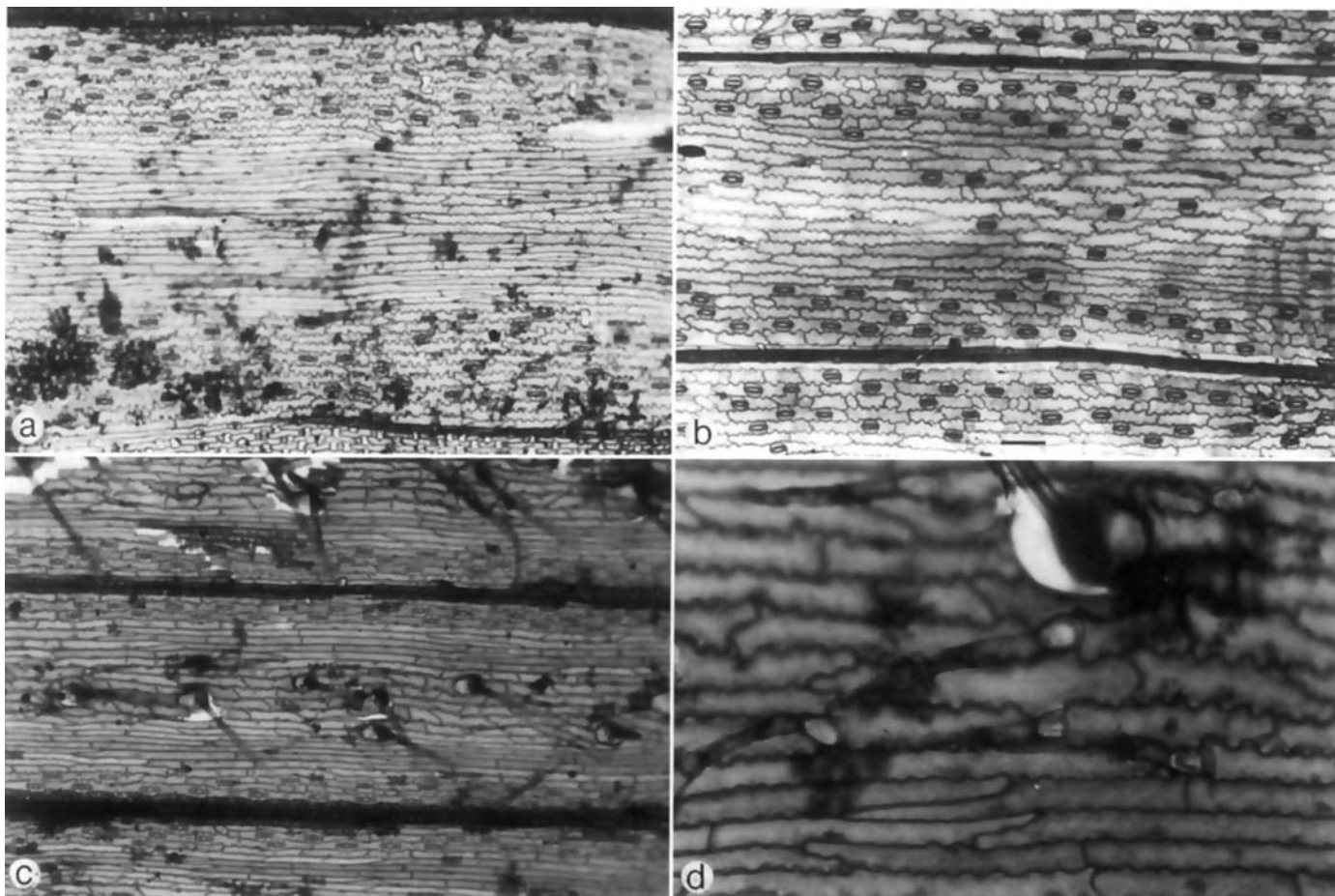


FIGURE 23.—Abaxial epidermides of *Streptochaeta* species: *a*, *S. sodiroana*, showing elongate mid-intercostal long cells; *b*, *S. spicata* subsp. *spicata*, showing shorter mid-intercostal long cells with more sinuous walls; *c, d*, *S. angustifolia*, showing (*c*) prominent mid-intercostal cilia and (*d*) bicellular microhairs. (*a* based on Soderstrom 1205, Costa Rica; *b* based on Soderstrom and Calderón 1861, Brazil; *c, d* based on Soderstrom and Sucre 1969, Brazil.) Scale bar: *a* = 60 μ m; *b* = 70 μ m; *c* = 80 μ m; *d* = 20 μ m.

