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Epidermal Features and Spikelet Micromorphology in *Oryza* and Related Genera (Poaceae: Oryzeae)

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ABSTRACT

Terrell, Edward E., Paul M. Peterson, and William P. Wergin. Epidermal Features and Spikelet Micromorphology in *Oryza* and Related Genera (Poaceae: Oryzeae). *Smithsonian Contributions to Botany,* number 91, 50 pages, 33 figures, 3 tables, appendix, 2001.—Using scanning electron microscopy, this study examines the spikelet morphology of sixteen species of *Oryza,* one species of *Leersi*a, and one species each of the monotypic genera *Porteresia* and *Rhynchoryza.* A detailed discussion of the spikelet epidermal features and their relationship to the pedicel and cupule is presented. As the pedicel and cupule of species of *Oryza* are below the point of articulation of the spikelet, have similar epidermal features, and are free from the vascular cylinder that proceeds upward (distally) into the spikelet, we conclude that the pedicel cupules are not glumes but are merely expanded apices of the pedicels. An original data set of 14 morphological characters was used to perform parsimony and UPGMA analyses. Of these 14 characters, six describe the lemma, three describe the rachilla, two describe the glumes, two describe the articulation point and callus shape, and one describes the embryo. Our classification of *Oryza* recognizes three subgenera: *Oryza* subg. *Oryza; O.* subg. *Brachyantha,* new combination and status; and *O.* subg. *Schlechteri*a, new combination and status. Within subgenus *Oryza* we recognize three sections: *Oryza* sect. *Oryza* (including *O.* ser. *Oryza* and *O.* ser. *Latifoliae*); *O.* sect. *Ridleyanae;* and *O.* sect. *Padia.*

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Contents

Epidermal Features and Spikelet Micromorphology in *Oryza* and Related Genera (Poaceae: Oryzeae)

Edward E. Terrell, Paul M. Peterson, and William P. Wergin

Introduction

The rice genus, *Oryza,* comprises approximately 22 species distributed in Asia, Africa, Australia, and the Americas. Using scanning electron microscopy this study examines the spikelet morphology of sixteen species of *Oryza,* one species of *Leersia,* and one species each of the monotypic genera *Porteresia* and *Rhynchoryza.* Previous studies have discussed the morphology and anatomy of the spikelets of *Oryza* (von Hohnel, 1875; Van Breda de Haan, 1911; Akemine, 1913; Graham, 1913; Weatherwax, 1929; Roschevitz, 1931; Santos, 1933; Juliano and Aldama, 1937; Jacques-Felix, 1955; Tateoka, 1962a, 1962b, 1963, 1964, 1965a, 1965b, 1965c; Tateoka and Pancho, 1963; Chang and Bardenas, 1965; Nunez, 1968; Roy, 1968; Katayama, 1969). Other papers employed scanning electron microscopy to illustrate parts of the rice spikelet (e.g., Maeda, 1972; Soni and Parry, 1973; Hoagland and Paul, 1978; Zee, 1981) or to describe silica localization in the spikelet tissues (Locci and Quaroni, 1975; Yoshida et al., 1962; Garrity et al., 1984). A previous study (Terrell et al., 1983) provided data on the epidermal features of the spikelets of the related genus *Leersia.* These same features were investigated in the oryzoid genus *Zizania* by Terrell and Wergin (1981).

Three new species of *Oryza* were not included in this study because they were unavailable and are thought to be closely related to other species included in this study, so they were not expected to contribute new data. They are *Oryza meridionalis* N.Q. Ng from Australia (Ng et al., 1981), which appears to be closely related to *O. sativa* and *O. rufipogon; O. rhizomatis* Vaughan from Sri Lanka (Vaughan, 1990), said by Vaughan to have the same genome as *O. officinalis* and *O. eichingeri* A. Peter; and *O. neocaledonica* Morat from New Caledonia, apparently related to *O. meyeriana* (Morat et al., 1994). Other taxa not included in our survey are *O. indandamanica* J.L. Ellis (Ellis, 1985a, 1985b), usually treated as a synonym of *O. meyeriana* var. *granulata* (Vaughan, 1989); *O. glumipatula* Steud., usually treated as a synonym of *O. rufipogon* (Tateoka, 1963); *O. nivara* Sharma & Shastry, considered conspecific with *O. sativa* (Duistermaat, 1987); *O. perennis* Moench, shown to be a vaguely described name of uncertain application (Tateoka, 1963; Clayton, 1968; Duistermaat, 1987).

The purposes of this study are to (1) describe and compare the epidermal features of the spikelets in species of *Oryza* and related genera, (2) confirm the relative silicon contents of the spikelet structures, (3) investigate the importance of the morphological data, using cladistic and phenetic techniques, as suggested by comparative morphology, and (4) determine the taxonomic significance of the comparative morphology of the taxa. In addition, we have provided a provisional classification within *Oryza* recognizing three subgenera, three sections in subg. *Oryza,* and two series within sect. *Oryza.*

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MATERIAL AND METHODS

The taxa examined in this study include 16 species of *Oryza,* and species of the following related genera: *Porteresia coarctata, Rhynchoryza subulata,* and *Leersia nematostachya* (Table 1, which includes authors of scientific names). Specimens were obtained through the United States Department of Agriculture (USDA), Beltsville, Maryland; from the herbarium of the National Museum of Natural History, Smithsonian Institution (US); from the United States National Arboretum (NA); or from the Royal Botanic Gardens, Kew (K), with the assistance of Stephen A. Renvoize. The designations in Table 1 of IRRI and IITA, refer, respectively, to the International Rice Research Institute, Los Baños, Philippines, and to the International Institute of Tropical Agriculture, Ibadan, Nigeria. Five accessions of *O. sativa* came from the USDA Rice Experiment Station, Crowley, Louisiana. The original source of material, however, was not always known by these institutions. Eight collections of *O. sativa* (Table 1) included certain cultivars and other specimens designated by USDA P.I. (Plant Introduction) numbers. Two cultivars, "Blackhull Red" and "Strawhull Red," the so-called red rice, considered by rice growers as an unwelcome weed, are herein presumed to be *O. sativa,* although they possibly include genes from *O. rufipogon.* Other examined accessions of *O. sativa* include the cultivars "Dawn," a long-grained rice; "Nortai," a short-grained rice; and "Saturn," a medium-grained rice. Voucher specimens are deposited in the USDA Seed Collection at Beltsville, Maryland, or in the listed herbaria.

All accessions were examined under a dissecting microscope and by scanning electron microscopy (SEM) at the USDA in Beltsville, Maryland. Specimens were air-dried, except for four of the *O. sativa* accessions (cv. "Nortai" and those designated by P.I. numbers). To preserve turgidity in the microhairs of these latter accessions, tissues were chemically fixed in vials containing 3% glutaraldehyde in 0.05M phosphate buffer, pH 6.8 at 22°C. Chemical fixation for 1.5 hr was followed by dehydration in an ethanol series and critical-point drying from liquid carbon dioxide. Next, the air-dried and the chemically fixed specimens were mounted on stubs, coated with 20 nm of gold-palladium in a Technics Hummer V sputtering device, and viewed in a Hitachi HHS-2R or Hitachi S-530 scanning electron microscope operating at 10–15 kV. Images of all the samples were recorded on Polaroid Type 55 P/N film.

TABLE 1.—Species of *Oryza, Porteresia, Rhynchoryza,* and *Leersia* examined using SEM. The designations IRRI and IITA refer, respectively, to the International Rice Research Institute, Los Baños, Philippines, and the International Institute of Tropical Agriculture, Ibadan, Nigeria.

Species	Source
Oryza alta Swallen	USDA reference collection, Brazil
O. australiensis Domin	*Blake 13641* (K), Queensland
O. barthii A. Chev.	IRRI 100119, French Sudan; IRRI 100224, Gambia
O. brachyantha A. Chev. & Roehr.	IRRI 101236, Mali; *Richards 9171* (K), Zambia
O. glaberrima Steud.	IITA, TOG5833, unknown source; IITA, TOG7141, unknown source
O. grandiglumis (Döll) Prod.	*Archer 8376* (US), Brazil
O. latifolia Desv.	*Standley 89614* (NA), Guatemala
O. longistaminata A. Chev. & Roehr.	IRRI 101199, Cameroun
O. meyeriana (Zoll. & Moritzi) Baill.	*Strain W1353* (K), N. Borneo, cult., Japan; *Meijer 50001* (US), Sabah; *Merrill 7244* (US), Palawan, Philippines
O. meyeriana var. *granulata* (Nees & Arn. ex G.Watt) Duist.	IRRI 100162, Malaya; *Kostermans 1200* (US), Thailand
O. minuta J. Presl	IRRI 101124, Philippines
O. officinalis Wall. ex G. Watt	IRRI, CAHUP 17423, Madagascar
O. punctata Kotschy ex Steud.	IRRI 100126, India
O. ridleyi Hook.f.	*IRRI 100820, Buwalda 6339* (US), Sumatra
O. rufipogon Griff.	*Clayton 5933* (US), Sri Lanka
O. sativa L. cv. Strawhull Red	USDA, Crowley, LA., U.S.A.
O. sativa L. cv. Blackhull Red	USDA, Crowley, LA., U.S.A.
O. sativa L. cv. Dawn	USDA, Crowley, LA., U.S.A.
O. sativa L. cv. Nortai	USDA, Crowley, LA., U.S.A.
O. sativa L. cv. Saturn	USDA, Crowley, LA., U.S.A.
O. sativa L. (P.I. 160978)	USDA, from China
O. sativa L. (P.I. 373210)	IRRI 11481, Japan via USDA
O. sativa L. (P.I. 391823)	IRRI 4213, Philippines via USDA
O. schlechteri Pilg.	*Pulle 377* (K), New Guinea
Porteresia coarctata (Roxb.) Tateoka	IRRI, collected by D. Auch, Bangadesh
Rhynchoryza subulata (Nees) Baill.	IRRI 100913, Argentina
Leersia nematostachya Launert	*Simon & Williamson 1987* (K), Zambia

TABLE 2.—Data set for 16 species of *Oryza*, and three outgroup species. (Character states from page 10; question marks=inapplicable data; – = data missing.)

Species	1. Spikelet articulation position	2. Callus shape	3. Glume position	4. Glume shape	5. Rachilla	6. Rachilla shape	7. Rachilla muricate	8. Lemma furrows	9. Lemma tubercles	10. Lemma tubercle shape	11. Lemma silica bodies	12. Lemma body stomata	13. Lemma awns	14. Embryo types
O. sativa	2	1	2	2	1	1	1	1	1	1	2	2	1	1
O. barthii	2	1	2	2	1	1	1	1	1	1	2	2	1	1
O. glaberrima	2	1	2	2	1	1	1	1	1	1	2	2	1	1
O. longistaminata	2	1	2	2	1	1	1	1	1	1	2	2	1	1
O. rufipogon	2	1	2	2	1	1	1	1	1	1	2	2	1	1
O. alta	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. australiensis	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. grandiglumis	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. latifolia	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. minuta	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. officinalis	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. punctata	1	1	1	2	1	2	1	1	1	1	2	2	1	1
O. meyeriana var. *meyeriana*	1	1	2	1	1	3	2	1	1	3	2	2	2	2
O. meyeriana var. *granulata*	1	1	2	1	1	3	2	1	1	3	2	2	2	2
O. ridleyi	1	1	2	1	1	3	2	1	1	2	2	2	1	2
O. brachyantha	2	2	3	1	2	?	?	1	2	?	2	2	1	2
O. schlechteri	1	1	1	2	2	?	?	3	2	?	1	2	2	–
Porteresia coarctata	1	3	2	1	2	?	?	1	2	?	2	1	1	3
Rhynchoryza subulata	1	1	2	3	2	?	?	2	1	4	2	1	1	1
Leersia nematostachya	2	2	?	?	2	?	?	1	2	?	1	2	1	–

For energy dispersive X-ray (EDX) analysis, flat specimens, which had been sputter-coated with gold-palladium, were inserted into the Hitachi HHS-2R scanning electron microscope and tilted to 45 degrees. X-ray mapping and line analysis for silicon were performed at 25 kV with a Kevex 5100 containing a 30 mm^2 Mark V detector. The excitation window was set at 1.62–1.86 KeV. The maps represent X-rays that were collected during a 200 second exposure on Polaroid Type 55 P/N film.

A character list and their states, with a discussion and explanation, were used in all ensuing numerical analyses (see page 10). The taxa were scored for 14 morphological characters (for data see Table 2). Of these 14 characters, six describe the lemma, three describe the rachilla, two describe the glumes, two describe the articulation point and callus shape, and one describes the embryo. Characters used in the phenetic analysis were incorporated in the cladistic analysis unless they were phylogenetically uninformative.

A preliminary unweighted pair-group mathematical average (UPGMA) phenetic evaluation of the morphological variation was made among 16 species of *Oryza*. The phenetic analysis was carried out with the UPGMA option in phylogenetic analysis, using parsimony (PAUP) test version 4d65 (issued 8 April 1999; Swofford, 1993).

In the parsimony (PAUP) analyses, files were input in nexus format, using the heuristic search option with tree bisection-reconnection (TBR), mulpars (multiple parsimonious trees) option, and a simple addition sequence. Strict consensus trees were calculated for the overall analysis. Although this technique has been widely criticized (e.g., West and Faith, 1990), it does provide an easy assessment for particular clades within a topology. Only parsimony-informative characters were used in the cladistic analysis. Bootstrap values were calculated using a MaxTrees setting of 100 or more, added sequentially, and are only reported where values are greater than 50% majority rule in the strict consensus tree. Multistate characters were treated as polymorphisms and were scored as unordered.

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Morphology of *Oryza*

EPIDERMIS

Terminology follows Metcalfe (1960) and Terrell et al. (1983), and we follow Snow (1996) in referring to prickles instead of prickle hairs.

One of the most conspicuous and common epidermal structures in the spikelets of *Oryza* are the bicellular microhairs. These have a short basal cell, about one-third to two-fifths as long as the microhair, and a slightly longer apical cell. The latter is especially fragile and frequently breaks off. Microhairs are usually collapsed in air-dried material and are turgid only in critical-point dried material (Figure 2). The living microhairs are filled with fluid, as illustrated for *Leersia* and *Zizania* (Terrell and Wergin, 1981; Terrell et al., 1983). Although we note differences in the size and shape of microhairs (e.g., Figures 2*c*, 4*c*, 16*b,d*), a much more detailed study of them would be necessary to determine their significance.

Prickles are one-celled, rigid, pointed structures that vary greatly in size and shape. They are one of the most abundant and widespread epidermal features of the pedicels and spikelets in *Oryza*. Prickles are commonly visible with the naked eye where they occur in rows over the nerves and margins of the lemmas and paleas. Under the microscope they are seen to occupy the ridges or the furrows of the lemmas and paleas, and in certain species they may arise from basal plates that are fused with the surrounding tissue (Figure 6).

Silica bodies are siliceous structures firmly embedded in the epidermis. Their shapes vary greatly from 2- to 4-lobed to almost entire or with irregular sinuses (e.g., Figures 3*b*, 11*b*) Silica bodies are primarily found in the rachillas, pedicels, calluses, glumes, and lemma apices.

Stomata occur in certain parts of the spikelets and in pedicels (e.g., Figure 2*b,d*) but are commonly absent from the main parts of the lemmas and paleas.

Papillae occur in all species on most parts of the spikelets. They are usually small rounded structures but can be large (e.g., Figures 2*d*, 6, 9), and their apices may have minute pores.

Tubercles are specialized, siliceous, 1- to 4-pronged structures that form the most conspicuous elements of the lemma and palea (e.g., Figure 4). They provide a formidable armor unique to *Oryza*. The tubercles are further described in the subsequent section.

We found a few, scattered, large, 3- or 4-celled hairs in *O. sativa* cultivars "Nortai" and "Saturn." They occurred in the lemma furrows among the usual appressed two-celled microhairs, with which they contrasted in being larger and ascending or erect. They were distributed randomly near or along the lemma margins and appeared to replace microhairs. Jacques-Felix (1955) alluded to the presence of such hairs on the lemmas of *O. glaberrima*, a species closely related to *O. sativa*.

SPIKELETS

Parts of the spikelet examined included the callus, the oryzal rachilla, the paired glumes (sterile lemmas), lemma, palea, apicular knobs, and awns. Above the point of articulation of the spikelet is a thickened, indurate structure, referred to as the callus. It sometimes bears silica bodies and/or stomata. Within *Oryza* we define the callus as extending from the point of articulation of the spikelets to the base of the first and second glumes. In species of *Oryza*, there is considerable variation in the size of the callus, and it is usually fused with the glume bases. In *O. brachyantha* and *Leersia nematostachya*, the unusually large callus, in the absence of a stipe or rachilla, forms a solid, indurate, homogeneous structure extending from the spikelet base to the base of the lemma (Figures 21, 28). We refer to this as a stipitate callus (term suggested by W.D. Clayton in 1983 and communicated to Terrell in correspondence with S.A. Renvoize).

The pedicel cupules, sometimes considered to be glumes, are discussed in the subsequent section. We consider the true glumes to be the paired, rigid, often lanceolate structures ("sterile or empty lemmas") below the lemmas. Each glume has one vascular bundle. These glumes are further differentiated from the pedicels and spikelet parts by having few or no epidermal features, usually only prickles, scattered silica bodies, or scattered microhairs (e.g., Figures 3*b*, 9*b*, 10*b*). The glumes differ further from other parts of the spikelet by their position and shape, and they resemble the glumes of other grass tribes and genera because they are opposite each other or, in some species, somewhat offset from or alternate with each other.

The structure generally called the rachilla in *Oryza* (e.g., Graham, 1913; Chang and Bardenas, 1965) is in the same position relative to the lemma that the rachilla occupies in some other grass tribes. In these other grasses, however, the rachilla is usually very slender or filiform and appears to be pedicel-like or stipoid. In *O. sativa* and related species, this structure is somewhat subglobose (e.g., Figure 3), and its surface is densely covered with small projections rather similar to the much larger tubercles on the lemma and palea. We refer to this condition as a muricate rachilla. The projections on the muricate rachillas are jumbled and locally coalesced (Figure 3*c*), in contrast to the orderly rows of tubercles in the lemmas and paleas. A few microhairs occur on the rachilla in certain species. In species of *Oryza* not closely related to *O. sativa*, the rachilla surface is not muricate and instead has silica bodies or lacks conspicuous epidermal features. These species (especially *O. meyeriana* and *O. ridleyi*) usually have cylindrical or broadly cylindrical rachillas (Figures 16*a*, 19*c*). We herein refer to both kinds of rachillas as oryzal rachillas because they are unlike the stipoid rachillas seen in other kinds of grasses.

Whether all of these grass rachillas are homologous remains to be determined.

The principal parts of the *Oryza* spikelet are the lemma and palea that are attached along their overlapping margins. The lemma is always larger, but the lemma and palea are identical in epidermal morphology. The palea has three nerves rather than two, as is usual in grasses, and several authors (e.g., Nunez, 1968) have discussed the origin and homology of the *Oryza* palea. We have not explored this problem and tentatively continue to use the term palea. The lemma and palea of *O. sativa* and closely related species bear large and conspicuous siliceous tubercles arranged in vertical tiers and horizontal rows that alternate with longitudinal furrows (e.g., Figure 4), resulting in one of the most remarkably specialized epidermal surfaces in the grasses. The tubercles usually have 1 to 4 conspicuous apical prongs. They may be apically shriveled or with terminal pores. Tubercles show considerable variation in size and shape, sometimes are dotted with papillae (e.g., *O. glaberrima;* Figure 9*d*), and may have coalescent basal plates that intrude into the adjacent furrows (e.g., *O. meyeriana;* Figures 16, 18). The furrows are lined with appressed microhairs, with one microhair attached opposite each tubercle (Figure 4). At intervals the microhairs may be replaced by relatively large prickles.

The anatomical and morphological features of the lemmas and paleas were briefly described by Kihara and Katayama (1959) and Katayama (1969). They also mentioned differences in the tubercles among four sections of *Oryza* and credited Roshevitz (1931) with previously recognizing the taxonomic importance of lemma surfaces in *Oryza.*

We used energy dispersive X-ray (EDX) analysis to chart the presence of silicon in the tubercles (Figure 5). A line scan shows the highest concentrations of silicon in the apices of the tubercles, whereas a line scan that intercepts the microhairs elsewhere or in the furrows showed less or no silicon. The X-ray map also illustrated the high silicon concentrations in the tubercles.

The apices or apiculus of the lemma and palea differ from the main body of the lemma and palea (Graham, 1913; Chang and Bardenas, 1965). The tubercles near the apices are jumbled and coalesced with each other (Figure 6) and occur with microhairs, prickles, and stomata (stomata are lacking in the main body of the lemma). Some prickles of the lemma and palea apices have large, plate-like bases that fuse or coalesce and the papillae may be numerous. *Oryza sativa* and related species have two small, knob-like swellings situated on the apiculus of the lemma near the base of the awn (Figures 6, 7). These knobs were described by rice specialists (Chang and Bardenas, 1965) and are said to be the termini of the lateral nerves of the lemma (Launert, 1965). Roy (1968) found that the nerves of the lemma converge and interconnect in the apicular region and continue into the awn. He proposed the term "apicular node" to designate the apicular region where interconnection of vascular elements take place (1968:10). He did not clearly designate a term for the external, knob-like structures, and we herein refer to them as apicular knobs. SEM micrographs show that the apicular knobs and the adjacent lemma and palea apices have the same surface epidermal features (Figure 6). We found that apicular knobs occur only in the five species of the *O. sativa* group (*O. barthii, O. glaberrima, O. longistaminata, O. rufipogon,* and *O. sativa*) and in *O. brachyantha.* They were not found and are believed to be absent in the other species of *Oryza.* This characteristic is sometimes very hard to interpret, however, and because we were unable to make an unambiguous determination of presence/absence in all species of this study, it was omitted from the numerical analyses.

Awn anatomy in *O. sativa* was described by Juliano and Aldama (1937). SEM views of awns appeared in Maeda (1972) and in Hoagland and Paul (1978). Roy (1968) described and illustrated details of awn anatomy in three species of *Oryza* and found that their awns had a single, ventral, vascular bundle. *Oryza sativa* and *O. australiensis* have two groups of phloem and one of xylem; however, *O. brachyantha* has two groups of phloem and two of xylem. Roy (1968) considered the latter species to have the plesiomorphic state.

Awns occur in most of the species of *Oryza* but are absent in the *O. meyeriana* complex and in *O. schlechteri.* They may or may not be present in *O. sativa.* In the *O. sativa* group (*O. barthii, O. glaberrima, O. longistaminata, O. rufipogon,* and *O. sativa*) and in *O. brachyantha,* the bases of the awns show a clear demarcation in epidermal features from the adjoining lemma apices (Figure 22*c*). In the *O. latifolia* group (*O. alta, O. australiensis, O. eichingeri, O. grandiglumis, O. latifolia, O. minuta, O. officinalis,* and *O. punctata*), there is no such demarcation other than sometimes a diminution in the density of prickles on the awns. Whether this demarcation in the *O. sativa* group is correlated with the presence of apicular knobs remains to be determined.

The epidermal features present on awns are listed in the individual descriptions and are shown in several micrographs (e.g., Figure 7). Commonly, awns have prickles, microhairs, and sometimes silica bodies and stomata. Awns in two cultivars of red rice (*O. sativa*) have prickles and microhairs only. The apices of awns generally vary from smooth (with reduced rounded to truncate swellings) to covered with projecting prickles.

EMBRYO

Tateoka (1964) investigated the embryo structure of species of *Oryza* and recognized three types in cross section. In type 1 the epiblast is fused with the lateral parts of the scutellum, and only the uppermost part is free from attachment. This type also has auricles between the epiblast and the coleoptile. Tateoka included all of the species of the *O. sativa* group (*O. barthii, O. glaberrima, O. longistaminata, O. rufipogon,* and *O. sativa*) in type 1. In type 2 there is no auricle and the epiblast is seen as distinct. This type includes *O. brachyantha, O. meyeriana,* and *O. ridleyi.* In type 3 there is a cleft between the scutellum and coleorhiza, an auricle is lacking, and the epiblast is very long and separate from the scutellum. This type is found only in *Porteresia coarctata,* a genus closely related to *Oryza.*

PEDICELS AND CUPULES

The apices of *Oryza* pedicels are expanded to form cupules that are often bilobed (Figures 2*c,* 12*b*). The structure of these lobed cupules in *Oryza* drew the attention of the eminent agrostologist Otto Stapf, who believed them to be glumes. The opposing concept considers the glumes to be the distinct paired structures, in the past called sterile or empty lemmas, located above the articulation point and closely resembling the conventional glumes of other grasses.

