The Silica Bodies of Tropical American Grasses: Morphology, Taxonomy, and Implications for Grass Systematics and Fossil Phytolith Identification

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ABSTRACT

Piperno, Dolores R., and Deborah M. Pearsall. The Silica Bodies of Tropical American Grasses: Morphology, Taxonomy, and Implications for Grass Systematics and Fossil Phytolith Identification. *Smithsonian Contributions to Botany,* number 85, 40 pages, 76 figures, 2 tables, 1998.—Silica bodies from over 200 species of Neotropical grasses comprising 80 different genera from all currently recognized subfamilies have been isolated from plant tissue and have been described. Silica-body shapes are significant at varying taxonomic levels, from the family to the genus. The Bambusoideae, especially, contribute large numbers of tribal- and genus-specific forms. Significant correlations are found between phytolith shape and the source plant's taxonomic relationships and postulated phylogeny. Disarticulated short-cell phytoliths occurring in ancient soils and sediments can be used to make identifications of certain taxa in the Poaceae below the level of family. Silica bodies observed in fossil grasses may elucidate the evolutionary history of the Poaceae.

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Introduction

Silica bodies are a type of phytolith that form in specialized epidermal cells of grass leaves. They have long been recognized as distinctive to the Poaceae (Grob, 1896; Prat, 1936; Blackman, 1971). Various workers have considered silica bodies to be diagnostic to family, and often they reflect the plants' subfamily affilations (Twiss et al., 1969; Brown, 1984; Mulholland, 1989). In paleoecological and archaeological sequences from North America, silica bodies have provided information on past environments and human subsistence, having been recovered in a virtually unaltered state from sediments up to 600,000 years old (Fredlund, 1986; Mulholland, 1993). They also have been recognized in fossilized remains of grasses dating to the Miocene where, in conjunction with other micromorphological characters of the leaf, they have provided information on the fossil's phylogeny and taxonomic relationships (Thomasson, 1984, 1987; Thomasson et al., 1986).

Although well established as significant and taxonomically important components of grasses, phytoliths rarely have been used independently either to positively identify specific taxa or to elucidate grass phylogeny. The prevailing assumption has been that grasses produce a limited range of silica-body shapes, which, at any rate, too often demonstrate overlap from subfamily to subfamily to be of critical use in the systematics and evolution of the Poaceae (Thomasson, 1987; but see Mulholland, 1989, and Ollendorf et al., 1988).

Compared to research carried out in temperate regions, far fewer studies involving grass phytoliths have been attempted in the Old and New World tropics (Piperno, 1988; Pearsall, 1989). As the Poaceae may have had its origins in moist tropical or subtropical lowlands (Stebbins, 1986), and as there has been a heightened interest in the determination of natural and human effects on lowland tropical environments during the Quaternary period (Leyden, 1987; Leyden et al., 1993; Piperno et al., 1990, 1991), the availability of phytolith keys with broad application to the grass family will become increasingly important in botanical research.

We have completed the first major survey of silica bodies in New World tropical grasses. Our goals were two-fold: (1) to provide a key to the kinds and distributions of short-cell phytoliths in the tropical American flora that will be of use in plant systematics and paleobotany, and (2) to determine to what extent identification of grass subfamilies, tribes, and genera can be made from individual phytoliths retrieved from ancient soils and sediments in Central and South America.

Our results indicate that certain kinds of silica bodies may be found in all of the subfamilies of the Poaceae and they can be used for discrimination below the family level only with caution. However, other short-cell phytoliths disarticulated from plant tissue are valid indicators of individual subfamilies, tribes, and genera of grasses, and these do provide valuable information on grass taxonomy and phylogeny.

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SAMPLING METHODS

Leaves, culms, and inflorescences from over 200 species of grasses comprising 80 different genera and representing a broad survey of all five subfamilies now recognized (Watson et al., 1985; Kellogg and Campbell, 1987) were studied. Assignation of individual genera to subfamily and tribe followed the current consensus in grass systematics (Soderstrom et al., 1987). Most of the species analyzed were sampled from annotated herbarium sheets at the Missouri Botanical Garden (in St. Louis and housed at the Smithsonian Tropical Research Institute, Panama) and the National Herbarium in Washington, D.C. A few species were collected in the field by the authors during field trips made to Latin America over the past 15 years.

For most species under consideration, at least two replicate specimens derived from different, local populations were analyzed. As bamboos inhabit a wide range of habitats and may constitute a significant component of the tropical flora, our sample included representatives of almost every genera and many species of the Bambusoideae reported from the Neotropics (Soderstrom and Ellis, 1987).

Phytoliths were extracted from plant material by the wet oxidation method described in Piperno (1988) and were mounted on slides in Permount, a histological fixative.

A multitude of short-cell phytolith types were isolated from the grasses analyzed. Many of them have not been reported previously in studies of North American and European grasses (e.g., Parry and Smithson, 1964, 1966; Twiss et al., 1969; Brown, 1984; Mulholland, 1989). This paper will discuss and illustrate the major distributional patterns demonstrated by the phytolith types, concentrating on those forms considered to be diagnostic of grasses below the family level, as well as on the forms that appear to be repeated often across major boundaries of the family.

General Patterns at the Subfamily Level

Table 1 summarizes the distribution of the short-cell phytoliths isolated from the grasses studied. Silica bodies classified as circular to oval- (rondels), saddle-, bilobate-, or cross-shaped are well-established diagnostic features of the leaf epidermis, occurring both over and between the leaf veins. This study shows that they also may be conspicuous components of the epidermis of inflorescence bracts, culms, and seeds, although the latter two structures often have a very low phytolith content and usually contribute other types of phytoliths.

In Table 1, the placement of phytoliths under the saddle-, rondel-, bilobate-, or cross-shaped category signifies that these bodies are of the classic shapes that have been commonly reported in previous grass studies. In other words, they are usually tabular, mirror-image forms that almost always assume saddle-, bilobate-, or cross-like orientations when observed in tissue and also when removed from plant parts and mounted on slides as separate entities.

In this study, many variations of these conventional, short-cell phytoliths were observed. Such phytoliths typically had only a single developed saddle- or bilobate-like face, and, as originally formed in the plant, they were thick with relatively deep extensions into the epidermal tissue. When removed from the plant and placed on slides they turned and assumed various kinds of wide, irregular shapes, with the saddle or bilobate face that had been observed in tissue becoming more difficult to define because it had become one of the lateral edges of the phytolith. In Table 1, these phytoliths were given either their own categories or were placed in the "Other" category. Most are described and illustrated.

Twiss et al. (1969) proposed three major divisions of short-cell phytoliths corresponding to three dominant subfamilies native to the Great Plains of the United States: bilobate/cross = Panicoideae, saddle = Chloridoideae, and circular/oval/rectangular = Pooideae. They recognized that some deviation from this typology occurred; for example, circular to oval bodies were observed in some panicoid grasses. Brown (1984) and Mulholland (1989) carried out more extensive studies of North American grasses and also found that although the three-part division generally held, there were significant deviations from the expected pattern. The same was true of the tropical grasses studied herein.

Circular to oval phytoliths or "rondels" (Mulholland, 1989), which are most closely associated with the Pooideae (Table 1), also are found in the Arundinoideae, Panicoideae, and, most prominently, in the inflorescences of the Bambusoideae (Figures 1–4, Table 1). Bilobate phytoliths, the most characteristic markers of the Panicoideae (Table 1), also are present in the Arundinoideae, Pooideae, Bambusoideae, and Chloridoideae (Figures 5–15). Indeed, bilobates are the most common kind of silica body in phytolith assemblages from certain genera in these subfamilies, such as *Aristida* (Arundinoideae), *Eragrostis* (Chloridoideae), and *Stipa* (Pooideae). The cross-shaped phytolith, another panicoid marker, is common in certain Bambusoideae (tribe Olyreae) (Table 1) and occurs in small numbers in the Chloridoideae, Arundinoideae, and Pooideae (*Brachypodium, Polypogon*) (Figures 16, 17).

Saddle-shaped phytoliths are the dominant phytolith class of the Chloridoideae (Table 1). They are also common in two subtribes of the Bambusoideae (Guaduinae and Chusqueinae)

(Table 1) and are present in two genera of the Arundinoideae (*Aristida, Phragmites*) (Figures 18–22).

Individual genera in the Arundinoideae are marked by highly divergent sets of phytoliths that may exhibit Panicoideae, Chloridoideae, or Pooideae tendencies (Table 1). Phytoliths with both saddle and bilobate tendencies, called "saddle/ bilobates," are common in this family, whereas the conventional kinds of saddle and rondel forms are relatively rare. These determinations are consistent with findings that the Arundinoideae is actually a hetereogeneous and poorly defined group of loosely related genera (Conert, 1987), and with the current belief that this subfamily is primitive and basal to all others of the Poaceae (Kellogg and Campbell, 1987).

It is evident from this analysis that the assignation of short-cell phytoliths found in ancient sediments and fossil plants to a particular grass subfamily will not always be possible. Compounding the difficulty is that several different plant structures may contribute confuser phytoliths. For example, rondels may be found in both the leaves and inflorescences of *Aristida*, whereas saddles occur in leaves, culms, and inflorescences of bamboos. However, a large number of other short-cell phytoliths that were observed in this study do appear to be both disjunct in distribution and diagnostic at and below the subfamily level. Some of them need to be isolated from plant tissue for proper study. Many have not been described previously in other phytolith studies. A summary of these phytoliths can be found in Table 2. There also appears to be considerable potential for discrimination of the conventional short-cell phytolith types using microdifferentiation of shape characteristics and phytolith size.

EXAMPLES OF PHYTOLITH DISCRIMINATION AT AND BELOW THE SUBFAMILY LEVEL

"Long, wavy trapezoids" (Brown, 1984) appear to be unique to the Pooideae and can be used to identify this group of mainly high-elevation tropical grasses (Figure 23). Square to rectangular short-cell phytoliths of the kind described by Twiss et al. (1969) also may be diagnostic of tropical Pooideae, as they were not observed in taxa from other subfamilies analyzed herein. Phytoliths called "plateaued saddles" were isolated in great number from the leaves of *Phragmites* (Figures 24, 25). More study is needed before they can be assigned genus-specific status, but they can be used as a marker of the Arundinoideae and to search for, or rule out, the possible presence of *Phragmites* in soil phytolith assemblages.

The Bambusoideae contribute a large number of types diagnostic at the family level (Table 2). Many of these are variations on saddle or bilobate themes. Typically, the phytolith, as found in tissue, is a thick structure with only one bilobate- or saddle-like face. When isolated from tissue, phytoliths turn from their original orientations to assume various kinds of shapes with acute points, "collapsed" sides, and other irregularities of structure (e.g., collapsed saddle, one-and two-spiked-side body, saddle with ridged platform, Chusqoid body, bilobate/saddle both sides; Figures 26–31). Phytoliths just described are commonly found in the bamboo subtribes Guaduinae and Chusquineae and occur rarely in other bamboo taxa, not being noted at all in the tribe Olyreae (Table 1).

The Bambusoideae also contribute a large number of phytoliths diagnostic at the tribal, subtribal, and genus levels. Bodies whose long axes have two points and two large, rounded lobes are diagnostic of *Chusquea*, and they have been observed thus far only in two species of the genus, *C. simpliciflora* and *C. pittieri* (Figure 32). *Chusquea* bodies with multifaceted faces were observed only in *C. pittieri*, a highland representative of the genus (Figure 33). This distribution probably allows differentiation of the single lowland species of the genus currently recognized, *C. simpliciflora*. Large, distinctive bodies are produced in *Streptochaeta* spp. (Figure 34), whereas *Neurolepis* contributes a diagnostic small and wide tent-shaped body (Figure 35). *Pharus* contributes a unique, wide body (Figure 36), whose smaller, lateral face presents as a biloboid structure in tissue. *Raddiela* spp. contribute bilobates and cross shapes that appear to be enclosed in siliceous plates (Figures 37, 38).