tendrulous awn, and the seventh and eighth bracts are inserted nearly side-by-side and have slightly recurved apices. Bract IX is only rarely present. Bracts X–XII are of nearly identical morphology and tightly invest the flower, which consists of six stamens (often delicately fused into a tube, at least near the base), and a gynecium with 3 hispid stigmas.

Fruit

STARCH GRAINS.—The endosperms of *Streptochaeta sodiroana* and *S. spicata* subsp. *spicata* are characterized by elliptical, highly compound grains, with 15–30 grains occurring in each endosperm cell. Each grain is 10–25(50) μm in diameter and is composed of 50–300 strongly angular granules that are approximately 2–4 μm in diameter.

EMBRYO.—Sections of the embryos of several specimens

of *S. sodiroana* and *S. spicata* subsp. *spicata* (Figure 13a,b) show that in median sagittal sections no mesocotyledonar internode is present between the scutellar and coleoptilar nodes of the vascular bundle (F), no trace of an epiblast is present (–), a small, shallow cleft is present between the lower part of the scutellum and the coleorhiza (P), and the embryonic leaf margins appear to overlap (P), giving a formula of F – PP (in the formula of Reeder, 1957). At least the margins of the coleoptile are not fused in the upper portions and there is a hint that they overlap. Five nerves were noted in the basal portion of the coleoptile and three in the first embryonic leaf.

CHROMOSOMES

There have been three gametic chromosome counts for two species of *Streptochaeta*: Pohl and Davidse (1971) and