J.D. Hooker ("Hook.f."), contributor of Gramineae to the *Flora of British India* (1896), described the pedicels of *Oryza* as being annular (ring-shaped) at the apex, and "Glumes I and II" as being what have since been called the sterile lemmas; thus, Hooker originally had a conventional concept of the glumes. Hooker (1900:182) later contributed the Gramineae for Trimen's work on the flora of Ceylon, but in this case he provided data from Stapf, as follows: "Dr. Stapf, who has made a careful study of the morphology of the spikelets of *Oryza,* informs me that it consists theoretically or normally of 5 glumes, of which the two lowest are very minute, are confluent with the tip of the pedicel, and rarely discernible. The spikelet is hence only apparently articulate with the pedicel, the real articulation being above these two suppressed glumes. The two following glumes, also empty, are always minute, and one, or rarely both, are sometimes suppressed." During the same year Stapf (1900) contributed the Gramineae to the *Flora Capensis. Oryza* is absent from the Cape region, but Stapf (1900:659) described the closely related genus *Leersia* as having "glumes reduced to an obscure hyaline entire or 2-lobed rim." Stapf (1917:22) stated the following in the tribal and generic key to Oryzeae and *Oryza* in the *Flora of Tropical Africa* (the Gramineae were never completed beyond genus 101; *Oryza* was genus 147): "Glumes very minute or confluent into an annular rim or suppressed."

Subsequently, authors have variously accepted or rejected Stapf's concept of the glumes in *Oryza.* Weatherwax (1929:548), in a detailed study of the spikelets of the Oryzeae, considered the glumes of *Oryza* to be the conventional, glume-like, sterile lemmas. He believed that the lobed sides of the end of the pedicel "possibly represent bractlets, and they are sometimes sufficiently elongated to be mistaken for glumes. The true glumes are above the articulation." Santos (1933) provided a detailed study of the morphology of *O. sativa* and had a concept like that of Weatherwax.

The most influential proponent of Stapf's concept was the eminent botanist Agnes Arber. In her book (Arber, 1934) she diagrammed a cross section of a spikelet of *O. sativa* and claimed that Stapf's concept was correct. She incorrectly cited Stapf's contribution as the *Flora of Tropical Africa* in 1898, a listing that has confused a number of later authors. Another influential botanist, the Kew agrostologist C.E. Hubbard (1934), accepted Stapf's interpretation of the structure of the glumes and sterile lemmas. He described the spikelets of *O. australiensis* as having glumes larger and more distinct than any other species of *Oryza.* His measurements showed the glumes to be 0.5 to 0.8 mm long, whereas the sterile lemmas were 1.5 to 2.5 mm long.

Michaud (1944) described abnormalities in the spikelets of *O. sativa* resulting in duplication of fertile lemmas and loss of sterile lemmas. These abnormalities bear mainly on the problem of the origin of the lemma and palea and are open to alternative interpretations.

Backer (1946) opposed Stapf's theory by claiming that the pedicel cupules were nothing more than the expanded ends of the pedicel. He pointed out the existence of an andropogonaceous grass, *Asthenochloa* Büse, that has a cup-shaped terminus on each branch, with a structure similar to that of species of *Oryza.* Backer (1946) mentioned other grasses with cup-shaped pedicel tips: *Rhynchelytrum* Nees (Paniceae), *Garnotia* Brongn. (Arundinelleae), and *Cyathopus* Stapf (Aveneae).

Chatterjee (1948), on the other hand, reviewed the previous literature and accepted Stapf's concept as correct. De Winter (1951) in treating the oryzaceous genus *Potamophila* R. Br. also accepted Stapf's concept. In the South African species *P. prehensilis* (Nees) Benth., De Winter described reduced glumes forming a small entire or bilobed hyaline cup. Schweickerdt and Marais (1956) presented an extensive study of abnormal spikelets in *O. barthii,* including abnormalities in the pedicel apices as well as in the spikelets. Like the work of Michaud (1944), this study of abnormalities is subject to more than one interpretation and involves the origin of the oryzal lemma and palea. Pyrah (1969), in a revision of *Leersia,* tentatively accepted Stapf's concept, but stated that more evidence was needed.

In connection with aberrant spikelets, we call attention to *O. grandiglumis* (Figure 14), a South American species having two extra bracts below the lemma and palea and lacking "sterile lemmas." The two extra bracts bear tubercles, so they are considered to be extra lemmas. This species needs further study.

Our study of three species (*O. sativa, O. grandiglumis,* and *O. meyeriana*) shows that the epidermal features present on their pedicels and cupules are microhairs, prickles, silica bodies, stomata, and papillae (Figures 2, 12). The relative abundance of a particular epidermal feature may vary locally; thus, the sides of cupules may have aggregations of microhairs (Figure 2). The cupules and their pedicels possess essentially the same features and differ only in the relative abundance of features. End views of the cupules show a thin cup of tissue surrounding, but free from, a central cylinder of vascular tissue (Figure 12*b*). Because the vascular cylinder is free from the surrounding cupule and prior to abscission passes upward into the spikelet, we conclude that the cupule, whether lobed or not, may function only as part of the support for the spikelet. We suspect that there are no separate, small, vascular bundles in the cupule. The diagram of Arber (1934:185, fig. 88, D2) designates the outer empty glume 1 (one of the two cupule lobes) as "non-vascular except for small bundle at side of base." It is difficult, however, to see where this bundle is located in the diagram. It is clear, however, that each sterile lemma has one vascular bundle.

We also examined the cupules of *O. australiensis* and found them to be slightly larger than in other species (as noted by Hubbard, 1934) and bent or somewhat reflexed. We consider this a difference in degree, which does not change our conclusions based on other data.

In previous investigations of the spikelets in *Leersia* (Terrell et al., 1983), the expanded end of the pedicel was considered as merely a cup-shaped pedicel apex. Recent examinations (in 1998) of several species of *Leersia* show that the cupules are often about 0.15 to 0.3 mm wide, with rims rounded or truncate, and sometimes slightly undulate. *Leersia lenticularis* Michx. cupules are more flattened and expanded and are obscurely bilobed. Other observations show that *Leersia* cupules are like those of *Oryza,* where the surrounding cupule is free from the central vascular cylinder. *Leersia* lacks sterile lemmas (true glumes). We found minute knobs on the calluses of the spikelet in *Leersia* as well; whether these are rudimentary remnants of the glumes remains to be determined. In the oryzaceous genus, *Zizania* L., glumes are lacking, and the cupules of the pedicels are conspicuously expanded, unlobed, and larger than in *Oryza* and *Leersia.* In the pistillate branches the pedicel apices are as wide as 1.2 mm (Terrell et al., 1997). Expanded cupules are known to occur in other grass tribes, as noted by Backer (1946, see above).

The following four points summarize our view of the nature of glumes in the Oryzeae: (1) the pedicel and its cupule are below the point of articulation of the spikelet and are therefore not part of the spikelet at all; (2) the pedicels and their cupules have the same kinds of epidermal features, and the cupules are not sufficiently differentiated from the contiguous pedicels to be a distinct structural entity; (3) the cupules, whether lobed or not, are free from the vascular cylinder that proceeds upward (distally) into the spikelet, and therefore serve only as part of the support of the spikelet; (4) *Leersia, Zizania,* and *Potamophila* (de Winter, 1951) also have expanded pedicel apices, although rarely lobed. If cupules are sometimes lobed, this suggests to us that they are simply following the basic tendency of stems/pedicels to branch dichotomously. We therefore conclude that in *Oryza* the pedicel cupules are not glumes but are merely the expanded apices of the pedicels, and all subsequent references to glumes are based on these conclusions.

Comparative Morphology of Species of *Oryza* and Related Genera

The *Oryza sativa* group includes about 13 species native to Asia, Africa, Australia, or South America. The main part of the *O. sativa* group includes the type species, *O. sativa,* which is also the best-known species because of its worldwide cultivation as one of the three most important crops. We recognize four other species in this main part, *O. barthii, O. glaberrima, O. longistaminata,* and *O. rufipogon. Oryza barthii* includes *O. breviligulata* A. Chev. & Roehr. (Clayton, 1968) and *O. stapfii* Roshev. (Tateoka, 1963). As noted by Vaughan (1989), the taxonomic relationships among these species need further study.

The epidermal features and spikelet structure of *O. sativa* are illustrated in Figures 1–7, and the remaining four species of this group are illustrated in Figures 8–11. The five species have a general basic morphology that provides a standard of comparison for the remaining species of the genus. They have the *O. sativa* type of spikelets showing a characteristic array of characters: large globose rachillas bearing muricate projections; furrowed lemmas and paleas with 1- to 4-pronged tubercles arranged in an orderly pattern of tiers and rows on the ridges of the lemmas; lateral articulation points (scars); lanceolate glumes; and type 1 embryos, as recognized by Tateoka (1964).

The second part of the *O. sativa* group is designated as the *O. latifolia* group, and includes *O. alta, O. australiensis, O. eichingeri, O. grandiglumis, O. latifolia, O. minuta, O. officinalis,* and *O. punctata* (Figures 12–15). Tateoka (1962a,b, 1964, 1965a,b) intensively investigated this group. The African species, *O. eichingeri,* was not included in our study, but it is clearly closely related to *O. punctata* and *O. officinalis* (Tateoka, 1965). *Oryza officinalis* was included in our study, although it is sometimes placed in synonymy under *O. minuta* (Duistermaat, 1987). *Oryza australiensis* appears to belong to this group because it has similar morphological characteristics.

The *O. latifolia* group is generally very similar to the main part of the *O. sativa* group in the features of the lemma and other spikelet parts and differs only in having the following characteristics: (1) although muricate, the rachillas are small to rudimentary compared to the large globose ones in the *O. sativa* group; (2) the point of articulation is horizontal or slightly oblique and the glumes are more or less opposite each other; and (3) the apicular knobs are absent or rudimentary.

Oryza meyeriana (Figures 16–18) was placed in section *Granulatae* by Roshevitz (1931), but this has been superseded by the earlier section *Padia.* Sectional ranking appears fully justified because of the distinctive morphological differences. *Oryza meyeriana* includes two varieties (Duistermaat, 1987), var. *meyeriana* (from Malesia) and var. *granulata* (from India, Thailand, Malesia, Southeast Asia). Duistermaat (1987) distinguished these varieties by the length/width ratios of the spikelets and caryopsis size. Tateoka (1962b) treated these as subspecies and also recognized *O. meyeriana* subsp. *abromeitiana* (Prod.) Tateoka, treated by Duistermaat (1987) as a synonym of *O. meyeriana* var. *meyeriana.*

Our sampling of this taxon includes two collections of each variety (Figures 16–18) and a fifth collection, which appears to be intermediate between the two varieties. The collections of *O. meyeriana* var. *meyeriana* have thick, indurate rachillas, whereas the collections of *O. meyeriana* var. *granulata* have non-indurate rachillas that appear wrinkled and somewhat compressed. These characters were not described by Duistermaat, and whether the presence or absence of indurate rachilla bases has taxonomic significance is a question beyond the scope of this paper.

The most conspicuous feature of the lemmas of *O. meyeriana* is the presence (in both varieties) of numerous complex tubercles centered over the furrows (Figures 16, 18). These tubercles are complex in having a sharply pointed, sometimes oblique or bent spine or prong, completely fused with the densely papillate or tuberculate adjacent base tissue. The tubercles are fused from one furrow to the next. The over-furrow position of the central spine suggests that a well-developed prickle forms the central part of the complex tubercles. These tubercles differ from those of the *Oryza sativa* group in having an over-furrow position and a more complex fused structure. They render the lemma of *O. meyeriana* (especially *O. meyeriana* var. *granulosa*) even more spiny than the lemmas of the *O. sativa* group.

Oryza meyeriana is characterized by glumes that are linear or subulate and only slightly longer than the rachilla (Figures 16, 17). Also, the glumes are somewhat offset from each other. Below the glumes is the base, including the callus, that bears stomata. Above the glumes are the short, broad, indurate or wrinkled rachillas bearing rounded silica bodies. The lemma and narrower palea lack awns and have merely short obtusely pointed apices that seem to lack apicular knobs.

In summary, the spikelets of *O. meyeriana* differ strongly from those of the *Oryza sativa* group as follows: (1) glumes are short and linear or subulate, not lanceolate; (2) the rachillas are not muricate and bear silica bodies; (3) the tubercles are positioned over the furrows instead of between the furrows; (4) the tubercles are larger and more complexly fused; (5) lemma apices lack apicular knobs; (6) the lemma and palea lack awns; and (7) the shape of the spikelet is more or less elliptical, with a blunt apex, which is quite unlike that of the *O. sativa* group.

Oryza ridleyi (Figures 19, 20) is native to Southeast Asia, Malesia, and New Guinea (Duistermaat, 1987). *Oryza longiglumis* Jansen (from Papua New Guinea) was not included in our study because of its similarity and close relationship to *O. ridleyi*. The shape of the spikelets in *O. ridleyi* is somewhat similar to that of the *Oryza sativa* group and differs from the elliptical spikelets in *O. meyeriana. Oryza ridleyi* lemmas also have conspicuous awns (Figure 19), whereas *O. meyeriana* has none. The linear or subulate glumes are somewhat offset from each other (Figure 19) and are unequal in length, with the longer one being as much as four-fifths as long as the spikelet. This species and *O. longiglumis* have the longest glumes in the genus (except possibly for *O. sativa* cultivated varieties and *O. glaberrima*). Above the glumes is a subcylindrical and indurate rachilla sometimes thickly beset with silica bodies. One sample of this species had an attached pedicel with a bilobed cupule, as is typical of other species of *Oryza*.

The lemma and somewhat narrower palea are beset with tubercles (Figure 20), which, like those of *O. meyeriana*, are positioned over the furrows. The tubercles differ, however, from those of *O. meyeriana* because they are simple and not complex. Prickles in rows also may occur on the lemmas and paleas and sometimes are modified to resemble the tubercles. Some of the papillae on the long cells may be enlarged and have apical pores (Figure 20*b*). The lemma and palea margins in our samples are ciliate with stiff prickles. The lemmas end in an awn, and the palea has only a short, awn-like point. The awn bases and palea tip bear prickles, stomata, and microhairs, but the ends of awns are so thickly beset with prickles that little else is visible.

Tateoka (1964) found that both *O. meyeriana* and *O. ridleyi* have type 2 embryos, but the several differences noted herein outweigh these similarities between the two species. Roshevitz (1931) placed *O. ridleyi* with *O. coarctata* Roxb., *O. brachyantha*, and *O. longiglumis*. Tateoka (1964) and subsequent authors have accepted the recognition of *O. coarctata* as a distinct genus, *Porteresia*. Tateoka (1964) placed *O. ridleyi, O. brachyantha*, and *O. longiglumis* in a new section, *Ridleyianae*.

Oryza brachyantha (Figures 21, 22) is native to West Africa, Congo, Sudan, and Zambia (Clayton, 1968). It has narrow spikelets with very long (to 17 cm) awns that differ from conventional awns in having two groups of xylem instead of one (Roy, 1968). The stipitate callus is very large, indurate, and homogeneous and is fused with the glume bases and extends from the spikelet base to the lemma base (Figure 21*a*). Its surface has silica bodies. The glumes are strongly offset from each other, one arising near the spikelet base, the other from the upper part of the callus. Just below the second glume is a lateral articulation point. A rachilla is lacking. The glumes are linear, quite unequal in length, and less than one-half as long as the lemma. Our samples did not have any conspicuous epidermal features. The lemma is much wider than the linear palea, lacks tubercles, and has microhairs, prickle hairs, and sometimes numerous papillae. There are large apicular knobs.

Although Tateoka (1964) included *O. brachyantha* with *O. ridleyi* in section *Ridleyianae*, comparison of *O. brachyantha* with other species of the genus show the following important characteristics: (1) strongly offset glumes; (2) very large, stipitate callus; (3) lemmas that lack tubercles, (4) absence of a rachilla; and (5) the presence of very long awns. These characteristics distinguish *O. brachyantha* as forming a distinct subgenus in *Oryza*. The resemblance and relationships of *O. brachyantha* and *Leersia nematostachya* are discussed under the latter taxon.

Oryza schlechteri (Figure 23) is native to northeastern New Guinea. The species is rare and is represented by very few herbarium specimens (Vaughan, 1989). It is a tufted perennial less than one meter tall, with a short panicle and muticous spikelets only about 1.75 to 2.15 mm long (Duistermaat, 1987; Vaughan, 1989). The base of the spikelet is small, fused with the glumes, and bears silica bodies. The two glumes (sometimes only one) are subopposite, lanceolate, short, unequal, and bear papillae, prickles, and silica bodies. A rachilla is lacking. The palea is much smaller than the lemma but is similar to it in texture. The distal half of the lemma has conspicuous furrows with microhairs and prickles (along the distal midnerve) but lacks silica bodies or tubercles. The basal one-fourth to one-half of the lemma lacks furrows, is entirely smooth, and bears conspicuous silica bodies. The apices of the lemma and palea are obtuse, and with coalesced stomata, microhairs, and reduced prickles. Apicular knobs and awns are lacking. The small ovate spikelets of *O. schlechteri* resemble those of *Leersia* in their shape and small size but differ in having a pair of glumes. Species of *Leersia,* besides lacking glumes, have lemmas with siliceous triads consisting of a central silica body flanked by a tubercle on each side (Terrell et al., 1983). One species, *Leersia lenticularis* Michx., has silica bodies but lacks lateral tubercles; in all other characters it is typical of *Leersia.* In *O. schlechteri* the "upper" (distal) furrowed parts of the lemma entirely lack silica bodies and tubercles, but the more basal smooth parts of the lemma have silica bodies without accompanying tubercles (Figure 23*c*). Thus, the lemma of *O. schlechteri* exhibits characters of both *Leersia* and *Oryza.*

After comparing *O. schlechteri* to species of *Leersia* and *Oryza,* Naredo et al. (1993) concluded that the presence of a glume (their material had only one) and the absence of triads on the lemma indicated that the species belonged in *Oryza.* We agree with this conclusion, although we point out the occurrence of silica bodies on the basal parts of the lemma in *O. schlechteri.*

Oryza schlechteri may represent an evolutionary stage somewhat intermediate between *Leersia* and *Oryza,* but with a preponderance of *Oryza* characters. We suggest its placement in a distinct subgenus of *Oryza.*

Porteresia is a monotypic genus and is represented by *Porteresia coarctata,* a species native to southern Asia. *Porteresia coarctata,* originally described as an *Oryza,* was shown by Tateoka (1964, 1965c) to be distinct from *Oryza* in having a large caryopsis with a bent apex, a large embryo, and short, petiolar, basal attachments. He described unusual characters in the leaf blades, such as the occurrence of two superposed bundles in each rib, air spaces within the mesophyll, and papillae with bifurcate tips (see also Clayton and Renvoize, 1986). Cope (1982) described *P. coarctata* as having extensive rhizomes and culms to two meters tall. He also noted that it forms dense mats at the mouth of the tidal Indus River in Pakistan and that it also occurs in India and Burma. Other authors have provided additional general data for this unique taxon (Dikshit et al., 1993).

The spikelets (Figures 24, 25) are narrowly oblong to narrowly ovate, 12 to 15 mm long (including the awn), and obliquely articulated with the pedicel. Our observations indicated that the unique callus is expanded as a rigid, transversely narrowed disk bearing silica bodies. The glumes are somewhat offset, linear, subequal, one-third as long as the spikelet, and lack apparent epidermal features. A rachilla is lacking. The lemma has a thin, wing-like portion. The palea is linear and almost as long as the lemma. The lemma has prominent long cells and lacks furrows. Tubercles also are lacking, but the lemma has small microhairs, stomata, and papillae. The lemma apex bears a rigid awn about 4 mm long, with microhairs and stomata. Apicular knobs are lacking. These distinctive spikelet features, along with other unique characteristics, lend support to recognition of this taxon as a separate genus.

Rhynchoryza is a monotypic genus that is represented by *R. subulata.* The species (Figures 26, 27) is native to Argentina, Brazil, Paraguay, and Uruguay. Its spikelets have several morphological features that set it apart from the *Oryza* species. The large spikelets are long and narrow, about 3.5 to 5 cm long, including the long awns. The base below the glumes has a solid, rounded, small callus bearing silica bodies. There is a horizontal or slightly oblique articulation point. The glumes (only 1 to 3 mm long) are opposite, somewhat ovate, and with two to a few acutely pointed lobes with conspicuously large marginal prickle hairs. The surface of the glumes has microhairs, papillae, and silica bodies. A rachilla is lacking. The lemma and palea are markedly unequal in size and shape. The palea is linear, shorter than the lemma, and with smaller tubercles. The long, narrow lemma has two sections. The basal half is coriaceous and lacks furrows, but it bears rows of rounded mammiform tubercles with pointed, withered apices. Also present are few and scattered microhairs and prickle hairs, along with papillae. The distal half of the lemma is chartaceous or somewhat soft and lacks tubercles but has microhairs, papillae, prickles, silica bodies, and unusual stomata conspicuously bordered by four papillae (Figure 27). The lemma tapers gradually into an awn (~2.5 cm long) bearing microhairs and prickles. Apicular knobs are lacking. Clayton and Renvoize (1986:72) described the distal section of the lemma as a "conical herbaceous beak composed of aerenchyma with transverse septa." This constituted a "flotation device built into the spikelet." *Rhynchoryza subulata* is so distinctive in relation to other species of *Oryza* that no one is likely to question its generic status.

Launert (1965) surveyed the African species of *Leersia* and noted that three of the species were difficult to assign to either *Leersia* or *Oryza.* These were *Leersia perrieri* (A. Camus) Launert, *L. tisserantii* (A. Chev.) Launert, and *L. nematostachya* Launert (formerly *L. angustifolia* C.E. Hubb.). The first two of these were found later to have siliceous triads like all other species of *Leersia* and were similar in other characteristics with *Leersia* (Terrell et al., 1983). The third species, however, lacks siliceous triads.

Hubbard (1951) and Launert (1965) noted the resemblance between *Leersia nematostachya* and *Oryza brachyantha.* Both species have very long slender awns (to 18 cm) and narrow spikelets with large indurate stipitate calluses (bearing numerous silica bodies) extending from the base of the spikelet to the base of the lemma. We contrasted other characters in this species with those of *O. brachyantha. Leersia nematostachya* grows in Zambia and Angola "in shallow laterite pans" and has delicate growth and convolute filiform leaves (Launert, 1965:131); in these respects it is uncharacteristic of species of *Oryza. Leersia nematostachya* (Figures 28, 29) lacks glumes, has silica bodies in the lemmatal furrows, lacks apicular knobs, and has chartaceous, irregularly angular awns (termed pseudo-awns by Launert, 1971) with three vascular bundles. In contrast, *O. brachyantha* has two glumes, lemmatal furrows lacking silica bodies, large apicular knobs, and coriaceous terete awns with one vascular bundle. Launert (1965) noted that three nerves entered the awn in those *Leersia* species having awns or awn-like extensions, whereas in *Oryza* species two of the lateral nerves end in the apical region, and only one nerve enters the awn. In addition, Launert found that the anatomical characters of the leaves in *L. nematostachya* were similar to those in other species of *Leersia*. Thus, the characters of *L. nematostachya* are predominantly those common to other species of *Leersia*, despite some resemblance to *O. brachyantha*. Within *Leersia* the closest relatives to *L. nematostachya* are *L. perrieri* and *L. tisserantii*.

Numerical Analyses

CHARACTERS AND THEIR STATES.—1. *Spikelet articulation position:* 1=horizontal or slightly oblique; 2=lateral. The point of articulation is located just below the glumes. In the lateral state (2) the articulation point is off to one side but still below the upper glume.

2. *Callus shape:* 1=rounded; 2=stipitate; 3=discoid. In *Oryza* the callus extends from the point of articulation of the spikelets to the base of the first and second glume, sometimes fused with the glume bases. At the base of the spikelet the small and rounded shape (1) is common in the *O. latifolia* group. In *O. brachyantha* and *Leersia nematostachya* the stipitate callus (2) forms a solid, indurate, homogeneous structure extending from the spikelet base to the base of the lemma. The callus here is extended and massive. The discoid callus (3) is a laterally expanded disk found only in *Porteresia*.

3. *Glume position:* 1=opposite; 2=slightly or somewhat offset (alternate); 3=strongly offset. In state three the glumes are separated by a considerable distance seen only in *O. brachyantha*. Although somewhat subjective, position of the glumes is consistent and useful in separating the species.

4. *Glume shape:* 1=linear or subulate; 2=lanceolate or narrowly lanceolate; 3=irregularly hastate or broadly ovate. State two is defined herein as widest near the base.

5. *Rachilla:* 1=present; 2=absent. The *Oryza* type of rachilla is of three types (see character 6) and not slender, filiform, pedicel-like, or stipoid as in most other grasses. The presence of a rachilla is found in members of subg. *Oryza*.

6. *Rachilla shape:* 1=subglobose (large, 0.5–2 mm long); 2=subglobose/rudimentary (small, 0.1–0.4 mm long); 3=cylindrical or broadly cylindrical. The *O. sativa* group is characterized by a large subglobose rachilla (1) whereas the *O. latifolia* group has a smaller subglobose/rudimentary rachilla (2). In *O. ridleyi* and *O. meyeriana* the rachilla is elongated, either cylindrical or broadly cylindrical (3). This character is inapplicable in *O. brachyantha, O. schlechteri,* and all outgroups because a rachilla is absent.