The Olyreae produce a number of different kinds of genus-specific forms that are irregular versions of complex bilobates or crosses. Their orientation in plant tissue reveals these basic, short-cell shapes (Figure 39). When isolated from tissue, they are oriented differently and assume a number of diagnostic forms. For example, those in *Maclurolyra* and *Pariana* have one sinuous shape (representing the turned bilobate) and one sloping edge, and they are extremely wide. (Figures 40, 41). Phytoliths from each of these genera appear to be differentiable on the basis of the regularity of the edge slope and the width of the body. *Arberella* contributes bodies with various irregular points and concavities on one edge (Figures 42–44).

Other phytoliths found in the Bambusoideae are diagnostic at the tribal level. Phytoliths previously described as irregular mesophyll (Piperno, 1988), but which are now also known to be irregular, complex short-cell phytoliths, are found in the Olyreae (Figures 45, 46). Cross-shaped bodies with partly or fully developed conical projections on one side, the "Variant 3 and 8" types (Piperno, 1988), also are diagnostic of the Olyreae (Figure 17). Many bilobates from this tribe also display the same Variant 3 and 8 attributes (Figures 47, 48). Cross-shaped bodies with three indentations, blocky structures, and concave faces, and with blocky structures, concave faces, and serrated short axes are characteristic of *Otatea fimbriata* and *Chusquea*, respectively (Figures 49, 50).

The documentation of many diagnostic phytoliths in bamboos is of considerable significance because the subfamily often exhibits habitat preferences that are very different from other tropical grasses. Bamboos are commonly found in the shady, cool understorey of tropical forests rather than in open

and disturbed vegetation. Bamboo phytoliths, then, can be important markers of various kinds of tropical forests in archaeological and paleoecological studies (see Piperno, 1988). The distribution of bamboo phytoliths by tribe and subtribe mirrors current taxonomic assessments of the family based on other anatomical and structural features (Soderstrom and Ellis, 1987), indicating the fundamental relationship of silica-body shape to Bambusoideae systematics.

Smaller numbers of one-to-one associations between a phytolith and a tribe or genus were observed in other subfamilies. They occurred in *Arundinella* (Panicoideae), *Aristida* (Arundinoideae), *Polypogon elongatus* (Pooideae), and *Aegopogon* and *Jouvea* (Panicoideae) (Figures 51–56). Phytoliths from *Aristida* are called "rondeloid/saddleloid" because they display characteristics intermediate between classic rondels and saddles. *Arundinella* possesses an unusual phytolith that is tall, thick, and more-or-less saddle shape when found in tissue, and then assumes a diagnostic form when removed from the leaf (Figures 51, 52). It is very similar to phytoliths found in the Arundinoideae taxon *Gynerium* (Figure 57) and to "saddle/bilobate, both sides" types of phytoliths that are common in bamboos (Figure 31).

Stebbins (1987) believed that the panicoid grasses derived via *Arundinella* from the Arundinoideae. The divergent set of phytoliths in *Arundinella* as compared to other species examined in the Panicoideae, as well as the similarity of the *Arundinella* leaf phytolith assemblage to that from some Arundinoideae taxa (predominance of wide, angled bodies and odd saddle shapes; few bilobates and crosses and no complex bilobates) are consistent with this proposed phylogeny.

As noted above, there also is considerable potential for short-cell phytolith discrimination using microshaped features of the conventionally defined short-cell phytolith types. For example, bilobates with rounded or semirounded lobes and long, thin shafts, or with squared lobes and distinct, thin shafts are common in panicoid taxa, but they were not observed in bamboos (Figures 5, 7). Bamboo bilobates, in contrast, usually are squat bodies with no or unremarkable shafts (Figures 11–13, 58, 59). Bilobates from the Chloridoideae (Figure 14) exhibit distinctively flared, convex edges that were first reported by Mulholland (1989).

Size differences in bilobates from different subfamilies also are apparent. Many bilobates isolated from panicoid grasses exceed 20 microns in length, whereas those from the Bambusoideae, Cloridoideae, and Pooideae (with the exception of *Stipa*) are almost without exception shorter.

Significant differences also are apparent from subfamily to subfamily in the type of saddle-shaped phytolith produced. Many phytolith assemblages from chloridoid grasses have significant proportions (32%–86%) of squat saddles, that is, the axis of the phytolith exhibiting the double-edge, saddle-like outline is wider than the other, or the two axes are equidimensional (Figures 18–20). In contrast, every species studied from the Bambusoideae and Arundinoideae produced

assemblages in which over 90% of saddles were longer than wide (Figures 21, 22, 60). Another difference between saddles from chloridoid and non-cloridoid grasses is that very tall saddles, those measuring longer than 15 microns, dominate bamboo assemblages, whereas saddles shorter than 15 microns long predominate in chloridoids (Figure 22).

PHYTOLITHS WITH LIMITED DISTRIBUTIONS IN THE POACEAE

Phytoliths called "narrow elliptates" were isolated in great number from the Bambusoideae, especially the Guaduinae and Chusqueinae, where they are a major component of the intercostal areas of the leaf epidermis (Figures 61, 62). They were not observed in the Olyreae, Streptochaeteae, Phareae, Streptogyneae, or Neurolepidinae. Narrow elliptates also occur in small numbers in the Arundinoideae, having been observed thus far only in *Gynerium* (Figure 63). These phytoliths have biloboid characteristics when viewed in tissue (Figures 61, 63), but they may assume other shapes when removed from the leaf (Figure 62).

Complex bilobates or trilobates and polylobates are common in phytolith assemblages from panicoid taxa. They were not observed, however, in the Bambusoideae and were extremely rare in the Arundinoideae, occurring in very small numbers (less than 1% of the short-cell assemblage) in a few culms. Complex bilobates also were observed in *Eragrostis* (Chloridoideae) and in *Stipa* (Pooideae).

OTHER KINDS OF SILICA BODIES AND PATTERNS OF SILICIFICATION

There are some types of phytoliths found in tropical grasses that do not lend themselves to easy description and classification. Many of them derive from culms, in which are typically found small, irregular phytoliths, especially in members of the Arundinoideae (Figures 64, 65). Other unusual phytoliths are insignificant components of assemblages from leaves and floral bracts (Figure 66). As no overlap occurs between these types of phytoliths and those from other families, they can be identified in soils or fossils as grass bodies. These phytoliths would repay further investigation, as some of them are likely to be of precise taxonomic value.

Patterns of silicification in certain members of the bamboo subtribe Arthyrostilidiinae are most interesting, as it appears that leaf silica bodies characteristic of bamboos or other grasses are seldom produced. Most genera are characterized instead by the presence of small, silicified cone-like structures that arise from the epidermis (Figures 67–69). The comment that "this subtribe is rather far removed from the Arundinariinae and Bambusinae and appears to have arisen from a single ancestor different from that which gave rise to other New World woody subtribes such as the Chusqueinae, Guaduinae, and Neurolepidinae" (Soderstrom and Ellis, 1987:234) is amply supported by its silicification patterns.

OTHER IMPORTANT PHYTOLITHS NOT DERIVED FROM SHORT CELLS

It is worthwhile to briefly review some other distinctive phytoliths that are formed in nonvegetative organs of the plant. Recent studies have shown that the silicification of epidermal tissue, proper, can result in distinctive phytolith shapes (Piperno and Pearsall, 1993). For example, the fruitcases of teosinte and *Tripsacum* produce genus- and, in the case of *Zea luxurians* (Guatemalan teosinte), species-specific forms (Figures 70, 71). Controversy surrounding the origin and evolution of these near relatives of maize, especially as they relate to maize evolution itself, has been long-standing and fervent. The distinctive fruitcase phytoliths may help to arrive at some resolution of the major conflicts.

Summary

GRASS TAXON IDENTIFICATION AND ENVIRONMENTAL RECONSTRUCTION FROM PHYTOLITHS RETRIEVED FROM ANCIENT TROPICAL SOILS AND SEDIMENTS

The information presented here demonstrates the importance of describing phytoliths after they are removed from plant tissue. Epidermal anatomy of many of the bamboo and other grass genera included in this research had been studied previously (Metcalfe 1960; Soderstrom et al., 1987; Soderstrom and Ellis 1987; Judziewicz and Soderstrom, 1989), but diagnostic phytoliths were missed because important shape attributes were hidden by plant tissue and, therefore, were difficult to ascertain. For example, Soderstrom et al. (1987) were able to note only that *Pharus* silica bodies (Figure 36) were horizontally elongated (having long axes aligned parallel to the long axis of the leaf) and bilobate-shape. Soderstrom and Ellis (1987) described the unique phytoliths from *Chusquea* simply as bilobate-shaped bodies (compare Figures 32 and 72) and suggested that the same bodies occured in *Pharus* (Figure 36). They were able to characterize the diagnostic *Streptochaeta* bodies only as a type of saddle shape and considered that they were very similar to those of *Maclurolyra* (compare Figures 34 and 40). Similarly, Metcalfe's (1960) monumental study of Poaceae anatomy using epidermal thin sections could not reveal the range of phytolith shapes described here for the same reasons.

This study has revealed a diverse and diagnostic set of phytoliths produced by bamboos, which should make bamboo presence quickly apparent in sediments. In many cases, tribal-and genus-specific identification will be possible. It already is clear that bamboo phytoliths attain a high representation in ancient sedimentary environments, as they have been identified with regularity in Late Pleistocene and Early Holocene-aged sites from Panama (Piperno, 1988; Piperno et al., 1991).

With regard to the identification of other subfamilies, one-to-one correspondences between individual phytoliths and subfamilies are found with wavy trapezoids (Pooideae) (Figure 23) and plateaued saddles (Arundinoideae) (Figures 24, 25). Other distinctive types limited in distribution to individual grass genera are described on page 4 and in Table 2.

In addition, some specific rules can be derived from this study and applied in soil and sediment analysis to identify grass subfamilies. For example, a soil phytolith assemblage with significant proportions (greater than 30%) of squat saddles (see page 4) can be said to contain representation from chloridoid grasses with a high degree of confidence. Squat saddles consistently shorter than 15 microns also can be said to probably derive from the Chloridoideae.

If the great majority (greater than 80%) of saddles are "tall," bamboo (probably Guaduinae or Chusquinae) or Arundinoideae (*Aristida* or *Phragmites*) representation is implicated. If the arundinoid taxon *Phragmites* is present, the assemblage also should contain significant proportions of "plateaued saddles." If an assemblage of tall saddles contains bamboo representation, it also should include one or more of the other types of phytoliths produced by bamboos (e.g., narrow elliptates, collapsed saddles, saddles with ridged platforms, etc.). Some primitive (see below) panicoids, such as *Isachne*, also have assemblages dominated by tall saddles (Figure 73), but they lack the other, irregular forms. A phytolith assemblage of very tall (longer than 15 microns) saddles also suggests bamboo presence.

Furthermore, a phytolith assemblage that contains bilobates with (1) semirounded or rounded lobes and long, thin shafts (Figures 5, 8), (2) squared lobes and distinct, thin or moderately thin shafts (Figure 7), or (3) lengths consistently (with a proportion of greater than 20% of all bilobates) longer than 20 microns probably contains representation from the Panicoideae, Arundinoideae (*Aristida*), or a genus in the Pooideae, *Stipa*. Presence of complex bilobates in this same assemblage indicates contribution by the Panicoideae and/or *Stipa* (actually, such a combination is precluded by the ecological habitats of these grasses, see below).

Attention to the above criteria, which can eliminate bilobate contribution by the Bambusoideae (Figures 10–13, 47, 48), is important in habitat reconstruction because the Panicoideae and *Aristida* typically occupy open and disturbed environments, not the shaded, forest environments preferred by the Bambusoideae. Habitat specificity of certain confuser taxa also can play a role in phytolith identification. For example, the Pooideae taxa that produce bilobates are high-elevation grasses; therefore, they probably can be ruled out as potential confusers in Holocene sediments from low- and mid-elevation tropical sites.

This study also suggests that tropical soil assemblages might contain a significant proportion of silica bodies that are unclassifiable below the family level. In addition to certain types of bilobates, cross-shapes, and rondels that occur in all of the subfamilies of the Poaceae, there are other short-cell phytolith shapes that presently can be taken only as general indicators of grass presence.

