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The Phareae and Streptogyneae (Poaceae) of Sri Lanka: A Morphological-Anatomical Study

Thomas R. Soderstrom, Roger P. Ellis
and Emmet J. Judziewicz

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ABSTRACT

Soderstrom, Thomas R., Roger P. Ellis, and Emmet J. Judziewicz. The Phareae and Streptogyneae (Poaceae) of Sri Lanka: A Morphological-Anatomical Study. *Smithsonian Contributions to Botany,* Number 65, 27 pages, 8 figures, 1987.—A morphological-anatomical study of the herbaceous bamboos (Poaceae: Bambusoideae) of Sri Lanka is presented. The occurrence of *Scrotochloa urceolata* and *Leptaspis zeylanica* of the Phareae and *Streptogyna crinita* of the Streptogyneae on the island represents the easternmost region in which these tribes of animal-dispersed, rain forest grasses are found together, a fact of phytogeographic significance, since both groups are the only herbaceous bamboo tribes found in both the Old World and the New World. Morphologically, *Leptaspis* and *Scrotochloa* possess strongly pseudopetiolate, inverted, obliquely-veined, usually broad leaves with an inner ligule and transverse veinlets. The inflorescence is an open panicle bearing unisexual, one-flowered spikelets; the mature female florets are inflated and covered with uncinate macrohairs that facilitate epizoochory, and the male spikelets have six stamens. *Streptogyna* has narrower, non-inverted, parallel-veined leaves that possess inner and outer ligules. The perfect, several-flowered spikelets have two or three stigmas and two stamens and are borne in a spikelike raceme; at maturity the florets may detach and adhere to animals by means of a complex of awns, retrorsely barbed stigmas, and rachilla internodes. Details of leaf anatomy indicate that both tribes are peripheral members of the Bambusoideae.

Transverse sections of the blades reveal typically bambusoid features such as a complex midrib vasculature, prominent fusoid cells, at least rudimentary arm cells, a multi-layered inner vascular bundle sheath composed of small, thick-walled cells, and an outer bundle sheath of large, colorless cells. The epidermides of the Phareae and Streptogyneae are quite distinct from each other and from typical bamboos. The pharoid grasses, unlike bamboos, possess intercostal fibrous bands, dumbbell-shaped, horizontal silica bodies, and poorly developed bulliform cells. *Streptogyna,* while less anomalous, also possesses somewhat fiber-like intercostal cells. Bicellular microhairs and well-developed, minute epidermal papillae, both typically bambusoid features, are absent from the leaf-blades of both tribes.

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Preface

The impetus for this paper came through an invitation from Dr. F. Raymond Fosberg to prepare an extensive treatment of the grasses of Ceylon to be included in "A Revised Handbook to the Flora of Ceylon." I gladly consented to do so, especially in view of the fact that Fosberg's Flora of Ceylon Project, headquartered at the Smithsonian Institution, would provide me with round-trip air transportation to that far-away island and cover all expenses of a three-month stay collecting grasses.

It occurred to me that it would be ideal if I could enlist the cooperation of other agrostologists, each visiting the island for a different three-month period to make general collections and be responsible for writing the treatments of a particular set of genera, especially in his field of expertise. This plan worked out admirably, and three leading agrostologists seized upon this opportunity. Dr. W. Derek Clayton of Kew travelled to Ceylon from January through March 1970, overlapping somewhat the period of March through May when Dr. Frank W. Gould of Texas A & M University and his wife, Lucile, visited the island. From July through September Dr. Michael Lazarides of C.S.I.R.O. in Australia collected in Ceylon. Dr. Norman Bor, who had published widely on the grasses of Southern Asia (1960) had kindly consented to identify the first set of specimens from Ceylon as they were assembled at Kew.

My own trip to Ceylon had been made the year before, from October through December, when I went to make collections of the bamboos. Mrs. Gesina Berendina Threlkeld, who had made many illustrations for me previously, accompanied me to Ceylon to work with fresh material. When flowering material was not available, dissections of herbarium specimens were made later in Washington and illustrations of these rendered by Alice R. Tangerini. The world's expert on bamboos and my mentor at the Smithsonian was Dr. F.A. McClure, who had agreed to prepare the bamboo treatment and also to go to Ceylon to collect. But shortly after our preliminary discussions in early 1969 he told me that he did not feel that his state of health would permit an arduous trip to Ceylon and he would not be able to go; furthermore he asked that I do the treatment with the assurance that he would help me along the way. Shortly after my return from Ceylon, my dear friend and mentor passed away on April 15, 1970.

The unexpected death of Dr. Bor on December 22, 1972, was a great loss to the field of agrostology and to our project in particular. I was fortunate to find another collaborator, Dr. Gerrit Davidse of the Missouri Botanical Garden, to write up the genera for which Bor was responsible. Our newest collaborator travelled to Ceylon in 1974, where he made a large and impressive collection of grasses and other plants during his stay there from October to mid-December.

My own assignment, the Bambusoideae, proved difficult from the beginning, as my previous studies had been confined to herbaceous bambusoid grasses, with little attention paid to the bamboos themselves during the time McClure was active. After McClure's death, I was thrust into the study of bamboos by editing his manuscript entitled, "Genera of Bamboos Native to the New World (Gramineae: Bambusoideae)," which appeared in 1973. Almost a whole year was devoted to this task and that of sorting out his office, in which I had the wonderful assistance of his wife, Ruth Drury McClure.

The state of taxonomy of the woody bamboos in general, not just those of Sri

Lanka, provided the impetus to undertake a broad survey of the leaf anatomy of the Bambusoideae; toward this end I began a collaborative effort in 1980 with Dr. Roger P. Ellis of the Botanical Research Institute in Pretoria, South Africa. This survey was a necessary step in understanding better the generic limits of the bamboos and in interpreting the genera of Sri Lanka. The results of this anatomical study are now being written up, as is the study of the Ceylonese bamboos themselves; and the *Grasses of Ceylon* volume is now being edited.

The present paper, which is a small portion of the entire study, covers only the herbaceous bamboos of Sri Lanka. When we wrote the first draft of this paper there were two described genera: *Streptogyna* and *Leptaspis.* During the past two years, a graduate student at the University of Wisconsin (Madison), Emmet J. Judziewicz, has made a study of the genus *Pharus,* which is confined to the New World. He is now continuing his investigations on its Old World sister genus, *Leptaspis* and a further genus, which he segregated from it and called *Scrotochloa.* Judziewicz is presently at the Smithsonian Institution as a pre-doctoral fellow (September 1985–August 1986) to carry out research on several herbaceous tribes of Bambusoideae, including the Anomochloeae, Phareae, Streptochaeteae, and Streptogyneae. Because of the expertise that he has acquired in the Phareae and his present studies on the Streptogyneae, we have asked him to contribute to this paper.

This publication is thus the result of a long series of events and, we hope, will be a worthy contribution to our understanding of these unusual herbaceous bamboos. We have attempted to present details of the morphology, along with those of leaf anatomy, of the two herbaceous tribes represented in Sri Lanka. More interesting, perhaps, than such details of the plants' structure is the distribution of the genera and their Singhalese connection. As the reader will learn, we have not denied ourselves the opportunity to speculate on this intriguing question.

T.R. Soderstrom
19 September 1985

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Introduction

In the shaded understories of the world's tropical forests occur seven or eight tribes and perhaps 150 species of herbaceous, broad-leaved grasses that, based on details of leaf anatomy and spikelet structure, are now generally considered to be allied to the woody Bambusoideae (Calderón and Soderstrom, 1980). Three tribes of these herbaceous bamboos, the Streptochaeteae, Streptogyneae, and Phareae, have mature spikelets that are variously adapted for dispersal via the fur and feathers of animals. These epizoochorous adaptations may be an important reason why these probably ancient, relictual grasses have been able to survive to the present day (Soderstrom, 1981), while distant cousins that lacked such adaptations have become extinct or nearly so. For example, *Anomochloa marantoidea* of the monotypic tribe Anomochloeae is now known only from a single forest in Brazil.

Sri Lanka marks the easternmost outpost in which two of these epizoochorous tribes co-occur. *Scrotochloa urceolata* and *Leptaspis zeylanica* (both Phareae) and *Streptogyna crinita* (Streptogyneae) are present on the island, and it is noteworthy that these groups are the only tribes of herbaceous bamboos that are native to both hemispheres. The Phareae are found in the tropical regions of Latin America, Africa, Southeast Asia, Australia, and Oceania; the Streptogyneae grow in tropical Latin America, Africa, southern India, and Sri Lanka. The occurrence of these grasses on Ceylon poses a question of great phytogeographical interest, and two explanations may be advanced for their pantropical distributions.

Based on their resemblance to the woody bamboos, both the Phareae and the Streptogyneae are probably quite ancient taxa, and so it is tempting to explain their amphi-Atlantic ranges on the basis of continental drift. In this scenario, the proto-pharoid and proto-streptogynoid stocks were present throughout the Gondwanaland super-continent, and upon the separation of South America from Africa during the Cretaceous (Raven and Axelrod, 1974) new climatic and biological parameters, aided by genetic isolation, allowed natural selection to proceed in different directions on both sides of the newly-formed Atlantic Ocean. Phylogenetic differentiation proceeded to the genus level in the Phareae and to the species level in the Streptogyneae. At the beginning of the Paleocene, South America and Africa were separated by about 800 km, or about ⅓ of their present distance, while to the east the Indian subcontinent, including Sri Lanka, had completed its separation from Madagascar. In succeeding eras the original Afro-Indian plants could then have been rafted northeastward; they probably migrated to Asia when that plate collided with the Indian plate in about the Middle Eocene. During this rafting period it is believed that India and Sri Lanka retained a warm, wet climate (R.O. Whyte, pers. comm.), and upon "impact" with Asia the pharoids could have spread eastward to Southeast Asia before the late Tertiary cooling and drying trend in world climate reduced their ranges to their present isolated sites at the southern tip of the Indian subcontinent. The streptogynoids either did not reach Southeast Asia or have since become extinct in the region. One difficulty with this hypothesis is that there is no evidence that the Poaceae were in existence during the Mesozoic; the earliest fossil grass pollen known is from the Paleocene and occurred in South America, Africa, and Australia (Muller, 1981).

A second explanation for the present distribution of the pharoid and streptogynoid grasses might invoke relatively

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recent (late Tertiary), long-distance dispersal by migrating or stray birds (Carlquist, 1974) as the means by which these taxa attained their present wide ranges. This process might have been facilitated by the manifestly epizoochorous nature of the disseminules in both tribes. The pharoid female floret is a compact, uncinate-covered structure, generally less than 1 cm long, that detaches singly from the branches of the inflorescence. That the Phareae can certainly travel is evidenced by their presence on many isolated islands. *Pharus lappulaceus* grows on many of the Lesser Antilles and also on the tiny Swan Islands north of Honduras. *Leptaspis angustifolia,* a clearly specialized taxon, has reached Fiji in the Pacific Ocean, and *L. zeylanica* grows on islands in three oceans: São Tomé in the Atlantic, the Comoro Islands, Madagascar, and Sri Lanka in the Indian Ocean, and New Britain, New Ireland, and Bougainville in the Pacific. The spikelets of *Streptogyna* are larger (2–3 cm long) and usually disarticulate as a group via a complex of awns and coiling stigmas, making the possibility less likely that a bird would complete a trans-oceanic journey with such a mass of large, foreign objects adhering to its feathers. The relatively awkward nature of this type of epizoochory may be reflected in the more continental distribution of the genus: the only islands from which *Streptogyna* is recorded are Trinidad and San José Island (Panama) in the New World and Fernando Po (Hubbard, 1956) and Sri Lanka in the Old World, all of which are less than 100 km from a continent.

The more likely method of dispersal of these grasses is continental drift, probably followed by over-water dispersal by birds when the American and African land masses were only a few hundred kilometers apart or bridged by island chains during the early Tertiary. The possibility remains that *Leptaspis, Scrotochloa,* and especially *Streptogyna* have continuously resided on Sri Lanka for tens of millions of years. To understand the full phytogeographic significance of the distribution of these extraordinary Singhalese grasses will require elucidation of the intra- and inter-tribal taxonomic relationships of all the tribes of herbaceous bamboos, based on careful anatomical and morphological studies. This study is a contribution toward that goal.

MATERIALS AND METHODS.—For anatomical studies of the leaf-blade in cross-section, dried (herbarium) material was hydrated by boiling or treatment with Contrad 70. Both dried and field-preserved (in a formalin-acetic acid solution) material was then treated with hydrofluoric acid to remove silica, dehydrated with 2-2-dimethoxypropane, embedded in paraffin, and sectioned on a rotary microtome at 10 or 13 μm. Staining was effected by either the safranin-fast green series or by chlorozol black E, and photographs were taken through a Leitz Ortholux compound microscope. Epidermal peels were prepared following the method of Tomlinson (1961), then stained in safranin O or chlarozol black E and mounted in clear resin under weighted cover slips. Pressed specimens were examined from the National Herbarium of Sri Lanka in Peradeniya (PDA), from the United States National Herbarium (US), and, for specimens of the pharoid genera from B, BR, GH, L, LE, NY, and P.

ACKNOWLEDGMENTS.—The first author is grateful to Dr. F. Raymond Fosberg for the opportunity afforded him to carry out fieldwork in Sri Lanka as a participant in the Flora of Ceylon project; and to the Smithsonian Research Opportunity Fund that made it possible to travel to South Africa in 1983 to work in the laboratory of Dr. Ellis. We thank Stanley Yankowski of the Smithsonian for preparing many of the leaf anatomical slides used in this study; and Alice R. Tangerini (ART) of the same institution for the several fine and detailed line drawings that she prepared for this paper. Thanks are also due to Mrs. Gesina Berendina Threlkeld (GBT), who prepared illustrations in Ceylon for all the bambusoid species.

Tribe PHAREAE

PHAREAE Stapf, 1898:319.

TYPE GENUS.—*Pharus* P. Browne.