7. *Rachilla muricate:* 1=present; 2=absent. These small, numerous projections are pointed, rounded or somewhat obtuse and are considerably smaller than lemma tubercles. Tubercles are larger and more prominent on the lemma and palea. The presence of a muricate rachilla is seen only in sect. *Oryza*.

8. *Lemma furrows:* 1=present; 2=absent; 3=absent only on the basal portion. Lemma furrows are folds in the epidermis/cuticle that run parallel with the keel and veins. Character state three is retained here to emphasize the unique feature of *O. schlechteri* where the furrows are absent on the basal one-fourth to one-half of the lemma.

9. *Lemma tubercles:* 1=present; 2=absent. These irregularly shaped structures have been found to contain high levels of silica. The tubercles are arranged in distinct rows in four major shapes (see character 10). This is an important character found in all members of subg. *Oryza*.

10. *Lemma tubercle shape:* 1=1- to 4-pronged on ridges; 2=1-pronged on furrows; 3=complex on furrows; 4=scattered mammiform. A pronged tubercle comes to a point above the surface; they can have up to four prongs. The important distinction is whether these tubercles are arranged on a ridge or a furrow. Complex tubercles are found in *O. meyeriana* where the tubercles are fused over the furrow. Mammiform tubercles are found in *Rhynchoryza*. This character is inapplicable in *O. brachyantha, O. schlechteri, Porteresia coarctata,* and *Leersia nematostachya* because tubercles are absent.

11. *Lemma silica bodies:* 1=present on lower three-fourths; 2=absent on lower three-fourths. These siliceous structures are firmly embedded in the epidermis and vary in shape from being 2- to 4-lobed to almost entire or with irregular sinuses.

12. *Lemma body (below apex) stomata:* 1=present; 2=absent. *Porteresia* and *Rhynchoryza* are the only taxa that have stomata. Therefore, this character is of little value.

13. *Lemma awns:* 1=present; 2=absent. Lemma awns are absent in *O. meyeriana* and *O. schlechteri*.

14. *Embryo types:* 1=type 1; 2=type 2; 3=type 3. In type 1 the epiblast is fused with the lateral parts of the scutellum and only the uppermost part is free from attachment with auricles between the epiblast and the coleoptile. In type 2 there is no auricle and the epiblast is seen as distinct. In type 3 there is a cleft between the scutellum and coleorhiza, no auricle, and the epiblast is very long and separate from the scutellum. This latter type is found only in the outgroup *Porteresia coarctata*. This character is undetermined for *O. schlechteri* and *Leersia nematostachya*.

UPGMA ANALYSIS.—Using the 14 morphological characters above as scored in Table 2, six (A–F) major groups in *Oryza* are shown in the phenogram (Figure 30). These are as follows: (A) *O. sativa, O. barthii, O. glaberrima, O. longistaminata, O. rufipogon*; (B) *O. alta, O. australiensis, O. grandiglumis, O. latifolia, O. minuta, O. officinalis, O. punctata*; (C) *O. meyeriana* var. *meyeriana, O. meyeriana* var. *granulata*; (D) *O. ridleyi*; (E) *O. brachyantha*; (F) *O. schlechteri*. Group A is characterized by having lateral spikelet articulation (character 1), slightly or somewhat offset glumes (character 3), and large subglobose muricate rachillas (character 6). Groups A and

B form a cluster that is supported by having muricate rachillas (character 7) and type 1 embryos (character 14). Group B is supported by having opposite glume insertion (character 3) and small, subglobose/rudimentary rachillas (character 6). Members of group C lack lemma awns (character 13) and share tubercle complexes on the furrows of the lemmas (character 10). *Oryza ridleyi* (D) has 1-pronged tubercles on the furrows of the lemma (character 10). Groups C and D form a cluster that is supported by cylindrical or broadly cylindrical rachillas (character 6) and 1-pronged lemma tubercles located on the ridges (character 10). Species that could not be grouped or showed weak assemblages in the phenetic analysis were *O. brachyantha* and *O. schlechteri*. *Oryza brachyantha* (E) has a stipitate callus (character 2) and strongly offset glumes (character 3), and *O. schlechteri* (F) lacks furrows on the basal portion of the lemma (character 8), has silica bodies on the basal three-fourths of the lemma (character 11), and lacks lemma awns (character 13).

PARSIMONY ANALYSIS.—A consensus tree of the 115 possible trees indicates that there are four clades within the species of *Oryza* that have a bootstrap value greater than 50% (Figure 31). These are group A (bootstrap value 71%, as above); group B (bootstrap value 54%, as above); group C (bootstrap value 70%, as above); and group E (bootstrap value 69%), which includes *O. brachyantha* and *Leersia nematostachya.* All other taxa included in this study form an unresolved network. The 115 trees differ primarily in placement of *O. ridleyi–O. meyeriana, O. schlechteri,* and *O. brachyantha–Leersia nematostachya.* The 17 taxa of *Oryza* consistently occur as a clade when using either *Porteresia* or *Rhynchoryza* as an outgroup without inclusion of *Leersia*. Whenever *Leersia nematostachya* is included in the analysis it forms a clade with *Oryza brachyantha,* thereby suggesting that *Oryza* is para or polyphyletic (see consensus tree in Figure 31). Most notably, *Oryza brachyantha* and *Leersia nematostachya* have a stipitate callus (character 2). This state is unique to these two taxa, whereas all others species of *Oryza* have a rounded callus. *Leersia nematostachya* lacks glumes, like other species in the genus, and has a pseudo-awn, unlike any species of *Oryza*. Because only a single species (*L. nematostachya*) is used to represent *Leersia,* and we are using only 14 characters, it seems a bit premature to place much confidence in this result. Based on our morphological observations, *Leersia* is the closest sister to *Oryza* because the shortest trees (21 steps) are formed when *Leersia* is used as the sole outgroup (Figure 32). The highest consistency index (CI=0.78) is obtained when *Porteresia* is the sole outgroup (Figure 33).

The cladogram shown in Figure 32 was chosen to illustrate one possible phylogeny within the ingroup. The genus *Oryza* is characterized by a single synapomorphy: absence of silica bodies on the lower three-fourths of the lemma (character 11). In this cladogram *Leersia* does not have any apomorphies because, as discussed previously, it shares characteristics with *O. brachyantha,* the most basal member of the *Oryza* clade with a single apomorphy of strongly offset glumes (character 3). The remaining species share two synapomorphies: horizontal or slightly oblique spikelet articulation (character 1) and a rounded callus (character 2) with *O. schlechteri,* the sister to a trichotomy containing three clades (*O. ridleyi,* two varieties of *O. meyeriana,* and groups A and B, see consensus tree, Figure 31). This trichotomy is supported by three synapomorphies: slightly or somewhat offset glume position (character 3), presence of an *Oryza* rachilla (character 5), and the presence of lemma tubercles (character 9). The clade containing groups A and B is supported by four apomorphies, of which two are non-homoplasious: subglobose rachillas (character 6) with muricate projections (character 7). Group B is supported with two apomorphies: subglobose/rudimentary rachillas (character 6) and opposite glumes (character 3), and group A is supported by the reversal of character 1 (to lateral spikelet articulation).

The cladogram rooted with *Porteresia coarctata* (Figure 33) is very similar to the one discussed in the previous paragraph because both share an identical trichotomy containing three clades (*O. ridleyi,* two varieties of *O. meyeriana,* and groups A and B). In this cladogram (Figure 33) the trichotomy is supported by only two (three in Figure 32) synapomorphies: the presence of a rachilla (character 5) and the presence of lemma tubercles (character 9). *Porteresia* and *Rhynchoryza* are characterized by a single symplesiomorphy: stomata on the lemma body (character 12). Another trichotomy is depicted just after this initial node or hypothesized speciation event in *Oryza* where *O. schlechteri* is supported by five apomorphies, two of these are non-homoplasious characters: lemma furrows absent only on basal portion (character 8) and lemma silica bodies present on the lower three-fourths (character 11); *O. brachyantha* is supported by three apomorphies, two of these are non-homoplasious characters: stipitate callus (character 2) and strongly offset glume position (character 3); the clade containing groups A and B is as discussed above.

Even though our data represent only a very few characters and would benefit greatly from investigations on a molecular level, we have considered many other morphological characters for our newly hypothesized classification. The topology of Figure 33 closely follows our hypothesized classification within *Oryza* where we recognize three subgenera (Table 3).

Classification of *Oryza*

The earliest classifications of *Oryza* that created formal ranks were those of Baillon (1894) and Roshevitz (1931). The classification of Roshevitz was part of an intensive study of the morphology and taxonomy of *Oryza*. He recognized four sections, three of which we list in our Table 3; the fourth section was *Coarctatae,* which included primarily *Oryza coarctata* Roxb. (later removed to a separate genus as *Porteresia coarctata*), and secondarily *O. ridleyi, O. brachyantha,* and *O. schlechteri.* Important additions and adjustments were made by Tateoka (1964) and Sharma and Shastry (1965). These classifications were discussed by others, notably by Nayar (1973) and

TABLE 3.—Infrageneric classification of *Oryza* with literature citations.

- *Oryza* subgenus *Oryza*.
  - *Oryza* section *Oryza* (section *Euoryza*, Baillon, 1894; section *Sativa*, Roshevitz, 1931).
    - Type: *O. sativa* L.
      - *O.* series *Oryza* [ser. *Sativae* Sharma & Shastry (1965)].
        - Type: *O. sativa* L.
        - Including *O. barthii, O. glaberrima, O. longistaminata, O. rufipogon,* and *O. sativa.*
      - *O.* series *Latifoliae* Tateoka ex Sharma & Shastry (1965) [ser. *Australienses* Tateoka ex Sharma & Shastry (1965)].
        - Type: *O. latifolia* Desv.
        - Including *O. alta, O. australiensis, O. eichingeri, O. grandiglumis, O. latifolia, O. minuta, O. officinalis, O. punctata.*
  - *O.* section *Padia* (Zoll. & Moritzi) Baill. (1894), based on *Padia* Zoll. & Moritzi, Syst. Verz. Zoll. 103 (1846); sect. *Granulatae* Roshev. (1931); ser. *Meyerianae* Sharma & Shastry 1965.
    - Type: *O. meyeriana* (Zoll. & Moritzi) Baill.
      - Including *O. meyeriana* var. *meyeriana*, *O. meyeriana* var. *granulata,* and *O. meyeriana* var. *abromeitiana.*
  - *O.* section *Ridleyanae* Tateoka (1964) [ser. *Ridleyanae* Sharma & Shastry (1965)].
    - Type: *O. ridleyi* Hook.f.
      - Including *O. ridleyi* and *O. longiglumis.*
- *O.* subgenus *Brachyantha* (Sharma & Shastry) Terrell, P.M. Peterson, & Wergin [based on *O.* ser. *Brachyanthae* S. Sampath ex Sharma & Shastry (1965)].
  - Type: *O. brachyantha* A. Chev. & Roehr.
- *O.* subgenus *Schlechteria* (Sharma & Shastry) Terrell, P.M. Peterson, & Wergin [based on *O.* ser. *Schlechterianae* Sharma & Shastry (1965)].
  - Type: *O. schlechteri* Pilg.

Tucker (1988). We also consulted Vaughan's (1989) extensive review of *Oryza.* In Table 3 we present further adjustments in classification, primarily on the basis of spikelet characters (which are fundamental reproductive characters). We recognize *O. ridleyi* as a distinct section, and *O. brachyantha* and *O. schlechteri* as separate subgenera (spellings of subgeneric names follows Greuter et al. (1994), particularly Articles 21 and 22). The other three genera examined herein are distinct genera and need no further reclassification.

Oryza subg. *Brachyantha* (S. Sampath ex Sharma & Shastry) Terrell, P.M. Peterson, & Wergin, comb. et stat. nov. Basionym: *O.* ser. *Brachyanthae* Sharma & Shastry, Indian J. Genet. Pl. Breed. 25:175. 1965.—Type: *Oryza brachyantha* A. Chev. & Roehr.

Oryza subg. *Schlechteria* (Sharma & Shastry) Terrell, P.M. Peterson, & Wergin, comb. et stat. nov. Basionym: *O.* ser. *Schlechterianae* Sharma & Shastry, Indian J. Genet. Pl. Breed. 25:174. 1965.—Type: *Oryza schlechteri* Pilg.

Appendix

Descriptions of Species Groups of *Oryza*

Oryza sect. *Sativa* ser. *Sativa*.—Spikelet with articulation point lateral; callus rounded at base, fused with glume bases; glumes slightly or somewhat offset, subequal, lanceolate or lance-ovate, extending to middle of lemma or rarely to top of lemma, lacking epidermal features or sometimes bearing prickles or silica bodies; rachillas large, subglobose, located above (distal to) both glumes, covered with muricate projections visible macroscopically, sometimes with microhairs, prickles; lemmas furrowed, tubercles large, with 1 to 4 sharp points, located on the ridges, with appressed microhairs and prickles in the furrows, papillae common; palea similar to lemma, narrower; lemma and palea apices with tubercles, microhairs, prickles, papillae; apicular knobs conspicuous at lemma tip; awns present or absent, with microhairs, prickles.

Oryza ser. *Latifoliae*.—Spikelet with articulation point horizontal or slightly oblique; callus small or somewhat larger, sometimes hardly visible below glume bases, flattish or rounded at base, horizontal or oblique, fused with glume bases; glumes appearing opposite, subequal, lanceolate or lance-ovate, very short to one-fourth or one-third as long as lemma, lacking epidermal features or sometimes bearing microhairs, prickles, papillae, silica bodies; rachillas small or rudimentary, a triangular area or barely discernible, located above (distal to) both glumes, covered with muricate projections visible macroscopically; lemmas furrowed, tubercles large, with 1 to 4 sharp points, located on the ridges, with appressed microhairs and prickles in the furrows, papillae common; palea similar to lemma, narrower; lemma and palea apices with tubercles, microhairs, prickles, papillae; apicular knobs none; awns present, with microhairs, prickles, silica bodies.

Oryza sect. *Padia*.—Spikelet obtuse or blunt; articulation point horizontal or slightly oblique; callus short, broad, fused with glume bases, bearing silica bodies and stomata; glumes slightly or somewhat offset, subequal, short, linear or subulate, with microhairs, prickles, silica bodies; rachillas cylindrical or broadly cylindrical, indurate or wrinkled, fused below with the glume bases; lemmas furrowed, tubercles large, complex, fused with prickles and papillae, on the furrows, usually with one short sharp point, with microhairs, prickles, papillae, tubercles smaller in *O. meyeriana* var. *meyeriana*; palea similar to lemma, narrower; lemma and palea apices with microhairs, stomata, prickles, papillae; apicular knobs none; awns none.

Oryza sect. *Ridleyanae*.—Spikelet with articulation point horizontal or slightly oblique; callus small, indurate, fused with glume bases; glumes slightly or somewhat offset, quite unequal, extending past mid-lemma, linear or subulate, with microhairs, prickles, silica bodies; rachillas cylindrical, fused below with glume bases; lemmas furrowed with 1-pronged tubercles on the furrows, with sharp or obtuse apices, microhairs, prickles, papillae numerous; lemma and palea apices with microhairs, prickles, stomata; palea as for lemma; apicular knobs none; awns with microhairs, prickles, stomata.

Oryza subg. *Brachyantha*.—Spikelet narrowly oblong; articulation point lateral; stipitate callus long and wide, extending to base of lemma, indurate, fused with glume bases, with silica bodies; glumes strongly offset, unequal, less than one-half as long as lemma, linear, lacking epidermal features; rachillas absent; lemma much wider than palea; lemma furrowed, lacking tubercles, with microhairs, prickles in furrows or prickles grouped in lines, with or without papillae; palea linear, muticous; lemma and palea apices with microhairs, prickles, papillae, some coalescence; apicular knobs large; awns very long, to 17 cm, with microhairs, prickles.

Oryza subg. *Schlechteria*.—Spikelet small, resembling *Leersia* spikelets in shape and size; articulation point horizontal or slightly oblique; callus very small, fused with glume bases, with silica bodies; glumes two, or sometimes only one, appearing opposite, unequal, small, shortly lanceolate, bearing silica bodies, prickles, papillae; rachillas absent; lemmas with distal section (two-thirds more or less of lemma) with conspicuous furrows, lacking tubercles, with microhairs, prickles, papillae; basal section of lemmas more or less smooth, lacking furrows, with conspicuous silica bodies; lemma and palea apices obtuse, with coalesced stomata, microhairs, reduced prickles; palea much narrower than lemma; more or less similar to lemma in epidermal features; apicular knobs none; awns none.

Figures

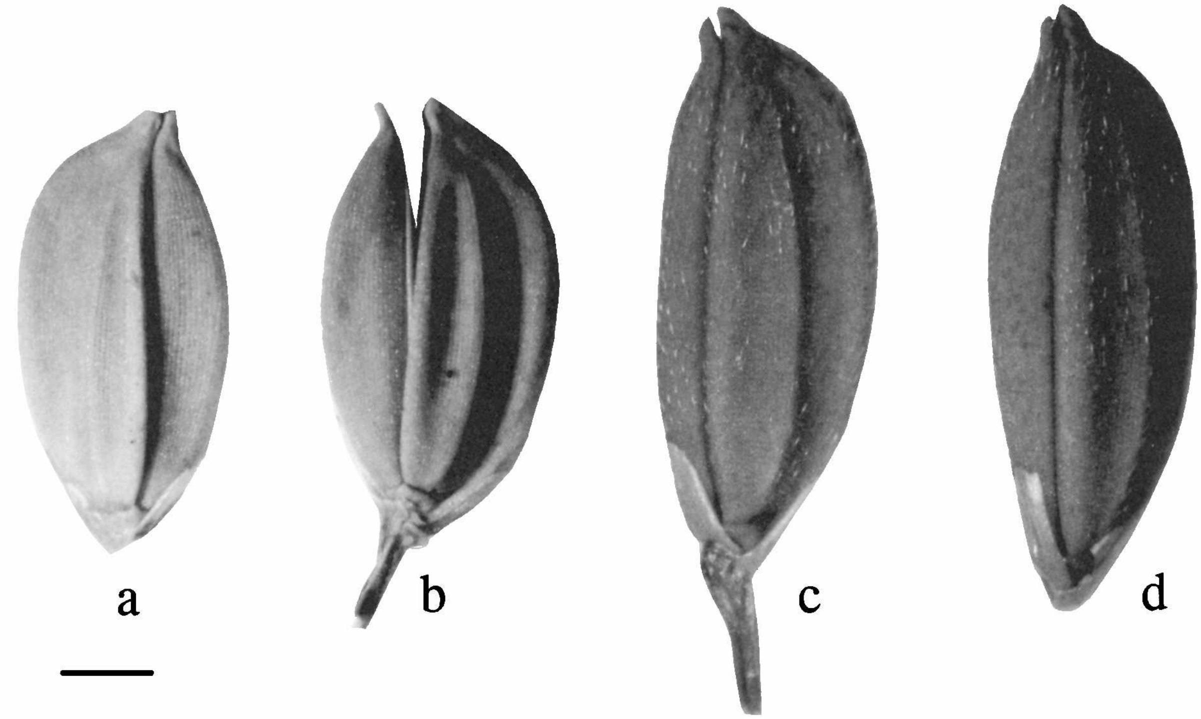

FIGURE 1.—Spikelets of *Oryza sativa* (*a,b, Watkins s. n.*, 17 Oct 1945, Upper Burma (US-2115904); *c,d, Chase 8550*, 20 Feb 1925, Brazil (US-1257171)): *a* and *d* with pedicels removed; *b* with glumes scarcely visible. (Scale =1 mm.)

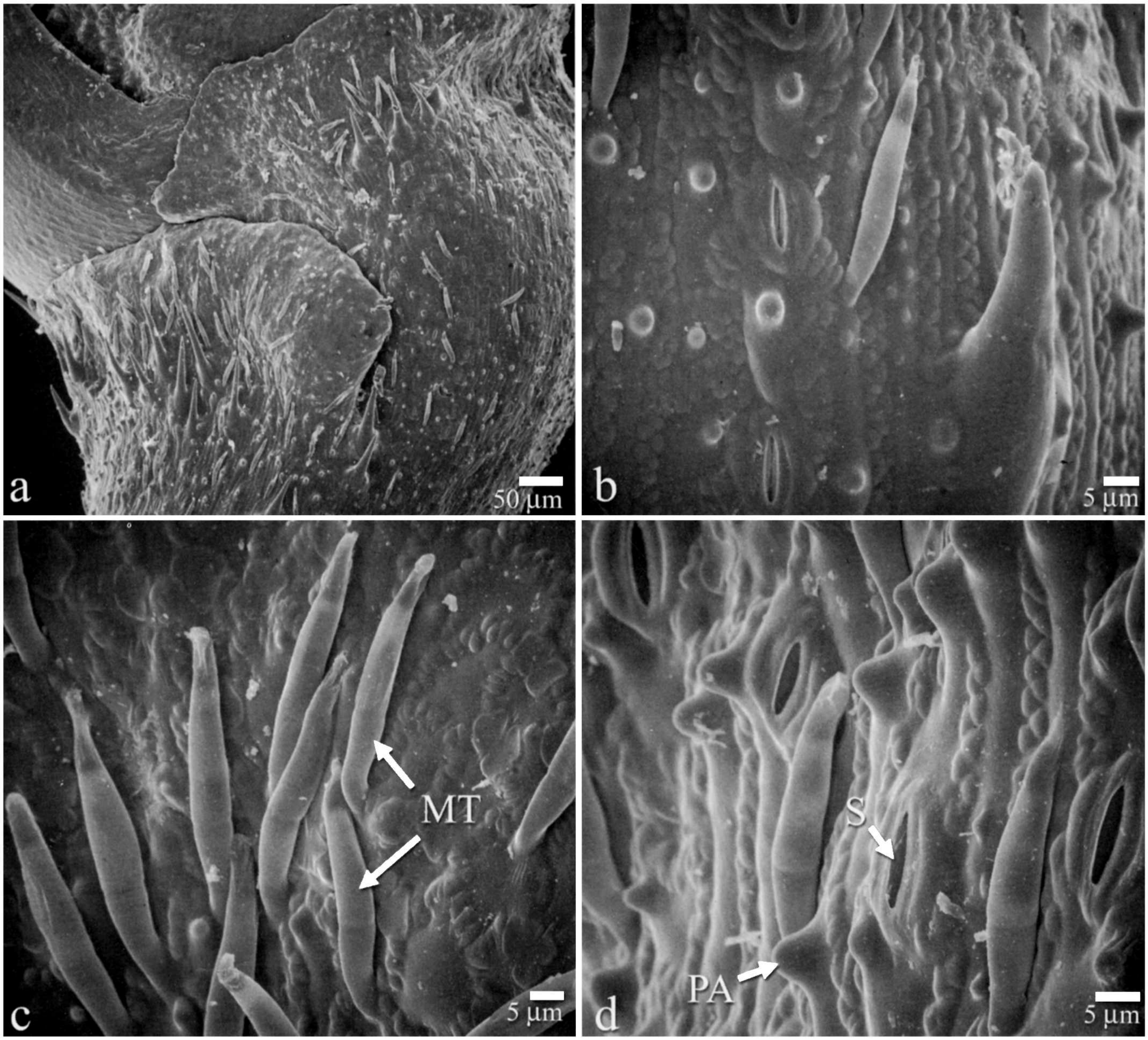

FIGURE 2.—Bilobed cupule and pedicel of *Oryza sativa* (P.I. 373210): *a,* cupule with microhairs, papillae; glume above left and globose rachilla to upper left; *b,* pedicel with large prickle, microhair, stomata, papillae; *c,* base of cupule with microhairs and silica bodies; *d,* cupule with microhairs and stomata. (MT=turgid microhairs; PA= papilla; S=stomate.)