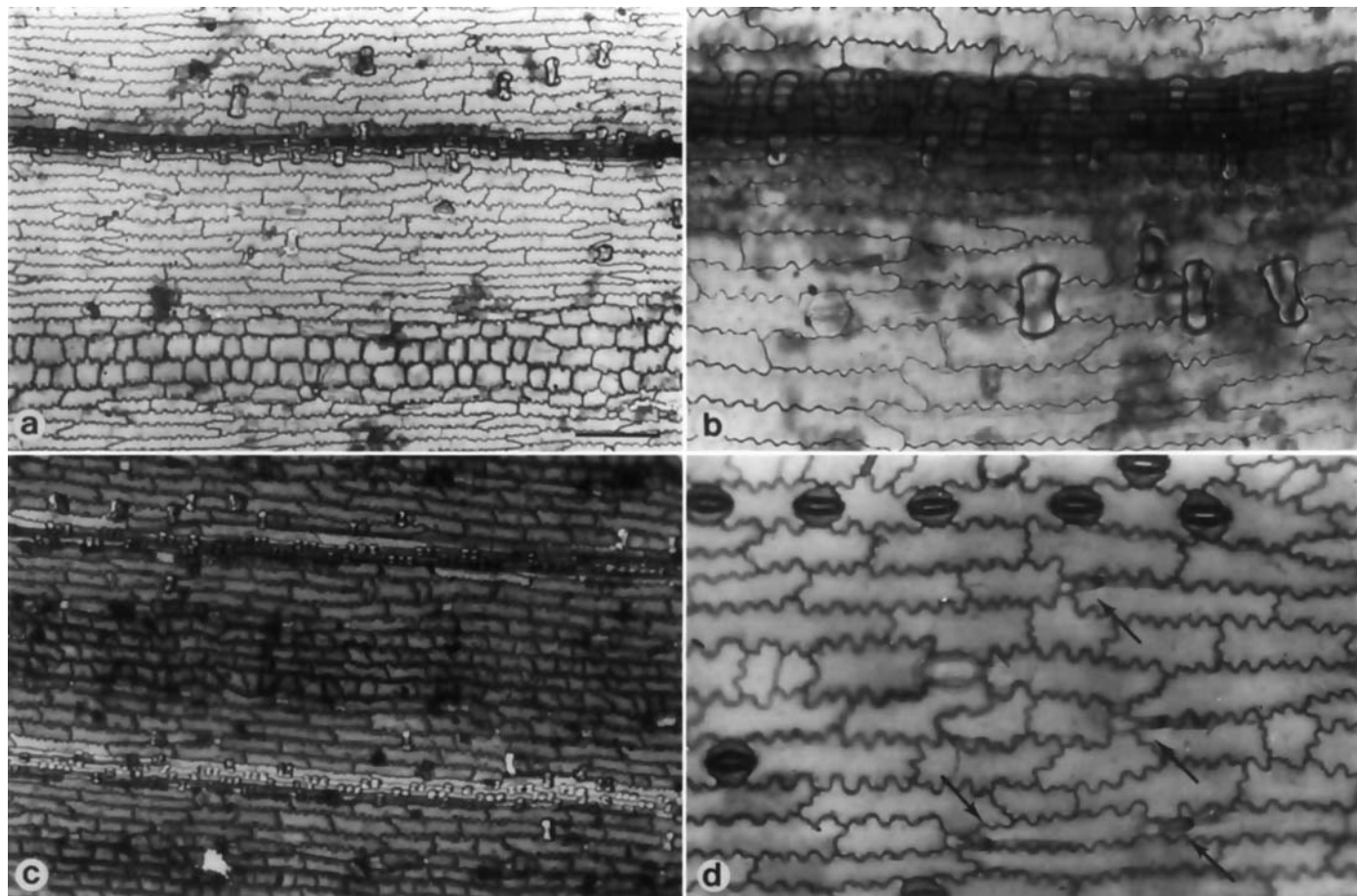


FIGURE 24.—Leaf epidermides of *Streptochaeta* species: a,b, adaxial view of *S. sodiroana* showing (a) bulliform cells (below) and (b) structure of costal and isolated intercostal silica cells; c, adaxial view of *S. angustifolia* showing poorly differentiated bulliform cells; d, abaxial, *S. spicata* subsp. *spicata*, showing bicellular microhairs (arrows). (a, b based on Soderstrom 1205, Costa Rica; c based on Soderstrom and Sucre 1969, Brazil; d based on Soderstrom and Calderón 1861, Brazil.) Scale bar: a = 100 μm ; b,d = 40 μm ; c = 120 μm .

Hunziker et al. (1982) studied *S. sodiroana*, and Valencia (1962) studied *S. spicata* subsp. *spicata*. All report that $n = 11$ with perfect pairing of bivalents.

DISCUSSION

Habit

Species of *Streptochaeta* are forest understory herbs to 1 meter tall. The plants are generally caespitose (Figure 1a) but apparently it is possible for a culm to become lodged in the soil, develop adventitious roots at the nodes, and spread vegetatively. Unlike *Anomochloa*, the culms of *Streptochaeta* are prominent and leafy and the leaf phyllotaxy represents a $2/5$ or $3/8$ spiral of a type rare in grasses (Page, 1951). In all taxa except *S. sodiroana* the upper portion of the culms may rebranch in a secund manner with each branch terminating in an inflorescence. Prominent prophylls are present as the first appendage of each lateral branch in such cases, but these organs are many-nerved, not bicarinate as are the prophylls of most grasses. The last leaf or two preceding the inflorescence is invariably a sheath lacking a blade.

The leaf sheaths of the plants are open. Neither an internal nor external ligule is found at the summit of the sheath, but lateral appendages of a type described for other bamboos by Tran Van Nam (1972) and minute oral setae are present, as is a prominent, turgid, hairy pulvinus. Cross-sections of the pulvinus reveal a complex vascular structure roughly similar to that of the upper pulvinus of *Anomochloa*. The blades of *Streptochaeta* are prominently tessellate and have a basically parallel venation. However, the venation is oblique to the extent that veins converge into the midrib for a distance of several centimeters above the base of the lamina.