DIAGNOSIS.—Herbaceous grasses of shaded forest understories. *Leaves* with a prominent pseudopetiole twisted 180° at the summit, thus bringing the morphologically abaxial surface into an upward-facing, functionally adaxial position; outer ligule absent; inner ligule small, membranous; blades with the lateral nerves diverging obliquely from the midnerve. *Inflorescence:* an open, terminal panicle, the rachis and branches covered with minute, uncinate hairs. *Spikelets:* unisexual, 1-flowered, mostly paired, the female spikelets large, subsessile to short-pedicelled, the male spikelet small, short- to long-pedicelled. *Female spikelets:* glumes 2, usually purple, shorter than the floret; lemmas indurate, covered wholly or in part by uncinate macrohairs; palea 2-nerved; lodicules apparently absent; ovary with a single style and 3 stigmas; fruit a caryopsis, the narrow hilum extending its entire length, the embryo small, basal. *Male spikelets:* membranous; glumes 2, shorter than the floret; lodicules 0–3; stamens 6; basic chromosome number $n = 12$ (Hunziker, Wulff, and Soderstrom, 1982).

The Phareae are an anomalous tribe of three well-defined genera and about a dozen species of tropical forest grasses. The genera are differentiated principally by the morphology of the mature female florets, which are covered with hooked hairs as an adaptation for external animal dispersal, and by the mode of disarticulation (if any) of the branches of the panicle. Two genera, *Leptaspis* and *Scrotochloa,* occur in Sri Lanka. *Leptaspis* may be the most primitive genus in the tribe, based on its persistent, non-disarticulating panicle branches and the presence of glume-like bracts subtending the 1st female glume and also the branchlet on which the female/male spikelet pair is borne. *Scrotochloa* is clearly advanced in its umbelliform panicles that detach from the summit of the peduncle. A third genus, *Pharus,* occurs in the New World and appears to be intermediate in terms of specialization.

DISTRIBUTION.—Three genera in the tropics of both hemispheres.

Key to the Genera of the Phareae

1. Mature female floret cylindrical, with strongly inrolled, usually free margins; axis of inflorescence prolonged into a naked or few-flowered bristle; male floret persistent; New World (7 species, Florida, Mexico to Argentina, Uruguay) .... ***Pharus***
1. Mature female floret globose, inflated, with fused margins; axis of inflorescence not prolonged into a bristle; male floret deciduous; Old World 2
    2. Mature female lemma urceolate, 13-nerved (at least at summit), the pore through which the style exits appearing terminal; some female spikelets solitary; main branches of inflorescence in verticils of 4–8, these and the associated node disarticulating as a unit from the summit of the peduncle at maturity; principal nodes of inflorescence 1 (rarely 2); female and male glumes blunt, caducous (2 species, Sri Lanka, India to Australia, Solomon Islands) .... ***Scrotochloa***
    2. Mature female lemma cochleate, strongly 7-nerved, the pore through which the style exits appearing lateral; female and male spikelets all paired; main branches of inflorescence borne singly, in pairs, or in verticils of 3, not disarticulating from the rachis at maturity; nodes of inflorescence 3–8; female and male glumes cuspidate, persistent (3 species, Guinea, Angola to Taiwan, Australia, Fiji) .... ***Leptaspis***

Genus *Scrotochloa*

Scrotochloa Judziewicz, 1984:299.

TYPE SPECIES.—*Scrotochloa urceolata* (Roxburgh) Judziewicz.

DIAGNOSIS.—Plants with hollow culms (or apparently solid in *S. tararaensis*), erect or with age becoming decumbent and rooting at the nodes. *Leaves:* sheaths somewhat compressed; blades narrow to broad. *Inflorescence:* long-pedunculate, umbelliform, with one principal node and 4–8 primary branches, the entire structure at maturity disarticulating at the summit of the peduncle, the rachis not prolonged into a bristle. *Spikelets:* paired or the female solitary; female spikelet short-pedicelled, the male spikelet long-pedicelled. *Female spikelets:* borne on slightly clavate pedicels; glumes caducous, blunt to acute, 5–7-nerved; lemmas urceolate, with connate margins and a terminal pore through which the style exits, indurate and densely covered with uncinate macrohairs at maturity; stigmas subplumose. *Male spikelets:* caducous; lemmas more or less tubular but with free margins; lodicules apparently lacking; basic chromosome number unknown.

DISTRIBUTION.—Sri Lanka and southern India to Vietnam, Indonesia, New Guinea, Australia, and the Solomon Islands.

SPECIES OF *Scrotochloa* IN SRI LANKA.— *Scrotochloa urceolata.*

Key to the Species of *Scrotochloa*

Leaf blades oblong, 4–8 cm wide, glabrous; female spikelets 4–6 mm long; range of the genus .... ***S. urceolata***

Leaf blades linear, about 1 cm wide, usually puberulent beneath (adaxially); female spikelets 3–4 mm long; rare, Papua, New Guinea and Australia ... ***S. tararaensis***

Scrotochloa urceolata

Scrotochloa urceolata (Roxburgh) Judziewicz, 1984:299.

Pharus urceolatus Roxburgh, 1832:611–612. [Type: Malaysia, Pulo Pinang, *without collector,* Herbarium Roxburgh. Holotype, BM!]

Leptaspis urceolata (Roxburgh) R. Brown in Bennett, 1838:23, pl. 6; Thwaites 1864:357; Hooker f., 1900:190–191; Senaratna, 1956:21–22; Bor, 1960:617,619.

Leptaspis manillensis Steudel, [1855]:8. [Type: Philippines, Leyte, *Cuming 1739.* Holotype, P!, isotypes BM!, L!, LE!, P!.]

MORPHOLOGY

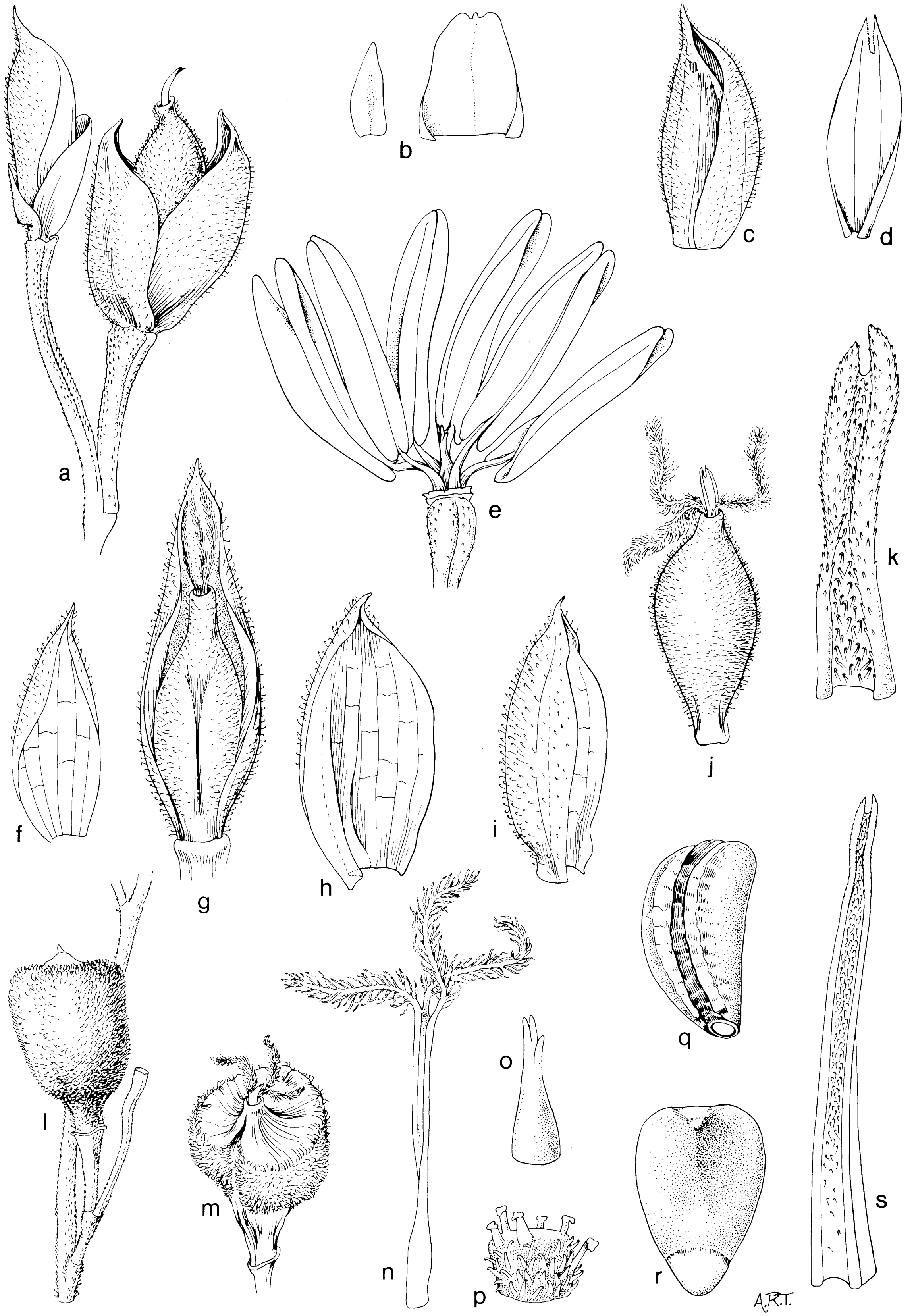
FIGURES 1, 2

DESCRIPTION.—*Plants:* with shallow rhizomes, the strongly ribbed internodes 1–4 cm long, the sheathed nodes each bearing 1 or 2 thick, hard, long primary (prop) roots, these 1–2 mm in diameter, naked for several cm before bearing secondary roots; rhizome continuous into the aerial axis (culm) of the plant, further culms often produced singly from the 2 or 3 rhizome nodes proximal to the main culm, resulting in formation of a clump of few individuals. *Culms:* to about 50 cm tall, covered by a thick, keeled layer of overlapping sheaths, the lowermost without blades, the succeeding ones with gradually larger blades. *Leaves:* sheaths elongate, glabrous, strongly ribbed, narrowed into a pseudopetiole about $\frac{1}{7}$ the length of the blade, manifestly tessellate on the inner (adaxial) surface, glabrous except at the narrowed and irregular transition zone between sheath and pseudopetiole where shortly appressed-pubescent; ribs of the sheath continuous with those of the outer (abaxial) side of the pseudopetiole and lower (morphologically adaxial) face of the blade; blades broadly obovate, 15–25 cm long, 4–6 cm wide, flexuous, tapering at the base, acuminate at the apex; upper (abaxial) surface glabrous, darker green than the lower, the midvein prominent, elevated, green, the primary veins emanating from it along the lower half; lower (adaxial) surface glabrous, pale green, strongly tessellate, the broad midvein level or slightly depressed, stramineous, smooth, shiny; ligule about 0.5 mm long, glabrous on the inner (adaxial) surface, densely ciliate on the outer surface. *Inflorescence:* terminal on an exserted peduncle; rachis about 12 cm long, strongly angled and densely covered by short uncinate hairs, bearing whorls of branches at the single principal node; primary branches of principal node about 6 to 14 cm long, at first ascending, at maturity stiffly spreading or some reflexed, densely covered with short uncinate hairs; upper nodes of inflorescence greatly reduced, the second node bearing about 3 short primary branches, successive nodes indistinct. Inflorescence at maturity falling entire, disarticulating just below the principal node, the whorled branches persistent or occasionally disarticulating from the rachis. Primary inflorescence branches bearing short, thin secondary branches, these terminating in a male spikelet; below this a pedicelled female spikelet. *Female spikelets:* 4–6 mm long, when young obovate and symmetrical, purplish-brown; glumes caducous, slightly coriaceous, greatly wrinkled; 1st glume shorter than the 2nd, about $\frac{4}{5}$ its length, more or less obovate, indistinctly 7–9-nerved, glabrous; 2nd glume the length of the spikelet at anthesis, broadly obovate and with inflexed margins, 2-keeled, concave between the keels, indistinctly 7-nerved, with some transverse veinlets, glabrous; lemmas at anthesis shorter than the 2nd glume, more or less fusiform, narrowed above into a short neck with an opening through which the stigmas and tip of the palea emerge, densely covered with delicate uncinate hairs, obscurely nerved; lemmas at maturity expanding into a hardened, inflated, urceolate structure with a narrowed, stipe-like base and a coarse abaxial groove, densely covered with stout uncinate macrohairs except at the flattened, slightly beaked summit, evidently 13-nerved only at the summit; palea longer than the lemma, tongue-like, 2-keeled, the sides parallel, glabrous below, the emergent tip densely covered on both surfaces by uncinate hairs. *Gynecium:* ovary gradually narrowed into an elongate style, dividing above into 3 subplumose stigmas; vestigial andrecium present as 6 minute staminodes situated asymmetrically around the base of the ovary; caryopsis not well-developed in the material examined but apparently about $\frac{1}{2}$ the length of the lemma, in front view more or less obtriangular, in lateral view strongly arched on the hilum (palea) side, deeply grooved, the broad hilum lying in the center of the groove; embryo about $\frac{1}{5}$ the length of the fruit. *Male spikelets:* overtopping the female and terminating the entire inflorescence, 3–4 mm long, ovoid, stramineous; 1st glume about $\frac{1}{3}$ the length of the spikelet, triangular with a broad apex, glabrous, nerveless; 2nd glume twice as long as the first, broadly obovate with an irregular dentate margin, 3-nerved; lemma more or less tubular and completely enclosing the andrecium, narrowing at the summit, covered by tiny appressed uncinate hairs, 7-nerved with some transverse veinlets; palea slightly shorter than the lemma, narrow with parallel sides and bifid at the apex; lodicules lacking. *Andrecium:* anthers orange-yellow, about 3 mm long, basifixed, the filament attached to the connective at the lower $\frac{1}{5}$ of the anther; vestigial gynecium present as a tiny, rudimentary, 3-pronged structure in the center of the andrecium.