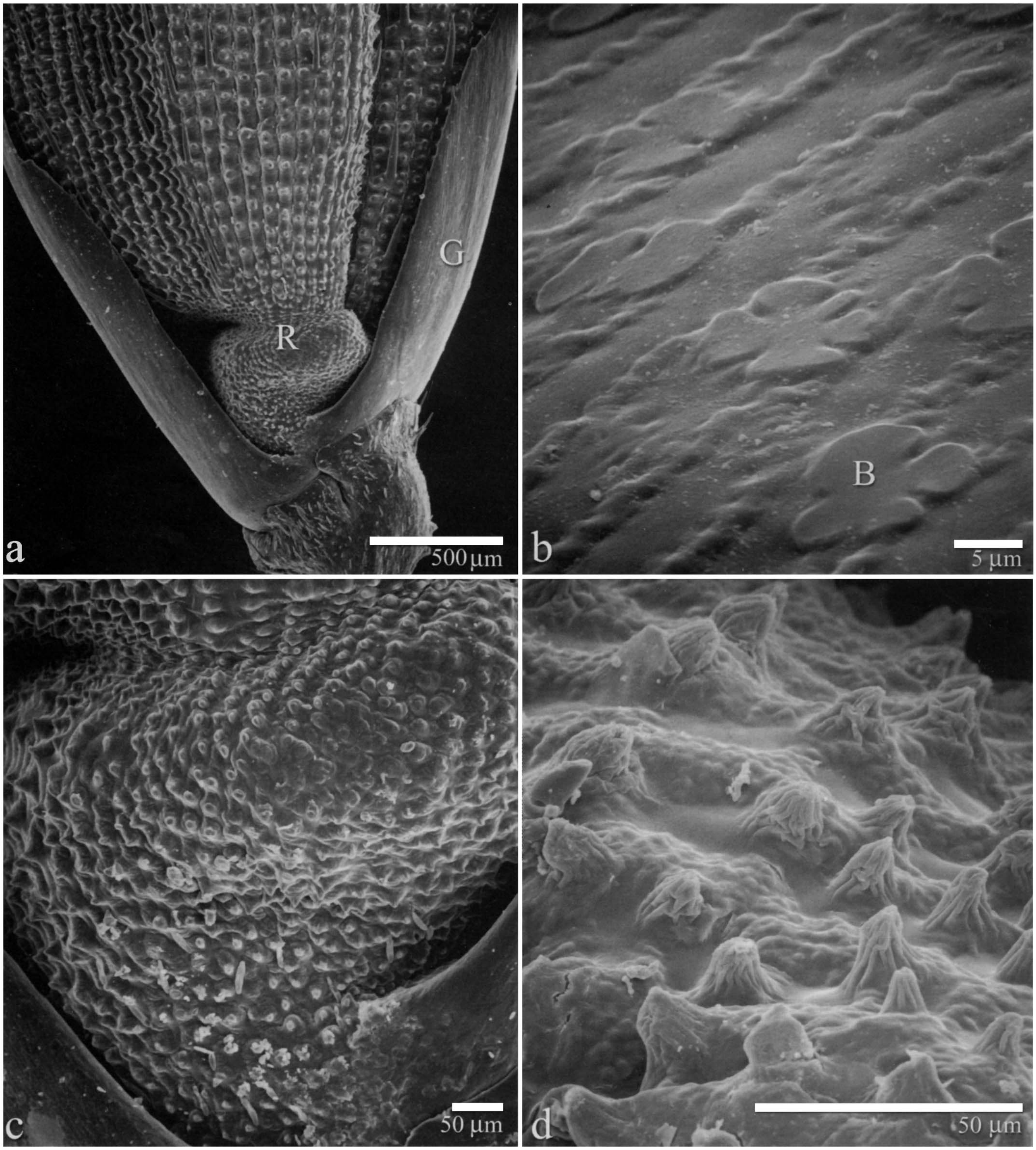

FIGURE 3.—Spikelets of *Oryza sativa* (*a,c,* P.I. 391823; *b,d,* P.I. 373210): *a,* lower part of spikelet showing cupule, glumes (offset), globose rachilla, base of lemma, and palea; *b,* glume with lobed silica bodies; *c,* globose muricate rachilla; *d,* same, projections enlarged. (B=silica body; G=glume; R=rachilla.)

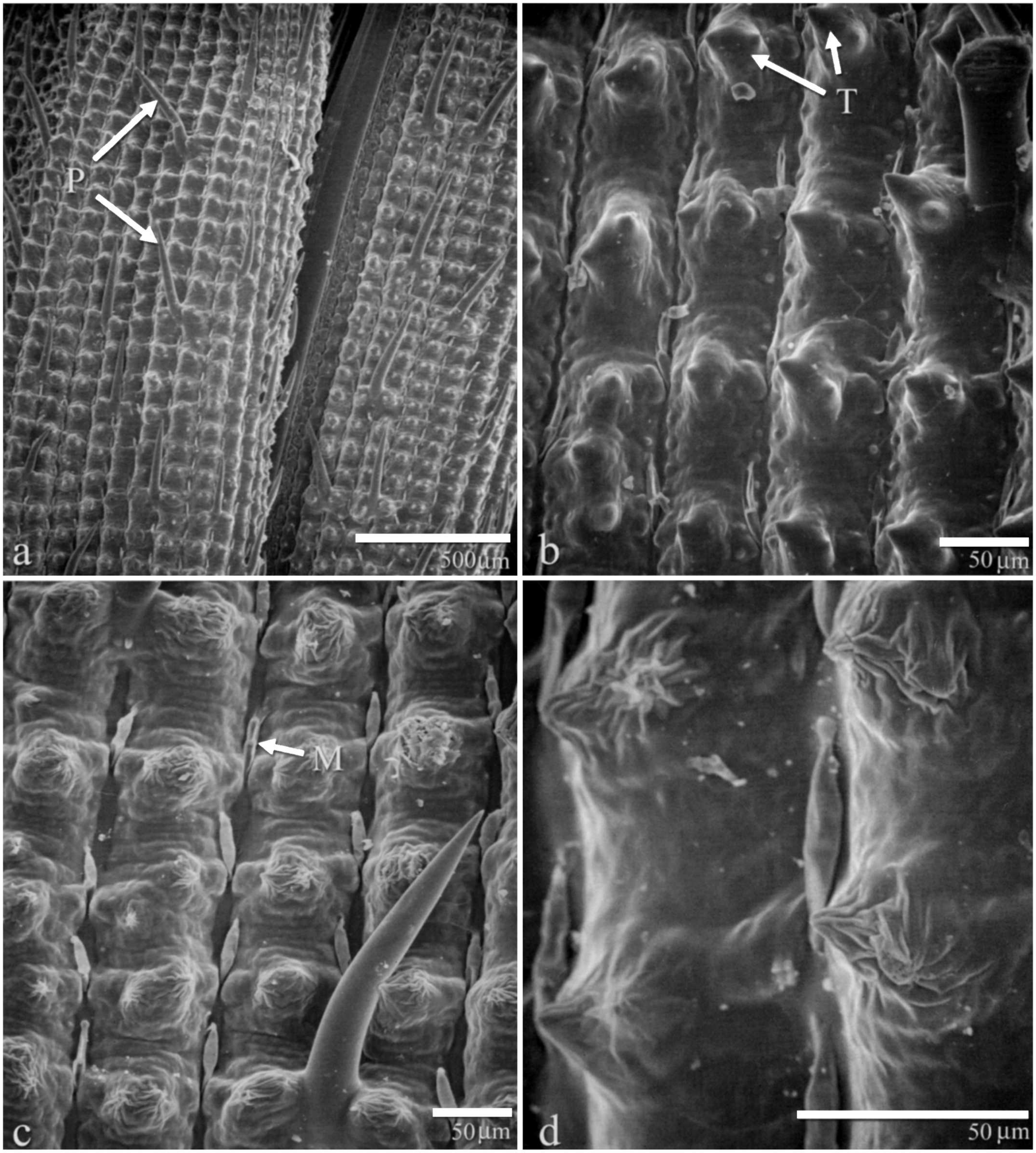

FIGURE 4.—Lemmas of *Oryza sativa* (*a,c,* P.I. 391823; *b,* cv. Strawhull Red; *d,* P.I. 373210): *a,* lemma (left) and palea with vertical tiers and horizontal rows of tubercles, scattered prickles; *b–d,* tubercles enlarged, microhairs in furrows. (M=microhair; P=prickles; T=tubercles.)

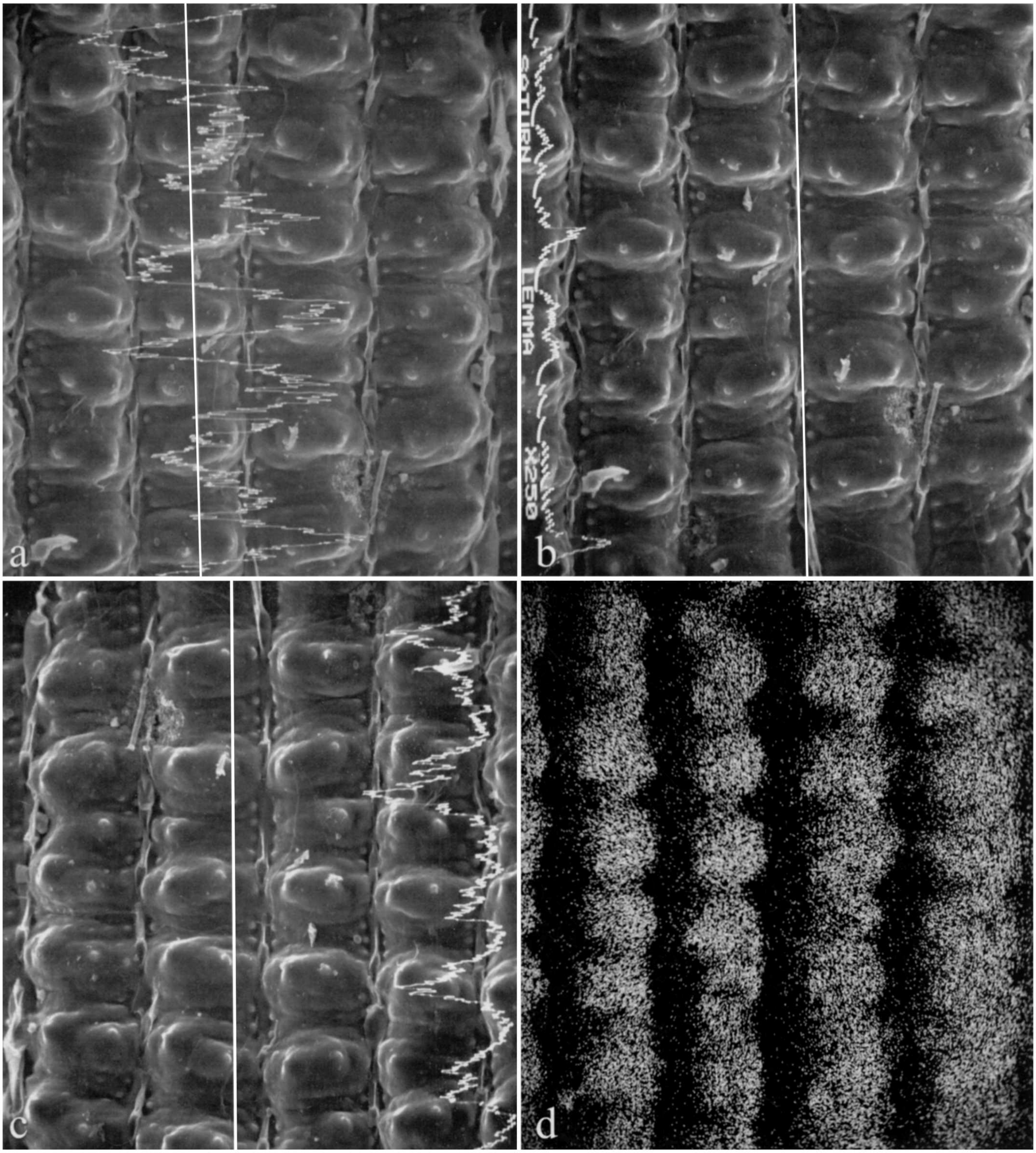

FIGURE 5.—Lemmas of *Oryza sativa* cv. Saturn by EDX analysis: *a–c*, line scan shows high silicon content in tubercles, low content in microhairs and furrows; *d*, X-ray mapping shows silicon in tubercles.

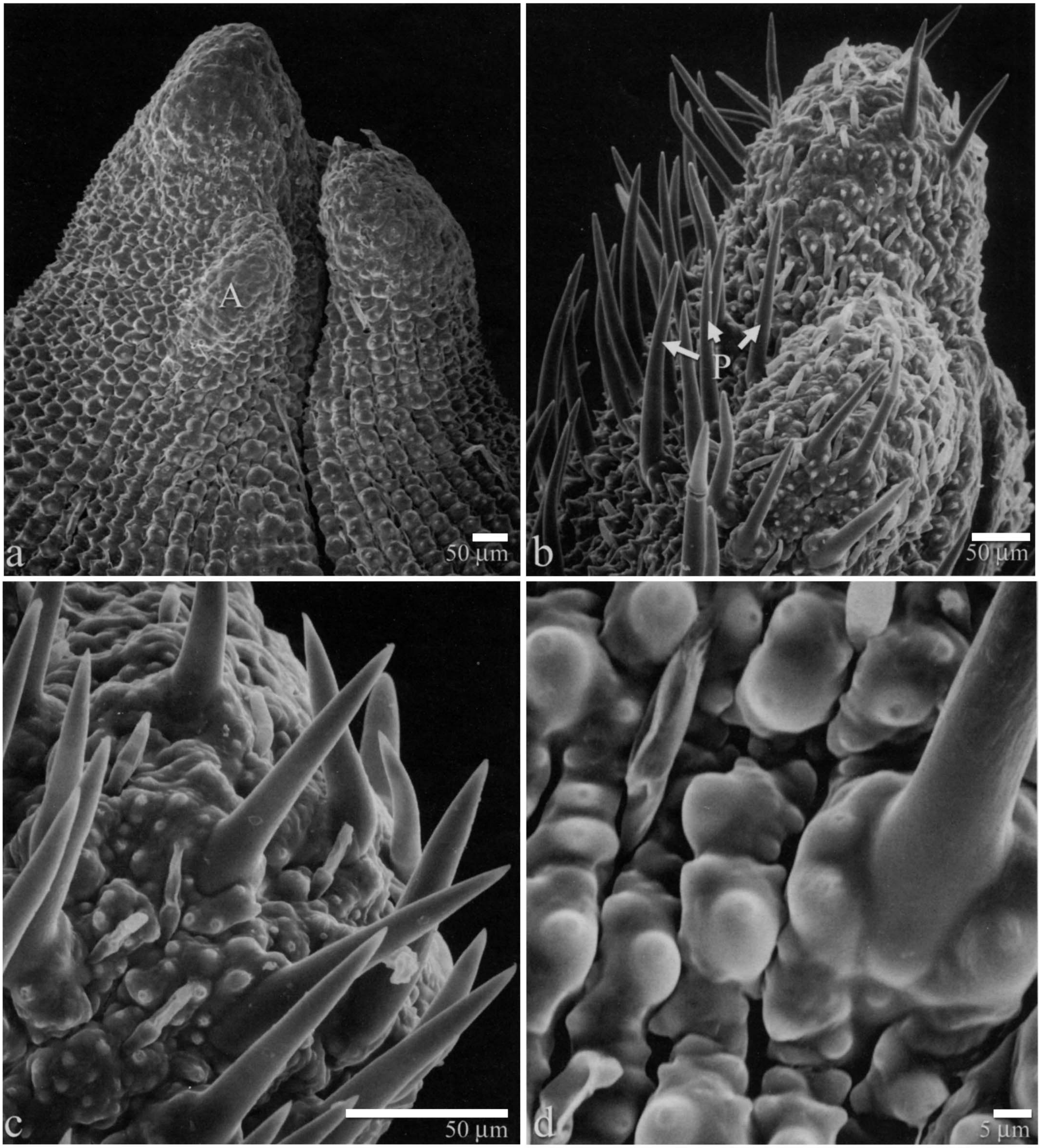

FIGURE 6.—Apices of spikelets of *Oryza sativa* (*a*, cv. Nortai; *b*, P.I. 391823; *c,d*, P.I. 160978): *a*, lemma apex with apicular knob opposite to palea apex; *b*, detail of lemma apex and apicular knob; *c*, same with microhairs, papillae, and prickles; *d*, same, enlarged, showing indurate fused base of a prickle. (A=apicular knob; P=prickles.)

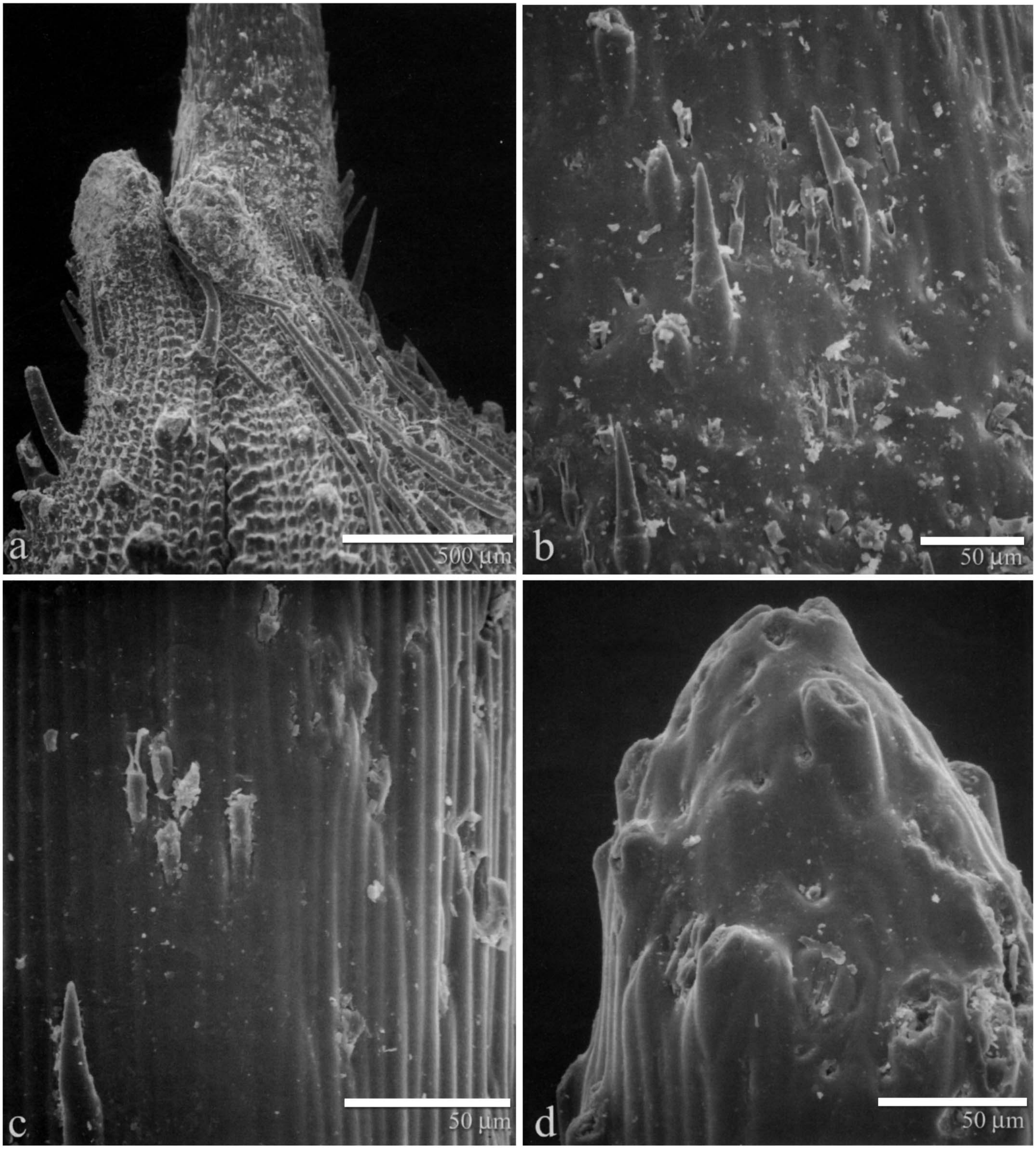

FIGURE 7.—Awns of *Oryza sativa* (*a,b,* cv. Blackhull Red; *c,d,* cv. Strawhull Red): *a,* palea apex (left) and lemma (right) with apicular knob and transition to awn base; *b,* awn base showing microhairs and prickles; *c,* median part of awn; *d,* awn tip showing bases of aborted prickles.

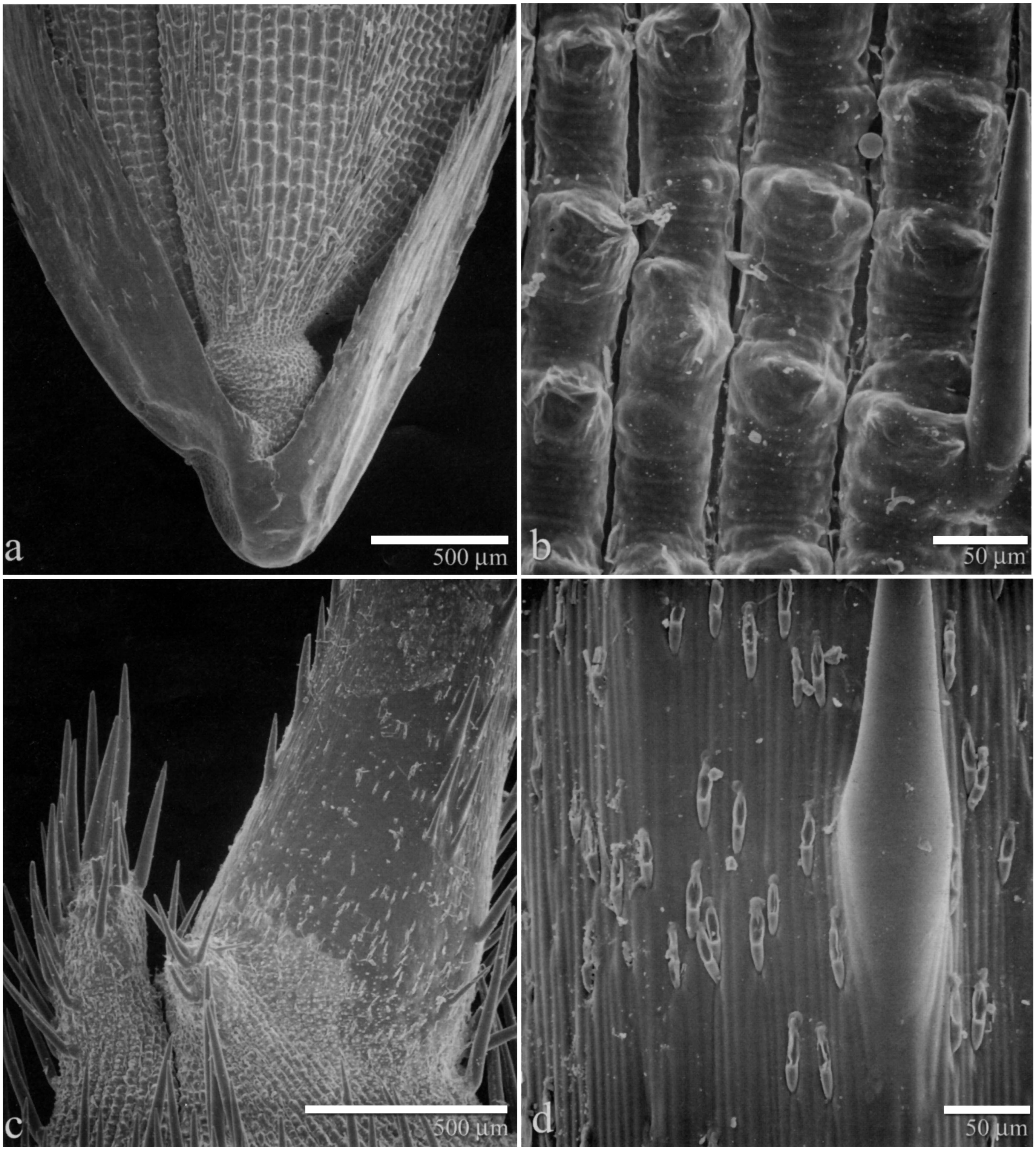

FIGURE 8.—*Oryza barthii* (*a,b,* IRRI 100224; *c,d,* IRRI 100119): *a,* lower part of spikelet showing callus at base, lateral articulation scar, glumes, globose rachilla, lemma, and palea bases; *b,* lemma with tubercles; *c,* palea tip (left) and lemma tip (right) with apicular knob and awn base; *d,* median part of awn showing microhairs and prickle.