Leaves

Cross-sections of the leaf blades of *Streptochaeta* reveal prominent fusoid cells and a distinctive midrib morphology, first noted by Metcalfe (1960:488), in which the adaxial keel is flat-topped and prominent while the abaxial keel is dome-shaped. The midrib retains its peculiar morphology and complex vasculature to near the apex of the blade. The development of the fusoid cells in *S. spicata* was studied by Page (1947).

The epidermides of *Streptochaeta* (Figures 23, 24) bear several resemblances to the bambusoid core group. The long cells are elongate with straight walls (*S. sodiroana*) to rectangular with sinuous walls, depending on the epidermis and species. Bulliform cells are well developed on the adaxial epidermis but epidermal papillae are totally lacking. Intercostal silica-cork cell pairs, characteristic of most bambusoid grasses, are absent in *Streptochaeta*. *Streptochaeta* has silica cells of a single type, vertical saddle-shape, although those silica cells found in the costal zones are smaller than the prominent isolated ones found in the intercostal zones. By contrast, *Anomochloa* has three types of silica cells (costal; intercostal

associated with cork cells; and isolated intercostal), all with different morphologies.

The microhairs of *Streptochaeta* are 2-celled and vary in length from 75–150 μm . The apical cell is about half again as long as the basal cell and is narrowly elliptic to linear, with a somewhat pointed apex (Figures 23d, 24d). The microhairs of the examined specimen of *S. spicata* subsp. *ecuatoriana* were remarkable for their very large size (120–150 μm), and in fact were half again as long as those of the other three species as noted both in our study and the survey of Metcalfe (1960:487). Based on a review of the grasses treated by Metcalfe (1960) and Tateoka et al. (1959), as well as our own studies, it appears that the bicellular microhairs of *S. spicata* subsp. *ecuatoriana* are the longest of any grass. The herbaceous bamboo *Guadua* has microhairs approaching 250 μm in length (Metcalfe, 1960:487; personal observation) but these hairs are multicellular, not bicellular. Tateoka and Takagi (1967) found that the microhairs on the epidermis of the "lodicules" (spikelet bracts X–XII) of *S. spicata* have an apical cell much shorter than the basal cell.

The three species of *Streptochaeta* differ in the abaxial leaf blade epidermides (Table 1). Leaves of *S. sodiroana* possess elongate, nearly straight-walled, tapering mid-intercostal long cells (Figure 23a) reminiscent of those of *Streptogyna* species (Soderstrom et al., 1987) and these are set off sharply from the interstomatal long cells, which are rectangular with strongly sinuous walls. In *S. spicata* there is barely any differentiation of the mid-intercostal long cells and interstomatal cells; both are rectangular with sinuous walls (Figure 23b).

The abaxial intercostal region of *Streptochaeta angustifolia* (Figure 23c) is differentiated into a central zone of rectangular, sinuous-walled long cells (these interspersed with ciliate macrohairs) flanked by two zones of elongate, slightly tapering long cells, and a zone of interstomatal cells that are elongate-rectangular with moderately sinuous walls. Cilia with broad inflated bases are common in the mid-intercostal regions of *S. angustifolia*, as are prickles. Both of these features, however, are rare or absent in *S. spicata* and are never seen in *S. sodiroana*. The abaxial epidermis of *S. sodiroana* exhibits occasional large, isolated silica cells enclosing ellipsoid-crenate silica bodies, a feature not observed in the abaxial intercostal zones of the other three species. *Streptochaeta sodiroana* has more rows of stomates flanking the veins than the other taxa.

The adaxial epidermis exhibits less interspecific differentiation, but the stomates appear to be randomly scattered in *S. sodiroana* but only occur in zones flanking the veins in *S. spicata*. Also, both epidermides of *S. sodiroana* lack prickles, a feature that has been observed in at least one epidermis in the other three taxa.

Inflorescence and Pseudospikelets

The inflorescences and pseudospikelets of *Streptochaeta* have been the objects of detailed studies, the most recent of

TABLE 1.—Comparison of leaf epidermal anatomy of *Streptochaeta* species.