The Place of Phytoliths in Paleoagrostology and Grass Systematics

To reiterate points discussed above, the correlation of circular to oval, saddle, bilobate, or cross-shaped phytoliths observed in fossil grass specimens with specific subfamiles or tribes should be made cautiously, as significant deviations from the expected pattern may occur, and phytoliths still embedded in plant tissue may display subfamily links more apparent than real. Nevertheless, phytoliths should play a more prominent role in paleoagrostology than has, heretofore, been the case, as silica-body shape in tropical grasses exhibits more diversity than that in grasses of other regions. Subfamily links based on microdifferentiation of silica bodies (tall vs. squat saddles; bilobates with and without shanks) are apparent, and overall patterns of leaf epidermal silicification may be diagnostic at several taxonomic levels. Examples include the Bambusoideae (many kinds of diagnostic patterns, including tall and very tall saddles and narrow elliptates), Arundinoideae, particularly *Phragmites* (combination of tall saddles and plateaued saddles in costal areas), Pooideae (dominance of circular to oval phytoliths in costal areas; presence of wavy trapezoids), and Chloridoideae (many squat saddles in the costal area).

Making precise identifications of fossil specimens from silica-body type will entail studying phytoliths in their natural orientations in leaves, where they tend to assume less distinctive shapes. At times, an identification should be possible, as the same phytolith, both when embedded in, and liberated from tissue, may assume idiosyncratic shapes that can be linked to each other (compare Figures 32 and 72, showing the *Chusquea* body as it is found in and out of leaf tissue).

Some cases of identification may prove more problematic, however, with the Bambusoideae also coming to mind in this regard. For example, the manifold shapes assummed by the irregular, multilobed short cells of genera in the bamboo tribe Olyreae (Figures 40–46) are not immediately apparent when they are still enclosed within tissue. Similarly, all of the distinctive *Arundinella* bodies (Figures 51, 52) appear as simple, tall, saddle-like shapes when viewed in tissue. The most preferable scenario for positive identification of fossil grasses may be one in which part of the specimen in question can be sacrificed in order to remove the phytoliths. Clearly, paleoagrostological studies would benefit from a systematic comparison of phytolith appearance in and out of leaves.

Patterns of silicification in structures other than leaves also may be diagnostic of certain taxa. For example, the inflorescence bracts of *Aristida* contain high numbers of rondeloids/saddeloids, and those of the Olyreae also produce irregular, multilobed short-cell phytoliths.

Also revealed by this study to be highly instructive in considerations of Poaceae taxonomy and phylogeny is phytolith shape in modern taxa. A review of Table 1 indicates that almost every taxon producing high amounts of atypical leaf phytoliths (those that are more characteristic of other subfami-

lies) occupies a primitive or otherwise singular position in its respective family. Some examples follow.

Isachne, a panicoid grass, but a producer of tall saddles similar to those in *Phragmites* (compare Figures 60 and 73), and phytoliths with both saddle and bilobate characteristics (Table 1), is thought to be a precursor of the Paniceae (Zuloaga, 1987) and may be basal in the Panicoideae (Kellogg and Campbell, 1987). *Eragrostis,* a C3 grass (a photosynthetic pathway highly unusual in the Chloridoideae), is a contributor of numerous bilobates as well as saddles (Table 1) and may be basal in the Chloridoideae (Kellogg and Campbell, 1987). *Stipa,* a pooid producer of bilobates, may be basal in the Pooideae (Kellogg and Campbell, 1987). Some analysts (Macfarlane, 1987) question whether the genus belongs in the subfamily Pooideae; Barkworth and Everett (1987) place it instead in the Arundinoideae. Anomalous characteristics of the pooid *Brachypodium* have long been recognized, and the genus has been accorded separate tribal status in the Pooideae (Macfarlane, 1987). The interesting Arundinoideae-like phytolith assemblages produced by the primitive panicoid taxon *Arundinella* have been noted above (page 4).

With the exception of *Brachypodium,* phytolith assemblages from all of the grasses just discussed are, on the whole, more similar to the Arundinoideae, from whose past members they are probably directly derived, than they are to other genera in their own subfamilies. It is clear that silica-body shape closely reflects phylogenetic relationships, and that phytolith shape changed along with other anatomical and micromorphological leaf characters in response to diversification and selective pressures during grass evolution.

The major directional trends taken by silica-body shape as grass evolution proceeded can be discerned from phytoliths in the modern flora. The predilection of more primitive taxa (Arundinoideae, Bambusoideae, *Isachne*) to have tall saddles has been discussed. These grasses also are marked by a high proportion of phytoliths that have just one complete saddle- or bilobate-like face, are thick (as oriented in leaf tissue), and that consequently turn when removed from tissue to assume various irregular, angular shapes (Figures 26, 28, 31, 42, 51, 52, 57, 74, 75). Primitive taxa contribute phytoliths that combine the characteristics of saddles, bilobates, and rondels, or small, irregular bodies that defy a conventional classification (Figures 53, 54, 64, 76).

It can be deduced that the earliest grass phytoliths were often thick pieces of silica with only one saddle- or bilobate-type face. Leaf epidermes may have contained a general assortment of saddle-, bilobate-, and rondel-like siliceous bodies, with forms assuming traits intermediate between these major classes also being common. Most regular saddles were tall. Leaf epidermal silicifications that result in a dominance of planar, mirror-image saddles and bilobates characteristic of mainstream genera in the Chloridoideae and Panicoideae appear to be later developments. It also can be argued that chloridoid ancestors had leaf epidermes with bilobate silica bodies and

that panicoid ancestors had leaf epidermes with saddle-shaped silica bodies.

In conclusion, this study has not described all of the short-cell phytoliths occurring in the tropical American flora. More studies are needed that include additional species in the larger genera of the Poaceae and also new taxa, as they continue to be described from the rain forest habitat. It also would be interesting to achieve a systematic study of the Old World tropical Poaceae in order to provide a key to geological/archaeological phytolith identification and to explore ancient grass biogeographical relationships. Because extensive studies of African leaf epidermes with silica-body descriptions already have been carried out (e.g., Palmer and Gerbeth-Jones, 1986, 1988 and references therein), a complementary analysis of disarticulated phytoliths is likely to enhance grass fossil identification in that part of the world.

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TABLE 1.—Distribution of phytolith types observed in the grasses studied. Within the Panicoideae, Chloridoideae, Arundinoideae, and Pooideae, x = characteristic of the taxon's subfamily; * = considered to be characteristic of other subfamilies, present in small numbers, i.e., <10% of the silica-body assemblage; o = considered to be characteristic of other subfamilies, present in substantial quantities, i.e., usually >20% of the silica-body assemblage. For all taxa, P in the "Other" category indicates the presence of other kinds of short-cell phytoliths in the assemblage; the letter P followed by the first letter of the genus in parentheses, e.g., P(T) for *Tripsacum*, indicates these phytoliths have not been observed in other taxa.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
PANICOIDEAE																						
Acrocereus zizianoides (H.B.K.) Dandy																						
seed	x																					
Aegopogon cenchroides H. & B. ex Willd.																						
leaf	x	x		*																		P(A)
Aegopogon tenellus (DC.) Trin																						
leaf	x	x																				P(A)
inflorescence	x	x																				P(A)
Andropogon bicornis L.																						
leaf	x	x																				
inflorescence	no phytoliths observed																					
Andropogon brevifolius Swartz																						
leaf	x	x																				
Andropogon leucostachyus Kunth																						
leaf	x	x																				
inflorescence	x	x																				
Andropogon liebmanni Hack.																						
leaf	x																					
inflorescence	x	x		o																		
Andropogon scoparius Michaux																						
leaf	x	x																				
Andropogon virginicus L.																						
leaf	x	x																				
inflorescence	x	x		o																		
Anthephora hermaphrodita (L.) Kuntze																						
leaf	x																					
Arundinella berteroniana (Schult.) Hitchc. & Chase																						
leaf	x	x	*																			P(A)
inflorescence				o																		P(A)
Arundinella deppeana Nees in Steud.																						
culm	x	x	o																			
inflorescence	no phytoliths observed		*	o																		P(A)
Arundinella hispida (H. & B.) Kuntze																						
leaf	x		o	o																		P(A)
culm			*	*																		P(A)
inflorescence	x		o	o																		P(A)

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Axonopus aureus Beauv.																						
leaf	x	x		*																		
inflorescence	x	x		o																		
Axonopus compressus (Sw.) Beauv.																						
leaf	x	x																				
inflorescence	x	x																				
Axonopus purpusii (Mez) Chase																						
leaf	x	x		o																		
inflorescence	x	x		o																		
Cenchrus brownii R. & S.																						
leaf	x	x		*																		
inflorescence	x	x		o																		
Cenchrus echinatus L.																						
leaf	x	x																				
inflorescence	x	x																				
Cenchrus pilosus H.B.K.																						
leaf	x	x																				
Chaetium bromoides (Presl) Benth. ex Hemsl.																						
leaf	x	x																				
inflorescence	x	x																				
Coelorhachis aurita (Steud.) A. camus																						
leaf	x	x																				
Ctenium concissum Swallen																						
leaf	x	x																				
inflorescence	x		*	*																		P
Echinochloa cruspavonis (H.B.K.) Schult.																						
leaf	x	x																				
inflorescence	x	x		*																		
Echinochloa holciformis (H.B.K.) Chase																						
leaf	x	x		*																		
inflorescence	x	x		*																		
Echinolaena gracilis Swallen																						
leaf	x	x		o																		
inflorescence	x	x		*																		
Hackelochloa granularis (L.) Kuntze																						
leaf	x	x																				
Heteropogon contortus (L.) Beauv.																						
leaf	x	x																				
inflorescence	x	x																				
Heteropogon melanocarpus (Ell.) Benth																						
leaf	x	x																				
inflorescence	x	x																				
Homolepis aturensis (H.B.K.) Chase																						
leaf	x																					
Hymenache amplexicaulis (Rudge) Nees																						
leaf	x	x																				

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Macluroiyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Hypogynium virgatum (Desv.) Dandy																						
leaf	x	x		*																		
inflorescence	x																					P
Ichnanthus nemorosus (Sw.) Doell in Mart																						
leaf	x	x																				
Imperata cordata																						
leaf	x	x																				
Isachne arundinaceae (Sw.) Griseb.																						
leaf			o																			P
Lasiacis linearis Swallen																						
leaf	x																					
Lasiacis oaxacensis (Steud.) Hitchc.																						
leaf	x	x																				
Leptocoryphium lanatum (H.B.K.) Nees																						
leaf	x			*																		
Luziola peruviana G.F.W. Mey. ex Benth																						
leaf	x	x																				
inflorescence	x	x		*																		
Mesosetum blakei Swallen																						
leaf	x	x		*																		
inflorescence	x	x		*																		
Mesosetum filifolium Hubb.																						
leaf	x	x		o																		
inflorescence	x	x		o																		
Optismenus burmanii (Retz.) Beauv.																						
leaf	x	x																				
Optismenus hirtellus (L.) Beauv.																						
leaf	x	x																				
Panicum fasciculatum Willd. ex Flugge																						
leaf	x																					
Paspalum paniculatum L.																						
leaf	x	x																				
Paspalum plicatulum Michx.																						
leaf	x	x																				
inflorescence	x	x																				
Paspalum virgatum L.																						
leaf	x	x																				
Pennisetum purpureum Schum.																						
leaf	x																					
Pseudochinolaena polystachya (H.B.K.) stapf in Prain																						
leaf		x																				P
Setaria scheelei (Steud.) Hitchc.																						
leaf	x																					
Setaria sp.																						
leaf	x																					

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Trachypogon filifolius (Hack.) Hitchc.																						
leaf	x																					
Trachypogon montuflora																						
leaf	x																					
Trichachne insularis (L.) Nees.																						
leaf	x	x																				
Tripsacum andersonii J.F. Gray																						
leaf	x	x		*																		P(T)
fruitcase	x	x																				
tassel	x	x																				
Tripsacum australe Cutler & Anderson																						
leaf	x	x																				P(T)
fruitcase	x	x		o																		
Tripsacum dactyloides (L.) L.																						
leaf	x	x																				P(T)
culm	x	x																				
fruitcase	x	x		*																		
tassel	x	x																				
Tripsacum lanceolatum Eupr. ex Benth																						
leaf	x	x																				P(T)
fruitcase	x	x		o																		
tassel	x	x																				
Tripsacum latifolium Hitchc.																						
fruitcase	x	x		*																		P(T)
tassel	x	x																				
Tripsacum laxum Nash																						
leaf	x	x		*																		P(T)
fruitcase	x	x																				
tassel	x	x																				
Tripsacum maizar E. Hernandez X. et Randolph																						
leaf	x	x		*																		P(T)
fruitcase	x	x																				
tassel	x	x																				
Tripsacum manisuroides de Wet & J.R. Harlan																						
leaf	x	x																				
Tripsacum pilosum Scribn. & Merr.																						
leaf	x	x		*																		P(T)
fruitcase	x	x																				P
tassel	x	x																				
CHLORIDOIDEAE																						
Bouteloua repens (Kunth) Scribn. & Merr																						
leaf			x																			
Chloris ciliata Swartz																						
leaf	*	*	x																			
Dactyloctenium aegyptium (L.) Aschers. & Schweinf																						
leaf			x																			