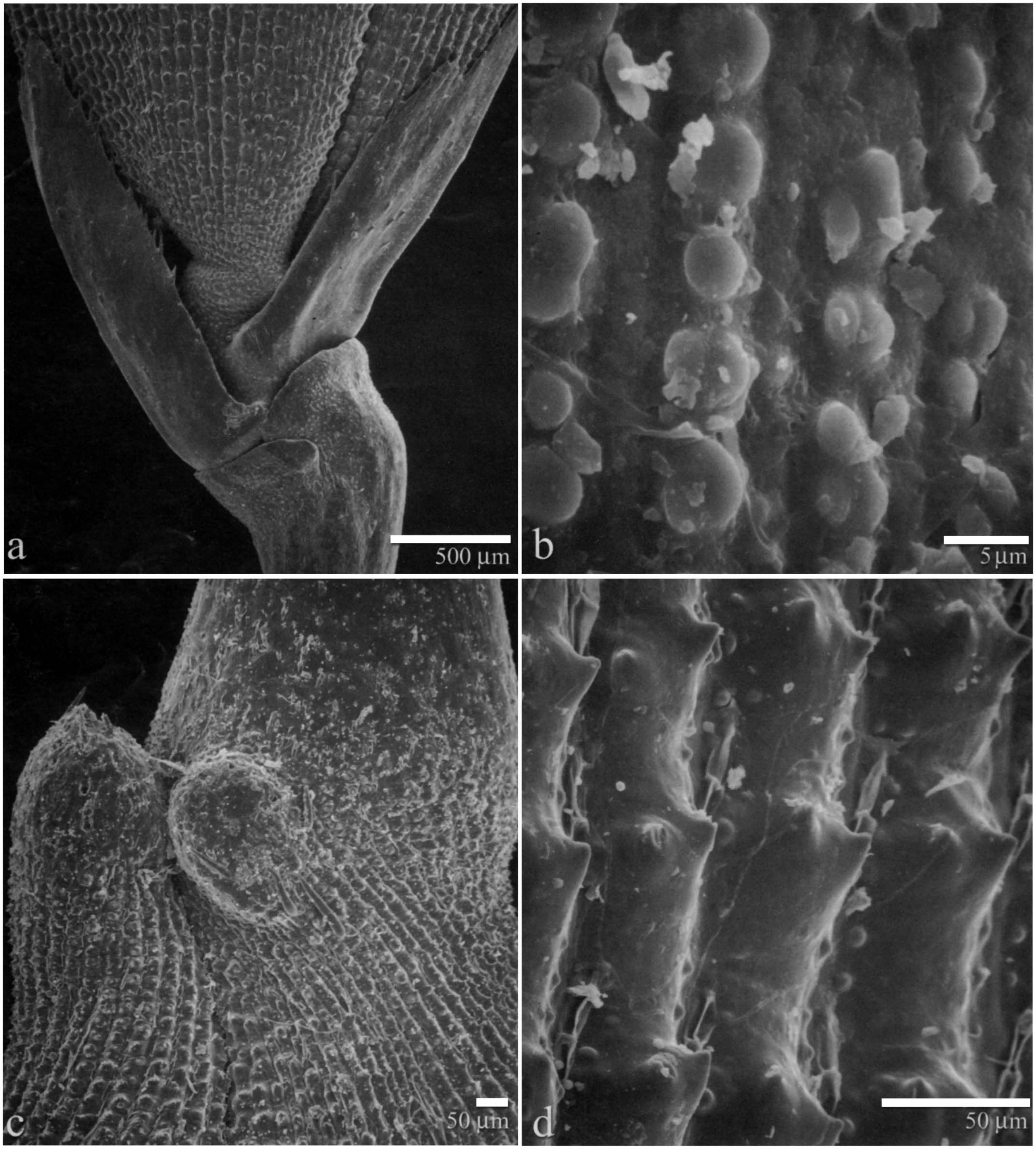

FIGURE 9.—*Oryza glaberrima* (*a,* TOG7141; *b–d,* TOG5833): *a,* lower part of spikelet showing pedicel and lobed cupule, glumes (offset), globose rachilla, lemma, and palea bases; *b,* glume with large papillae; *c,* lemma and palea (left) apices, apicular knob, and base of awn; *d,* lemma showing tubercles, microhairs in furrows, and scattered papillae.

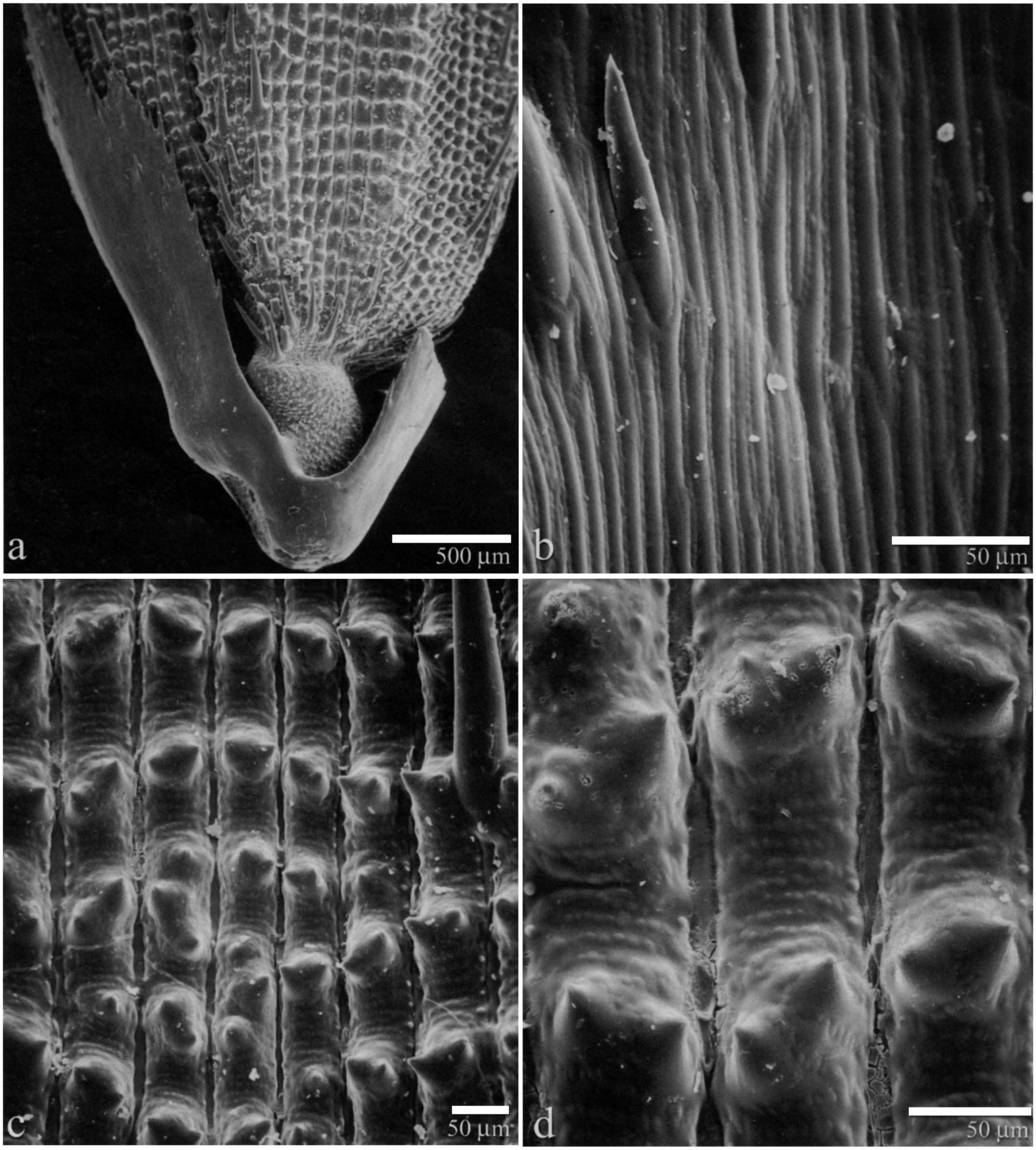

FIGURE 10.—*Oryza longistaminata: a,* lower part of spikelet showing callus at base with lateral articulation scar, globose rachilla, one glume broken off, lemma, and palea bases; *b,* glume with two prickles; *c,d,* lemma with tubercles, microhairs in furrows.

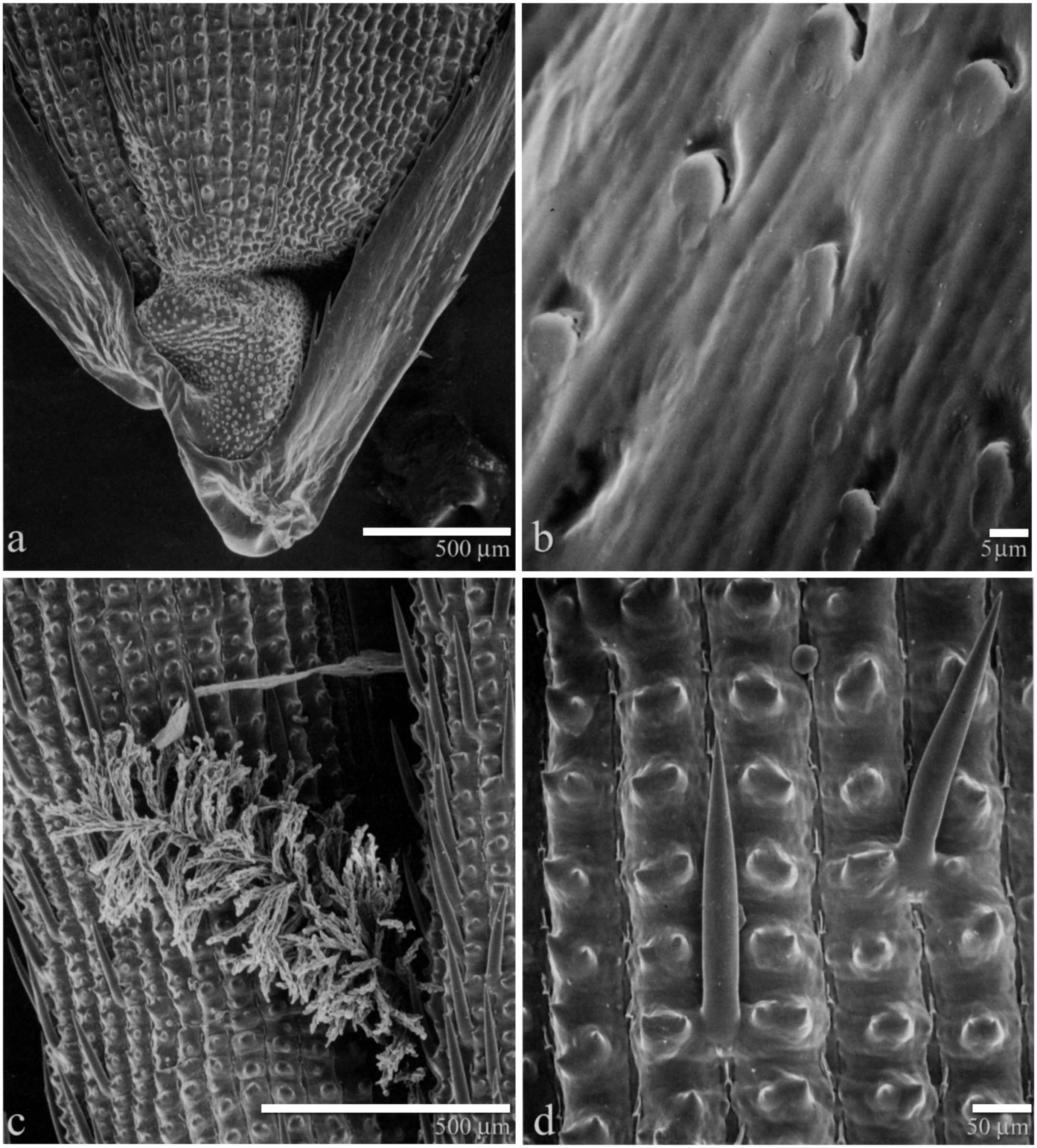

FIGURE 11.—*Oryza rufipogon: a,* lower part of spikelet showing callus with lateral articulation scar, glumes (offset), globose rachilla, lemma, and palea bases; *b,* glume with silica bodies; *c,* lemma and palea with exserted stigmas; *d,* lemma with tubercles, microhairs, and prickles.

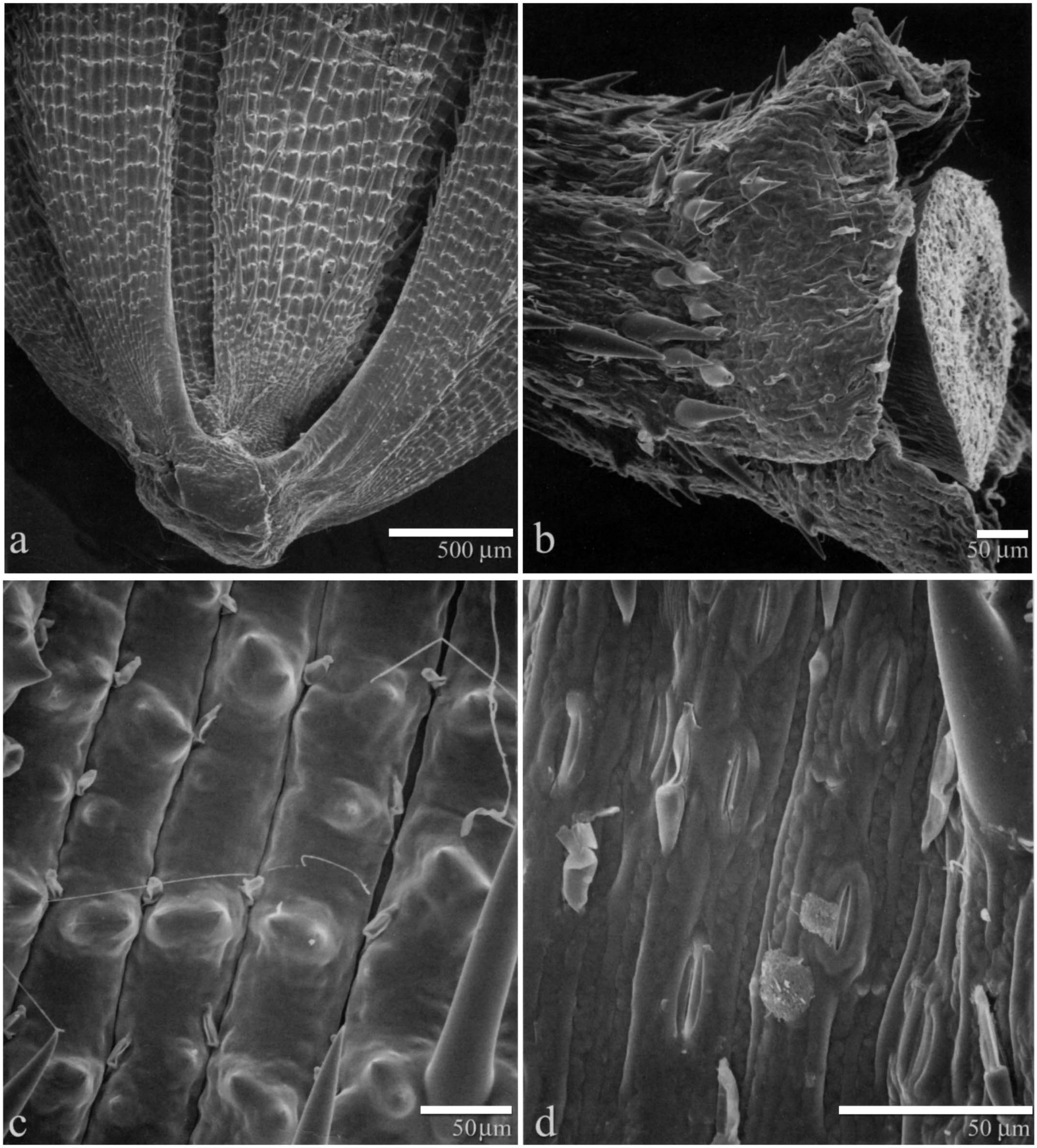

FIGURE 12.—*Oryza grandiglumis: a,* lower part of spikelet showing small callus at base, glumes absent, extra pair of lemmas (outer), small rachilla, inner lemma, and palea; *b,* pedicel with cupule surrounding vascular cylinder but free distally from it; *c,* lemma showing tubercles and microhairs; *d,* pedicel showing microhairs, stomata, and prickle.

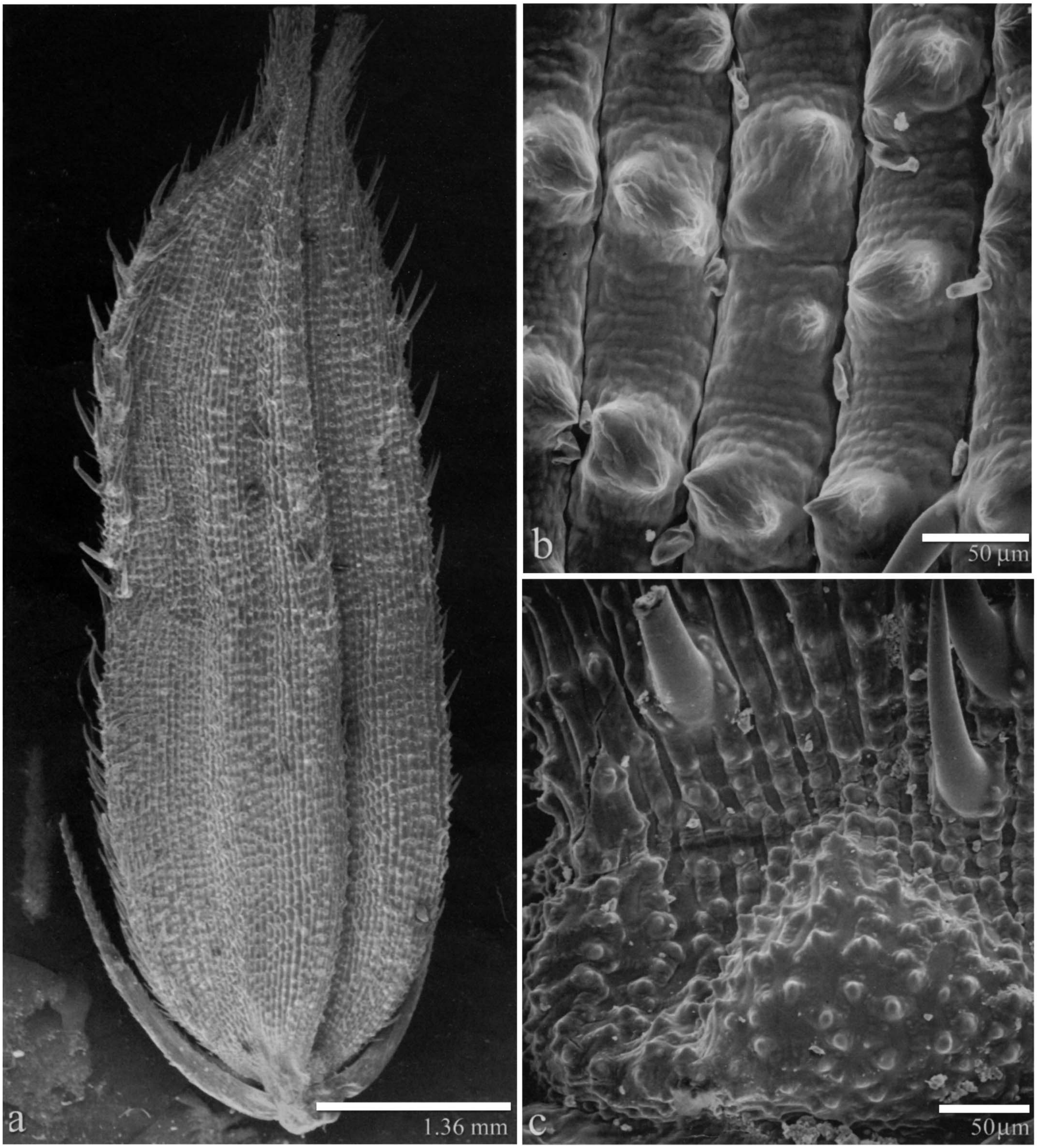

FIGURE 13.—*Oryza alta* (*a,b*), *Oryza latifolia* (*c*): *a,* spikelet showing small callus at base, glumes, very small rachilla, lemma, palea, marginal prickles, and base of awns; *b,* lemma showing tubercles and microhairs, *c,* small muricate rachilla.

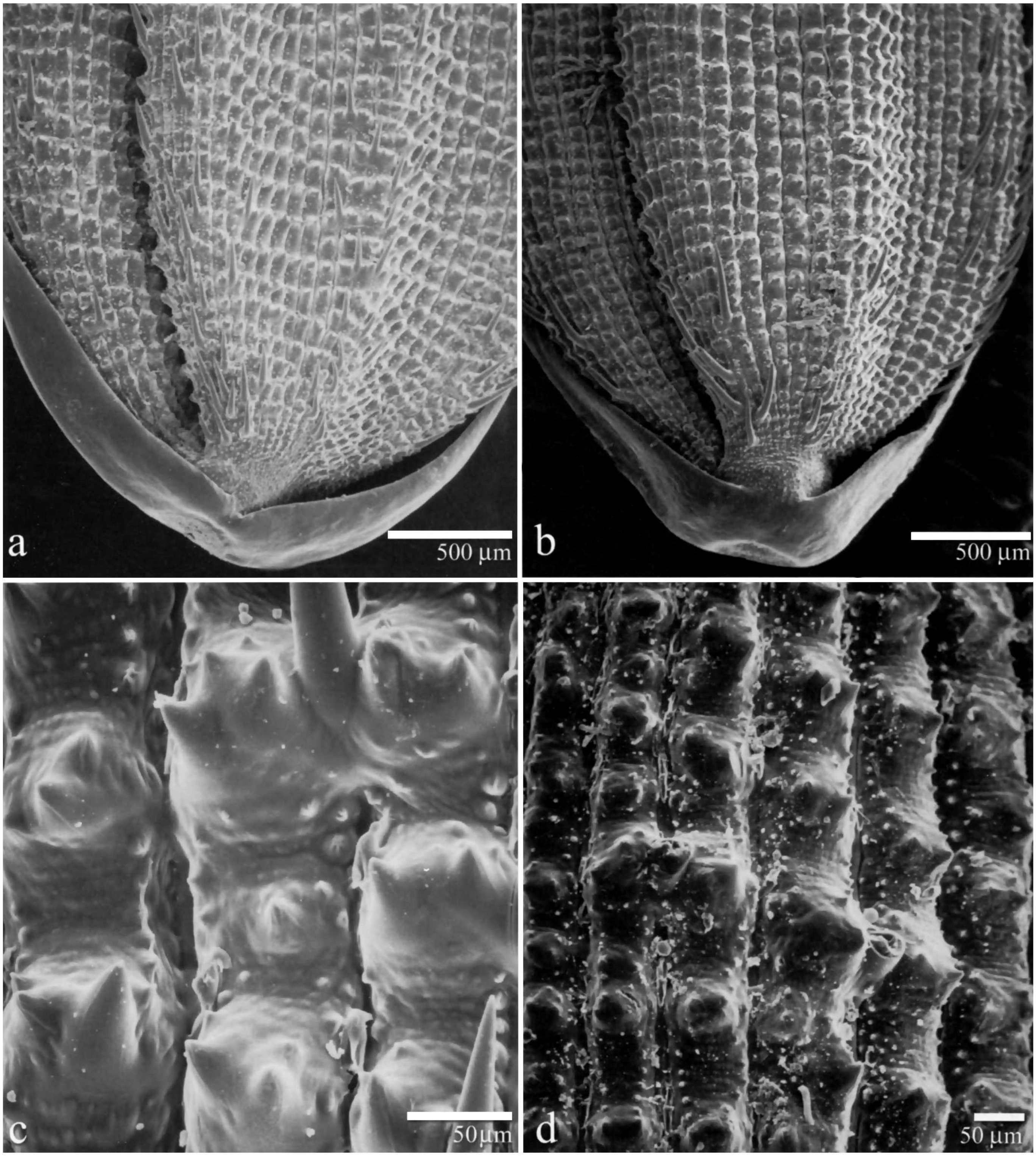

FIGURE 14.—*Oryza australiensis* (*a,c*), *Oryza punctata* (*b,d*): *a,b,* lower parts of spikelets showing callus at base with oblique articulation scar, glumes, small muricate rachilla, lemma, and palea; *c,d,* lemmas with tubercles, microhairs in furrows, and scattered papillae.