Character	<i>S. sodiroana</i>	<i>S. spicata</i>		<i>S. angustifolia</i>
		<i>ssp. ecuatoriana</i>	<i>ssp. spicata</i>	
LOWER (ABAXIAL) EPIDERMIS:				
Intercostal long cells	Elongate; walls not sinuous	Elongate-rectangular; walls sinuous	Rectangular; walls strongly sinuous	Elongate-rectangular; walls moderately sinuous
Rows of stomates flanking each side of vein	7–9	2	2–4	2 or 3
Interstomatal long cells	Very sinuous	Moderately sinuous	Moderately sinuous	Not sinuous
Bicellular microhairs (length in μm)	Present only in stomatal regions (75–90)	Present in all intercostal regions (120–150)	Present in all intercostal regions (85–105)	Present in all intercostal regions (90–115)
Macrohairs	Absent	Absent	Rarely present	Present, mostly in center of intercostal zone
Intercostal prickles	Absent	Common	Common	Absent
Costal prickles and microhairs	Absent	Absent	Absent	Present
Vein spacing (mm)	0.7–0.9	0.7–0.8	0.4–0.6	0.3–0.4
Costal short cells	Solitary, paired, or in threes	Solitary, paired, or in threes	Solitary, paired, or mostly in short rows (3–8 cells)	Solitary, paired, or mostly in short rows (3–8 cells)
Intercostal silica cells	Present	Absent	Absent	Absent
UPPER (ADAXIAL) EPIDERMIS:				
Stomates	Scattered throughout intercostal areas	Uncommon, in rows flanking veins	Uncommon, in rows flanking veins	Rare
Intercostal silica cells	Very large, saddle-shaped, in intercostal areas	Uncommon, near veins	Moderately large, only very close to veins	Uncommon, near veins
Prickles	Absent	Absent	Edges of and among bulliform cells	Edges of (but not among) bulliform cells
Bicellular microhairs	Throughout intercostal zone, but not among bulliform cells	Edges of zone of bulliform cells	Edges of (rarely among) zone of bulliform cells	Edges of zone of bulliform cells

which have been Page (1951) and Soderstrom (1981a); both are recommended for their reviews of the many previous studies of this genus. Soderstrom interpreted the spikelet-like diaspores as consisting of a series of “bracts on different axes of a highly modified pseudospikelet,” basing this view on (among other features) the occasional presence of buds in the axils of bracts I–V and the anomalous structure and arrangement of the putative “lodicules” (bracts X–XII).

Fruit

CARYOPSIS.—The hila in the caryopses of *Streptochaeta spicata* subsp. *spicata* and *S. sodiroana* are quite different in morphology; in the former the hilum is strictly linear (Figure 20o) while in the latter there is an elliptical trough occupying the center of the ventral face (Figure 17q). This is interesting in that hilum morphology is generally considered to be a

conservative character even at the subfamilial level in the Poaceae. The Bambusoideae are usually considered to be characterized by a strictly linear hilum (Calderón and Soderstrom, 1980:11). However, nonlinear hila somewhat resembling the type found in *S. sodiroana* are known from species of the olyroid genera *Raddiella* (Calderón and Soderstrom, 1967, fig. 9a) and *Diandrolyra* (Soderstrom and Zuloaga, 1985, fig. 1o).

STARCH GRAINS.—The endosperm starch grains of *Streptochaeta spicata* were first studied by Yakovlev (1950, fig. 20), who illustrated them as strongly compound. Tateoka (1962) studied an unspecified species of *Streptochaeta* and reported that the grains were of his Type IV; that is, strictly compound with eight to numerous granules in each grain. He noted that this type is typical of festucoid, eragrostoid, and oryzoid grasses, and that the olyroid herbaceous bamboos show a similar type that differed in having only 3 to 10 granules per grain. Our findings of highly compound grains for both *S. sodiroana* and *S. spicata* confirm these studies.