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Eleusine indica (L.) Gaertn.																						
leaf	*		x																			
Eragrostis ciliaris (L.) R. Br. in Tuckey																						
leaf	o	*	x																			
Eragrostis mexicana (Hornem.) Link																						
leaf	o	o	x	*																		
Leptochloa dominguensis (Jacq.) Trinius																						
leaf	o		x																			
Leptochloa scabra Nees																						
leaf	o	*																				
inflorescence	o	o		o																		
Muhlenbergia distans Swallen																						
leaf	*		x																			
inflorescence			x																			
Muhlenbergia emersleyi Vasey																						
leaf			x																			
inflorescence			x																			
Muhlenbergia implicata (Kunth) Kunth																						
leaf	*	*	x																			
inflorescence	*	*	x																			
Muhlenbergia lehmanniana Henr.																						
leaf		*																				
culm		*																				
Sporobolus cryptandrus (Torrey) A. Gray																						
leaf		*	x																			
ARUNDINOIDEAE																						
Aristida capillacea Lam.																						
leaf	*			*																		
inflorescence	o			*																		
Aristida divaricata H. & B. ex Willd.																						
leaf	o	*	*	o																		P
inflorescence	o	*	*	o																		P(A)
Aristida jorullensis Kunth																						
leaf	o			*																		
inflorescence	*	*	*																			
Aristida orizabensis Fourn.																						
leaf	o	*	*	*																		P
inflorescence	o		o																			P
Aristida orizaliensis																						
leaf	o																					P(A)
culm	o																					
inflorescence	o			*																		P(A)
Aristida orizaliensis																						
leaf	o			*																		P(A)
inflorescence	o	*	*	*																		

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Aristida recurvata H.B.K.																						
leaf	o																					
culm	*			*																		
inflorescence	o																					P(A)
Aristida ternipes Cav.																						
leaf	o		*																			
culm	o			*																		P
inflorescence	o																					P
Gynerium sagittatum (Aubl.) Beauv.																						
leaf	*	*																				
culm	*	o		o																		P
inflorescence	o	o																				
Orthoclada laxa (L. Rich.) Beauv.																						
leaf	o	o																				
Phragmites australis (Cav.) Trin. ex Steud.																						
leaf			o																			P
POOIDEAE																						
Agrostis tolocensis Kunth																						
leaf				x	x																	
inflorescence				x																		
Brachypodium mexicanum (R. & S.) Link																						
leaf	o	*		x	x																	
inflorescence				x																		
Bromus sp.																						
leaf				x	x																	
Bromus brevis Nees ex Steud.																						
leaf, culm, sheath				x	x																	
inflorescence				x																		
Bromus carinatus Hooker & Arnott																						
leaf and sheath				x	x																	
inflorescence				x																		
Bromus exaltatus Bernh.																						
leaf and sheath					x																	
inflorescence				x																		
Calamagrostis eminens (Presl.) Steud.																						
culm				x																		
inflorescence	no phytoliths observed																					
Calamagrostis humboltiana Steud.																						
leaf					x																	
culm	no phytoliths observed																					
inflorescence				x																		
Calamagrostis macrophylla (Pilger) Pilger																						
leaf					x																	
culm	no phytoliths observed																					
inflorescence				x																		

TABLE 1.—Continued.

| Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow ellipate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Cinna poaeformis (Kunth) Scribn. & Merr.																						
leaf				x																		
inflorescence				x	x																	
Dicctomis fastigiata (Sw.) H.B.K.																						
leaf	x																					
Holcus lanatus L.																						
leaf				x	x																	
culm				x																		P
Lolium multiflorum Lam.																						
leaf				x																		
inflorescence				x	x																	
Polypogon elongatus H.B.K.																						
leaf	*	0,12			x																	P(P)
inflorescence				x																		P
Polypogon elongatus H.B.K.																						
leaf	*	0,12			x																	P(P)
inflorescence				x																		P
Polypogon elongatus H.B.K.																						
leaf	*	0,12			x																	P(P)
inflorescence				x																		P
Stipa ichu (Ruiz & Pavon) Kunth																						
leaf	o																					
culm	o																					
inflorescence	no phytoliths observed																					
Stipa mucronata H.B.K.																						
leaf	o			x																		
culm	o			x																		
inflorescence	*																					
Trisetum deyeuxioides (Kunth) Kunth																						
leaf	no phytoliths observed																					
culm					x																	P
inflorescence				x																		
Trisetum tonduzii Hitchc.																						
leaf				x																		P(T)
culm				x	x																	
inflorescence				x	x																	
BAMBUSOIDEAE																						
OLYREAE																						
Arberella dressleri Soders. & Calderon																						
leaf	x	x3,8									x	x										
Arberella longifolia Soders. & Zuloaga																						
leaf	x	x3,8									x	x										
Cryptochloa dressleri Soders.																						
leaf	x	x									x											
inflorescence	x	x15																				
Lithachne pauciflora (Sw.) Beauv. ex Poir																						
leaf	x	x3									x											

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Maclurolyra tecta Calderon & Soders.																						
leaf	x	x11												x								
inflorescence	x	x15																				
Olyra cordifolia H.B.K.																						
leaf	x	x8									x											
Olyra latifolia L.																						
leaf	x	x8									x											
inflorescence		x13									x											
Olyra micrantha H.B.K.																						
leaf	x	x3,8									x											
inflorescence	x	x																				
Pariana campestris Aubl.																						
leaf	x	x									x											
inflorescence	x	x		x																		
Raddiella esenbeckii (Steud.) Calderon & Soders.																						
leaf	x	x3									x								x			
Raddiella nana (Doell) Swallen																						
leaf	x	x3	x								x								x			P
CHUSQUEINAE																						
Chusquea grandiflora Clark																						
leaf and sheath	x	x	x			x	x	x								x						P
inflorescence	x	x		x																		
Chusquea longifolia Swallen																						
leaf and culm	x	x	x			x	x	x	x							x					x	
inflorescence	x	x		x																		
Chusquea patens Clark																						
leaf	x	x	x				x															
Chusquea pittieri Hack.																						
leaf	x	x	x				x						x									P
culm	x																					
Chusquea pohli Clark																						
leaf	x	x	x				x									x						
Chusquea simpliciflora Munro																						
leaf	x	x8					x						x									
Chusquea virgata Hack.																						
leaf	x	x	x													x						
inflorescence	x	x	x	x																		
Chusquea vulcanalis Soders. & Calderon																						
leaf and culm	x	x	x				x		x							x						
inflorescence		x		x												x						
NEUROLEPIDINAE																						
Neurolepis pittieri McClure																						
leaf	x																x					P
inflorescence	x	x		x																		P

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
GUADUINEAE																						
Criciuma asymmetrica Soders. & Londoño leaf			x				x		x							x						P
Criciuma asymmetrica Soders. & Londoño leaf			x						x							x						P
Guadua amplexifolia (Presl.) Schult. f. leaf sheath				x																		
culm				x																		
Guadua amplexifolia (Presl.) Schult. f. inflorescence	x			x																		
Guadua amplexifolia (Presl.) Schult. f. leaf			x			x									x	x						
culm				x																		
leaf sheath and culm				x																		
Guadua angustifolia Kunth leaf	x		x			x									x	x						
inflorescence				x																		P
Guadua angustifolia Kunth leaf			x	x		x									x							
culm			x	x																		P
Guadua latifolia H. & B. leaf			x			x									x	x						
inflorescence																						
Guadua latifolia H. & B. leaf			x			x									x	x						P
culm			x													x						
Olmeca recta Soders. leaf	x		x	x		x	x		x						x	x						P
inflorescence						no phytoliths observed																
Olmeca recta Soders. leaf	x		x			x	x								x	x						
fruit								x	x						x	x						
Olmeca reflexa Soders. leaf	x		x			x																
Otatea acuminata Calderon & Soders. leaf	x	x	x				x								x							P
inflorescence	x	x																				
Otatea fimbriata Calderon & Soders. leaf	x	x	x			x	x									x						
culm	x									x												P
STREPTOCHAETEAE																						
Streptochaeta sodiroana Hack. leaf																				x		
inflorescence						no phytoliths observed																
Streptochaeta spicata Schrad. ex Nees leaf			x																	x		

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
PHAREAE																						
Pharus latifolius L.																						
leaf																		x				P
Pharus parvifolius Nash																						
leaf																		x				P
STREPTOGYNEAE																						
Streptogyne americana C.E. Hubb.																						
leaf			x						x													P
ARTHROSTYLIDIINAE																						
Actinocladum merticulatum																						
leaf										x												
inflorescence				x																		
Arthrostylidium fimbriatum Griseb.																						
leaf				x						x												
inflorescence										x												
Arthrostylidium unenguelae Ruprecht																						
leaf										x												
sheath/culm										x												
Atractantha longispiculata McClure																						
leaf			x			x			x							x						
inflorescence			x			x																
Atractantha radiata McClure																						
leaf				x					x							x						
inflorescence	x			x						x												
Aulonemia aristulata (Doell) McClure																						
leaf	x			x						x												
inflorescence		x								x												
Aulonemia queko Guodot																						
leaf				x						x						x						
inflorescence				x						x												P
Colanthelia cingulata McClure & L.B. Smith																						
leaf				x						x												
culm				x																		
Colanthelia cingulata McClure & L.B. Smith																						
leaf				x						x												
culm	no phytoliths observed																					
inflorescence				x						x												
Colanthelia lanciflora McClure & L.B. Smith																						
leaf				x						x												
inflorescence																						
Colanthelia intermedia McClure & L.B. Smith																						
leaf				x																		
inflorescence				x																		
Colanthelia intermedia McClure & L.B. Smith																						
leaf				x																		
inflorescence				x																		

TABLE 1.—Continued.

Taxon	Bilobate	Cross	Saddle	Rondel	Wavy Trapezoid	Bilobate/Saddle, on both sides	Collapsed saddle	Saddle with ridged platform	Chusquoid	Conical	Multilobed short cells	Arberella body	Chusquea body	Maclurolyra body	Elliptate/Bilobate	Narrow elliptate	Neurolepis body	Pharus body	Raddiela body	Streptochaeta body	1- and 2-spiked top	Other
Elytrostachys clanisera McClure																						
leaf	no phytoliths observed																					
culm	x									x												
inflorescence				x																		
Merostachys multiramea Hack.																						
leaf				x						x												
Merostachys argyronema Lindm.																						
leaf	no phytoliths observed																					
culm				x						x												
Myriocladus cardonae Swallen																						
leaf	x									x												
inflorescence				x																		

TABLE 2.—The occurrence and distribution of phytoliths diagnostic at and below the subfamily level.