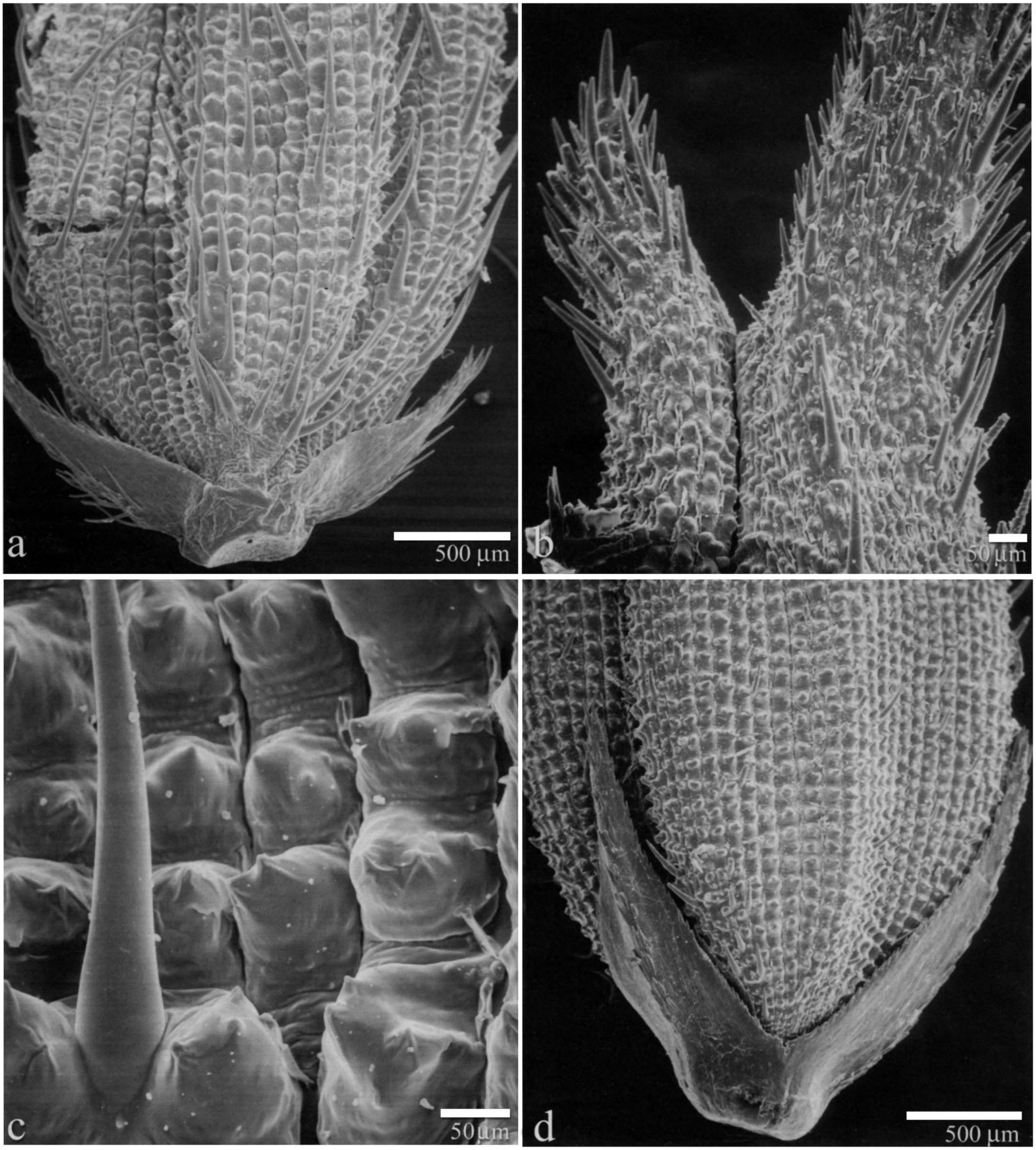

FIGURE 15.—*Oryza minuta* (*a,c*), *Oryza officinalis* (*b,d*): *a,* lower part of spikelet showing callus at base with basal articulation scar, glumes, very small rachilla, lemma, and palea; *b,* palea (left), lemma apex, and awn base; *c,* lemma with tubercles, microhairs, and prickle; *d,* lower part of spikelet, parts as in (*a*).

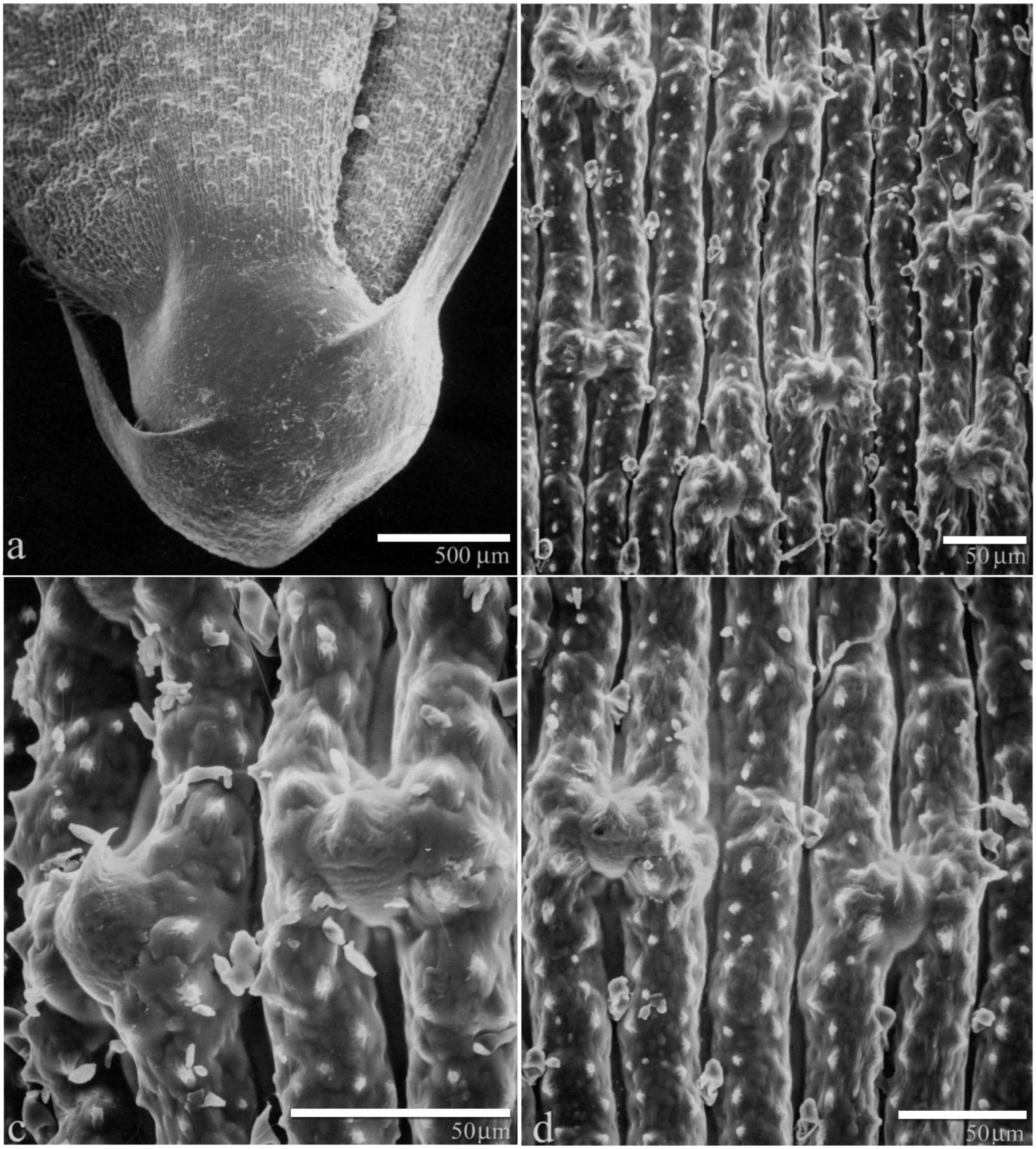

FIGURE 16.—*Oryza meyeriana* var. *meyeriana* (*Strain W1353*): *a,* lower part of spikelet showing callus at base with oblique articulation scar, offset glumes, broad indurate rachilla, bases of lemma, and palea; *b–d,* lemmas showing complex tubercles over furrows and very small microhairs in furrows.

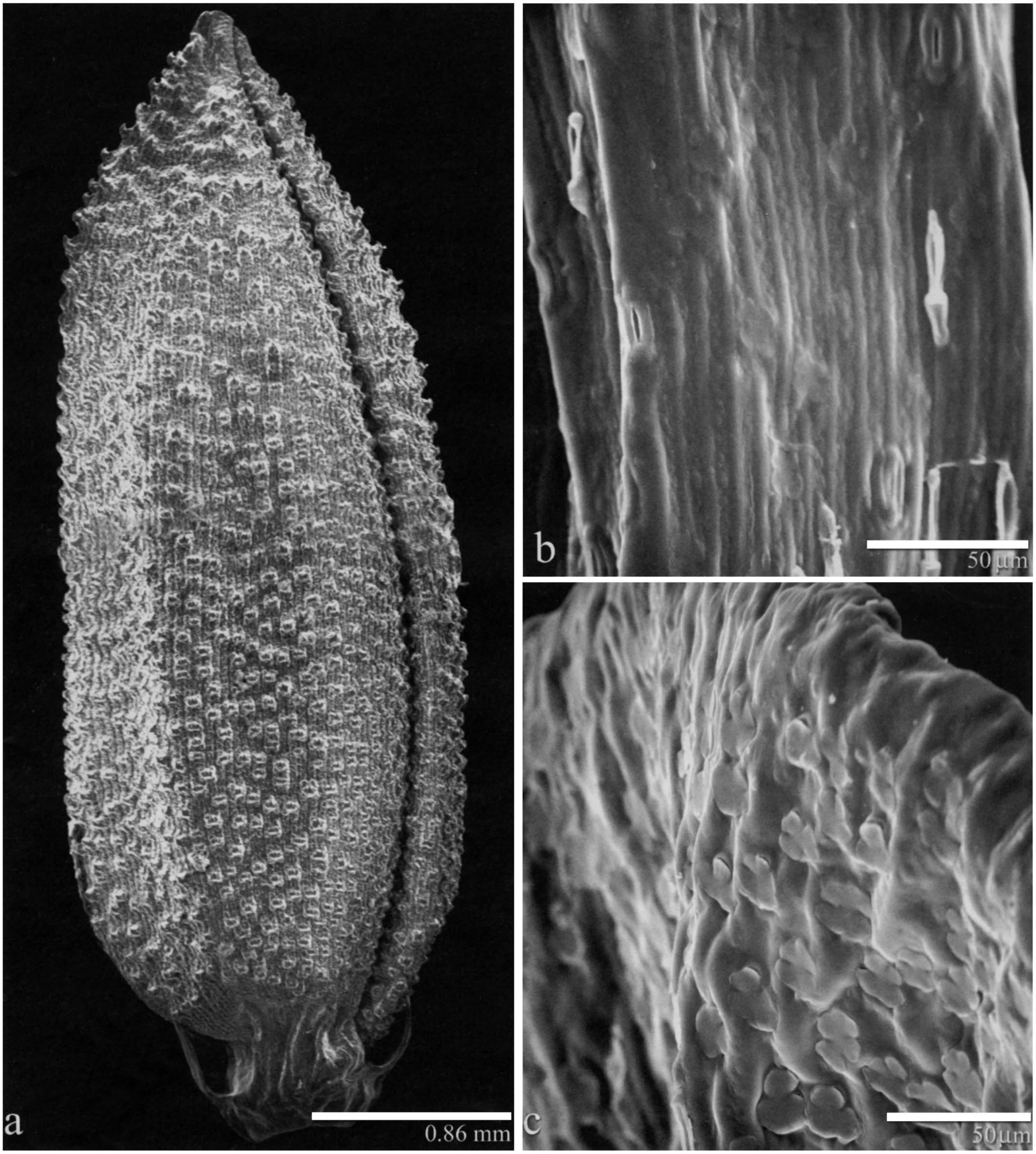

FIGURE 17.—*Oryza meyeriana* var. *granulata* (*a, Kostermans 1200*; *b,c,* IRRI 100162): *a,* spikelet showing callus, small glumes, wrinkled cylindrical rachilla, lemma, and palea, awn lacking; *b,* pedicel with microhairs, silica bodies, and stomata; *c,* cupule with prominent silica bodies.

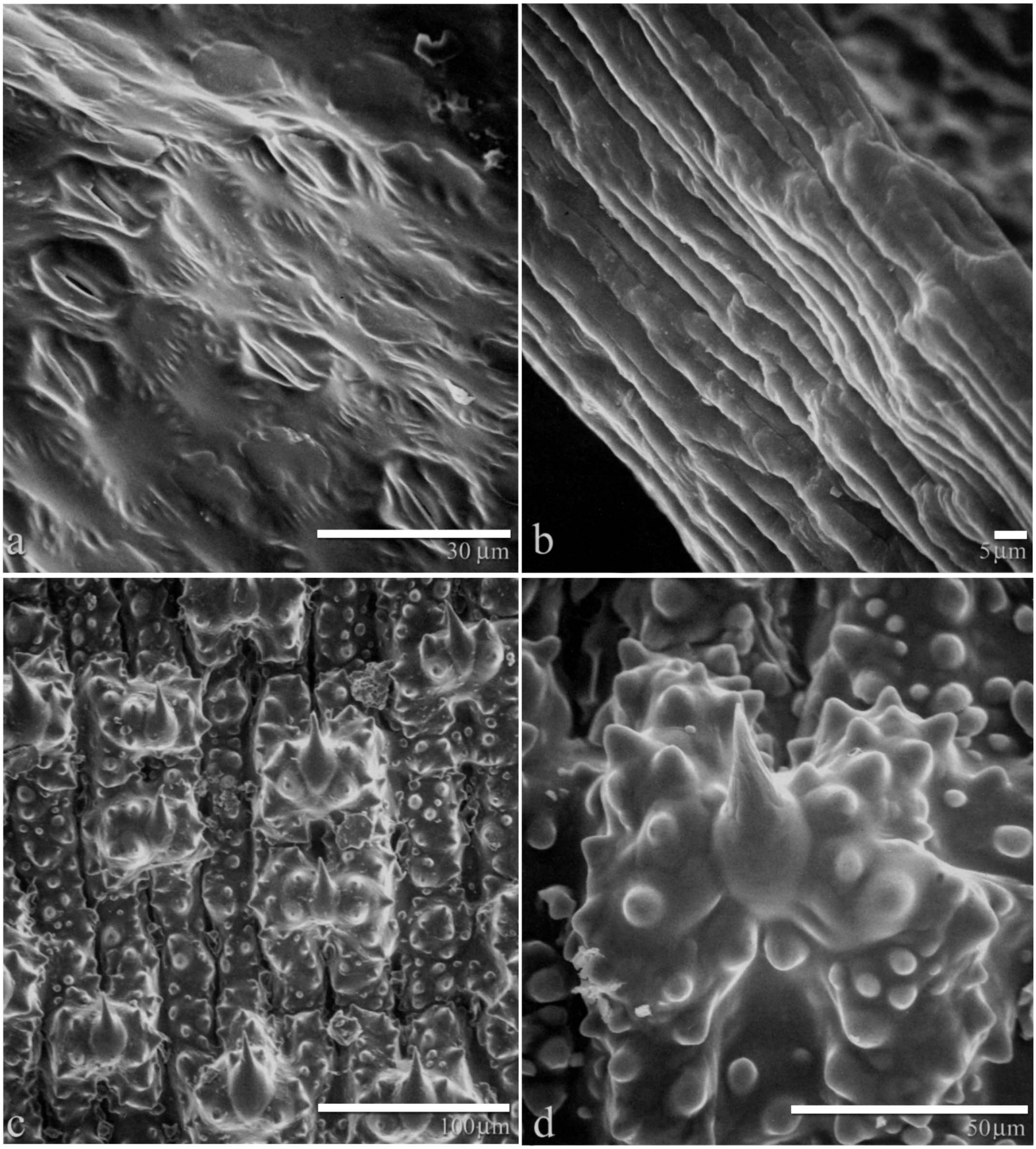

FIGURE 18.—*Oryza meyeriana* var. *granulata* (*a,c, Kostermans 1200*; *b,d,* IRRI 100162): *a,* callus surface with silica bodies and stomata; *b,* glume lacking apparent epidermal features; *c,d,* lemmas with complex tubercles over furrows, numerous free and fused papillae.

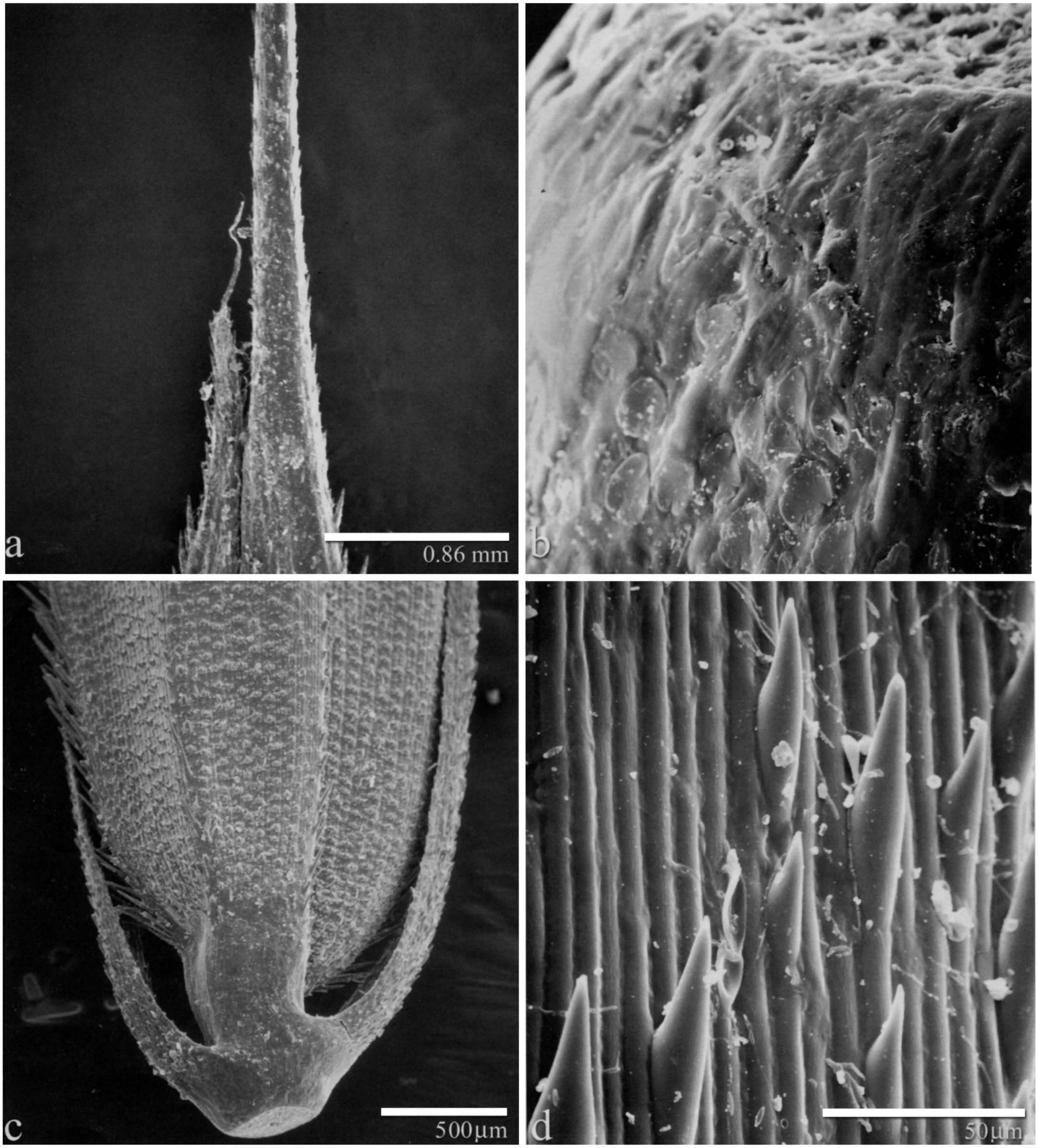

FIGURE 19.—*Oryza ridleyi* (*a, Buwalda 6339*; *b–d,* IRRI 100820): *a,* apices of palea and lemma, lower part of awn; *b,* callus with silica bodies; *c,* spikelet with callus at base, offset glumes, cylindrical rachilla, lemma, and palea; *d,* glume with microhairs and prickles.

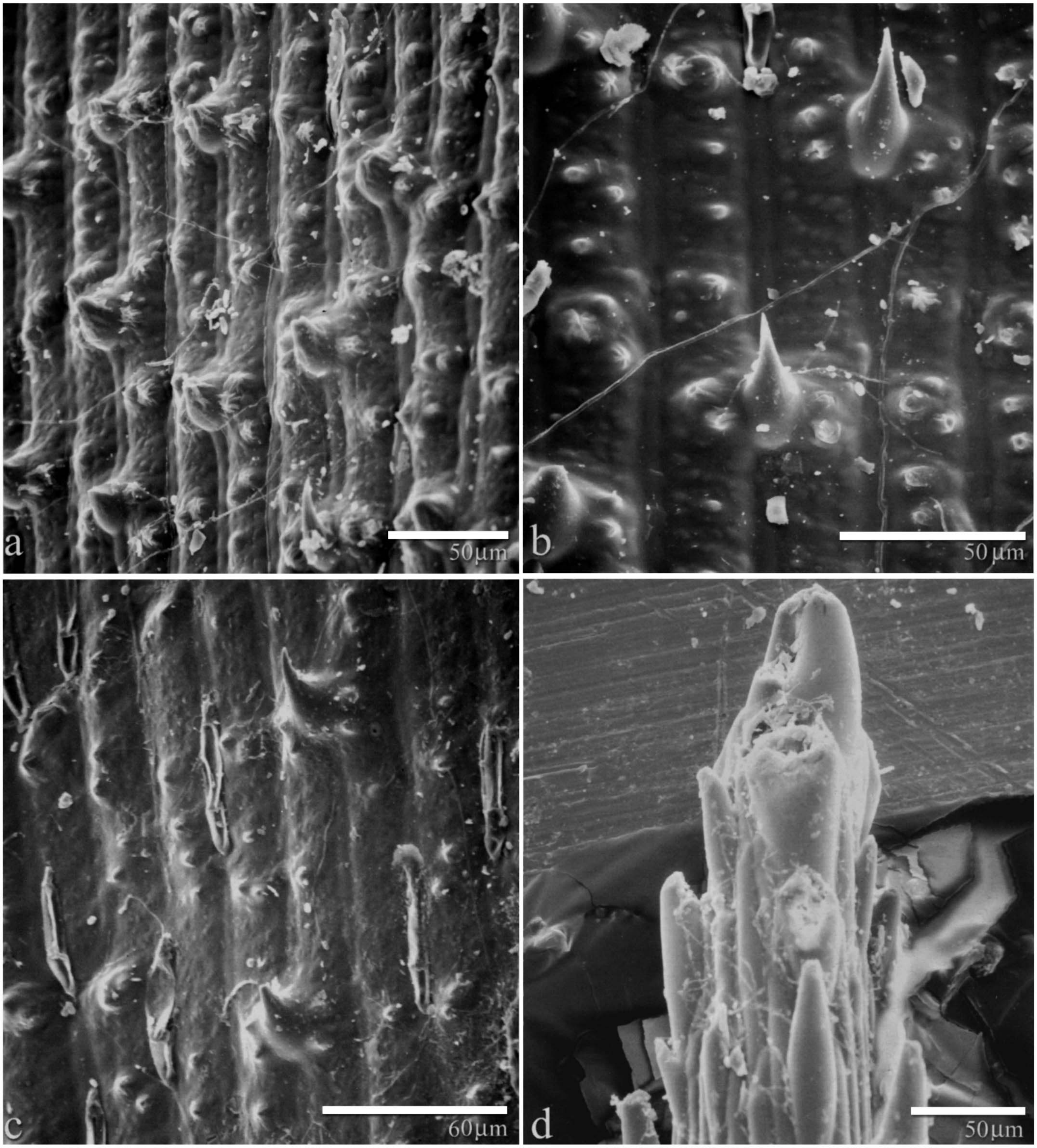

FIGURE 20.—*Oryza ridleyi* (*a,b,d,* IRRI 100820; *c, Buwalda 6339*): *a–c,* lemma with tubercles, microhairs, and prickles; *d,* awn tip.

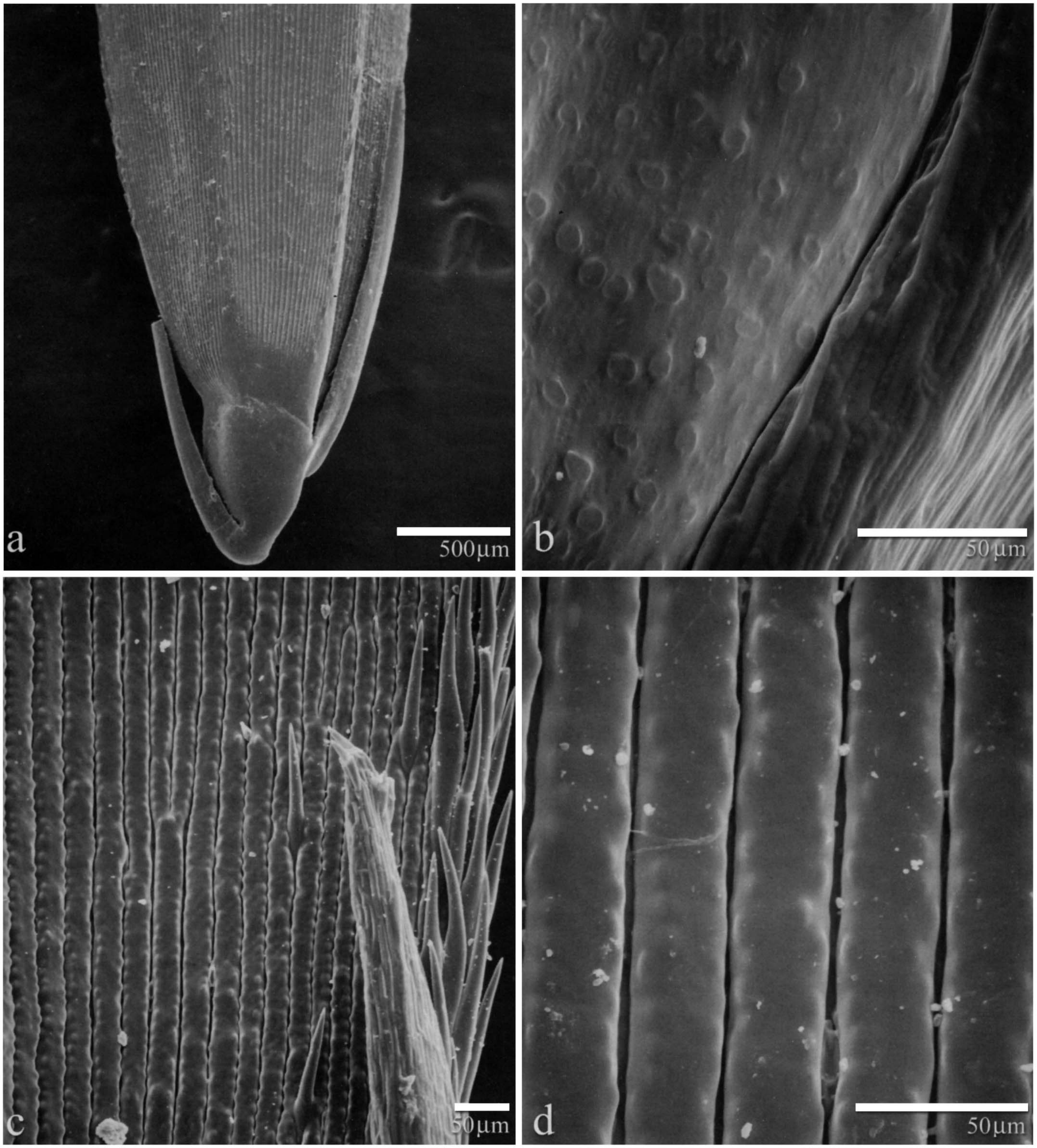

FIGURE 21.—*Oryza brachyantha* (*a,d,* IRRI 101236; *b,c, Richards 9171*): *a,* lower part of spikelet showing large stipitate callus extending to lemma base, strongly offset glumes, upper glume located just above lateral articulation scar, palea (narrow) to right, rachilla lacking; *b,* glume base (right), callus (left) with silica bodies; *c,* lemma with prickles, glume tip, and papillae; *d,* lemma, enlarged, lacking tubercles.