EMBRYO.—Yakovlev's (1950, fig. 78) illustration of a longitudinal section of the embryo of *Streptochaeta spicata* shows a cleft between the scutellum and the coleorhiza, no mesocotyledonar internode, and no evident epiblast. The embryo of the same species was studied in detail by Reeder (1953), who reported that *Streptochaeta* was unique among grasses in possessing a coleoptile with unfused, overlapping margins and 5 nerves. He recorded the presence of a short midnerve but noted that it was not prominent and disappeared soon above the base. Reeder was also impressed by the unfused, overlapping margins of the coleoptile. Most bambusoid grasses examined have coleoptiles with margins that are unfused for at least part of their length and some have the free portions of these margins overlapping (Ghosal and Ram, 1985; Usui, 1957; Philip and Haccius, 1976; de la Cruz, 1985; X. Londoño (Instituto Vallecaucano de Investigaciones Científicas, Cali, Colombia; pers. comm.) for a fleshy-fruited species of *Guadua*; sections by the present authors of most olyroid and pharoid genera). Later, in general surveys of grass embryos, Reeder (1962) reported a formula of F – PP for *Streptochaeta*, that is, typically bambusoid except for the absence of an epiblast. No other bambusoid grasses are known that lack an epiblast, except possibly for some woody, fleshy-fruited Indian species (Ghosal and Ram, 1985). Our sections of the embryos of several specimens of *S. sodiroana* and *S. spicata* confirm the findings of Yakovlev (1950:195) and Reeder (1953).

Reproductive Biology

Observations of *Streptochaeta sodiroana* at La Selva, Costa Rica, in February 1983 indicated that the pseudospikelets bloomed protogynously and in a basipetal sequence in the inflorescence.

At maturity the pseudospikelets become detached from the

rachis and become intertwined with the bract VI awns of the other pseudospikelets in a tangled, often pendent mass (Figures 1a, 16a, 19a) adapted for external animal dispersal (epizoochory; Ridley, 1930, Van der Pijl, 1982). In *S. spicata* the upper part of the rachis and the pedicels of the pseudopetioles are covered with hooked hairs (Figure 20a) that aid in securing the spikelets by the bract VI awns. The pseudospikelets then serve as diaspores that become entangled, often en masse, in the fur of mammals or in clothing; the Schipp collection of *S. sodiroana* from Belize bears the comment that the species is "one of the worse grass pests we have in the colony." The slightly recurved apices of bracts I–V, VII, and VIII may help to secure the pseudospikelet in the pelage of the disperser.

Interspecific Relationships

Streptochaeta sodiroana is quite distinct from the taxa of the *S. spicata* group. The depressed, trough-like area in the hilum of the caryopsis, the fiber-like mid-intercostal long cells on the abaxial leaf epidermis (Figure 23a), and the absence of foliar prickles may all be interpreted as specializations when *S. sodiroana* is compared with possible outgroups of the genus, such as *Anomochloa* or the Olyreae. Members of the *S. spicata* group also have some specializations: branched culms; the tendency of the andrecium to form a stamen tube; the presence of hooked hairs on the pedicels of the pseudospikelets and summit of the rachis; and the restriction of bicellular microhairs on the adaxial leaf epidermis to the areas immediately adjacent to the bulliform cells. The presence of these apomorphic characters may indicate that neither group is directly ancestral to the other.

Phylogenetic Position of *Anomochloa* and *Streptochaeta*

The affinities of *Anomochloa marantoidea* have long puzzled agrostologists. Brongniart (1851) suggested that *Anomochloa* might be related to the Oryzae, based on its resemblance to *Oryza* in its many-nerved (according to his interpretation) palea, possession of more than three stamens, and 1-flowered, terminal spikelets without glumes. Lacking material for further studies later authors had to concur with this placement (Doell, 1871:24; Hackel, 1887:42; Baillon, 1893:297; Schuster, 1909:32), although Bentham (1883:1111) tentatively placed the genus, along with other herbaceous bamboos, in the Paniceae. Early and mid-twentieth century agrostologists emphasized the distinctiveness of *Anomochloa*. Hubbard (1934:219) erected the tribe Anomochloae for the genus but did not allocate any of his tribes to subfamilies. Pilger (ex Potztl, 1957) placed it in its own subfamily, the Anomochlooideae. Exceptions to this trend of recognition at successively higher taxonomic levels were Stapf (1898) and Roshevits (1937:199), who placed *Anomochloa* in the Phareae, along with several olyroid genera. The anatomical work of Page (1947) and Metcalfe (1960:29) revealed that the

epidermal and cross-sectional leaf anatomy of *Anomochloa*, with its prominent fusoid cells, was similar to the bamboos. Later authors (Calderón and Soderstrom, 1980:16; Watson et al., 1985:460; Clayton and Renvoize, 1986:57), therefore, have maintained the plant in its own tribe within the Bambusoideae.