SPECIMENS EXAMINED.—KANDY DISTRICT: Peradeniya Botanical Garden [cultivated?], *without collector,* anno 1903 (NSW). KURUNEGALA DISTRICT: Kurunegala [as Kurunagalle], Aug 1847, *Gardner s.n., C.P. 972* (PDA); Dolukanda, *Soderstrom 2562* (US); [as Doluwa Kande], Dec 1883, *Trimen s.n.* (PDA); *Hinadure [as Himidoor], May 18[5]5, without collector, C.P. 972* (PDA). KEGALLA DISTRICT: Ca. 40 miles SE of Kandy, across river from Kitugala, *Gould and N. Balakrishnan 13874* (PDA, US); Kelaniya River, near Kitulgalle, *Kostermans 28395* (AAU). RATNAPURA DISTRICT: Sri Palabaddala, *Waas 419* (NY, PDA, US); *Gilimale, N. Balakrishnan 620* (PDA, US); Horagalkanda, Sinharaja, *Waas*

FIGURE 1.—*Scrotochloa urceolata: a,* habit of basal part of plant, showing decumbent culm with thick prop roots (× 0.6); *b,* habit of upper part of plant (× 0.6); *c,* enlargement of section of blade to show transverse veinlets; *d,* ligule, with twisted pseudopetiole (× 4); *e,* pseudopetiole showing twisting at summit (× 2); *f,* inflorescence showing point of disarticulation from peduncle (× 0.6); *g,* enlargement of surface of female glumes to show uncinate macrohairs. All drawings based on *Balakrishnan 620,* from Sri Lanka.


a
b
c
d
e
f
g
A.R.T.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2016 (NY, PDA, US). GALLE DISTRICT: Hinidun-kanda, *Jayasuriya et al. 1795* (PDA, US). DISTRICT UNKNOWN: Kekuna Ethula Mukalane, 3-2-[19]24, *de Silva s.n.* (PDA); Kopa Kande, Marawa Kale, 28 Feb. 1881, *without collector* (PDA); Kalugammana, *J.M. Silva 46* (BM, NSW, NY). LOCALITY UNKNOWN: *Walker* [*as Walk*] *1404* (PDA); *Walker s.n.* (GH); *C.P. 972* (BR, GH, LE, MEL, P, US).

DISCUSSION.—*Scrotochloa urceolata,* the only widespread species in this small, recent segregate of *Leptaspis,* reaches the western limits of its range in the wet forests of southwestern Sri Lanka and southern India. Both this species and its relative, *Leptaspis zeylanica,* occur in shaded forests, where individuals may form clones by decumbent culms that root at the lower and middle nodes. Because of the paucity of collections from Sri Lanka it is not possible to give the blooming phenology of this species for the island, but based on African and Asian collections it appears that both pharoid genera exhibit a flowering peak in the local rainy season.

The dispersal mechanism of *Scrotochloa urceolata* is quite specialized. The number of conspicuous or principal nodes in the rachis of the inflorescence is reduced to one, although often one or two naked, knob-like swellings are found on the peduncle between the uppermost foliage leaf and the whorl of panicle branches, indicating where additional panicle branches have been reduced and lost. At maturity the principal node of the inflorescence with its whorl of branches disarticulates from the summit of the peduncle (Figure 1*f*), and since the branches and female florets are covered with a dense indumentum of hooked macrohairs the entire structure is easily capable of adhering to animals. Unlike *Leptaspis zeylanica,* the inflated female florets are neither conspicuously ribbed nor brightly colored at maturity.

The Singhalese specimens of *S. urceolata* at our disposal did not include young inflorescences or mature fruits, so some material from Sumatra (*Bartlett 8223*) and New Guinea (*Brass 32709*) was used to prepare portions of the species description and illustration.

FIGURE 2.—*Scrotochloa urceolata,* dissection of spikelets: *a,* pair of spikelets: male left, female right, on clavate pedicel (× 12); *b,* glumes, 1st (left) and 2nd (right) of male spikelet (× 12); *c,* lemma of male spikelet (× 12); *d,* palea of male spikelet (× 18); *e,* andrecium with 6 stamens and pistillodium in center (× 12); *f,* 1st glume of female spikelet (× 12); *g,* 1st glume removed on female spikelet to show young fusiform anthecium with stigmas beginning to exit through apical pore (x 12); *h,* 2nd glume of female spikelet, inner view (× 12); *i,* 2nd glume of female spikelet, side view (× 12); *j,* lemma of young female spikelet covered with uncinate hairs and with stigmas and palea exiting through apical pore (× 12); k, tip of female palea enlarged (× 48); *l,* mature female spikelet, side view (× 6); *m,* mature female spikelet as viewed from above (× 6); *n,* gynecium showing the 3 subplumose stigmas (x 12); *o,* pistilodium (× 32); *p,* 6 staminodes at base of ovary (× 32); *q,* caryopsis showing broad linear hilum in groove (× 12); *r,* caryopsis showing basal embryo (× 12); *s,* palea of female spikelet (× 16). Drawings *a-e* and *o* based on *Bartlett 8223,* Sumatra; *f-k,n,p,* and *s* on *Brass 32709,* New Guinea; *l* and *m* on *Balakrishnan 620; q* and *r* on *Gardner s.n.* from Sri Lanka.

ANATOMY

FIGURE 3

(cf. Figures 7 and 8)

DESCRIPTION.—*Leaf-blade in transverse section. Outline:* blade flat, expanded, the margins somewhat reflexed; lamina thickness 175 μm. *Ribs and furrows:* absent, and no undulations associated with vascular bundles. *Midrib outline:* distinct abaxially projecting keel (Figure 3*a*), this representing the functionally adaxial side of blade as the pseudopetiole is twisted through 180° at its summit; symmetrical and semicircular or rounded in shape; no lacunae in parenchymatous ground tissue of keel. *Midrib abaxial vascular bundles:* 1 median and 2 minor vascular bundles present; median bundle with well-developed abaxial cap of sclerenchyma present, but with no girder linking it to the epidermis (Figure 3*a*), the fibrous tissue surrounding the phloem separated from the epidermis by a continuous layer of mesophyll cells; minor bundles also lacking girders. *Midrib adaxial vascular bundles:* 1 minor bundle, partially embedded in a thin, broad plate of sclerenchyma extending the width of the midrib. *Vascular bundle arrangement in lamina:* 9 first-order bundles present in leaf section, including single first-order bundle in keel. Number of third-order bundles between successive first-order bundles variable from midrib to margin: 5–7 present between midrib and first lateral first-order bundle, 10–12 separating central first-order vascular bundles and 5 or 6 between first-order bundles near margin. All bundles located in center of blade. *Vascular bundle description:* first-order bundles ovate, with broader side uppermost (Figure 3*b*); lysigenous cavity present; metaxylem vessels circular, with unthickened walls, of about the same diameter as the outer bundle sheath cells. Third-order vascular bundles elongated vertically, tall, angular, and narrow; xylem and phloem tissue distinguishable. *Vascular bundle sheaths of primary bundles:* double sheath present. Outer sheath square, composed of 16–18 cells with straight, vertical sides (Figure 3*b*), entire, although adaxial and abaxial cells much smaller than lateral cells; no bundle sheath extensions present. Cells achlorophyllous, regular in shape and distinct from chlorenchyma cells, although virtually same size, square-shaped with straight radial and outer tangential walls, the walls without secondary thickening. Inner mestome sheath entire, consisting of at least 2 layers of cells with uniformly thickened walls (Figure 3*b*). *Sclerenchyma:* girders not associated with vascular bundles but adaxial strands developed adjacent to all bundles (Figure 3*b*); minute abaxial strands sometimes associated with bundles. Thickened, lignified pairs of epidermal cells occurring throughout both epidermides, in surface view ap-

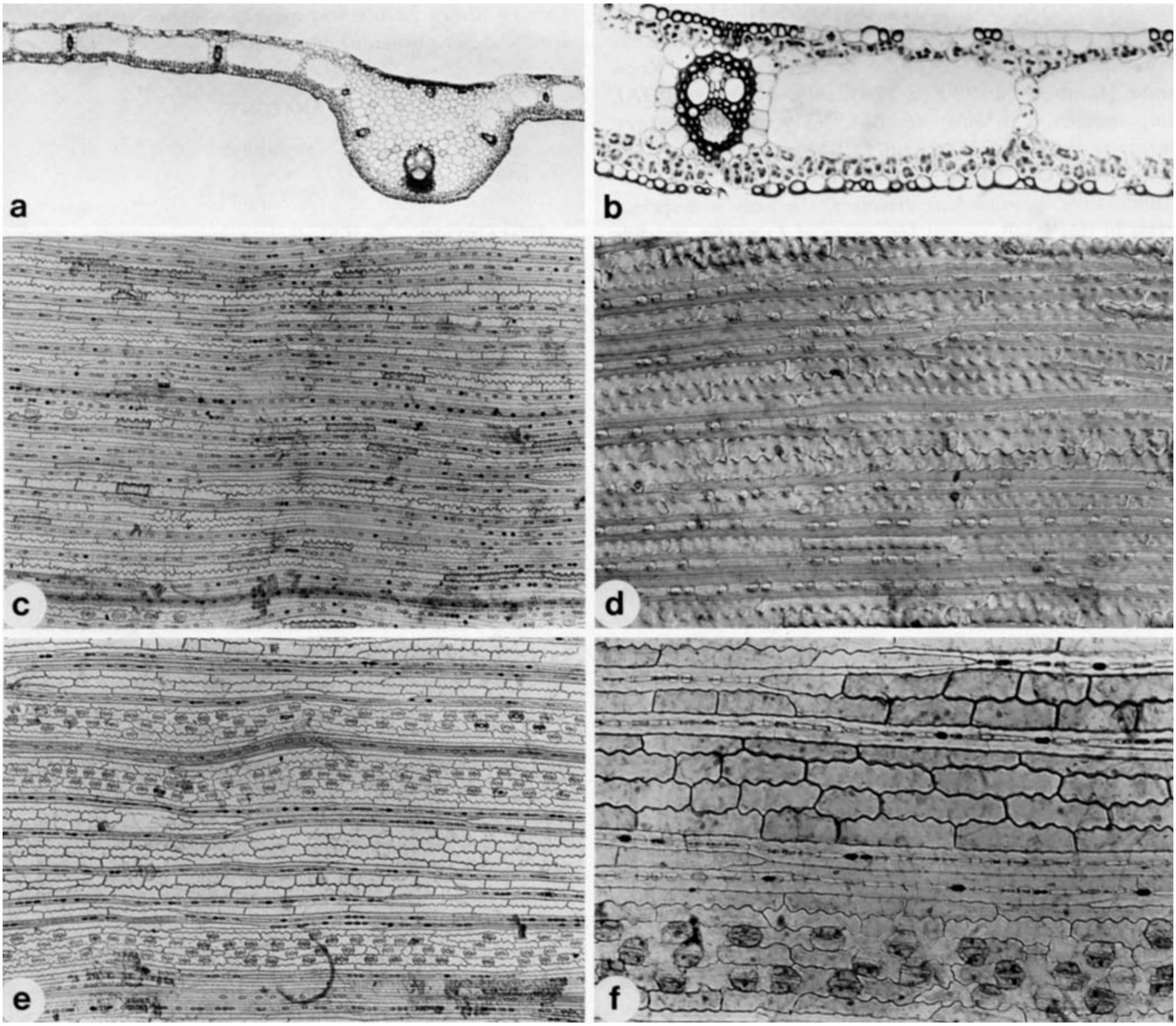

FIGURE 3.—Leaf anatomy of *Scrotochloa urceolata: a* and *b,* leaf-blade anatomy as seen in transverse section, the adaxial (downward-facing) surface facing up in these views; *a,* outline of midrib showing shape and vasculature (× 55); *b,* anatomical detail with fusoid cell shape, multi-layered mestome sheath and epidermal fibers in the intercostal zones visible (× 225); *c* and *d,* abaxial (upper) epidermis in surface view, the long axis of the leaf horizontal; *c,* general cellular arrangement showing little differentiation into costal and intercostal zones (× 90); a vein in located near the bottom, and many fibrous bands are visible in the upper portion; *d,* detailed structure of the intercostal fibrous bands showing their tapering and interconnecting ends and associated silica bodies, interference contrast, (× 225); *e* and *f,* adaxial (lower) epidermal structure. Note the strongly sinuous long cells; *e,* distinct stomatal bands flanking two veins, the intercostal zones composed of alternating areas of files of fibrous bands and long cells (× 90); *f,* stomatal band above vein (lower), fibrous bands and long cells (upper) (× 225). Based on *Soderstrom 2562* from Sri Lanka.

pearing as fibers (Figure 3*c–f*), each pair enclosing a short or long cell; no sclerenchyma present between bundles except for these fibrous bands scattered throughout both epidermides. Leaf margin with a small cap of fibrous tissue projecting into short, narrow point. *Mesophyll:* chlorenchyma not radiate, consisting of single layers of cells located immediately subjacent to both upper and lower epidermides; remainder of leaf thickness occupied by fusoid cell cavities. Uniseriate columns of chlorenchyma connecting adaxial and abaxial layers of chlorenchyma cells between adjacent fusoid cavities. Cells of abaxial (upper) chlorenchyma layer somewhat palisade-like, vertically oriented, tightly packed, larger than adaxial cells; arm cells poorly-developed, with only relatively short and indistinct inward-facing invaginations. Colorless parenchyma cells not present. *Bulliform cells:* absent on both epidermides. *Macrohairs,* *prickles, minute papillae:* absent on both epidermides. *Abaxial epidermal cells:* Long cells small, inflated, each with an individual cuticle on their outer tangential walls. Groups of fibrous bands occurring at regular intervals among files of typical long cells (Figure 3*b*); stomata not observed. *Adaxial epidermal cells:* intercostal long cells small, uniform in size, thin-walled, without distinct cuticle; groups of lignified fibrous bands interspersed among these normal long cells. Stomata occurring in bands on either side of vascular bundles, serving to indicate position of costal zones overlying the vascular bundles.