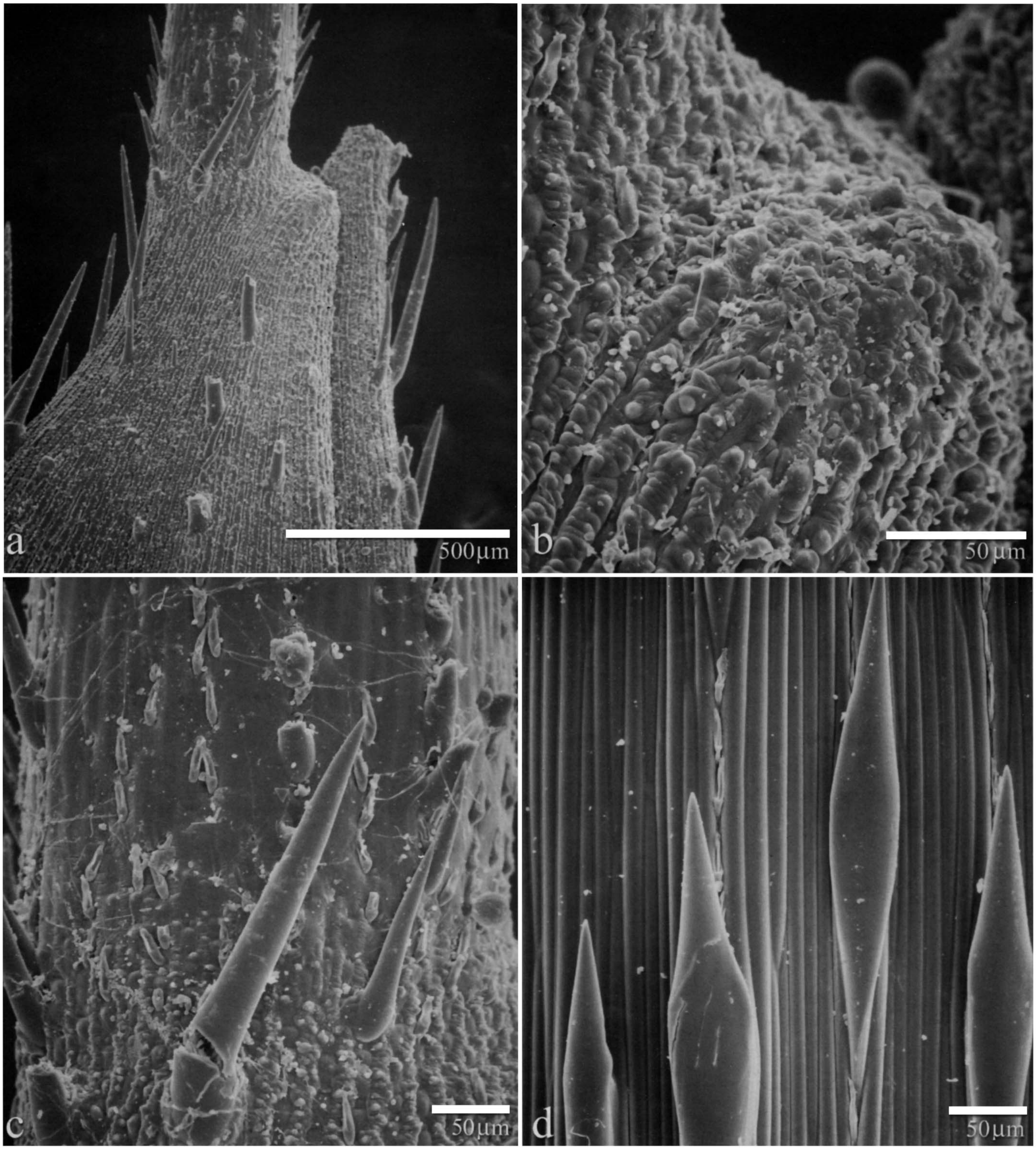

FIGURE 22.—*Oryza brachyantha* (*a–c*, IRRI 101236; *d*, *Richards 9171*): *a*, palea tip (right) and lemma with apicular knob and transition to awn; *b*, lemma apex showing coalesced papillae and microhairs; *c*, transition between lemma and awn; *d*, awn with microhairs and prickles.

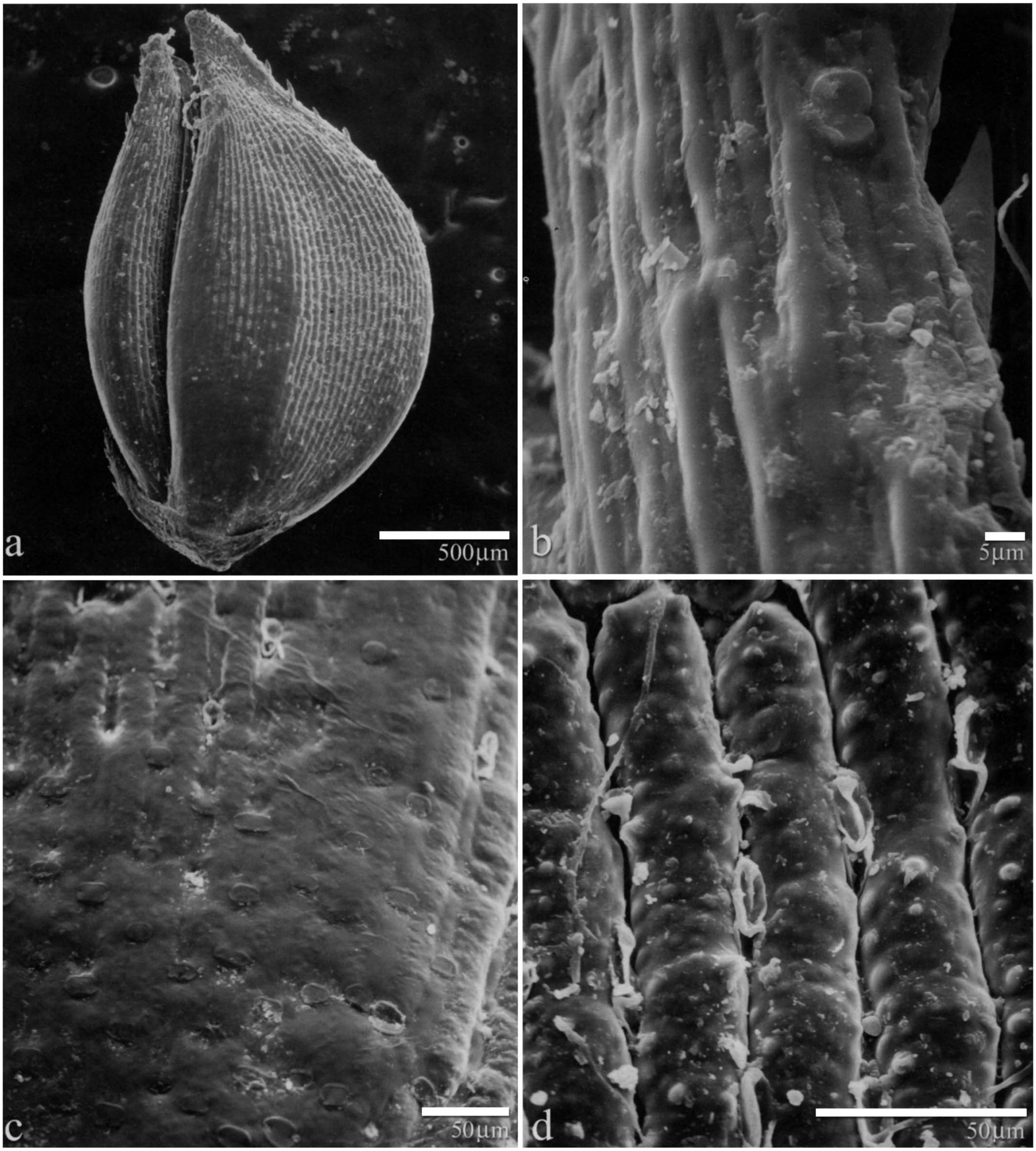

FIGURE 23.—*Oryza schlechteri: a,* spikelet showing very small callus, small glumes, lemma and palea smooth toward their bases; *b,* glume with silica body; *c,* lower smooth part of lemma with silica bodies; *d,* upper furrowed part of lemma with microhairs in furrows, lacking tubercles.

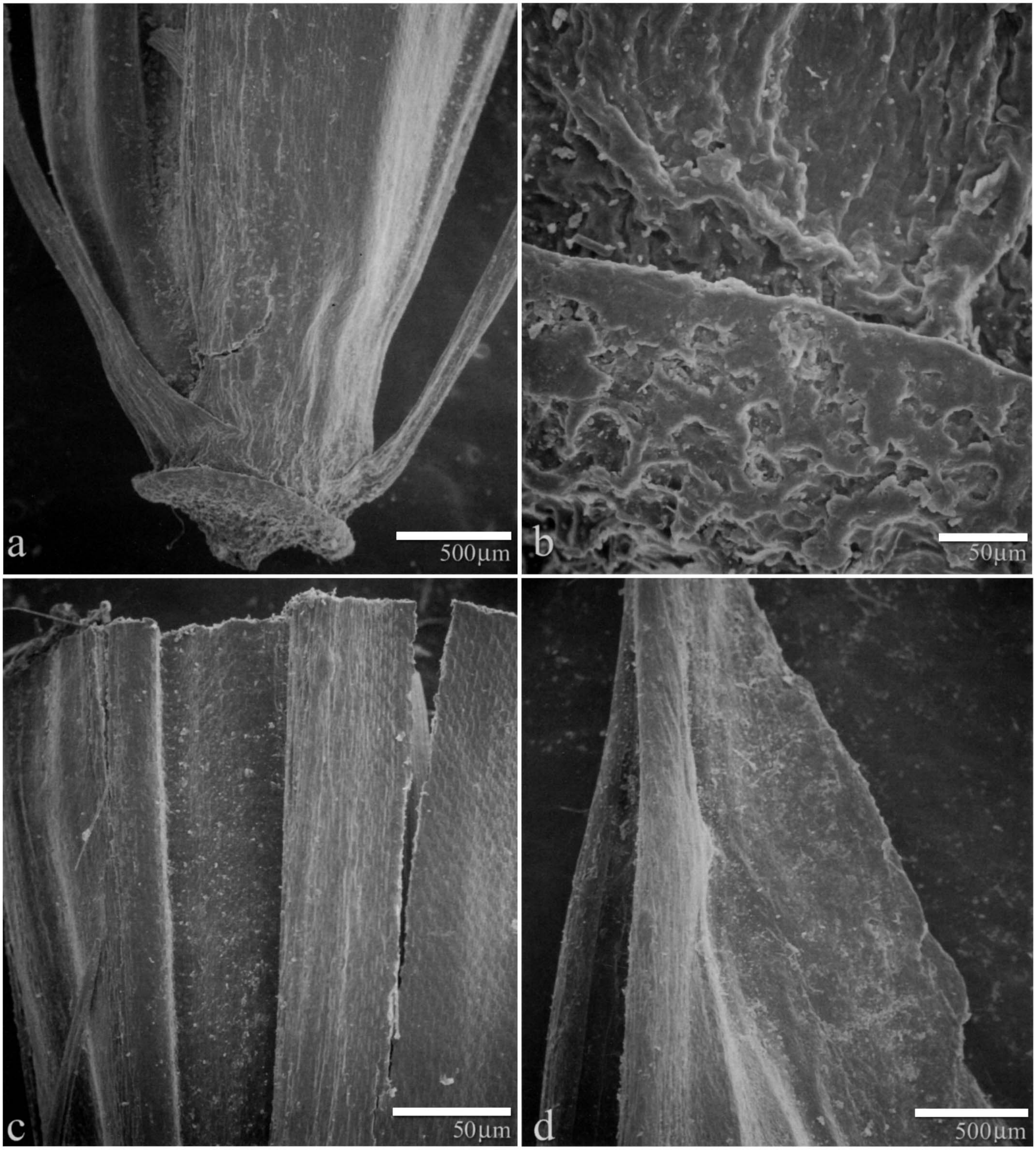

FIGURE 24.—*Porteresia coarctata: a,* lower part of spikelet showing callus expanded and disk-like, rachilla lacking, with glumes, lemma, and palea; *b,* callus below, apparently lacking features; *c,* left side of lemma; *d,* lemma, near its apex.

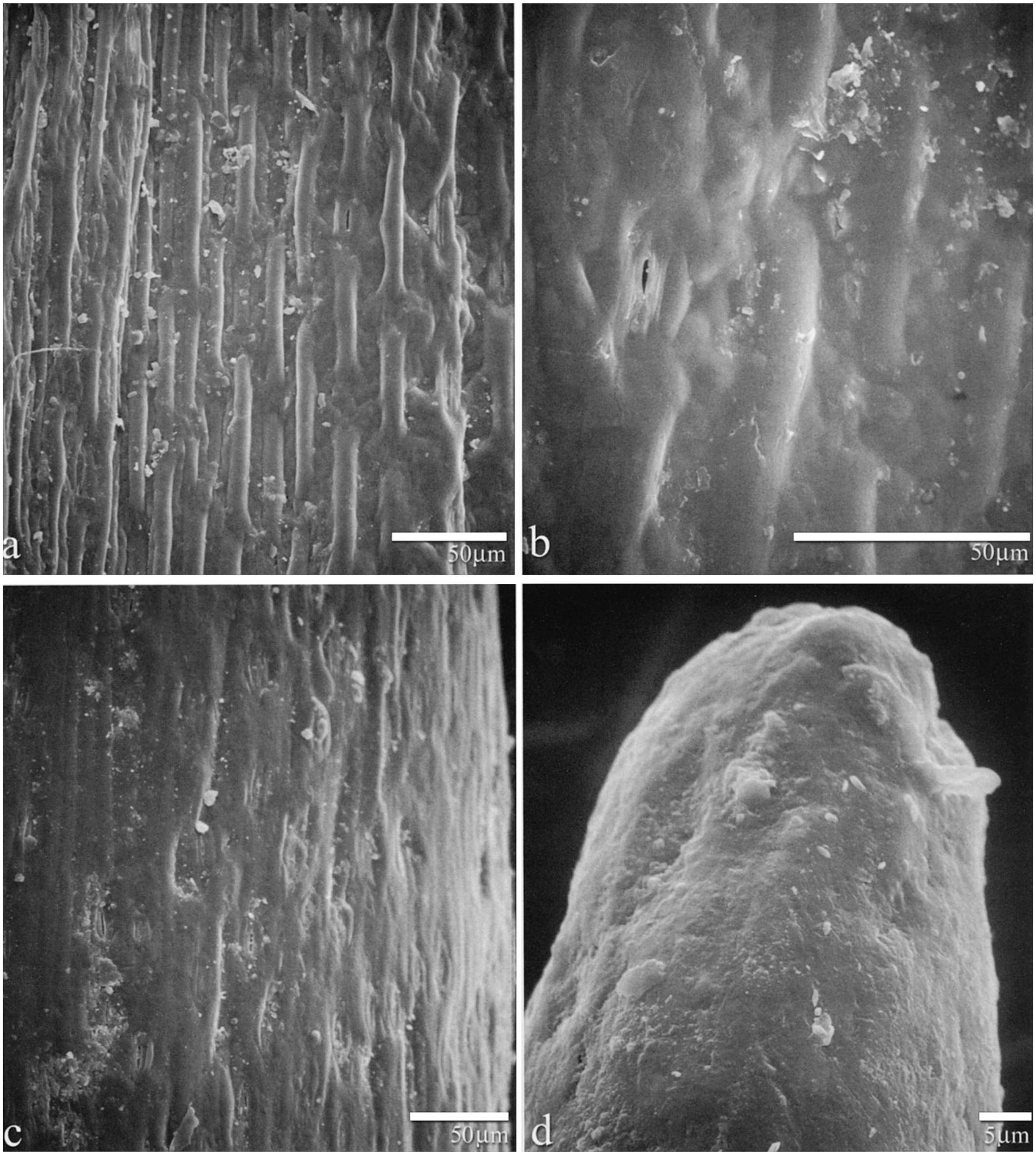

FIGURE 25.—*Porteresia coarctata: a,b,* lemma with stomata, tubercles lacking; *c,* awn base with stomata; *d,* awn tip.

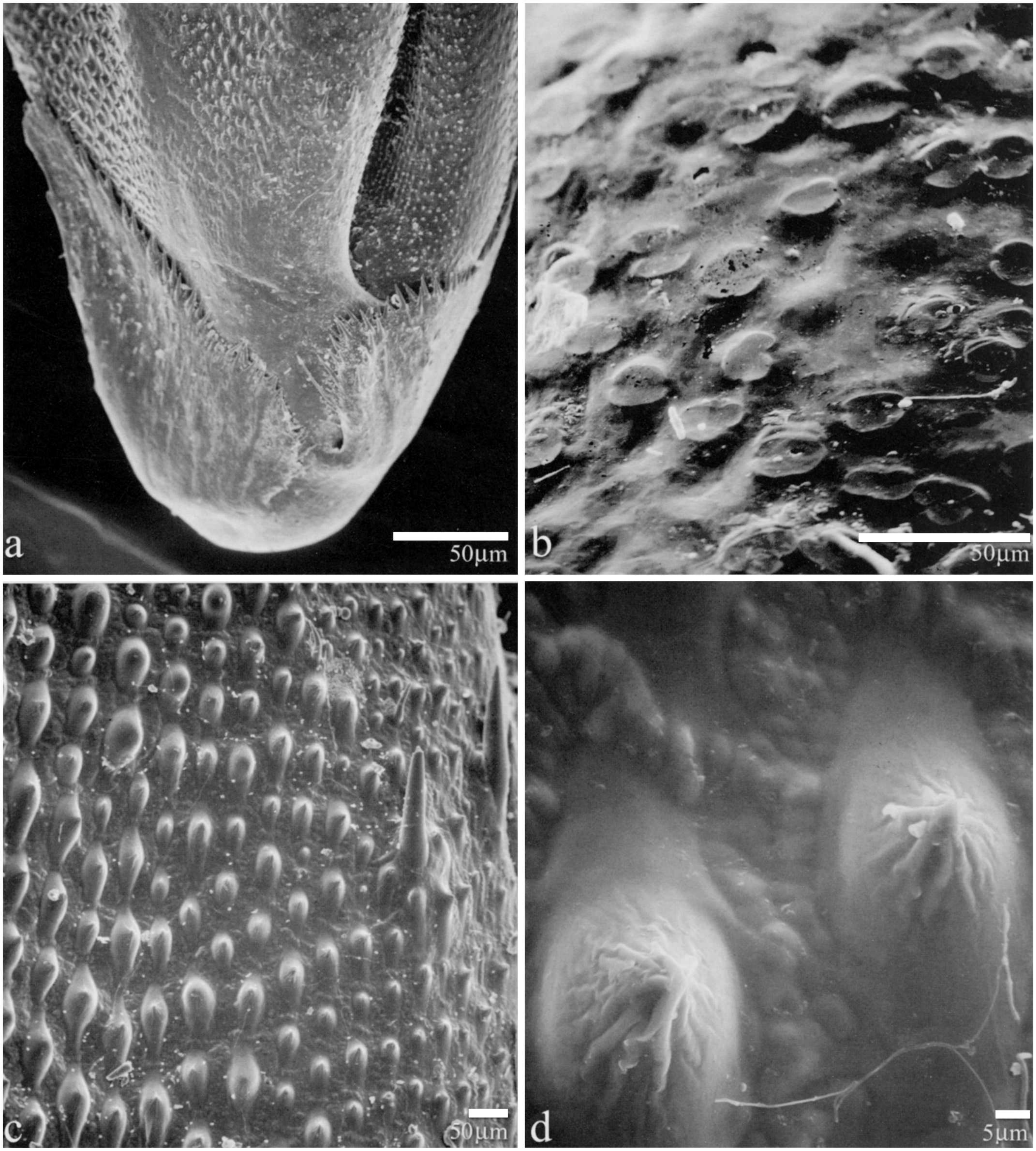

FIGURE 26.—*Rhynchoryza subulata: a,* lower part of spikelet showing rounded callus, ovate glumes with prickles on margin, lemma, and palea, rachilla lacking; *b,* callus with silica bodies; *c,* lemma with mammiform tubercles and prickles; *d,* mammiform tubercles enlarged.

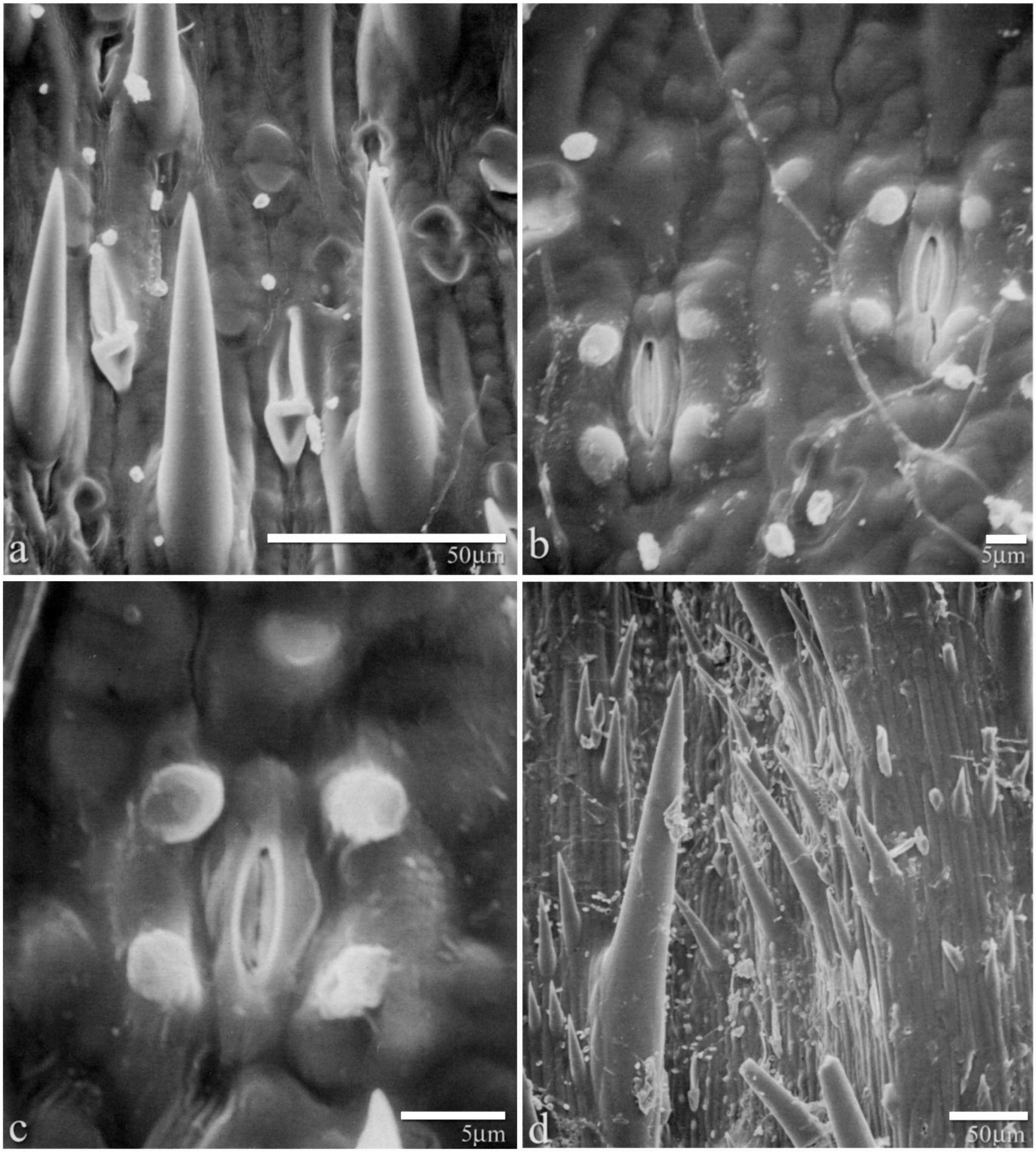

FIGURE 27.—*Rhynchoryza subulata: a,* upper (distal) part of lemma showing microhairs, prickles, and silica bodies; *b,c,* lemma showing stomata, each with four bordering papillae; *d,* awn with microhairs and prickles.