The highly bracteate nature of the inflorescence of *Streptochaeta* has long hinted at its affinities to the woody bamboos, as recognized by Nees von Esenbeck (1835), who placed the genus in a group that corresponds to the modern broad view of the Bambusoideae. Both Steudel (1855:339) and Doell (1877:217) agreed that the affinities of *Streptochaeta* were, if anything, to the bamboos. Most later 19th century authors, however, placed the genus in either the Oryzeae (Hackel, 1887:42; Baillon, 1893:296) or Paniceae (Kunth, 1833:164; Bentham, 1883:1111). In the present century most agrostologists have placed the genus close to the bamboos. Hubbard (1934:205) placed *Streptochaeta* in its own tribe, the Streptochaeteae, near the Bambuseae, and Roshevits (1937:157) included the tribe in his "Séries Bambusiformes" along with the Phareae and Bambuseae. Subsequent authors (Parodi, 1961; Soderstrom, 1981a:17; Clayton and Renvoize, 1986:58) have recognized this grass as a monotypic tribe and included it in the Bambusoideae, although Butzin (1973:121) established the Streptochaetoideae with the Streptochaeteae as its only tribe.

Most evidence of relationships of *Anomochloa* and *Streptochaeta* to other herbaceous bamboos is of a negative nature, that is, two or more of the tribes often lack a feature found in the others. For example, the Anomochloae, Streptochaeteae, Phareae, Streptogyneae, and Puelieae lack the prominent epidermal papillae and well-developed arm cells found in the Bambuseae, Buergersiochloae, Olyreae, Guaduelleae, and many oryzoids; *Anomochloa* and *Streptochaeta* lack the membranous inner ligules found in all other bambusoids except for the African *Puelia schumanniana*, which is highly specialized. Because of the possibility of independent loss, however, the shared absence of a feature is not as strong an indication of relationship as the shared presence of a derived character.

There are some characters that may indicate a distant relationship between *Streptochaeta* and *Anomochloa* and the olyroid bamboos. A single meiotic chromosome count has been made for *Anomochloa marantoides* recently, and a gametic number of $n = 18$ has been observed (J.H. Hunziker and A. Wulff, pers. comm.). The chromosome number of $n = 18$ is uncommon but scattered in the grass family. *Joinvillea* (Joinvilleaceae), which has been suggested as closely related to the grasses (Dahlgren et al., 1985:425; Campbell and Kellogg, 1987), however, has an identical count (Newell, 1969). It is interesting to note that the only bambusoid grass known with a chromosome number equaling half that of *Anomochloa* is the olyroid *Diandrolyra bicolor* ($n = 9$; Daker, 1968). The basic number of *Streptochaeta* ($n = 11$) is quite common in the Olyreae. Besides its similar basic chromosome number, the seedling of *S. spicata* subsp. *spicata* is of the typical olyroid/bambusoid type, with a few bladeless or

reduced-leafy sheaths preceding the first fully developed leaf, which bears a broad, horizontal lamina (Soderstrom, 1981a:24). The highly compound starch grains of both *Anomochloa* and *Streptochaeta* are common in the Oryzeae and in several olyroid genera, such as *Maclurolyra* (Calderón and Soderstrom, 1973, fig. 14f). Compound grains of this type are also found in *Joinvillea* (Joinvilleaceae; personal observation) and *Restio* (Restionaceae; Yakovlev, 1950, fig. 39), both putative relatives of the grasses. The isolated intercostal silica cells of *Anomochloa* enclose typical olyroid (vertical-crenate) silica bodies; silica-cork cell pairs are common throughout the intercostal zones, as in the many olyroids; the partial inflorescences recall those of many olyroid genera (cf. Calderón and Soderstrom, 1973, fig. 11); and the leaf venation is of the parallel type found in the olyroids.