Abaxial epidermis: Costal and intercostal zones sometimes difficult to distinguish in surface view, as vascular bundles often not connected to epidermis by sclerenchyma girders. *Epidermal long cells:* consisting of two intergrading types. Normal long cells elongate-rectangular (length/width ratio 5:1; Figure 3*d*) with thin, often very sinuous lateral anticlinal walls and straight end walls, these grading into thick-walled, very elongate (length/width ratio over 100:1), lignified fibers with tapering ends, the latter occurring laterally in files of three contiguous cells, the central file containing costal-type silica bodies and small, short, thin-walled long cells, the two sandwiching lateral files of each group quite fibrous, exceedingly long (l.5–4 mm) and tapering, and either interlocking with another fiber or diverging into a V configuration, and making contact with normal intercostal long cells. Fibrous bands typically 6–10 between each costal zone, not continuous along leaf length but ending abruptly among normal intercostal long cells. *Bulliform cells:* absent. *Stomata:* infrequent in short, interrupted files (Figure 3*c*); subsidiary cells dome-shaped, sometimes with slightly flattened tops. *Intercostal short cells:* present only as interrupted files of silica cells interposed between the files of fibers in the fibrous bands; normal long cells not separated by short cells. *Papillae:* absent. *Prickles:* not present on specimens examined. *Microhairs:* none seen. *Macrohairs:* absent. *Silica bodies:* much narrower than other epidermal cells; small, horizontally elongated, round to oblong or somewhat dumbbell-shaped, usually single but sometimes paired and alternating with short to long cells between epidermal fibers; granules or vesicles present in all bodies. *Costal cells:* very narrow, with silica bodies present only as single files between epidermal fibers; of short to medium length and often appearing to be silicified. Files of fibers located below vascular bundles probably continuous along the whole length of associated bundle.

Adaxial epidermis: Similar to abaxial epidermis, but with costal and intercostal zones well-demarcated. *Stomata:* occurring in bands of 3–4 cells on both sides of the costal zones (Figure 3*e*); subsidiary cells dome-shaped but appearing to be flat-topped, as stomatal complexes are located below the level of the adjacent long cells (Figure 3*f*); stomatal rows adjacent to one another, a single interstomatal long cell separating successive stomata in a file. *Intercostal fibrous bands:* present, fewer in number (5–7) than on abaxial epidermis, and with no fibrous cells transitional to normal long cells. Fibers tapering to long, sharp points, occasionally branching. *Intercostal long cells:* of normal type, shorter, wider, and slightly less sinuous than their abaxial counterparts (Figure 3*c–f*).

SPECIMENS EXAMINED.—*S. urceolata: Soderstrom 2562,* Sri Lanka (US); *Brass 29119,* New Guinea (US).

DISCUSSION.—The prominent fusoid cells and complex midrib vasculature observed in leaf cross-sections of this species are familiar bambusoid features, but the intercostal fibrous bands of *Scrotochloa* (Rao and Naidu, 1981; Renvoize, 1985; Figure 3) and its relatives, *Leptaspis* (Metcalfe, 1960; Clifford and Watson, 1977; Palmer and Tucker, 1981) and *Pharus* (Metcalfe, 1960; Renvoize, 1985; Figure 8) are without exact parallel in the family. Each band consists of lateral files of elongate, thick-walled, tapering fibers that invariably enclose a single central file of silica cells, prickles, or modified, small long cells. On the abaxial surface of *Scrotochloa urceolata* (Figure 3*c*) there appears to be a complete gradient between these fibers and typical thin-walled, sinuous long cells. On the adaxial surface of the species, however, as well as on the abaxial epidermides of all the *Pharus* species examined for this study (Figure 8), there is a fairly sharp demarcation between the two types. Thus, preliminary evidence indicates that *Scrotochloa,* although advanced morphologically, may be primitive with respect to this character.

Genus *Leptaspis*

Leptaspis R. Brown, 1810:211.

TYPE SPECIES.—*L. banksii* R. Brown.

DIAGNOSIS.—Plants cespitose or spreading by decumbent, rooting culms; culms solid. *Leaves:* sheaths compressed; blades narrow and linear to broadly elliptic. *Inflorescence:* a long-pedunculate panicle bearing appressed or spreading, single or whorled, persistent branches. *Spikelets:* paired, the female large, subsessile, the male small, pedicelled. *Female spikelets:* sometimes subtended by a glume-like bract; true glumes 2, persistent, cuspidate; lemmas with fused margins, at maturity becoming bladder-like and forming a shell-shaped (cochleate) utricle, strongly 7-ribbed, covered with uncinate macrohairs, somewhat indurate, the style exiting through a lateral pore; palea narrow, longer than the lemma and exiting through the pore; stigmas subplumose. *Male spikelets:* glumes persistent, shorter than the deciduous floret; lemmas more or less tubular; lodicules 0–3; basic chromosome number, $n = 12$ (Hunziker, Wulff, and Soderstrom, 1982).

DISTRIBUTION.—Tropics of the Old World, from Guinea eastward to Madagascar, Sri Lanka, Taiwan, Australia, New Caledonia, and the Fiji Islands.

SPECIES OF *Leptaspis* IN SRI LANKA.—*Leptaspis zeylanica.*

Key to the Species of *Leptaspis*

1\. Main inflorescence branches in whorls of 3; leaf-blades 2.5–6 cm wide, glabrous; bract subtending 1st female glume present; Guinea, Sri Lanka, to New Guinea, Bougainville . . . . **L. zeylanica**
1\. Main inflorescence branches borne singly at the nodes; leaf-blades 1–2.5 (–3.5) cm wide, glabrous or puberulent beneath (adaxially); bract subtending 1st female glume typically absent 2
    2\. Leaf-blades lanceolate, (1.5–) 2–3 (–3.5) cm wide, puberulent beneath; Taiwan, Indonesia to New Caledonia, Australia . . . . **L. banksii**
    2\. Leaf-blades linear, about 1 cm wide, glabrous; Fiji Islands . . . **L. angustifolia**

Leptaspis zeylanica

Leptaspis zeylanica Nees ex Steudel, 1853:8. [Type: Sri Lanka. Neotype, here designated: Sri Lanka, without locality or collector, C.P. 896, B!]

Leptaspis cochleata Thwaites, 1864:357. [Type: Sri Lanka, Central Provinces. Lectotype [chosen by C.C. Mez in 1922]: Sri Lanka, without locality or collector, C.P. 896, B!] Hooker f., 1900:191; Senaratna, 1956:22; Bor, 1960:617, fig. 73.

Leptaspis conchifera Hackel, 1887:211–212, pl. G, fig. A. [Type: São Tomé, "prope Morros de Monte Café ad 850 m (Moller) et prope Mongo ad 480 m (Moller); Angolares (F. Quintas)." Holotype, *Moller and Quintas 148,* W, not seen; isotype, K, not seen; fragment of holotype, US! sheet no. 81844.]

Leptaspis comorensis A. Camus, 1924:513. [Type: Comoro Islands, *Humblot 321.* Holotype, P!; isotypes, BM!, K, not seen.]

MORPHOLOGY

FIGURE 4

DESCRIPTION.—*Plants:* with shallow rhizomes, the strongly ribbed internodes 1–6 cm long, the sheathed nodes each bearing a thick, hard, long, adventitious (prop) root, this bearing fibrous roots; rhizome continuous into the aerial axis (culm) of the plant, or new culms sometimes borne from a decumbent node. *Culms:* up to 1 m tall, covered by overlapping sheaths. *Leaves:* sheaths elongate, glabrous, strongly ribbed, narrowed to the ligule and continuous with the pseudopetiole, sparingly tessellate on the outer surface, glabrous, the ribs of the sheath continuous with those of the abaxial face of the blade; blades oblong-lanceolate, 10–20 cm long, 2.5–5 cm wide, flat, narrowed at the base into a pseudopetiole $^1/_{10}$–$^1/_{15}$ the length of the blade, the apex acute; upper (morphologically abaxial) surface glabrous except for the pilose adaxial surface of the pseudopetiole, the midvein slightly elevated, green, strongly ribbed, the primary veins emanating from it along the lower half, tessellate; lower (morphologically adaxial) surface glabrous, strongly tessellate, the broad midvein flush with the epidermis, stramineous, smooth, shiny; ligule about 0.25 mm long, membranous, densely ciliate on the abaxial surface. *Peduncle:* exserted, 5–10 cm long, densely covered with uncinate hairs. *Inflorescence:* a narrowly ovoid panicle to 30 cm long, the rachis strongly angled and covered with uncinate macrohairs, bearing whorls of branches at the nodes; primary branches ascending or held at an acute angle or sometimes elongate, lax, and horizontally positioned, covered with a fine mat of uncinate hairs, 3 (–5) branches to about 15 cm long radiating from the lower nodes and fewer and shorter branches from the upper nodes, pulvinate at the base on the upper surface, the branches not disarticulating at maturity. Branchlets bearing spikelets sometimes subtended by a deciduous, narrow, glume-like bract about 1 mm long (Figure 4*e*, arrow), terminating in a male spikelet and bearing about 1–2 mm below it a subsessile female spikelet. *Female spikelets:* subtended by a deciduous, lanceolate-triangular glume-like bract 3–4 mm long placed below and slightly lateral to the 1st glume and separated from it by a short internode; glumes 2, subequal, broadly ovate with a cuspidate tip, about 2–2.5 mm long, 1(–3)-nerved, persistent, becoming horizontal and relatively indistinct under the expanded lemma; floret 4–5 mm long, ovate and symmetric when young, purplish-brown, at maturity greatly inflated, cochleate, the surface stramineous, pinkish, or purplish and covered with a dense mat of small uncinate hairs, strongly 7-nerved, the nerves elevated; palea about half the length of the lemma, broader at the base and flat, becoming sulcate above between the 2 keels, bifid at the apex, glabrous; ovary glabrous; style 1, stigmas 3, subplumose; andrecium not seen in material examined; caryopsis not seen. *Male spikelets:* slightly overtopping the female, terminating the entire inflorescence, about 3.5 mm long, ovoid, purplish-brown, the glumes broadly ovate, narrowed abruptly to a cuspidate tip, subequal, about 1.2 mm long, glabrous, 1-nerved, persistent; lemmas broad, somewhat inflated, 3-nerved, covered with minute dark brown hairs, 3.3–3.5 mm long; palea

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FIGURE 4.—*Leptaspis zeylanica: a,* habit of plant showing decumbent culm with prop roots (× 0.6); *b,* upper leaves of culm (× 0.6); *c,* inflorescence, showing primary branches in whorls of 3 (× 0.6); *d,* branches of inflorescence enlarged to show pulvini (× 5.5); *e,* pair of young spikelets (× 11), male left, female, right; note glume-like bract subtending the 1st female glume, and second bract (arrow) subtending the branchlet bearing the male-female spikelet pair; *f,* andrecium of 6 stamens with pistillodium in center and palea extending behind (× 23); *g,* mature spikelet pair, male on left, female with inflated lemma on right (× 7.5). Drawings *a, c,* and *e* based on *Gardner s.n.,* Matale, Dec 1846, *C.P. 896; b, d, f,* and *g* on *Sumithraarachchi 602,* both from Sri Lanka.


g
d
b
c
f
a
e
A.R.T.

shorter than the lemma, about 2.6 mm long, linear, bifid at the apex, membranous; lodicules 3, the anterior pair broad, rounded, glabrous, nerveless, about 0.3 mm long, the posterior reduced; stamens 6, the anthers orange-yellow, 2.1–2.6 mm long, basifixed, the filament attached to the connective at the lower ⅕ of the anther; rudimentary gynecium not seen.

SPECIMENS EXAMINED.—MATALE DISTRICT: Gammaduwa, *Alston 670* (PDA); *C.P. 896* (PDA), *O. C.* [?] *1045* (PDA); Matale, *C.P. 896* (PDA); *Gardner s.n.*, Dec 1846 (PDA); *C.P. 896* (US). KANDY DISTRICT: Hantane, *Gardner 1045* (NY); Boyagoda Kanda, near Galagedera, 7°23′N, 80°30′E, *Sumithraarachchi 602* (B, PDA, US). LOCALITY UNKNOWN: *C.P. 896* (BM, BR, LE, P); anno 1827–1830, *Macrae 810* (BM).

DISCUSSION.—*Leptaspis zeylanica* has one of the widest ranges of any herbaceous bamboo, extending nearly halfway around the globe (160° of longitude), from the west coast of Africa to the Solomon Islands. The genus is unusual in the tribe in that neither the inflorescence nor its branches disarticulate at maturity, although the mature female florets readily detach from the glumes and adhere to clothing and presumably also fur and feathers. Label data of collectors on specimens from outside of Sri Lanka indicate that these shell-like, utriculate diaspores often have a showy, pink or purple color at maturity, and that the prominent ribs are white or dark-colored. Clearly, animal interactions with this grass must be complex, and our understanding of the subject would benefit from further study.

Very few good Sri Lanka collections of this species were available for study. Most male florets had already fallen from our material, and it was difficult to find any with the stamens still present. Measurements of these organs were therefore taken from those of a plant collected in Cameroon (*Mildbraed 7856*, US).

Steudel (1853) described *Leptaspis zeylanica* as having "oblong leaves and pseudopetioles pubescent below toward the midrib, variable in having a composite raceme with subrotund, cuspidate valves [female florets] and a simple raceme with ovate-acuminate valves" [translated from the Latin]. In the same work he also described *L. manillensis* (with a "verticilled panicle" and "oblong valves"), since shown to be the same as *Scrotochloa (Leptaspis) urceolata*, with which the author was evidently not familiar. The two genera of Ceylonese Phareae are quite similar vegetatively in that both have oblong leaf blades that narrow below into twisted pseudopetioles. In *S. urceolata*, however, the pseudopetioles are completely glabrous, while in *L. zeylanica* they are densely pubescent on the inner surfaces. Also, the female florets in this species are subrotund, not oblong as in *Scrotochloa*, and the inflorescence does resemble a "composite raceme," whereas *Scrotochloa* has an umbelliform panicle. It is evident that Thwaites (1864) described *Leptaspis cochleata* because he mistakenly considered *L. zeylanica* to be synonymous with *Scrotochloa (Leptaspis) urceolata. Leptaspis zeylanica* Steudel thus takes precedence over the later name of Thwaites, and we here designate the Berlin specimen from Sri Lanka, labelled "C.P. [Ceylon Plants] 896," to serve as the neotype. This specimen has also been chosen as the type of *Leptaspis cochleata* Thwaites by C.C. Mez in March 1922, as indicated by his annotation of the Berlin specimen. Sheets marked "C.P. 896" are found in many European herbaria, but since the "C.P." series numbers were essentially species numbers it is impossible to be certain that they all come from the same locality.