Phytolith	Taxa
Long, wavy trapezoids (Figure 23).	Pooideae, not observed in *Calamagrostis* or *Stipa*.
Plateaued saddles (Figures 24, 25).	*Phragmites*.
Collapsed saddles (Figures 26, 27); two-spiked body (Figure 28); saddle with ridged platform (Figure 29); *Chusqoid* body (Figure 30); saddle/bilobate both sides (Figure 31).	Bambusoideae. Most common in the subtribes Guaduinae and Chusquineae. Not observed in the Olyreae.
Chusquea body (Figures 32, 33).	*Chusquea*. Absent from most members of the genus studied.
Pharus body (Figure 36).	*Pharus*. An idiosyncratic type of phytolith, even for bamboos.
Enclosed in siliceous plates (Figures 37, 38).	*Raddiela*. These phytoliths seem to have hyperdeveloped Olyreae characteristics.
Irregular and extremely wide, with one sinuous and one sloping edge (Figure 40).	*Maclurolyra*. Morphology similar to those in *Pariana*, but bodies are much larger.
Irregular and wide, with one sinuous and one sloping, pointed edge (Figures 42–44).	*Arberella*. Differentiated from *Mclurolyra* and *Pariana* by one edge with irregular concavities and points.
Irregular, complex short-cell phytoliths (Figures 45, 46).	Olyreae. Of the same origin as phytoliths described from *Arberella* and *Maclurolyra* but more widespread in distribution.
Cross-shaped and bilobate phytoliths, with one tier having conical protrusions, called the "Variant 3 and 8" types (Figures 17, 47, 48).	Olyreae. A three-dimensional structure of silica bodies that is highly useful in grass discrimination.
Considerably wide; marked by the presence of one somewhat concave and one somewhat sloping edge (Figures 51, 52).	*Arundinella*.
"Rondeloid/Saddeloid" (Figure 53).	*Aristida*.
Cross-shaped and bilobate, with one tier having a saddle-like structure that extends only about two-thirds of the length of the longer cross or bilobate side (Figure 55).	*Polypogon*.