Streptochaeta bears less of a resemblance to the Olyreae in exhibiting a distinctly oblique type of leaf venation (at least in the lower quarter of the blade) never found in the olyroids but found in the African tribe Puelieae, and especially well developed in the Phareae. The leaves have vertical silica bodies of a saddle-shape type, rather than the crenate type found in the olyroids; the embryo of *Streptochaeta* lacks an epiblast, which is found in all olyroid genera examined.

It is natural to begin the search for a sibling group of *Anomochloa* with *Streptochaeta*, because both genera are the only herbaceous bamboos that have inflorescences and spikelets (or the functional equivalents of spikelets) that are difficult to interpret in conventional agrostological terms. Further study, however, has made it clear that the inflorescences and spikelets of the two genera have little in common. The spikelet-equivalent in *Streptochaeta* is a pseudospikelet composed of 12 spirally arranged bracts (Soderstrom, 1981a, fig. 8j), and the pseudospikelets are borne spirally in a spike-like arrangement. We have shown that in *Anomochloa* the 2-bracted spikelets, except for the solitary terminal one, are borne in alternating scorpioid cyme-like partial inflorescences subtended by prominent general bracts.

Anomochloa and *Streptochaeta* share features of leaf anatomy and fruit morphology that may qualify as shared-derived characters (synapomorphies).

1. A similar leaf midrib structure in which the keel projects both abaxially (as a small dome) and adaxially in a prominent 'anvil' or 'keystone' configuration. This distinctive morphology has not been found in any other bambusoid genus studied by us. Both genera also have a complex vasculature, *Streptochaeta* along the entire length of the blade, *Anomochloa* in at least the lower half.

2. Exceptionally large (75–150 μm long) bicellular microhairs of a distinctive type, with the pointed apical cell averaging at least half again as long as the basal cell and with the basal cell having an apparent constriction about one-third of the way from the base (also a feature not seen in other bamboos). Most bambusoid grasses have microhairs ranging from 40–75 μm in length, with the unconstricted basal cell longer than the blunt apical cell (Metcalf, 1960, fig. 16).

3. Isolated, vertically elongated silica cells on the leaf epidermis. Isolated intercostal short cells that project above and below the file in which they are borne are typical of the Olyreae, but in that tribe they never project so prominently above and below the file in which they are situated as they do in *Anomochloa* and *Streptochaeta*.

4. Strongly compound starch grains of a type common in the Oryzae but less common in the core group of the Bambusoideae.

5. Five-nerved coleoptiles with unfused margins in which the midnerve is soon lost distally, although recent anatomical studies of woody bamboos have revealed that several have many-nerved coleoptiles with at least partially unfused margins (Ghopal and Ram, 1985).

These five features may constitute evidence for a relatively close relationship between *Anomochloa* and *Streptochaeta*. It must be emphasized, however, that in many ways besides inflorescence and spikelet structure the two genera are amply distinct from each other, including significant differences in chromosome number ($n = 18$ and $n = 11$, respectively), embryo

structure (epiblast present in *Anomochloa* but absent in *Streptochaeta*), and leaf epidermal anatomy (typical silica cells crescent to roundish in *Anomochloa*, tall saddle-shape in *Streptochaeta*); the phenetic studies of Watson et al. (1985:463) have led them to place *Streptochaeta* in their supertribe Bambusanae (with the woody bamboos and the several-flowered herbaceous bamboo tribes) and *Anomochloa* in their Oryzanae (with the single-flowered tribes of herbaceous bamboos). Based on their common possession of 1-flowered spikelets, symmetrical, predominantly adaxially projecting leaf midribs, herbaceous culms, and noncyclic flowering, Soderstrom and Ellis (1987) place the Anomochloae and Streptochaeteae in their supertribe Olyrodae, along with the Olyreae and Buergersiochloae. We still must examine the seedling of *Anomochloa* before coming to definite conclusions about its affinities. Despite its bizarre inflorescence, the leaf anatomy and embryo structure of *Anomochloa marantoidea* are not so different from that of the olyroid grasses. The species is definitely a member of the grass family.

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