ANATOMY

No preserved anatomical material of *Leptaspis zeylanica* was available for this study, but based on the descriptions and illustrations of African material of this species by Metcalfe (1960), Jacques-Félix (1962), Palmer and Tucker (1981), and research in progress, the leaf anatomy of this taxon appears to be quite similar to that of the species of *Scrotochloa* (Figure 3) and *Pharus* (Figures 7 and 8) examined. In transverse blade sections *L. zeylanica* is hardly distinguishable from its sister genera, but in epidermal views it rather surprisingly bears a closer resemblance to *Pharus* than it does to *Scrotochloa.* In common with all *Pharus* species, but unlike *Scrotochloa,* the abaxial (lower) blade surface of *L. zeylanica* exhibits prominent inflated interstomatal cells (see Palmer and Tucker, 1981), and the silica bodies are consistently dumbbell-shaped. As is typical of pharoid grasses, intercostal fibrous bands are prominent on at least one epidermis.

Tribe STREPTOGYNEAE

STREPTOGYNEAE C.E. Hubbard ex Calderón and Soderstrom, 1980:18.

TYPE GENUS.—*Streptogyna* P. Beauvois.

DIAGNOSIS.—Forest grasses forming cespitose clumps or spreading by rhizomes. *Leaves:* blades linear-lanceolate to broadly lanceolate, narrowed below to a pseudopetiole-like base, the nerves parallel, transverse veinlets not manifest, the midvein and secondary nerves clearly manifest on the lower surface; outer ligule present as a small hard rim with irregular margins; inner ligule short, membranous. *Inflorescence:* an erect one-sided raceme. *Spikelets:* several-flowered; florets hermaphrodite, the upper ones reduced and not fertile, disarticulating between the fertile florets above the glumes, each floret falling attached to the extended curved rachilla segment above it; glumes 2, persistent, the lower shorter than the upper, the upper convolute and enclosing the floret at its base; lemmas narrow, elongate, awned, many-nerved; paleas strongly 2-keeled, sulcate between the keels; lodicules 3; stamens 2 or reportedly 3; ovary with a long style and 2 or 3 spiraling stigmas, these becoming hardened and persistent, intertwined at maturity with the stigmas of other florets in the same spikelet and inflorescence; fruit a linear caryopsis, with a narrow hilum equaling its length; embryo small, basal. Basic chromosome number, $n = 12$ (Tateoka, 1958b).

DISTRIBUTION.—One genus of two species occurring in the tropics of Latin America, Africa, southern India, and Sri Lanka. The range of *Streptogyna* is strikingly paralleled by that of the centothecoid genus, *Orthoclada.*

This is the only genus of herbaceous bamboos that is native to the tropics of both hemispheres and studies are underway to determine the relationships of the species to each other and to the other herbaceous bamboos.

Genus *Streptogyna*

Streptogyna Palisot de Beauvois, 1812:80.

TYPE SPECIES.—*S. crinita* P. Beauvois.

SPECIES OF *Streptogyna* IN SRI LANKA.—*Streptogyna crinita.*

Key to the Species of *Streptogyna*

Stigmas 2; plants rhizomatous; leaf-blades (10–) 15–36 mm wide; callus of floret pilose; Paleotropical .... ***S. crinita***

Stigmas 3; plants cespitose; leaf-blades 8–16 (–24) mm wide; callus of floret glabrous; Neotropical .... ***S. americana***

Streptogyna crinita

Streptogyna crinita Palisot de Beauvois, 1812:80 + pl. 16, fig. 8. [Type (*fide* Hubbard, 1956): Nigeria, *Palisot de Beauvois s.n.* Holotype: P, not seen.] Thwaites, 1864:374; Bor, 1960:649.

Streptogyna gerontogaea Hooker f., 1900:301–302. [Type (*fide* Hubbard, 1956): Sri Lanka, *without locality or collector, C.P. 922.* Holotype, K, not seen.] Senaratna, 1956:34.

MORPHOLOGY

FIGURE 5

DESCRIPTION.—*Culms:* erect 75–100 cm tall, each representing the aerial extension of an upturned sympodial rhizome, the culm itself producing at its base 1–3 additional rhizomes to 25 cm long, these with short internodes about 1 cm long covered by the overlapping sheaths. *Leaves:* evenly distributed along the culm, the sheaths not overlapping; sheaths glabrous, strongly ribbed, extending upward along both sides of the blade pseudopetiole and contiguous with the inner ligule; blades up to 26 cm long, 2.5 cm wide, broadly lanceolate and tapering at both ends, acute at the tip, narrowed below to a pseudopetiolate base, narrower than the summit of the sheath, 6 primary nerves present on either side of the midrib; upper blade surface pale green, with scattered spinelike hairs, lacking manifest transverse veinlets, the midrib not pronounced; lower surface darker green than the upper, glabrous, transverse veinlets manifest, the midvein conspicuous, thick, shiny; outer ligule about 0.5 mm long, indurate; inner ligule about 1.2 mm long, the upper margin erose, ciliate on the abaxial (outer) surface, glabrous on the adaxial surface. *Inflorescence:* terminating the culm, racemiform, 20–22 cm long, secund, containing 20–25 overlapping spikelets; axis appressed-pubescent, rounded on the back, with the outer surface flat or grooved; rachis slightly twisted, bringing all spikelets into alignment. *Spikelets:* pale green, 4- or 5-flowered, slightly laterally compressed, the first floret most developed, with reduction upwards; 1st glume about 12 mm long, linear-lanceolate, glabrous, 3-nerved, transversely veined, attached to the side of the thickened pedicel that supports the second glume; 2nd glume about 26 mm long, elliptic-lanceolate, glabrous, 17-nerved, the nerves of various thicknesses, not all extending the length of the glume, with numerous transverse veinlets and an antrorsely scabrous awn 1–2 mm long; lemma of lowest floret about 19 mm long, lanceolate, firm and thick except for the broad scarious margins, 9-nerved, the two halves tightly folded, sparingly appressed-pubescent on the lower half, the base extended beyond the attachment of the lemma and palea into a pubescent stipe (glabrous in the upper reduced florets), the midnerve thickening above into an antrorsely scabrous awn about 15 mm long, this becoming elongated and coiled at maturity; palea about 13 mm long, glabrous and bowed-out below, narrowed above and puberulent, strongly 2-keeled, the keels close together and grooved between them; rachilla internodes elongated, glabrous, curved, with an oblique apex and base; lodicules 3, thin, narrowly obovate, glabrous, with a few tiny hairs at the tip, the anterior pair 1.6–2.4 mm long, 1–5-nerved, the posterior one a little shorter, 1.6–1.8 mm long, 1–3-nerved. *Andrecium:* stamens 2, the filament weak and ribbonlike, the anthers yellow, basifixed. *Gynecium:* ovary fusiform, long-ciliate on the upper third and lower part of the style; style long, flattened, with sparse appressed hairs; stigmas 2, strongly retrorsely barbed above, the barbed portions elongating and coiling with age, eventually becoming entangled with each other and with the awns of the lemmas; fruit a caryopsis about 15 mm long, narrow, elongated, slightly tapering, the ciliate summit of the ovary persistent at its apex; hilum narrow, linear, extending the full length of the fruit; embryo about 1/11 the length of the caryopsis.


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SPECIMENS EXAMINED.—KURUNEGALA DISTRICT: Dolukanda, *Senaratna 2700* (PDA). MATALE DISTRICT: Matale, Dec 1846, *Gardner s.n., C.P. 922* (PDA). COLOMBO DISTRICT: Henaratgoda, 3 Jan 1881, *Ferguson s.n.* (PDA). MONERAGALA DISTRICT: Buttala to Sirigala, 3 Mar 1907, *Rock s.n.* (PDA).

DISCUSSION.—The stigmas of this genus are unusual, and perhaps unique in the grasses, in that they continue to grow after performing the usual function of pollen reception. *S. crinita,* especially, is unusual in that the stigmas develop hardened, retrorse barbs. The filaments of the stamens are weak and ribbon-like, and field observations will be needed to determine whether the anthers are exserted or not. Although only two stamens were observed in the florets of the material studied, both Bentham (1881) and Jacques-Félix (1962) report that this genus may also have three stamens. The description and illustration of the caryopsis was based on a specimen from Cameroon (Africa) (*Buesgen 530*).

Hubbard (1956) pointed out that the name *S. crinita* had long been misapplied to the American species, and that Hooker (1900), unaware of this, renamed the Ceylonese species *S. gerontogaea,* basing that epithet on a Kew specimen labelled *C.P. 922.* Realizing that *S. crinita* applied to the Asiatic specimens and that the American species was without a name, Hubbard therefore described the latter as *S. americana.* As in the case of *Leptaspis zeylanica,* other sheets labelled "C.P. 922" cannot unequivocally be considered to represent type material.

At maturity the antrorsely scabrous lemma-awns and all spikelets in the inflorescence are collectively bound together by the retrorsely barbed stigmas, which coil around each other. The entire mass then has the potential to disarticulate and adhere to passing forest animals. The pointed callus of the lemma and the persistent rachilla internode may also facilitate adherence to fur or feathers. The survival of *Streptogyna* in both hemispheres may have been due in part to this epizoochorous dispersal mechanism. The two species are so similar in details of inflorescence and spikelet structure that they cannot be separated into two genera, and it is not obvious which taxon is more primitive. Studies of the anatomy and morphology of both species are underway.

FIGURE 5.—*Streptogyna crinita: a,* base of plant showing sympodial habit of rhizomes (× 0.6) *b,* leafy portion of mature culm terminating in young inflorescence (× 0.6); *c,* mature inflorescence (× 0.6); *d,* ligular region, showing inner and outer ligules (× 7); *e,* young spikelet (× 2.5); *f,* glumes (× 3.5); *g,* spikelet without glumes (× 3.5); *h,* section of lemma awn showing antrorse scabrosity (× 30); *i,* base of lower fertile floret and succeeding rachilla segment (× 11); *j,* palea of fertile floret with succeeding rachilla segment (× 7); *k,* lodicules, at left the posterior lodicule and others the anterior lodicules (× 15); *l,* andrecium of 2 stamens with ribbonlike filaments and gynecium showing the hairy ovary and style and 2 stigmas (× 7); *m,* section of stigma showing retrorse scabrosity (× 30); *n,* caryopsis, showing small embryo at base and persistent hairy apex of ovary (× 5.5); *o,* caryopsis, showing narrow, elongated hilum, and persistent hairy apex of ovary (× 5.5). Drawing *a* based on *Rock s.n.,* 8 Mar 1907, Sri Lanka; *b-i* on *Senaratna 2700,* Sri Lanka; *j, l, and m* on *Trimen s.n.,* Henaratgoda, 3 Jan 1881, Sri Lanka; *k* on *Gardner s.n.,* Dec 1826, Sri Lanka; *n* and *o* on *Buesgen 530,* Cameroon, Africa.

ANATOMY

FIGURE 6

DESCRIPTION.—*Leaf-blade in transverse section. Outline:* blade flat to broadly U-shaped with margins curved slightly upwards. *Ribs and furrows:* slight ribs and furrows present (Figures 6*e–f*). *Midrib outline:* keel present, triangular, with complex vasculature; abaxially projecting. *Midrib abaxial vascular bundles:* large median bundle present, this connected to the epidermis by an anchor-shaped girder of sclerenchyma; two additional first-order bundles present, these connected to the epidermis by smaller sclerenchyma girders; smaller bundles 8, 5 of these variously oriented and embedded in the mass of fibrous tissue (Figure 6*e*) supporting the median bundle. *Midrib adaxial vascular bundles:* large first-order bundle present, this with a cap of fibers only barely touching the epidermis; minor bundles 2, without sclerenchyma girders. *Vascular bundle arrangement in lamina:* first-order bundles 13; third-order bundles 6 or 7 between consecutive large bundles; all bundles located slightly towards the abaxial side of blade. *Vascular bundle description:* first-order bundles ovate with broadest side adaxial; phloem surrounded by fibers; lysigenous cavity and protoxylem vessel present; metaxylem vessels thickened, circular, with diameters greater than the outer bundle sheath cells; third-order bundles vertically elongated, elliptical; phloem easily distinguishable. *Vascular bundle sheaths:* outer bundle sheaths of first-order vascular bundles ovoid, consisting of about 20 cells, with narrow adaxial and wide abaxial interruptions (Figure 6*b,f*); bundle sheath extensions absent; chloroplasts absent, the cells thus distinct from chlorenchyma cells; inner (mestome) sheath of first-order vascular bundles complete; cell layers 2 or 3 (Figure 6*b,f*), the cells with uniformly thickened walls; outer sheath surrounding third-order bundles entire, consisting of 7–11 cells, a distinct gradation in size occurring between the large lateral outer bundle sheath cells and the very small adaxial cells, which are about the same size as inner sheath cells (Figure 6*b*). *Sclerenchyma:* small trapezoidal adaxial girders developed in association with all vascular bundles. *Mesophyll:* arm cells relatively conspicuous (Figure 6*f*); no tendency toward a palisade-like arrangement of adaxial chlorenchyma cells displayed; chlorenchyma subjacent to adaxial epidermis 2 or 3 cell layers thick, and that subjacent to abaxial epidermis 1 or 2 layers thick; fusoid cells distinct and clearly demarcated, short and ovoid in shape, successive fusoid cells separated by 3 or more arm cells; colorless parenchyma cells absent. *Bulliform cells:* present on adaxial