Irregular bodies marked by one highly decorated lateral edge (Figure 56).	*Aegopogon*.
Bodies with elliptoid/biloboid tendencies (Figures 61–63).	Bambusoideae, especially intercostal areas of the Guaduinae and Chusqueinae, and *Gynerium* (Arundinoideae).
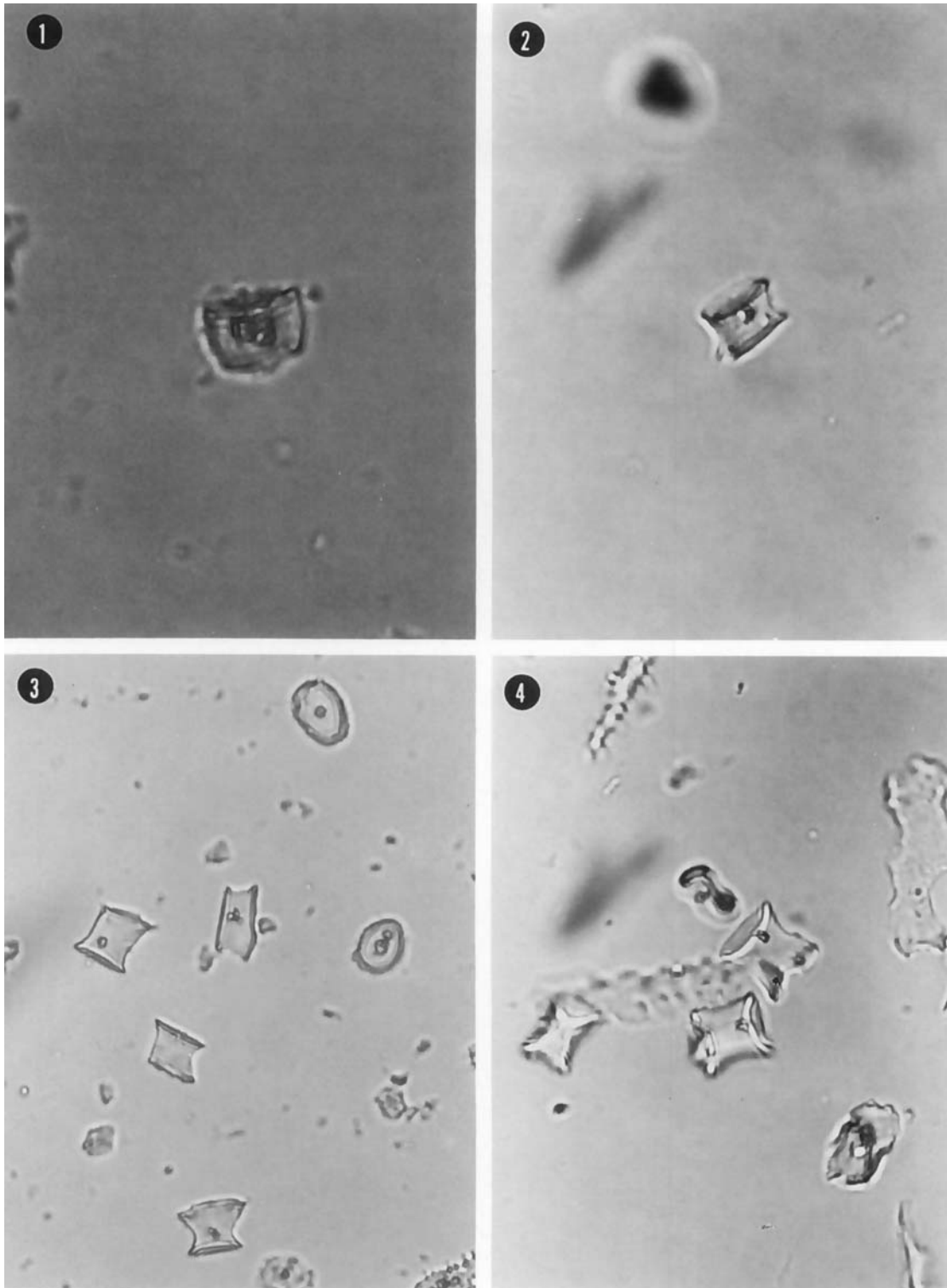
FIGURES 1–4.—1, A rondel from *Stipa ichu* (×400). 2, A rondel from the culm of *Guadua angustifolia* (×400). 3, Rondels from the cob of *Zea mays* L., race Maiz Ancho (×400). As the rondel phytoliths from maize, and especially bamboos (Figures 1, 3), tend to be thick when formed in the plant, the rondel faces that are orientated toward the investigator in plant tissue become the lateral edges of the phytoliths after they are removed from the plant and mounted on slides. 4, Center, three rondels from the inflorescence of *Guadua latifolia*. The phytolith at the top is a bilobate (×400).
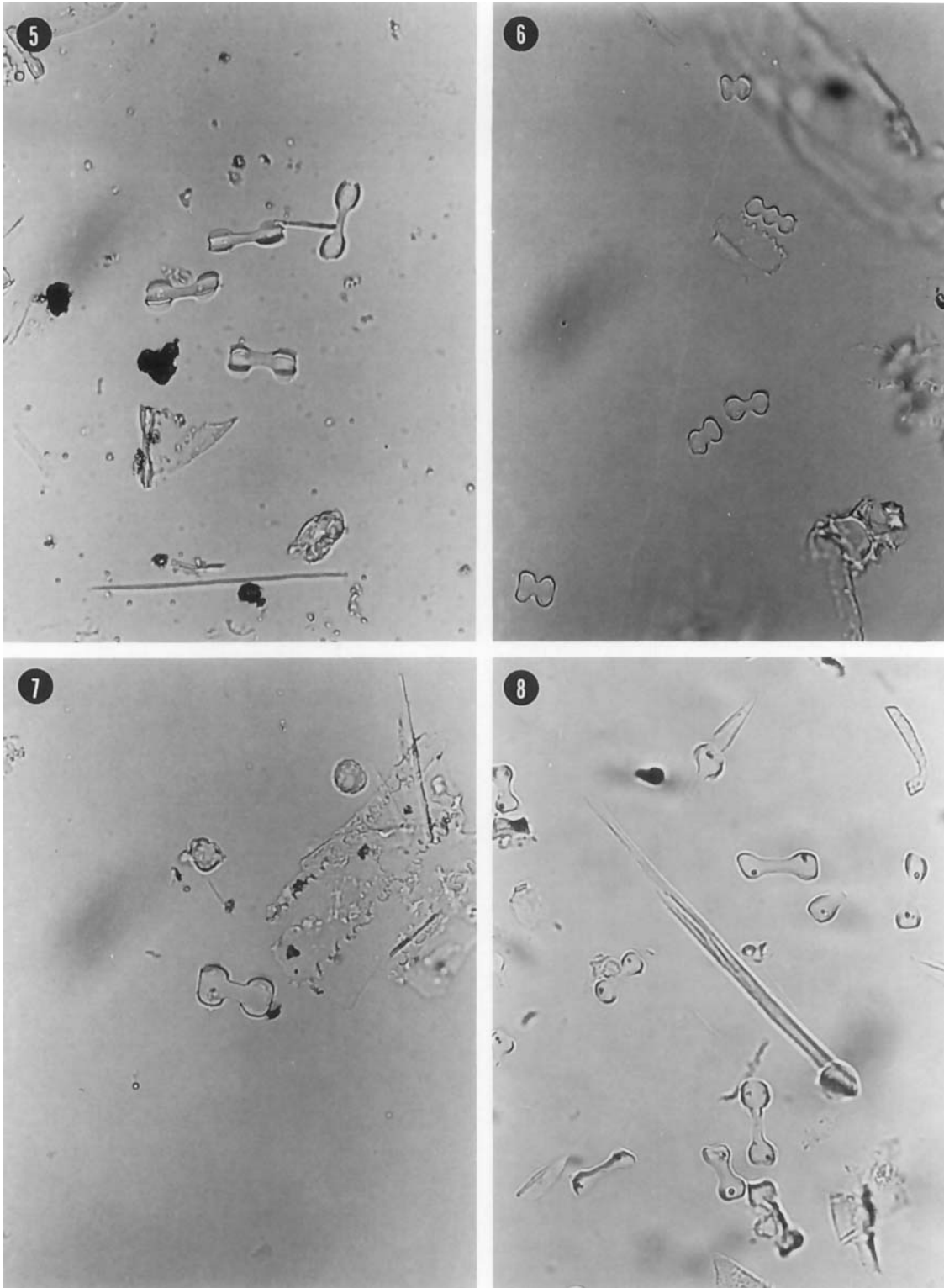
FIGURES 5–8.—5, Bilobates with semirounded lobes and long, thin shafts from *Andropogon leuchostachya* (×200). 6, Bilobates and a complex bilobate from *Panicum fasciculatum* (×200). 7, Center, a bilobate with squared lobes and a distinct, moderately thin shaft from *Andropogon bicornis* (×200). 8, Bilobates with semirounded lobes and long, thin shafts from *Aristida orizaliensis* (×200).
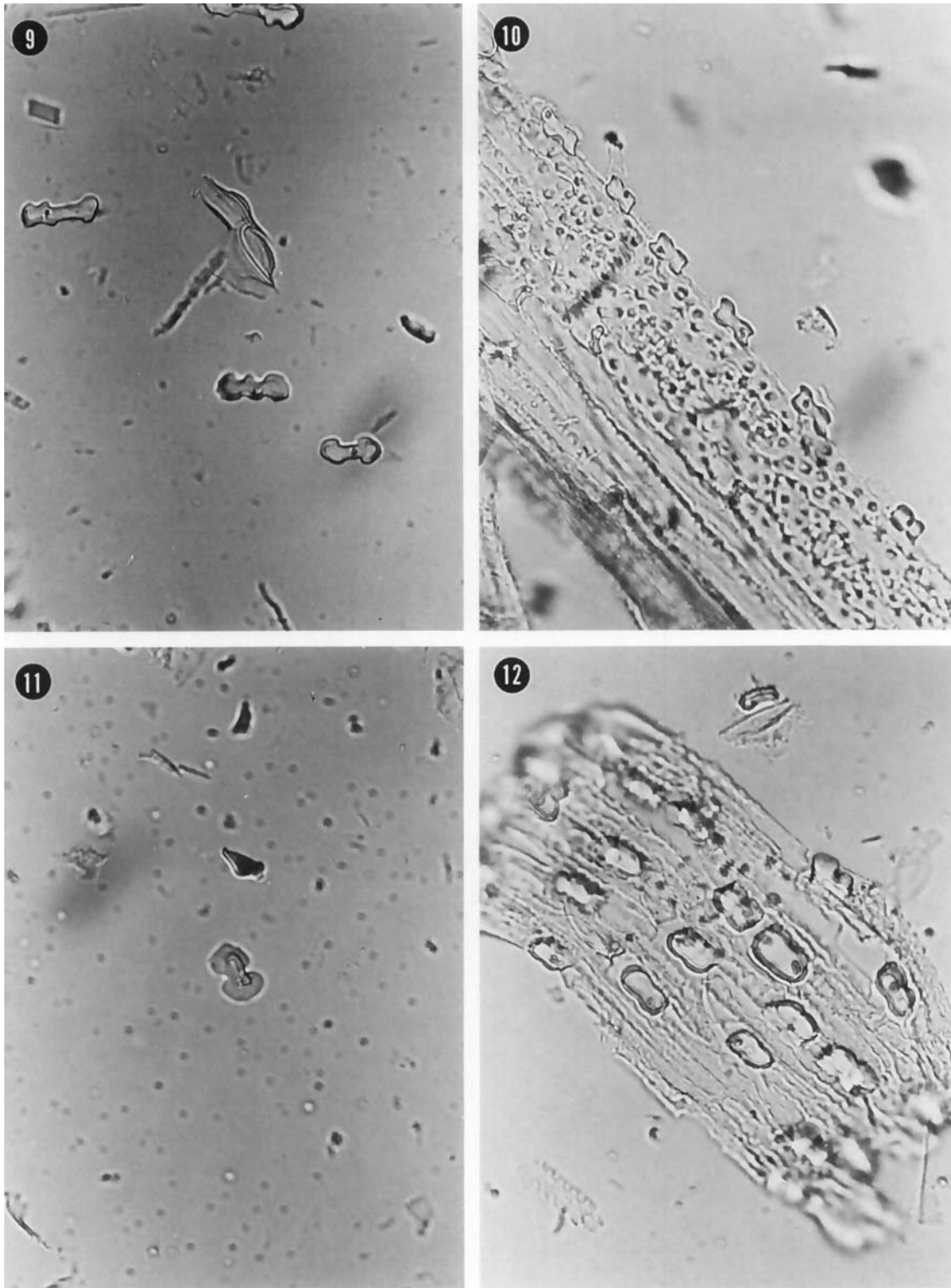
FIGURES 9–12.—9, Bilobates and complex bilobates from *Stipa mucronata* (×200). 10, A row of bilobates from *Chusquea patens* (×200). Their morphology, although not ovelapping the panicoid types, is unusual for bamboos. 11, A bilobate from *Maclurolyra tecta* (×200). 12, Bilobates in tissue from *Chusquea pohli* (×200).
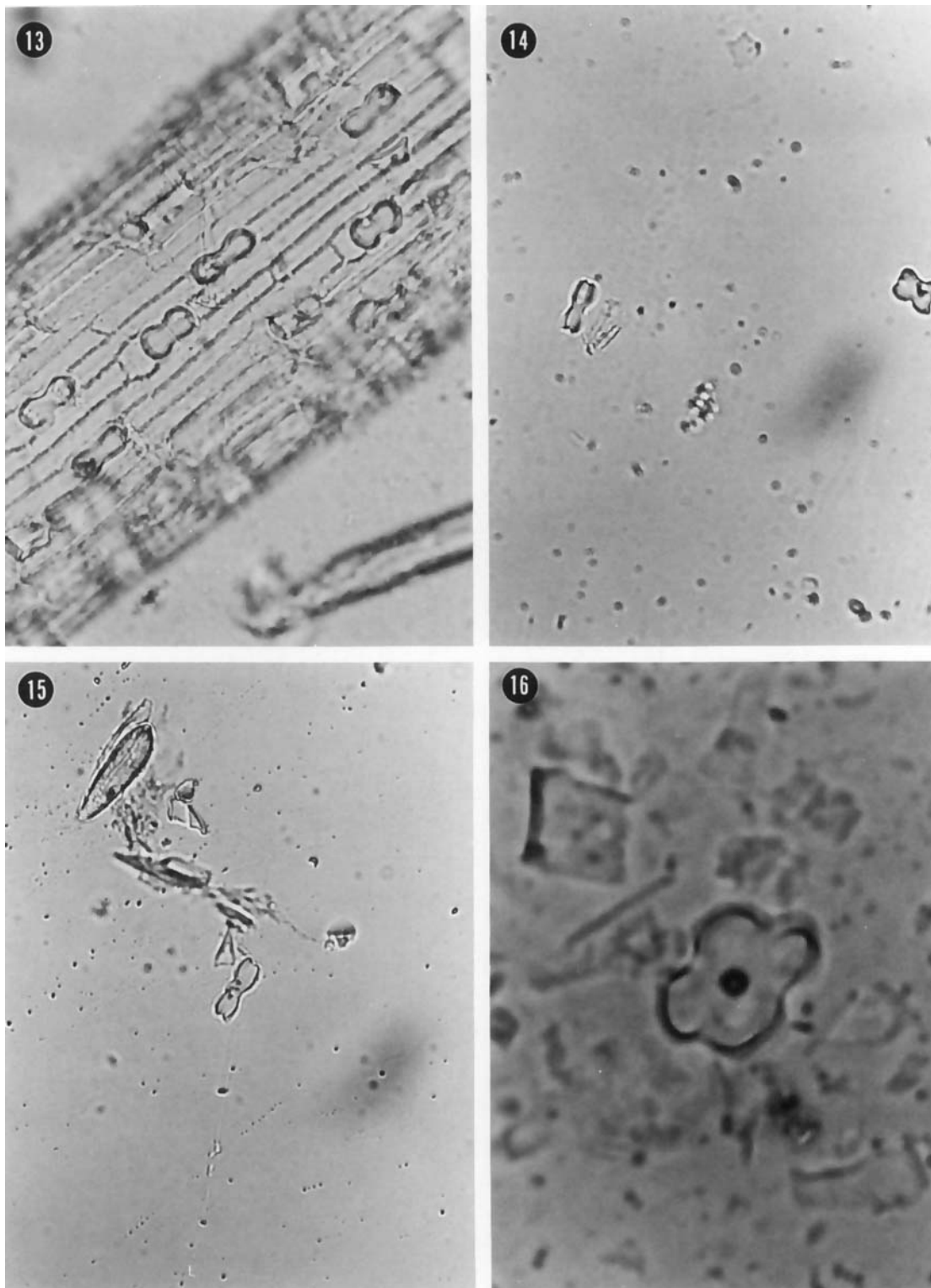