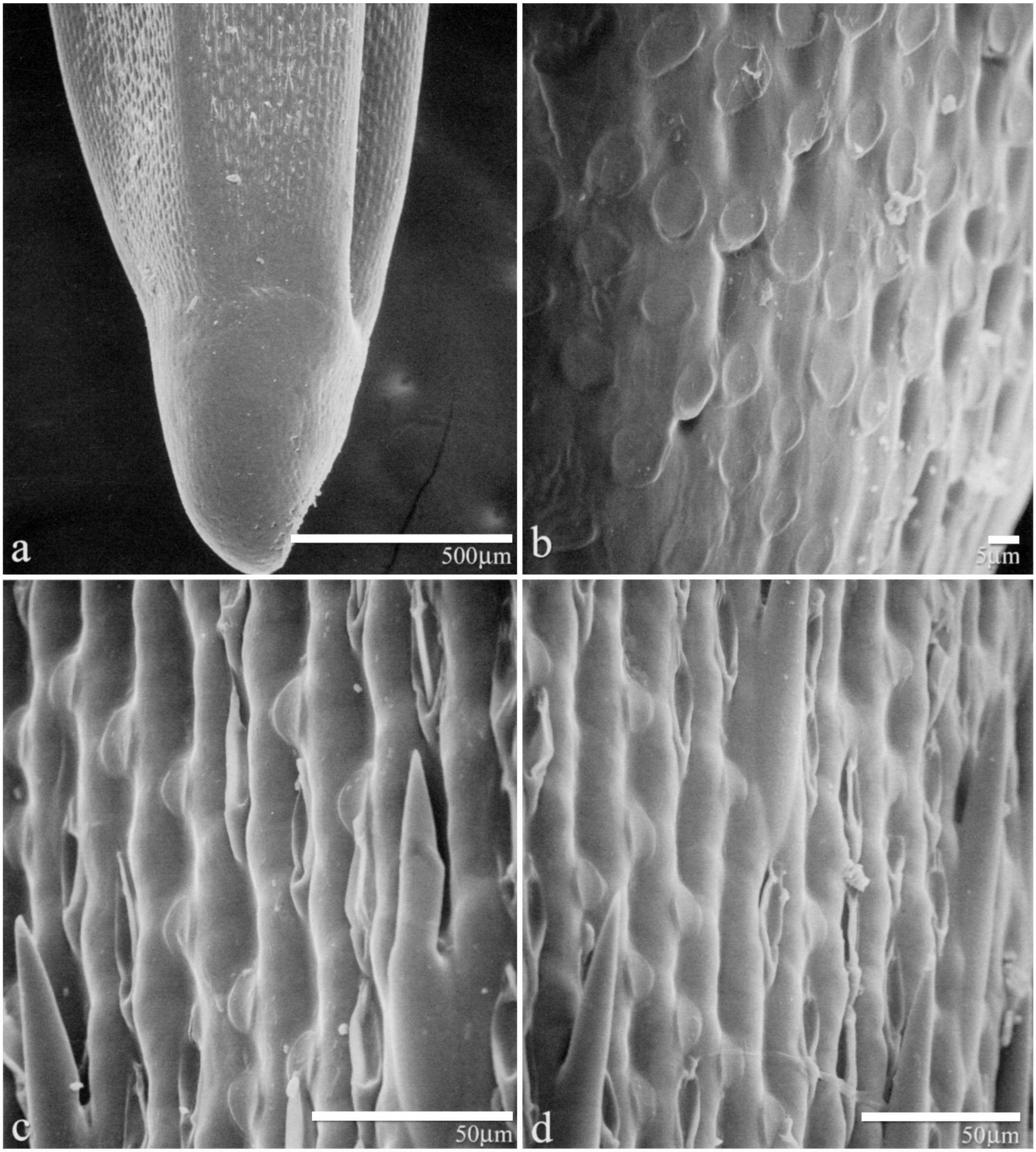

FIGURE 28.—*Leersia nematostachya: a,* lower part of spikelet showing stipitate callus with lateral articulation scar (right), lemma, and palea, rachilla lacking; *b,* upper part of callus with silica bodies; *c,* lemma showing silica bodies, microhairs, and prickles, tubercles lacking; *d,* palea, same as preceding.

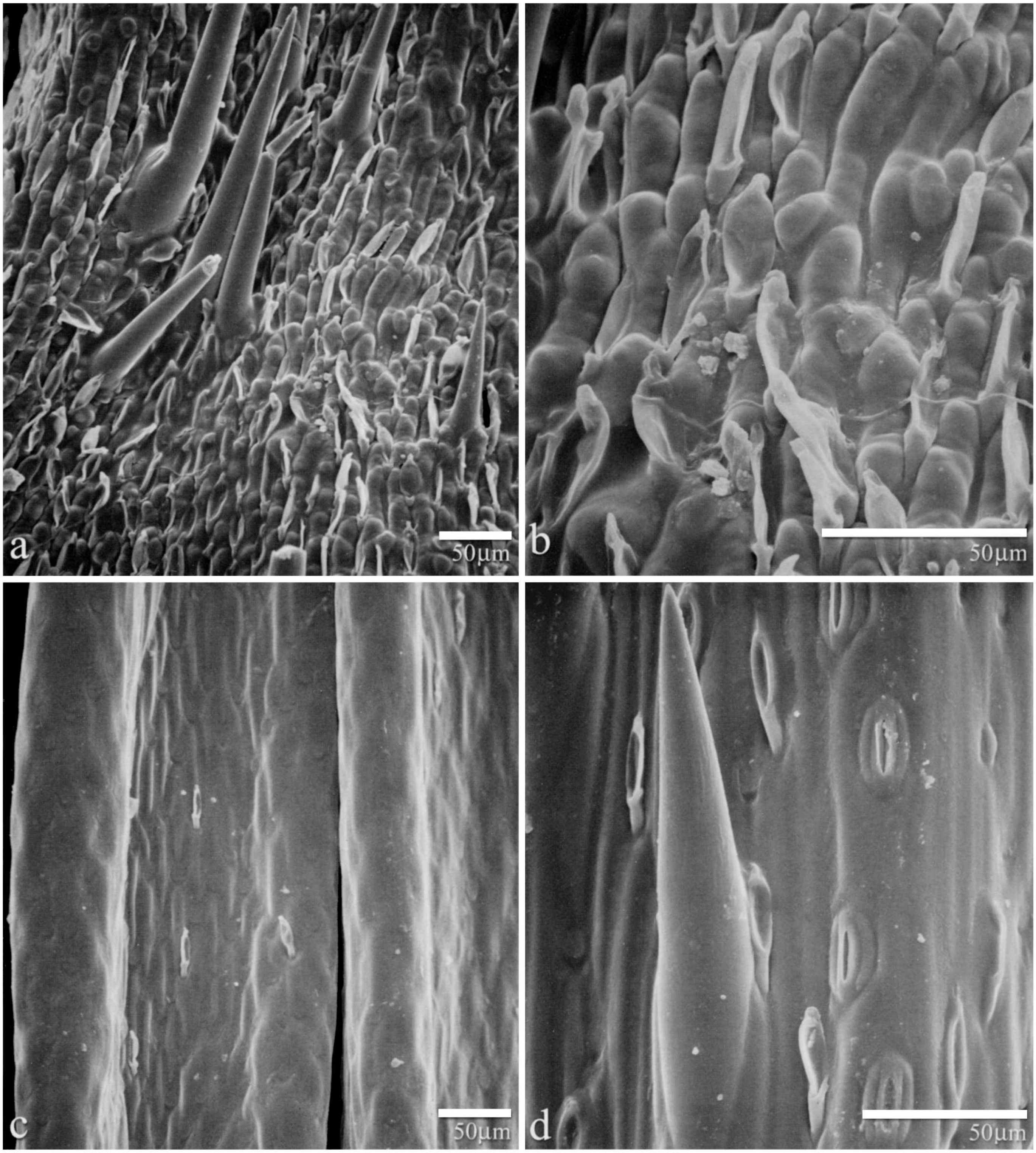

FIGURE 29.—*Leersia nematostachya: a,b,* transition, lemma apex, and awn base showing coalesced papillae, microhairs, and prickles; *c,d,* awns showing microhairs, stomata, and prickles.

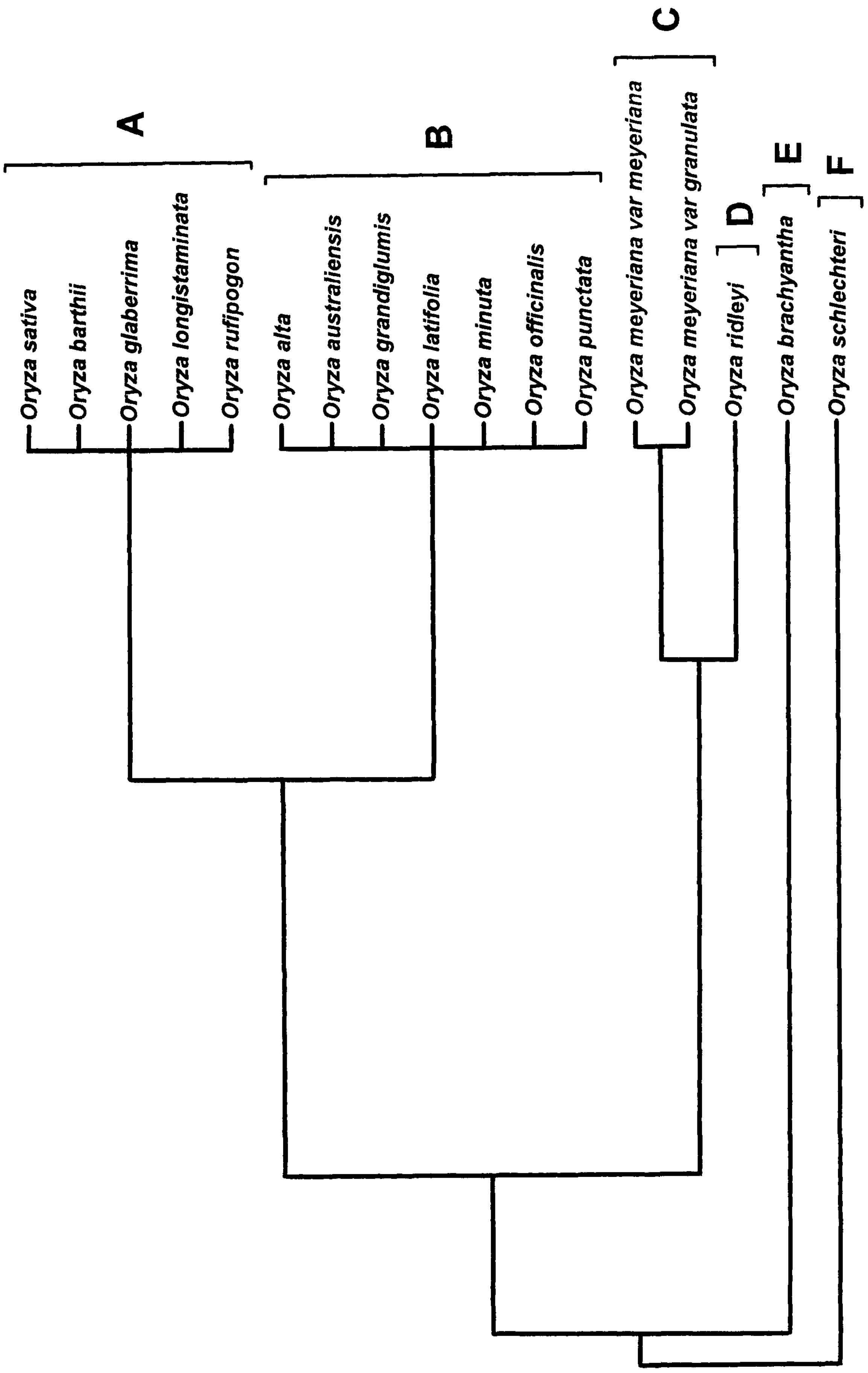

FIGURE 30.—UPGMA cluster phenogram of 16 species of *Oryza*. (Refer to Table 2 for data set and text for description of characters. Groups A, B, C, D, E, and F discussed in text.)

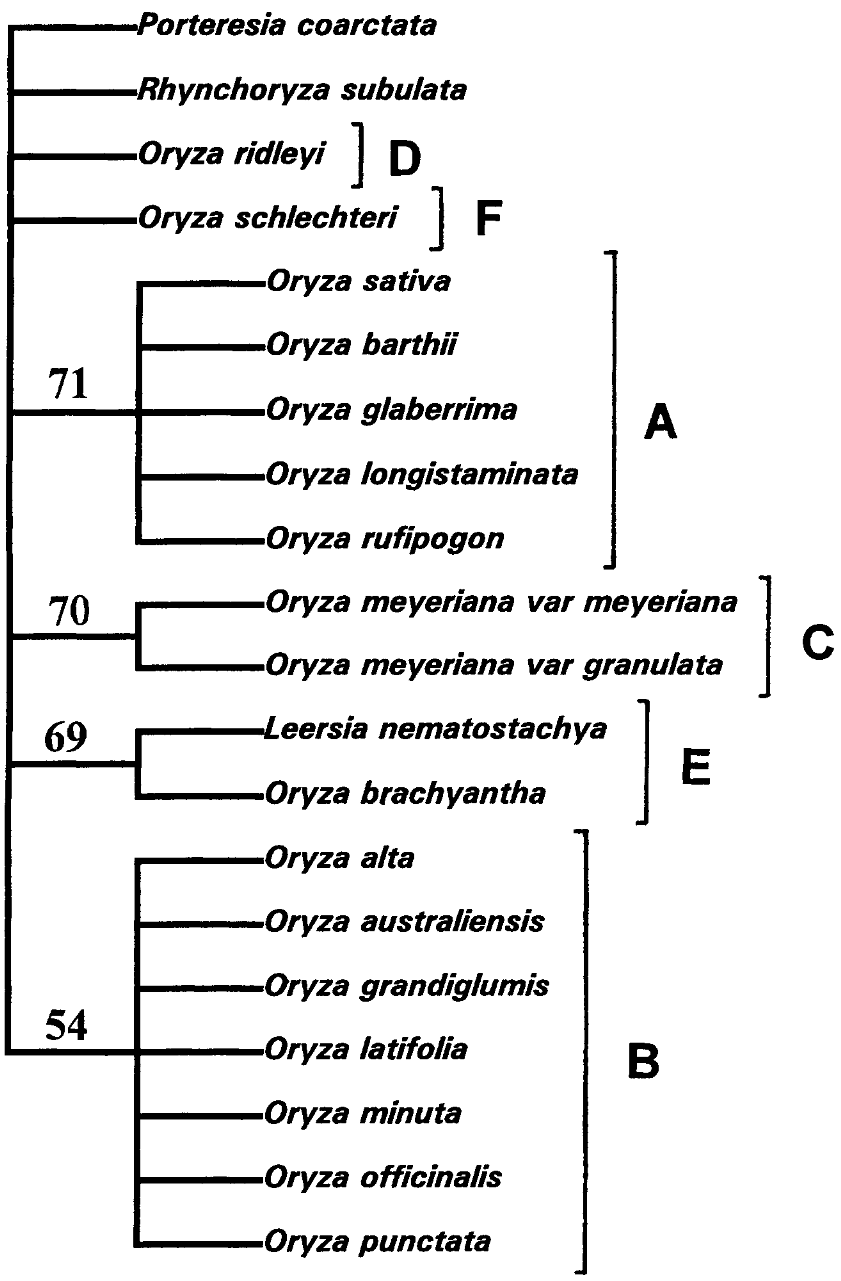

FIGURE 31.—Strict consensus tree based on parsimony analysis of 16 species of *Oryza*, using 14 characters described in text and Table 2 (data set). (Bootstrap values indicated where greater than 50% majority rule. Groups A, B, C, D, E, and F discussed in text.)

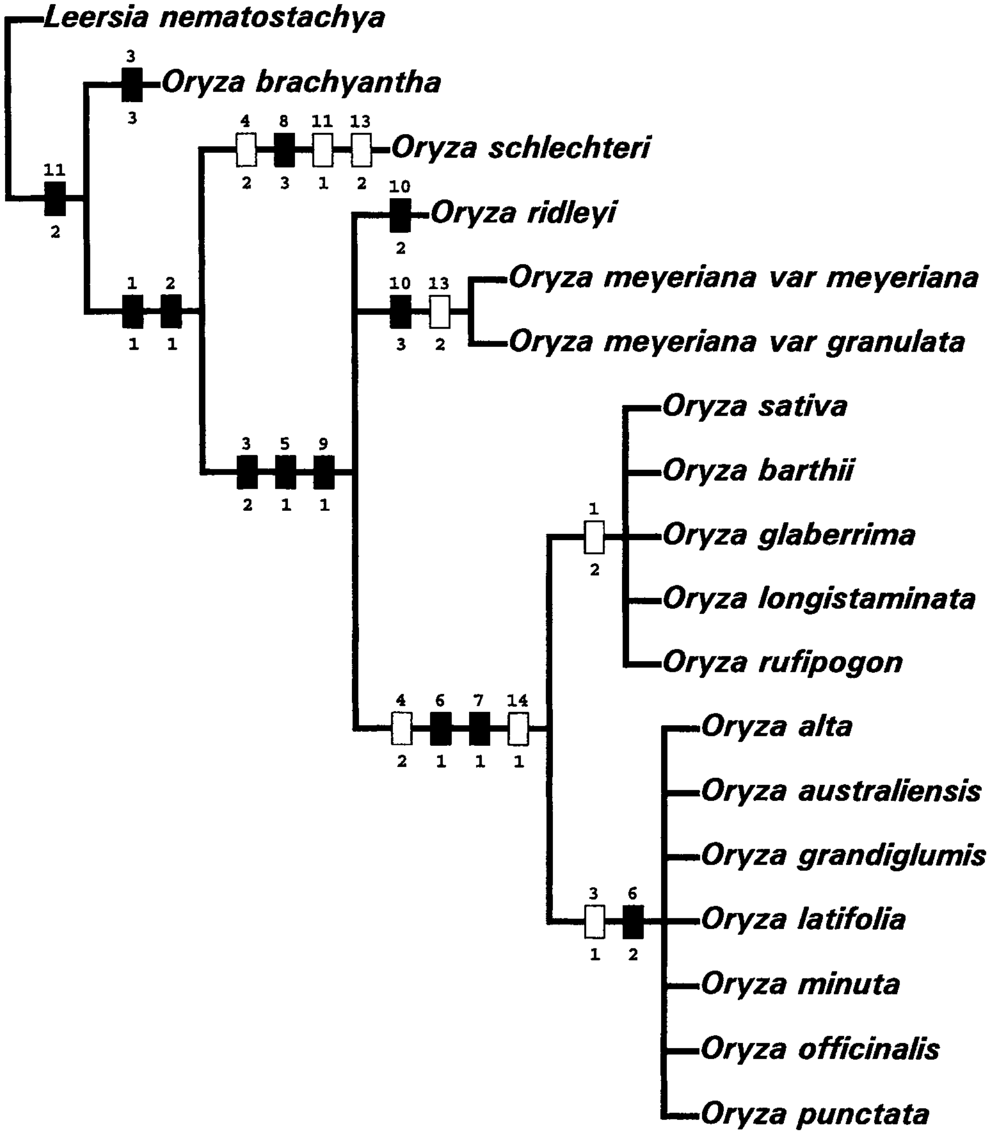

FIGURE 32.—One of 15 equally parsimonious trees (length=21 steps, CI excluding uninformative characters = 0.75; RI=0.86) analyzing 16 species of *Oryza* with *Leersia* as an outgroup. (Solid bars=unique origin of states (synapomorphies) and hollow bars=reversals or parallel states.)

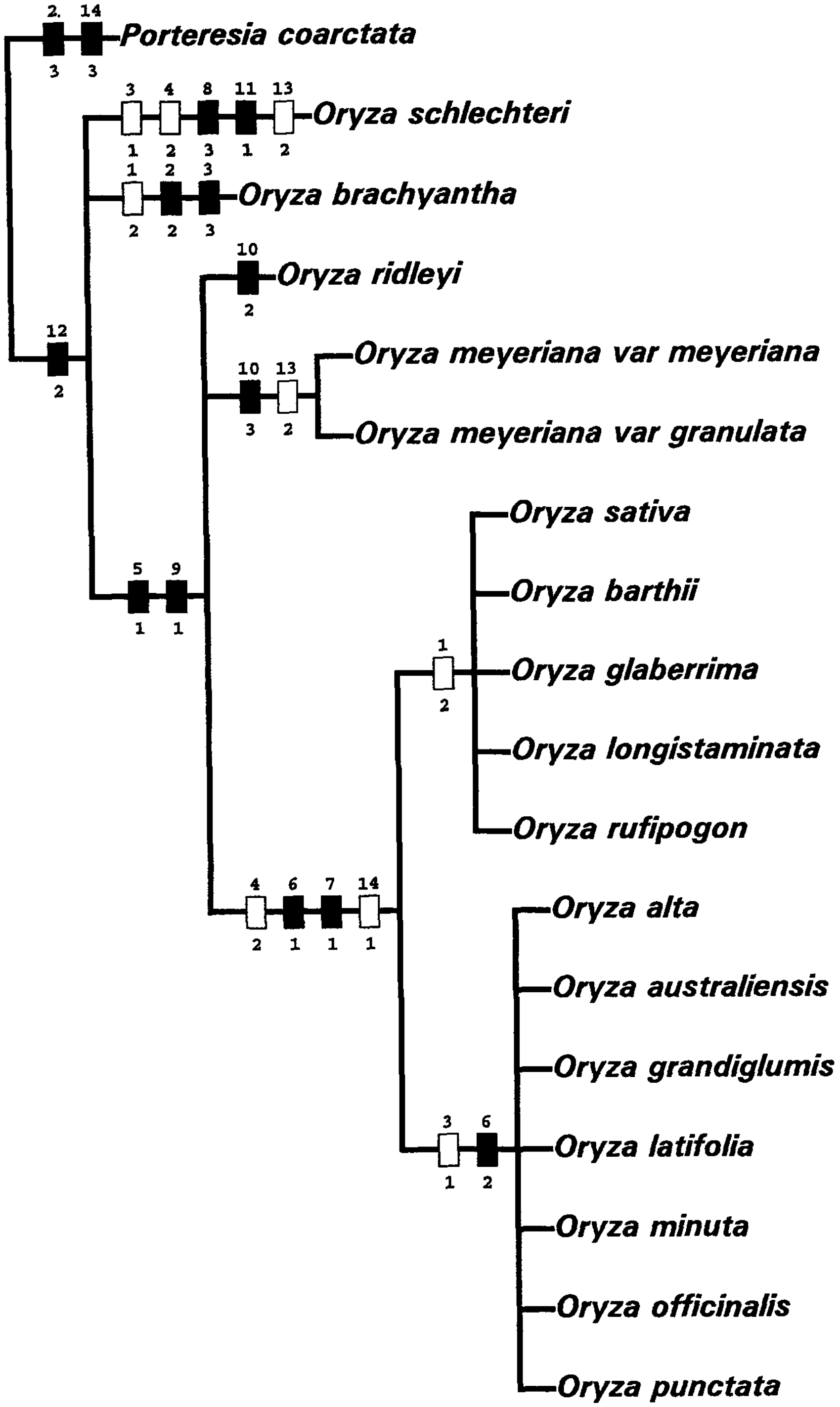

FIGURE 33.—One of 16 equally parsimonious trees (length=23 steps, CI excluding uninformative characters=0.78; RI=0.88) analyzing 16 species of *Oryza* with *Porteresia* as an outgroup. (Solid bars=unique origin of states (synapomorphies) and hollow bars=reversals or parallel states.)

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