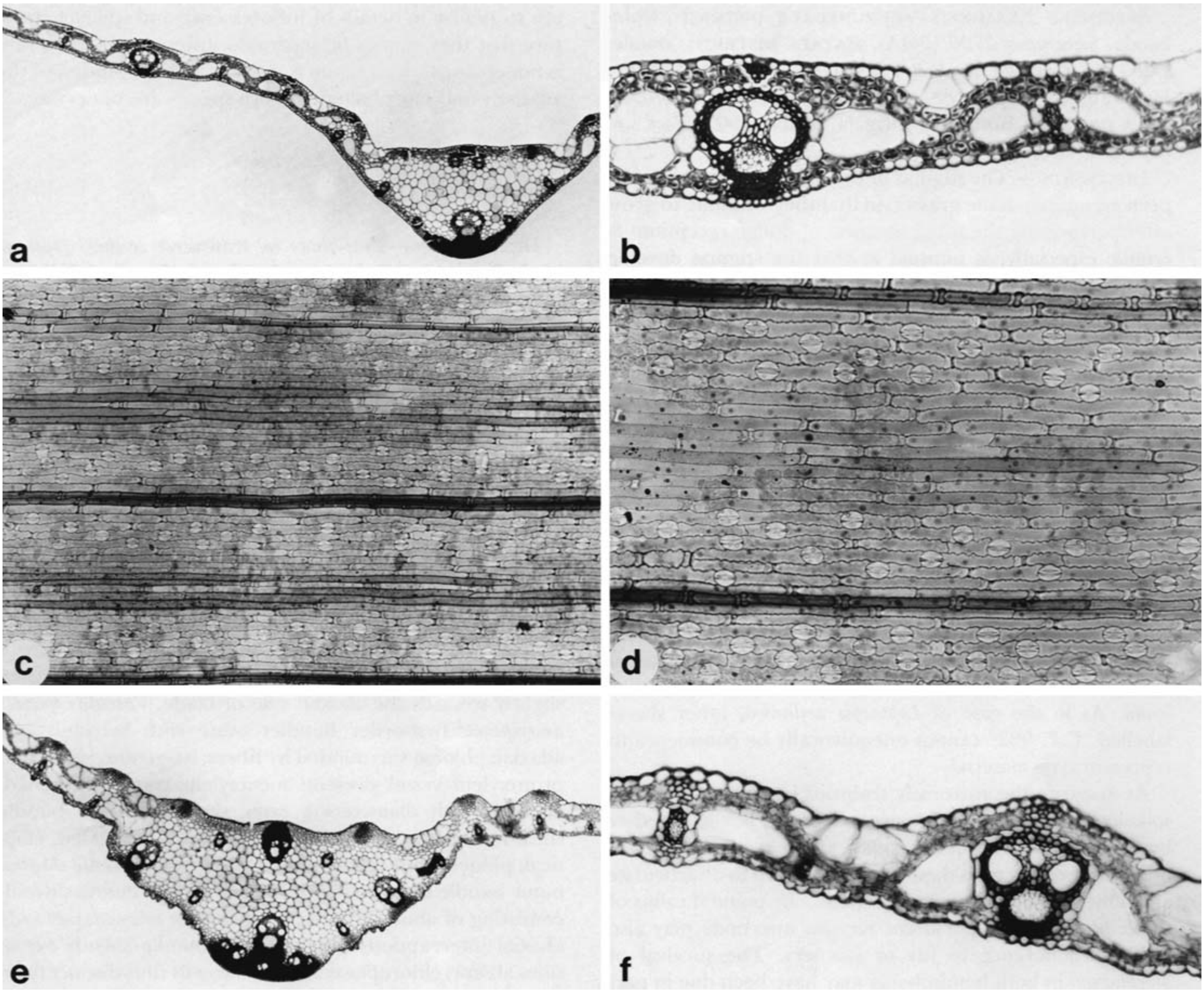


FIGURE 6.—Leaf anatomy of the genus *Streptogyna: a-d, S. americana: a,* outline of midrib showing shape and complex vasculature of the keel (× 60); *b,* anatomical detail showing fusoid cell shape and multi-layered inner bundle sheath of first-order vascular bundles (× 240); *c,* abaxial epidermis showing poorly differentiated costal zones (× 150); *d,* abaxial epidermis illustrating fiber-like long cells in centre of intercostal zones and absence of papillae and epidermal appendages (× 240); *e* and *f, S. crinita: e,* outline of leaf blade in region of keel (× 60); *f,* detail of leaf blade anatomy with double inner bundle sheath (× 240). *Streptogyna americana* from *Soderstrom and Sucre 1906,* Brazil; *S. crinita* from *Linder 1012,* Liberia.

surface only, in discrete, fan-shaped groups between all vascular bundles, occupying about one-third of the blade thickness, each group consisting of 3 or 4 cells with the outer tangential walls shorter than the inner walls; lateral walls straight (Figure 6*b,f*). *Adaxial epidermal cells:* bulliform cells present; outer tangential wall of all epidermal cells, except bulliform cells, covered by distinct, continuous cuticle; macrohairs, prickles, and papillae not seen. *Abaxial epidermal cells:* bulliform cells absent; outer tangential wall with continuous cuticle; macrohairs and papillae absent; prickles present.

Abaxial epidermis. Intercostal long cells: markedly elongated, particularly in center of intercostal zones; cells somewhat fiber-like, with tapering ends and much more than 3 times longer than wide (Figure 6*c,d*); side walls parallel, end walls vertical; horizontal anticlinal walls only slightly undulating; shape of all abaxial long cells (both costal and intercostal) remarkably similar and constant throughout abaxial epidermis; most long cells separated from horizontally adjacent neighbors by single short cells or silico-suberose couples; interstomatal cells with relatively sinuous walls. *Stomata:* 4 or 5 irregular horizontal files of stomata present on either side of costal zones, some files present in adjacent files of intercostal long cells, the two stomatal zones in each intercostal zone separated by up to 10 files of fiber-like long cells; individual stomata in a file separated by 1 or 2 interstomatal long cells, these elongated and where adjoining one another separated by paired short cells (Figure 6*d*); subsidiary cells uniformly low-domed-shaped, their papillae small, indistinct or absent. *Intercostal short cells:* paired or rarely solitary, present between virtually all intercostal long cells; cork cell tall and narrow, with a somewhat crenate outline; silica body saddle-shaped but vertically elongated. *Papillae:* absent except for minute and indistinct papillae present only on subsidiary cells. *Prickles:* none seen. *Microhairs:* none seen. *Macro-hairs:* absent. *Silica bodies:* vertically elongated, tall saddle-shaped; costal and intercostal silica bodies of similar shape, of same width as associated long cells; invariably associated with cork cells, these cork-silica cell pairs separated by elongated long cells. *Costal zones:* very narrow, 1–3 cells wide, consisting of parallel-sided, elongated long cells with slightly thickened walls.

Adaxial epidermis: Similar to abaxial epidermis, except that 3 or 4 files of colorless, equidimensional, hexagonal bulliform cells are present in center of intercostal zones, these angular, straight-walled, and interlocking with one another. A few small prickles present on edges of files of bulliform cells.

SPECIMEN EXAMINED.—*S. crinita: Linder 1012,* Liberia (K).

DISCUSSION.—The multi-layered mestome or inner sheath observed in Liberian material is also clearly illustrated by Jacques-Félix (1962) for African *S. crinita,* but Tateoka's (1958a) drawing of a Sri Lanka specimen shows only a single-layered inner sheath, and the multi-layered condition is not mentioned by Metcalfe (1960), who also examined the Linder collection cited above, or by Renvoize (1985), who studied material from Ghana.

The structure of the adaxial chlorenchyma tissue is not palisade-like in either of the specimens we examined (Figure 6*b,f*), or in the drawings of *S. crinita* published by Tateoka (1958a) and Jacques-Félix (1962). The unfixed specimen of *S. crinita* examined in this study had chlorenchyma with distinct arm-like invaginations and closely resembles the condition shown in the plate of Jacques-Félix (1962). The Ceylonese specimen studied by Tateoka (1958a) apparently lacks well-developed arm cells, but perhaps the drawing may simply lack this detail. It is possible that Asian and African *S. crinita* specimens, then, show slight but distinct differences in arm cell development and in the nature of the inner bundle sheath; clearly, more material of this species and its New World congener needs to be examined with regard to these characters. The Brazilian specimen of *S. americana* (Figure 6*b*) studied lacks distinct arm cells and its adaxial and abaxial chlorenchyma cells are only two layers and one layer thick, respectively.

Bulliform cell groups are well developed in *Streptogyna* and the fusoid cavities of both species are fully developed across the full width of the leaf. This led Metcalfe (1956) to suggest bambusoid affinities for the genus.

The epidermal structure of *Streptogyna* is of particular interest in that it differs somewhat from the typical bambusoid configuration. The extremely long, fiber-like cells in the centers of the abaxial intercostal zones of *S. americana* (Figure 6*c*) have not been referred to before; the epidermis illustrated by Jacques-Félix (1962) for *S. crinita* does not appear to possess this type of cell (although the drawing does not include a full intercostal zone), and Renvoize's (1985) drawing of this epidermis shows elongate cells with sinuous walls. In transverse sections of *S. americana* examined (Figure 6*a*) there is no indication that these cells are actually fibers; indeed, they closely resemble normal long cells when viewed in this plane. This unusual cell type may conceivably indicate a relationship with the pharoid grasses and it will be interesting to determine whether they occur consistently in one or both *Streptogyna* species.

Streptogyna possesses few epidermal appendages, although prickles have been reported in *S. crinita* by Metcalfe (1960), Jacques-Félix (1962), Palmer and Tucker (1981), and Renvoize (1985), the last author illustrating them as abundant on the abaxial epidermis. In the present study no prickles were observed on the abaxial epidermis of *S. crinita,* although a few were present on the adaxial surface. Very scattered delicate, spinelike macrohairs are present in the leaves of many African collections (e.g., *Fosberg 40539,* Ivory Coast, US), but the absence of microhairs and distinct, minute papillae in the genus is supported by all workers who have studied its anatomy. This condition is rare in bambusoid grasses.

Phylogenetic Considerations

MORPHOLOGICAL AND ANATOMICAL DIAGNOSIS OF THE BAMBUSOIDEAE

Given the importance of leaf anatomy in delimiting the graminoid subfamilies and the broad sense in which the Bambusoideae is now interpreted, it is difficult to present an unambiguous morphological diagnosis of the group. Soderstrom's (1981) characterization of the main morphological features of the subfamily, excluding the Oryzeae, includes the following very general tendencies that are found in most tribes: Leaf blades broad, transversely-veined, pseudopetiolate; pseudospikelets present; lodicules 3; stamens 3 or 6; stigmas 2 or 3; fruit a caryopsis with a long, linear hilum and small embryo; and seedling with coleoptile not elevated from the caryopsis, the first seedling leaves bladeless. We emphasize that there are many exceptions to even this skeletal summary of bambusoid morphology, particularly in outlying tribes such as the Oryzeae and Phareae.

Anatomical characteristics of the leaf-blade are now widely recognized as being very important in the diagnosis of the five subfamilies of the Poaceae that are now generally accepted by most agrostologists. Each of these subfamilies can be characterized by a unique combination of leaf blade anatomical features possessed by their constituent representatives, and the delimitation of subfamilies is now firmly based upon differences in leaf blade anatomy (Watson and Clifford, 1976; Clifford and Watson, 1977; Renvoize, 1981). The bambusoid type of leaf anatomy has been defined as follows by Metcalfe (1956, 1960), Calderón and Soderstrom (1973), Soderstrom (1981), and Renvoize (1981) and further elaborated upon by our own work.

Outline: leaf-blade flat and expanded, the two halves of the lamina often asymmetrical about the midrib, this asymmetry evident in transverse section by the S-shaped midrib and the difference in shape of the two margins, which differ in the degree of tapering as well as in the degree of development of the lateral adaxial ribs.

Transverse veinlets (or commissural veins) usually present and conspicuous, connecting the parallel, first- and third-order longitudinal vascular bundles.

Midribs invariably well developed and conspicuous, often in the form of prominent, asymmetrical keels with colorless parenchyma ground tissue and containing complex vascular systems, with bundles located in two planes close to both the abaxial as well as the adaxial epidermides; keel bundles usually embedded in and supported by elaborate systems of sclerenchyma tissue.

Bundle sheaths always double; outer (parenchyma) sheath composed of a single layer (at least laterally) of large cells with few chloroplasts; inner (mestome) sheath conspicuous, one or usually two cell layers thick, the cells small and with uniformly thickened walls.

Chlorenchyma cell arrangement without exception non-radiate, with a lateral cell count greater than four; the anatomy is, therefore, non-Kranz, with the C3 photosynthetic pathway being operational (Brown, 1977); chlorenchyma always composed of arm cells arranged in a few horizontal layers adjacent to and parallel with the upper and lower epidermides; chlorenchyma with invaginations or arms projecting inwards towards the fusoid cells or fusoid cell cavities; fusoid cells and fusoid cell cavities located on either side of each vascular bundle, enclosed between the adaxial and abaxial layers of arm cells and in contact with the outer bundle sheaths; adjacent fusoid cells separated by narrow columns (1–several cells wide) of arm cells.

Epidermal structure complex, far from uniform throughout the subfamily, with many different types of epidermal appendages present.

Long cells uniform in type with thickened, usually very sinuous anticlinal walls; in outline, the cells elongate-rectangular with parallel side walls; bulliform cells equidimensional, hexagonal, typically present on adaxial epidermis.

Stomata with subsidiary cells either dome-shaped or triangular; shape of subsidiary cells often obscured by overarching papillae.

Papillae common in most tribes, often abundant on epidermal long cells; many small, cutinized papillae typically occurring on each cell, these often overarching the stomata.

Microhairs usually present, finger-like and bicellular; both cells elongated, more or less equal in length, uniform in diameter, the distal cell with a rounded apex and not tapering to a point.

Silica bodies variable in shape and usually transversely elongated in the direction of the long axis of the leaf; tall, saddle-shaped types predominate but cross-shaped, olyroid types, and horizontally-elongated dumbbell-shaped types also occur.

Short cells paired, or sometimes in short rows.

Relationships of the Phareae to the Bambusoideae

Until the past quarter-century there has been little taxonomic consensus on the correct subfamilial placement of the pharoid genera. Some early authors, perhaps noting the rice-like appearance of the female spikelets of several common species of *Pharus,* placed the group in the Oryzeae (Kunth, 1835). Bentham (1881) stressed the similarity of the indurate female lemmas of *Pharus* and *Olyra* to the panicoid grasses and therefore placed them hesitantly in the Paniceae. Following the anatomical studies of Brandis (1907) and especially Metcalfe (1956, 1960), however, it became apparent that the Phareae were more closely related to the true bamboos than to any other grass group, and later workers (Calderón and Soderstrom, 1980) have placed the tribe in the Bambusoideae, or near to the bamboos in the Olyroideae (Pilger, 1954; Jacques-Félix, 1962).