FIGURES 13–16.—13, Bilobates from the culm of *Chusquea longifolia* (×400). 14, A bilobate (left) and a cross-shaped phytolith (right) from *Eragrostis mexicana* (×200). The bilobate has four indentations and both phytoliths have the flared edges typical of the Chloridoideae. 15, Center, a complex bilobate from *Eragrostis mexicana* with multiple indentations (×200). 16, A Variant 1 (mirror-image) cross-shaped phytolith from *Zea mays* (×400).
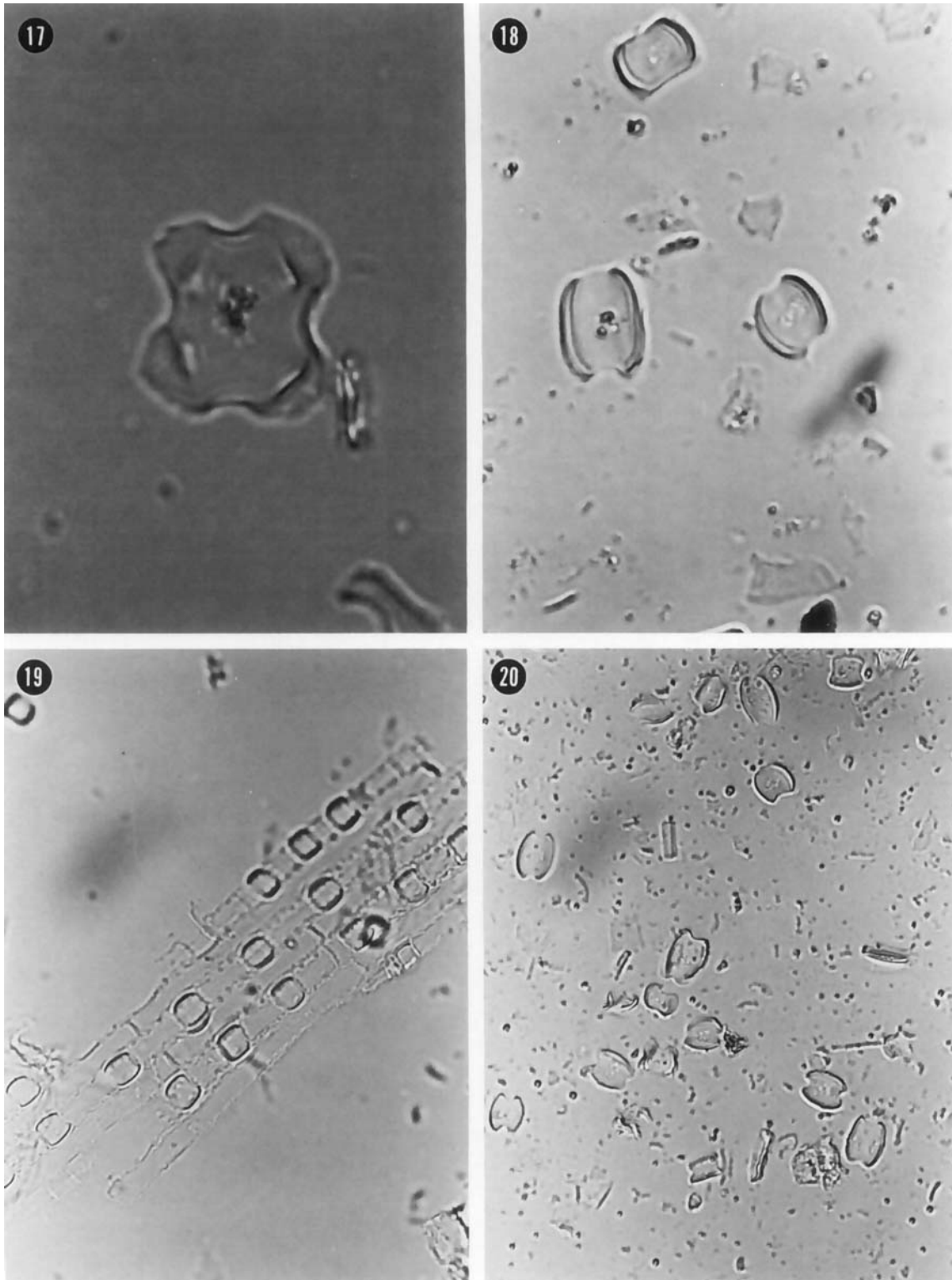
FIGURES 17-20.—17, A Variant 3 cross-shaped phytolith from *Arberella dressleri* with conical protrusions on the upper face (×400). 18, Center, two squat saddles, and top, a tall saddle from *Chloris eiliata* (×400). 19, Saddle-shaped phytoliths from *Muhlenbergii emersleyi*. Many of them are squat saddles (×200). 20, Saddle-shaped phytoliths from *Dactylactenium aegpticum*. Many of them are squat (×200).
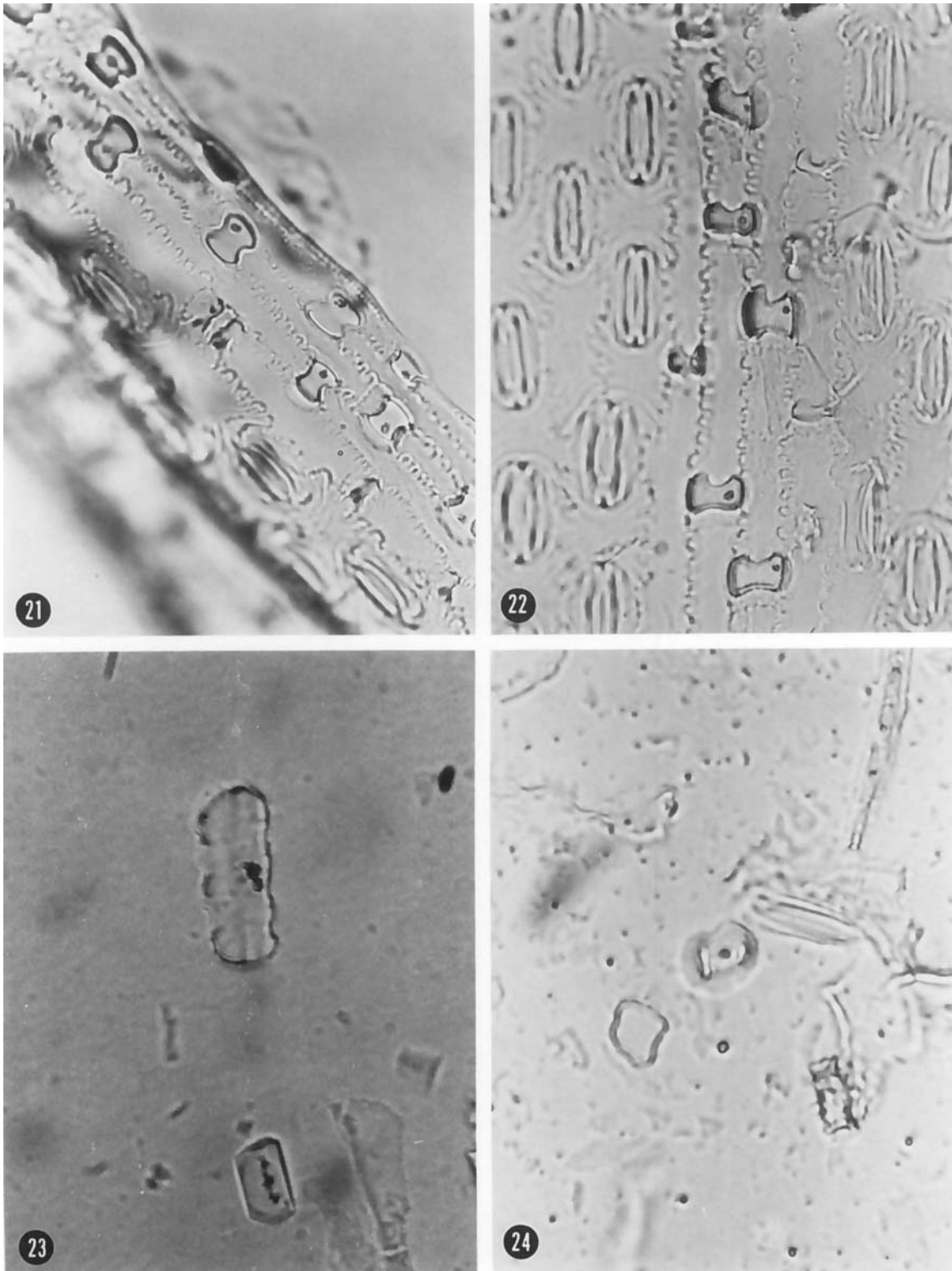
FIGURES 21–24.—21, Saddle-shaped phytoliths from *Guadua amplexifolia*. All but one are tall (×200). 22, Saddle-shaped and narrow-elliptical phytoliths from *Guadua amplexifolia*. All of the saddles are very tall (×200). 23, Top, a long, wavy trapezoid from *Triticum aestivum* (×400). 24, Center, a plateaued saddle from *Phragmites australis* (×400).
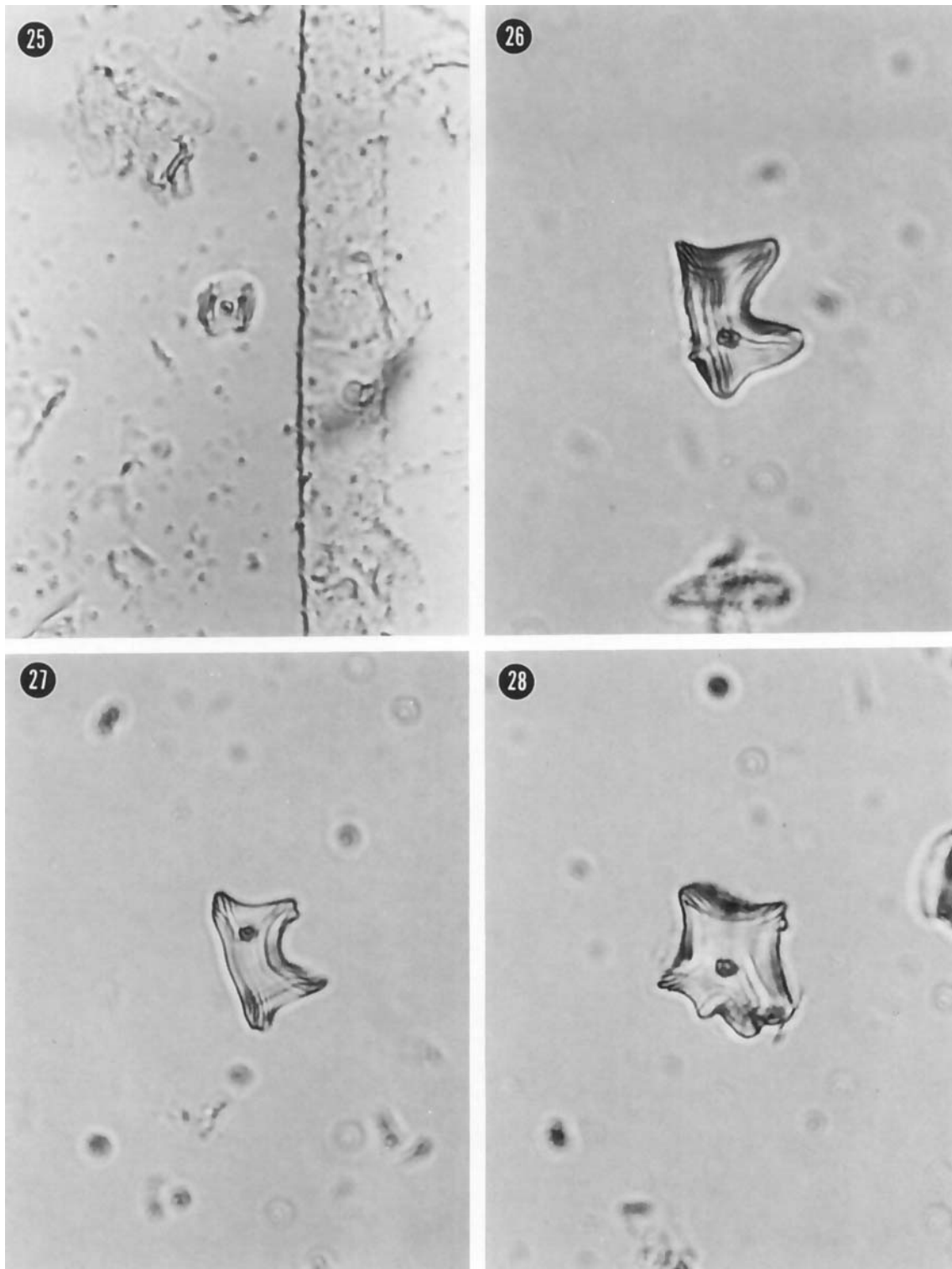
FIGURES 25–28.—25, A plateaued saddle from *Phragmites australis* (×400). 26, A collapsed saddle from *Chusquea grandiflora* (×400). 27, A partially collapsed saddle from *Chusquea grandiflora* (×400). 28, A two-spiked-side phytolith from *Chusquea grandiflora*. Spikes are present on the bottom of the phytolith (×400).
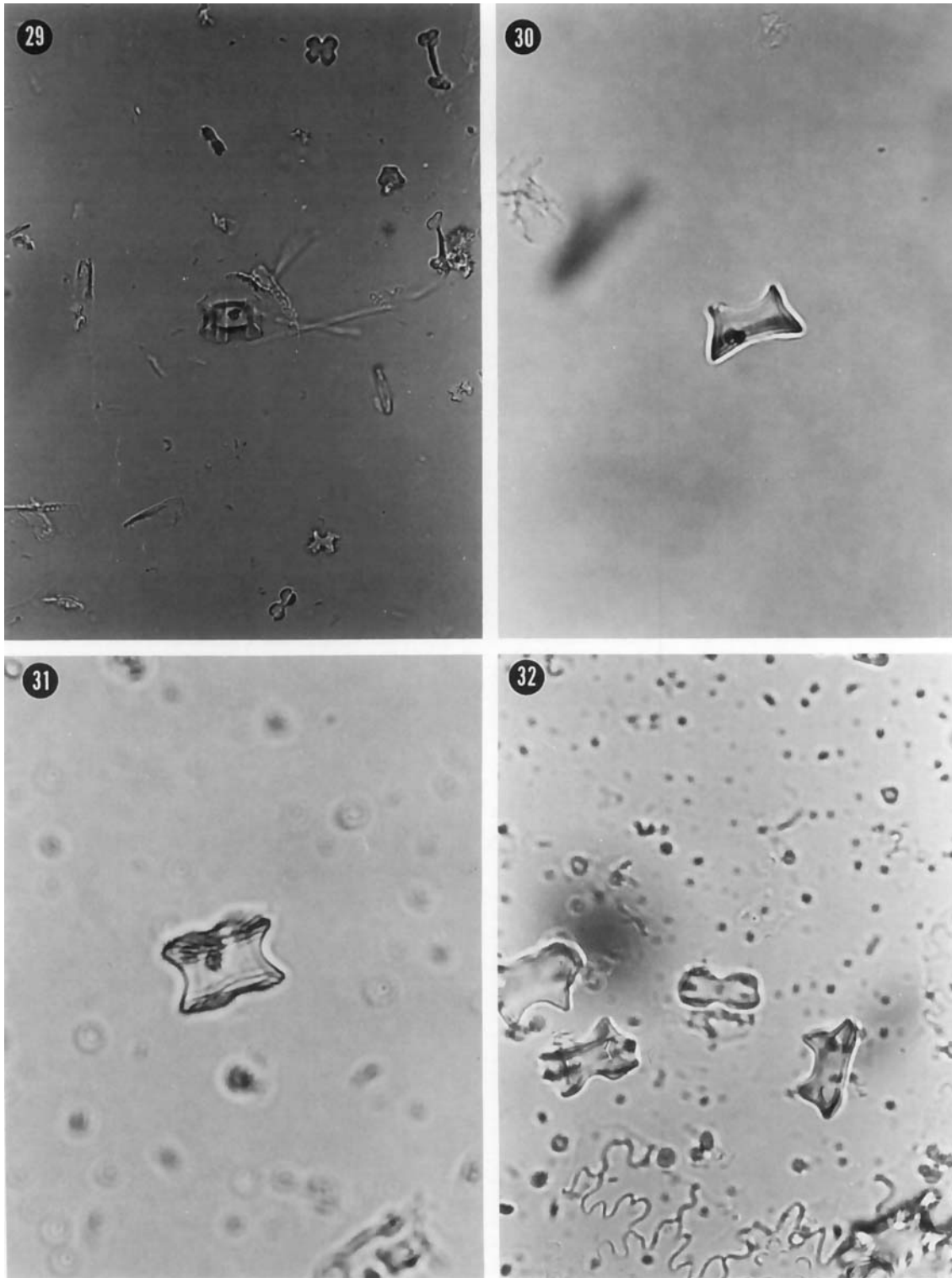
FIGURES 29–32.—29, Center, a saddle with a ridged platform from *Chusquea grandiflora* (×400). 30, A Chusqoid body from *Criciuma asymmetrica*. This phytolith, unlike the *Chusquea* body, is fairly widely distributed in bamboos (×400). 31, A saddle/bilobate both sides type of phytolith from *Chusquea grandiflora* (×400). 32, Right and left, *Chusquea*-body phytoliths diagnostic of this genus from *Chusquea simpliciflora*. The phytolith on the bottom left is still orientated as it would appear in the leaf (×200). The center phytolith is a bilobate.