MORPHOLOGY.—In gross morphology, all three genera of pharoid grasses resemble the core group of the bamboo subfamily in possessing pseudopetiolate, usually broad leaf blades with evident transverse veinlets. Those species with very narrow blades lacking evident commissural veins (*Leptaspis angustifolia,* certain races of *Pharus lappulaceus,* and *Scrotochloa tararaensis*) are clearly specialized taxa that have been derived from broad-leaved ancestors.

The Phareae differ from all other bambusoids in their obliquely veined, inverted leaf blades. Too much emphasis must not be placed on these features, however, since oblique venation has been independently derived in at least one other subfamily of grasses. *Setaria paniculifera* and related species in the Panicoideae have this type of venation, yet they otherwise fit comfortably into a genus and subfamily with parallel-veined leaves. *Maclurolyra tecta* has semi-inverted leaf blades (Calderón and Soderstrom, 1973), yet other morphological and anatomical data clearly place the genus in the Olyreae.

In critical details of spikelet structure, too, the Phareae resemble the bamboo core group in possessing six stamens and three stigmas, and at least some species have male spikelets with three lodicules, though the latter structures are atypical in their lack of hairs and vascular bundles. The fruit in the tribe is a caryopsis with a long, linear hilum and a small embryo, again features that are typically bambusoid, although the first seedling leaf is usually not transitional in size to the adult blades (Soderstrom, 1981), and so in this respect does not resemble a typical bamboo. Sections of the embryos of pharoid genera have not been made for this study, but Reeder (1962) reports that *Pharus,* at least, has an embryological formula that does not differ from the four genera of woody bamboos that he investigated. Hunziker, Wulff, and Soderstrom (1982) report a basic chromosome number of $n = 12$ for the group, again consistent with the Bambusoideae.

LEAF ANATOMY IN TRANSVERSE SECTION.—For purposes of comparison with *Scrotochloa* and *Leptaspis,* and to illustrate the cohesiveness of the Phareae, we also examined blade cross-sections and epidermides of several species of *Pharus* (Figures 7 and 8).

In transverse section, the leaf outline of the pharoid grasses is symmetrical about the midrib and both margins taper to a distinct pointed apex. This differs significantly from the condition in the woody bamboos. The Olyreae also lack a marked asymmetry in the midrib outline and yet are widely considered to belong to the Bambusoideae; therefore, although the Phareae deviate from the subfamily definition with regard to this feature, little emphasis should be accorded this difference. In fact, this asymmetric tendency is only clearly applicable to the woody core group of the subfamily, and is rarely noted in non-woody genera.

The midrib of the Phareae is in the form of a prominent keel with a complex vasculature (Figures 3*a;* 7*a,d*). This is characteristic of all the bambusoid grasses and strongly suggests affinities with this subfamily. The pharoid keel structure differs from the Bambuseae, however, in being symmetrical and semicircular and in lacking an elaborate system of sclerenchyma in which the vascular bundles are embedded. The pharoid keel projects abaxially (upwards), not adaxially as in the Olyreae, but it must be realized that it is functionally adaxially located due to the 180° twisting of the pseudopetiole, which results in the inversion of the blade. Thus, both pharoid and olyroid leaves effectively have adaxially projecting midribs, an unusual condition in the Poaceae. The advantage, if any, of this upward-facing central support of the blade in both of these groups of umbrophilic grasses is not clear, but it is interesting to note that selection has produced an apparent convergence in this evolutionarily somewhat distant pair of grass groups.

The usually prominent transverse veins in *Leptaspis, Pharus,* and *Scrotochloa* conform to the condition in the subfamily. These veins occur in many other grasses, however, particularly those from shaded forest habitats as in *Zeugites* of the Centotheceae (Camus, 1945), and perhaps they reflect a common ecological adaptation without phylogenetic significance.

The double vascular bundle sheaths of the Phareae (Metcalfe, 1960; Renvoize, 1985; Figures 3*b*; 7*c,e*) are typically bambusoid. Of particular interest is the multi-layered inner sheath of small, uniformly thickened cells, a condition known only in the Bambusoideae. This feature, then, strongly links the two groups; all other subfamilies have but a single inner sheath of cells with endodermal-like thickenings.

The arm and fusoid cells of both *Leptaspis* and *Scrotochloa,* along with *Pharus,* are strictly bambusoid features which indicate close relationships. Again, these structures in the Phareae diverge considerably from the typical condition in the Bambusoideae. The arm cell wall invaginations are poorly developed and are best observed in the palisade-like abaxial chlorenchyma (Figure 7*c*). This tendency again reflects the torsion of the leaf blade in the pharoids; the abaxial side of the leaf is functionally adaxial (upward-facing), hence the palisade-like nature of the arm cells. Arm cells are usually best developed in the adaxial chlorenchyma in typical bambusoid grasses. The fusoid cells of the Phareae are interesting in that they do not appear to collapse into narrow plate-like structures with narrow lumina as they do in the other bambusoid grasses. Instead, even at maturity, they remain large, inflated, transversely elongated, and bladder-like, with exceptionally thin walls (Page, 1947; Rao and Naidu, 1981). In transverse sections, the fusoid cells are tightly packed along either side of each vascular bundle and extend halfway to the adjacent vascular bundle (Figure 7*e*). Fusoid cavities are, therefore, not observed in leaf sections of the Phareae; the actual cells are always sectioned. This feature can clearly be seen in some epidermal preparations, particularly in macerations in which all of the mesophyll tissue is not cleanly removed.

LEAF BLADE EPIDERMAL ANATOMY.—The anatomical features of the leaf blade in transverse section thus show that the Phareae closely resemble the bamboo core group or Bambuseae. This clear indication conflicts with the epidermal evidence, however, as the pharoid epidermis is unique in the Poaceae and differs substantially from the typical bambusoid condition. In fact, pharoid epidermal characteristics give little indication of even graminoid affinities and remain the major reason why there is still disagreement among agrostologists as to the taxonomic placement of the group.

The intercostal zones of both epidermides of the Phareae are occupied by two distinct types of cells: normal intercostal long cells and groups of fibrous bands. The normal type of long cell is typically bambusoid, with thickened, very sinuous anticlinal walls. The presence of these striking fibrous bands (Metcalfe, 1960; Renvoize, 1985; Figures 3, 8), each

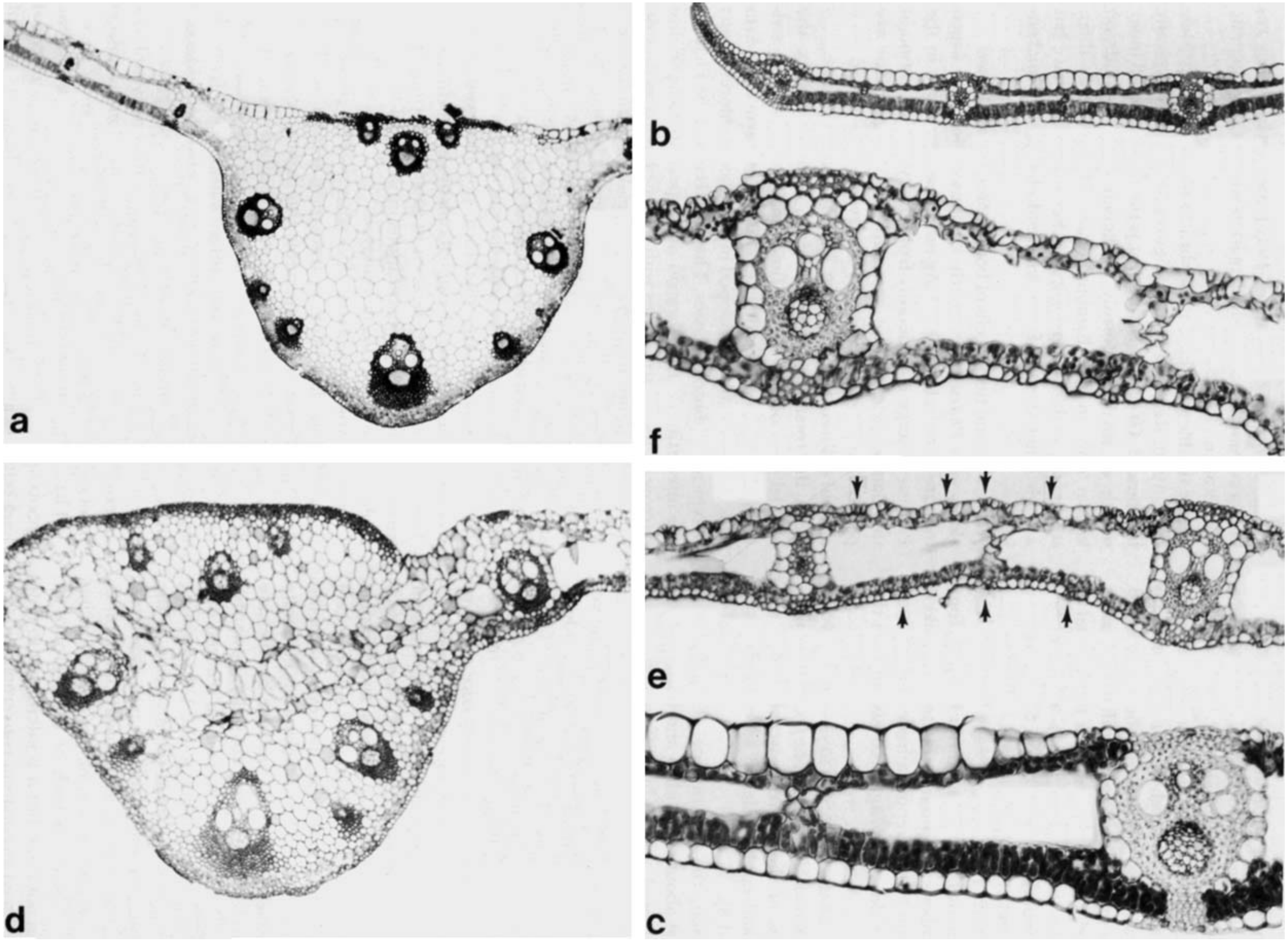


FIGURE 7.—Leaf anatomy of the genus *Pharus* as seen in transverse sections; the adaxial (downward-facing) surface faces upwards in these views: *a-c*, *P. lappulaceus*; ***a***, outline of midrib showing complex vasculature (× 66); ***b***, tapering sclerenchyma cap of the leaf margin and narrow lateral fusoid cells; note the absence of intercostal fibrous bands on the adaxial surface, and their paucity on the abaxial surface (× 165); *c*, detail of first-order vascular bundle with mestome sheath consisting of several layers as well as fusoid and arm cell structure; abaxial long cells quite bulliform-like (× 264); *d-f*, *P. parvifolius* subsp. *elongatus*; ***d***, outline of keel (× 106); e, mid-laminar region with fusoid cells and first- and third-order vascular bundles; note abundance of intercostal fibrous bands (arrows) on both surfaces (× 165); f, detail of first-order vascular bundle, fusoid cells and chlorenchyma (× 264). *P. lappulaceus* from *Soderstrom 1805*, Puerto Rico and *P. parvifolius* subsp. *elongatus* from *Calderón and Dressler 2152*, Panama.

of which is composed of a file of short cells positioned between a pair of fibers, is of extreme taxonomic importance, and their phylogenetic significance is undoubtedly great. These intercalating fibers, or fiber-like tracheids (Rao and Naidu, 1981) are unique and have not been reported in any other representative of the Poaceae, although the occurrence of leaf epidermal tracheids in other families (e.g., Theophrastaceae) is well documented in the literature. The possession of this unique feature tempts one to postulate that the pharoid grasses are not closely allied to any present day grass taxon, but the evidence of the leaf in cross section strongly suggests bambusoid affinities and too much significance should not be attached to one single outstanding characteristic.

Perhaps correlated with the prominence of the intercostal fibrous bands, bulliform cells are absent from the epidermides of *Leptaspis* and *Scrotochloa.* In the species of *Pharus* in which the adaxial epidermis lacks these bands, however, the intercostal long cells farthest from the veins are somewhat larger than those closer to the veins and could be interpreted as poorly developed bulliform cells (Renvoize, 1985; Figure 7*b–c*). Bulliform cells are common in the woody core group of the subfamily.

The stomatal subsidiary cells of *Leptaspis, Scrotochloa,* and *Pharus* are dome-shaped (Figure 3*f*) and conform to the bambusoid type. This subsidiary cell shape is not, however, exclusive to the Bambusoideae, being found also in the Panicoideae and Arundinoideae (Renvoize, 1981), and consequently no great importance should be attached to this character state.

Though common in the woody bamboo core group, minute, cutinized, epidermal papillae are poorly developed or totally absent in the pharoid grasses as they are in other peripheral bambusoids such as *Anomochloa* (Anomochloeae), *Streptochaeta* (Streptochaeteae), and *Streptogyna* (Streptogyneae). The absence of papillae, therefore, does not imply that the Phareae cannot be classified with the Bambusoideae but, again, indicates a peripheral position for this anomalous group.

Microhairs appear to be absent from the leaves of the Phareae, corroborating the observations of Metcalfe (1960), Jacques-Félix (1962), Palmer and Tucker (1981), and Renvoize (1985). Thus, *Pharus, Scrotochloa,* and *Leptaspis* join *Streptogyna* and *Puelia* in being the only bambusoids without microhairs, structures that are often considered to be universally present in non-festucoid grass genera (Johnston and Watson, 1977). This strengthens the case for removing these peripheral groups from the bambusoid nucleus.

The silica bodies of the Phareae are quite different from the diagnostic bamboo type. In the pharoids these bodies are horizontally elongated and dumbbell-shaped, an exceptional configuration in the Bambusoideae. Pharoid silica bodies are closely associated with the unique epidermal fibrous bands, and thus the shape of these structures may be largely determined by their close association with these fibers.

Based on epidermal structure, it is not possible to accommodate this tribe within the core of the bamboo subfamily, but based on leaf blade cross-sectional anatomy, the Phareae undoubtedly belong with this group rather than with any of the other subfamilies. If a broad view is taken of the circumscription of the Bambusoideae, then the Phareae can be accommodated together with the other herbaceous bamboo tribes and the Oryzeae outside the bambusoid core yet within a wider concept of the subfamily. The Phareae, then, constitute a separate tribe within the Bambusoideae sensu lato with diagnostic leaf blade anatomical characters as listed below.

Midrib symmetrical, keels semi-circular, abaxially projecting; vasculature complex.

Inner bundle sheath multiple-layered around the primary vascular bundles; cells small, uniformly thickened.

Arm cells invaginations poorly developed but most evident on the adaxial side of abaxially located mesophyll cells.

Fusoid cells prominent; do not appear to collapse at maturity.

Bulliform cells absent on the abaxial surface; poorly developed or absent on the adaxial surface.

Intercostal epidermal fibers common in both adaxial and abaxial epidermides in both costal and intercostal zones, except for certain species of *Pharus,* which lack adaxial intercostal fibers; always in pairs enclosing a file of short or modified long cells. A unique feature of this group.

Stomata more common on adaxial epidermal surface; subsidiary cells more or less dome-shaped.

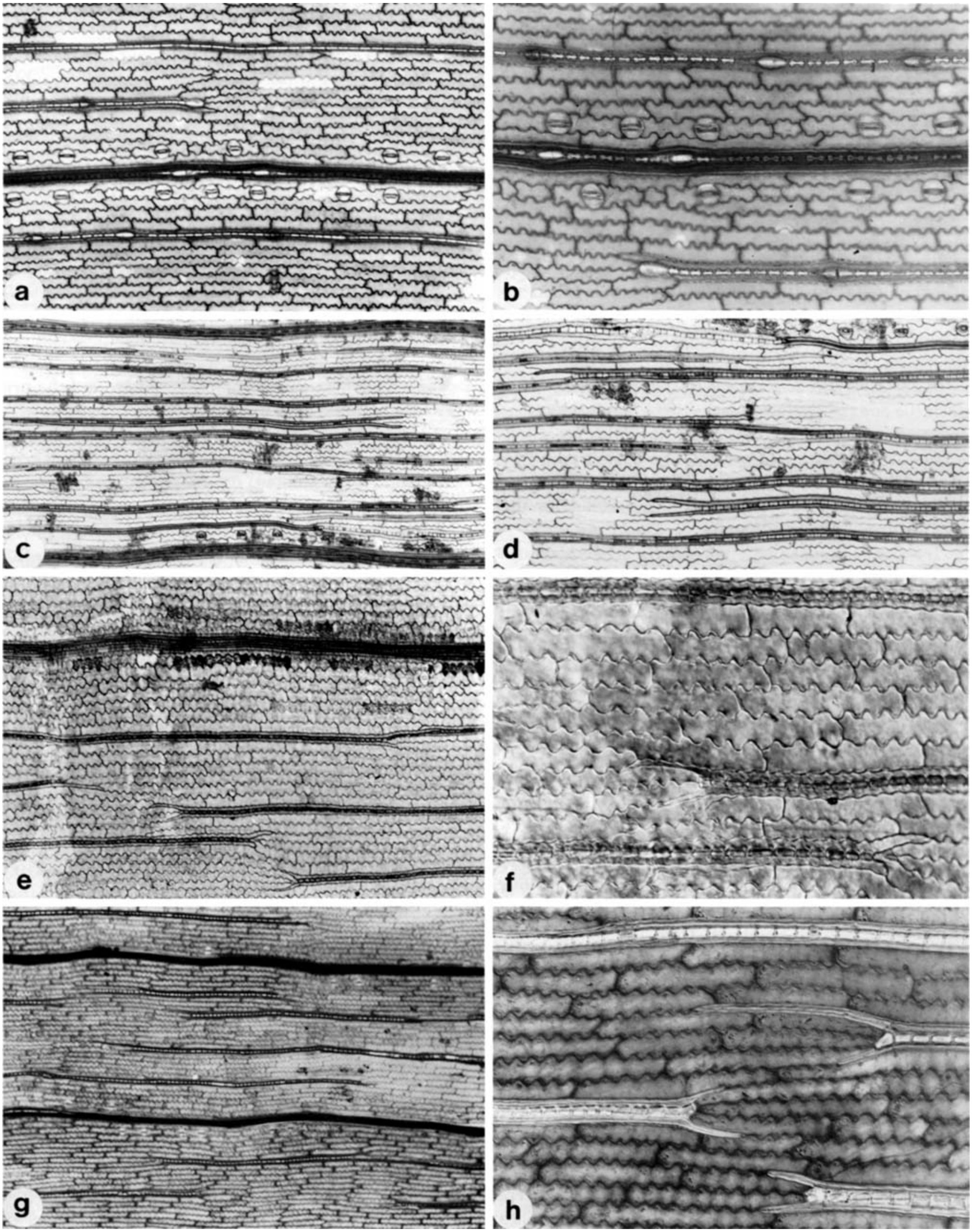
Papillae absent on both surfaces.

Microhairs appear to be absent.

Silica bodies horizontally elongated; round, oblong, rectangular, or most characteristically saddle-shaped.

RELATIONSHIPS OF THE STREPTOGYNEAE TO THE BAMBUSOIDEAE

Streptogyna has been variously classified by different authors. Early agrostologists noted the similarity of its spikelets to those of the pooid grasses, and thus placed the genus in the Festuceae (Kunth, 1835, as Festucaceae; Bentham, 1881). This disposition was long accepted, and as late as 1954 Pilger placed *Streptogyna* in this tribe, albeit in its own subtribe, the Streptogyninae. The anatomical studies of Metcalfe (1956, 1960) gave preliminary evidence that *Streptogyna* might be close to the bambusoids and led other workers to modify their placement of the group, Jacques-Félix (1962) putting the genus in its own "Série" (corresponding roughly to a subfamily), and Tateoka (1958a) grouping it with the pharoids. From this diverse classifactory history it is obvious that the taxonomic placement of *Streptogyna* has caused considerable difficulty in the past,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but the genus is now generally placed in its own tribe within the Bambusoideae (Calderón and Soderstrom, 1980).

MORPHOLOGY.—At first glance, the narrow-leaved *Streptogyna* species appear to be quite unlike any bamboo. Similarities between the two groups do exist, however. Both groups have pseudopetiolate, tessellate leaf blades with an outer ligule, features otherwise rare in the Poaceae, and there is also agreement in such technical features as number of lodicules (three in each group) and basic chromosome number ($n = 12$; Hunziker, Wulff, and Soderstrom, 1982). The partial embryo structural formula given by Jacques-Félix (1962) is similar to that of the woody bamboos. Only in the apparent lack of a transitional first seedling leaf, at least in *S. americana* (Soderstrom, 1981), does the genus depart significantly from the usual bambusoid type.

ANATOMY OF LEAF BLADE IN TRANSVERSE SECTION.—The outline in transverse section of the leaf blade of *Streptogyna* is not asymmetrical, as in the woody core group of the subfamily. This is particularly evident in that part of the lamina immediately adjacent to the midrib and the keel itself. As noted, this symmetrical nature of the two halves of the lamina also occurs in the Phareae and other herbaceous bamboos, which may all be included in the Bambusoideae in its broadest sense. The copious sclerenchyma associated with the median abaxial vascular bundle is a typical bambusoid characteristic (Metcalfe, 1956), and some of the minor bundles are actually embedded in this sclerenchyma tissue, a condition also illustrated by Jacques-Félix (1962). The adaxially located midrib bundles of both *Streptogyna* species are also embedded in fibrous tissue and Metcalfe (1956) considers the vasculature of the midrib of the genus to resemble that of the true bamboos.

The outer vascular bundle sheath is composed of relatively large, thin-walled cells that lack chloroplasts, and the multi-layered inner bundle sheath, with small cells having uniform wall thickenings (Figure 6*b,f*), are features confined to the Bambusoideae and in this respect *Streptogyna* conforms to the classical bambusoid condition.

The mesophyll of *Streptogyna* is bambusoid in the presence of fusoid cavities on either side of each vascular bundle and in *S. crinita* small arm-like extensions are present in the chlorenchyma. Fusoid cells and arm cells are confined to the Bambusoideae and it was on the basis of this observation that Metcalfe (1956) suggested affinities between *Streptogyna* and the bamboos. The leaf-blade anatomy as seen in transverse section, therefore, diverges very little from the bambusoid condition and confirms the assignment of the Streptogyneae to the Bambusoideae.

LEAF BLADE EPIDERMAL ANATOMY.—The intercostal long cells of the specimens of *Streptogyna* examined (Figure 6*c,d*) are unusual in not having markedly sinuous walls; in fact, the exceptionally long, tapering, fiber-like central long cells found on the abaxial epidermis of *S. americana* are hardly bamboo-like. More study of this feature is required, as Jacques-Félix (1962) and Renvoize (1985) illustrate and describe the long cells of *S. crinita* as moderately sinuous and Metcalfe (1960) describes them as coarsely sinuous. The lack of microhairs and well-developed papillae in the genus is most unusual in the subfamily, and is paralleled only by their absence in the Phareae and *Puelia*. The vertically orientated silica bodies somewhat resemble the bambusoid type but they are not as well-developed as they are in most bambusoid tribes. Fan-shaped, well-developed, typically bambusoid clusters of bulliform cells are present on the adaxial surface of the blade. In summary, *Streptogyna* has many cross-sectional and several epidermal features that indicate bambusoid affinities, and retention of this tribe in the Bambusoideae appears justified on present evidence if the concept of the subfamily is broadened to include bamboo-like grasses that cannot be accommodated in the woody core of the group.

The Streptogyneae constitutes a small but distinct tribe within the Bambusoideae and has the following leaf anatomical characteristics.

Midrib symmetrical, abaxially projecting; keel triangular, with complex vasculature; vascular bundles at least partially embedded in sclerenchymatous tissue.

Inner bundle sheath multiple-layered around the first-order vascular bundles; cells small, uniformly thickened.

Arm cells invaginations poorly to moderately well-developed.

Fusoid cells well-developed across the width of the leaf blade.

Bulliform cells well-developed adaxially, in fan-shaped groups of 4 or 5.

Epidermal long cells central files of intercostal zones with exceptionally long, tapered, fiber-like cells. Long cells with straight to sinuous anticlinal walls.

FIGURE 8.—Abaxial (upward-facing) epidermal structure of the genus *Pharus* as seen in surface view; note prominent intercostal fibrous bands, each composed on two files of elongate, tapering fibers that enclose a row of short cells: *a* and *b, P. lappulaceus; a,* intercostal fibrous bands, long cells and infrequent stomata along a costal zone (center) (× 135); *b,* costal zone with files of fibers and dumbbell-shaped silica bodies, flanked on each side by a row of stomates. The normal intercostal long cells have sinuous walls (× 220); *c* and *d, P. parvifolius* subsp. *elongatus; c,* arrangement of costal (upper and lower) and intercostal zones, the latter with fibrous bands (× 85); *d,* intercostal zone showing tapering ends of fibrous bands (× 135); *e* and *f, P. latifolius; e,* costal (upper) and intercostal zones (× 85); f, detail of tapering ends of epidermal fibers, interference contrast (× 220); *g* and *h, P. virescens; g,* general appearance of epidermis showing two dark, narrow, costal zones (× 55); *h,* detailed structure of intercostal epidermal fibers and associated silica cells, interference contrast (× 220). *P. lappulaceus* from *Venturi 7895,* Argentina; *P. parvifolius* subsp. *elongatus* from *Calderón and Dressler 2152,* Panama; *P. latifolius* from *Soderstrom and Sucre 1886,* Brazil; and *P. virescens* from *Irwin et al. 55044,* Surinam.

Stomata dome-shaped; not overarched by papillae.

Papillae poorly developed or absent on both surfaces.

Microhairs absent.

A final decision on the phylogenetic classification of the Phareae and the Streptogyneae will require an evaluation of all the relevant anatomical characters in combination in all of the tribes of herbaceous bamboos. These anatomical criteria should also be considered in conjunction with other proven and conservative taxonomic characters such as seedlings (Soderstrom, 1981), embryos (Reeder, 1962), and cytology (Hunziker, Wulff, and Soderstrom, 1982).

List of Taxa

- ANOMOCHLOEAE C.E. Hubbard in Hutchinson
  - Anomochloa Brongniart
    - A. marantoidea Brongniart
  - Leptaspis R. Brown
    - L. angustifolia Summerhayes and Hubbard
    - L. banksii R. Brown
    - L. cochleata Thwaites
    - L. comoroensis A. Camus
    - L. conchifera Hackel
    - L. manillensis Steudel
    - L. urceolata (Roxburgh) R. Brown in Bennett
    - L. zeylanica Nees ex Steudel

    - Maclurolyra tecta Calderón and Soderstrom

  - Olyra Linnaeus

  - Orthoclada Palisot de Beauvois

- PHAREAE Stapf in Thiselton-Dyer
  - Pharus P. Browne
    - P. lappulaceus Aublet
    - P. latifolius Linnaeus
    - P. parvifolius Nash
    - P. parvifolius subsp. elongatus Judziewicz
    - P. urceolatus Roxburgh
    - P. virescens Doell in Martius

  - Puelia Franchet

  - Scrotochloa Judziewicz
    - S. tararaensis (P. Jansen) Judziewicz
    - S. urceolata (Roxburgh) Judziewicz

    - Setaria paniculifera (Steudel) Fournier

- STREPTOCHAETEAE C.E. Hubbard in Hutchinson
  - Streptochaeta Schrader ex Nees
- STREPTOGYNEAE C.E. Hubbard ex Calderón and Soderstrom
  - Streptogyna Palisot de Beauvois
    - S. americana C.E. Hubbard
    - S. crinita Palisot de Beauvois
    - S. gerontogaea J.D. Hooker in Trimen

  - Zeugites P. Browne

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