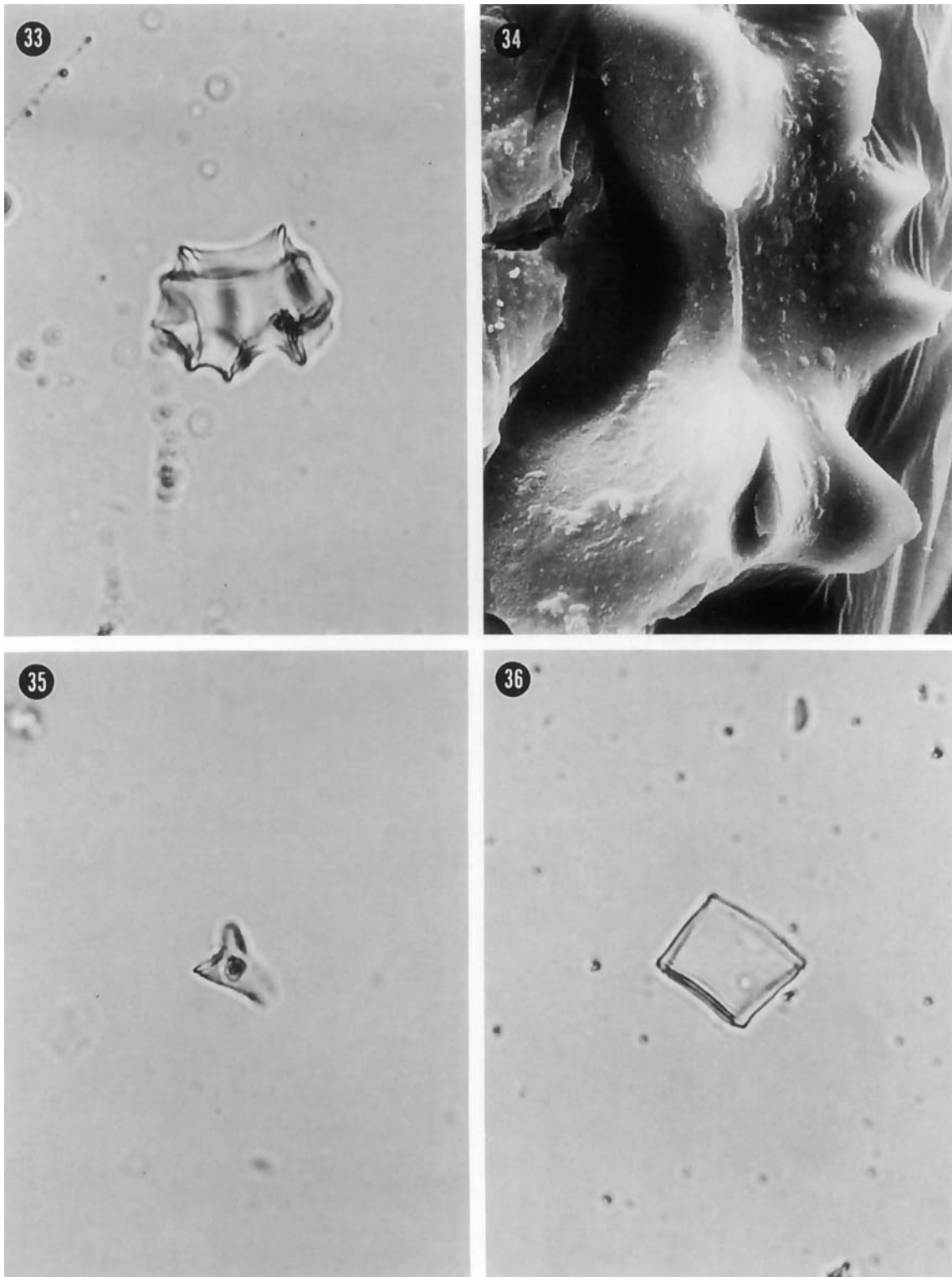
FIGURES 33–36.—33, A multifaceted *Chusquea*-body phytolith from *Chusquea pittiera* (×400). 34, SEM photograph of a *Streptochaeta*-body phytolith from *Streptochaeta sodiroana,* with lateral edges consisting of (left) a concave bilobate and (right) several saddle-like structures (×1000). 35, A small, wide, tent-shaped body from *Neurolepis pittiera* (×400). 36, A *Pharus* body characterized by its flatness, considerable width, and presence of (bottom left) dumbboid and (upper right) rectanguloid lateral edges (×400).
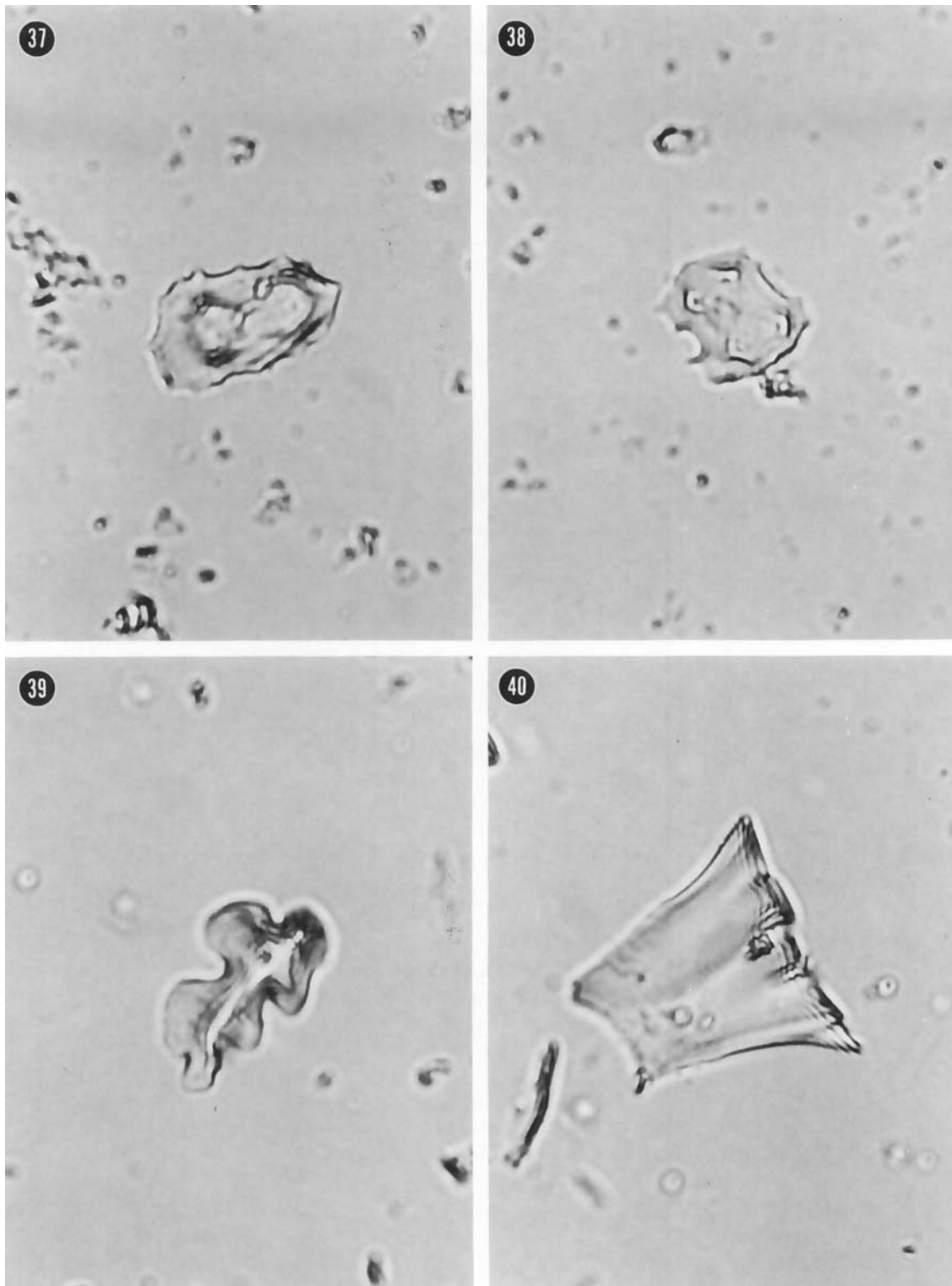
FIGURES 37–40.—37. A biloboid from *Raddiela nana* enclosed in a siliceous plate (×400). 38, A cross-shaped-like phytolith from *Raddiela nana* enclosed in a siliceous plate (×400). 39, An irregular, complex short-cell phytolith from *Maclurolyra tecta* orientated as it would be in leaf tissue (×400). Compare with Figure 40. 40, An irregular, complex short-cell phytolith from *Maclurolyra tecta* exhibiting extreme width and one sinuous and one sloping edge (×400).
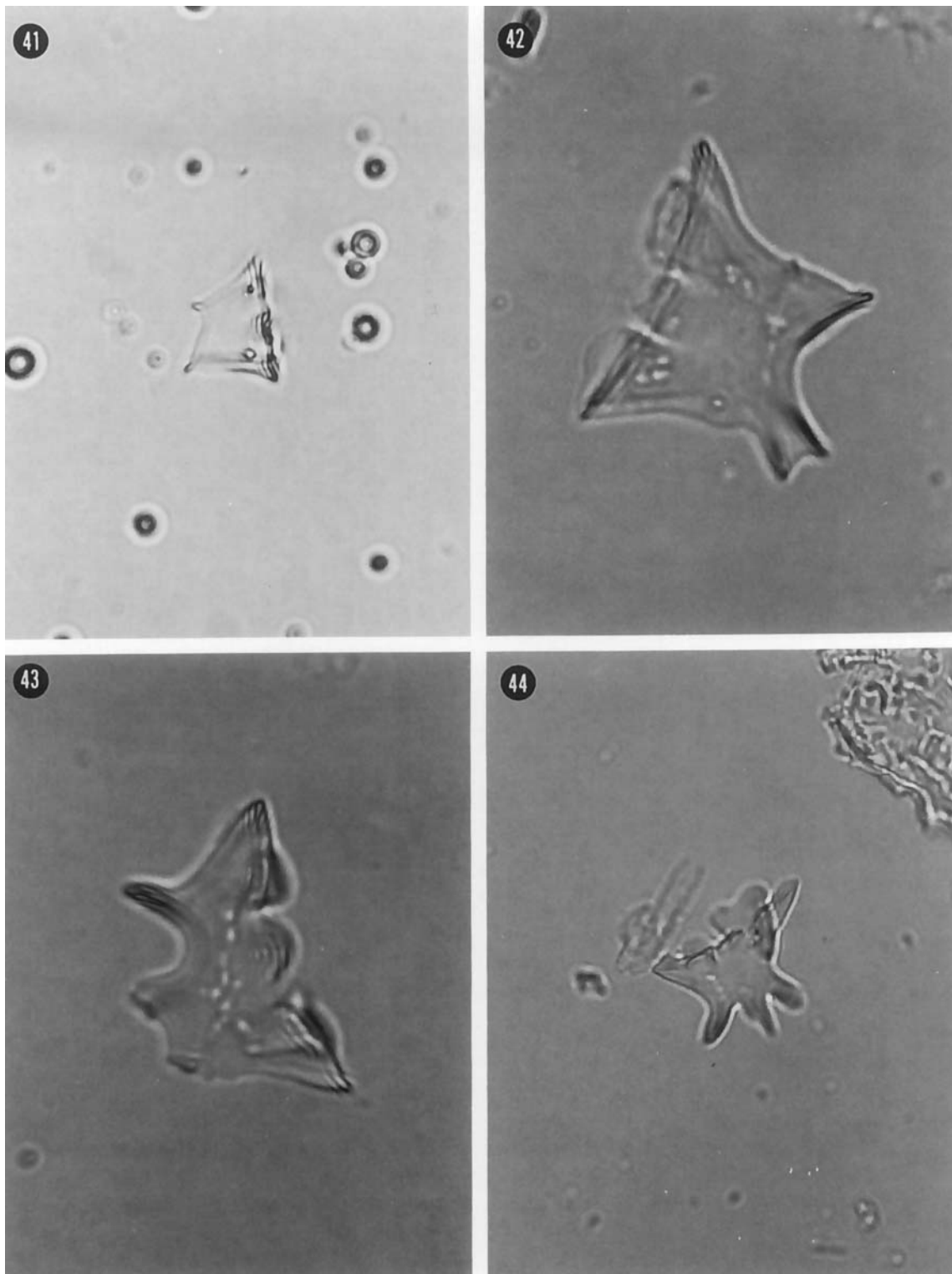
FIGURES 41–44.—41, A phytolith from *Pariana campestris* with one sinuous and one sloping edge. It is neither as tall nor as wide as that from *Maclurolyra tecta* (×400). 42, A phytolith from *Arberella dressleri* with one sinuous and one concave, irregularly pointed edge (×400). 43, A phytolith from *Arberella dressleri* with one sinuous and one concave, irregularly pointed edge (×400). 44, A phytolith from *Arberella dressleri* with one sinuous and one irregularly pointed edge (×400).
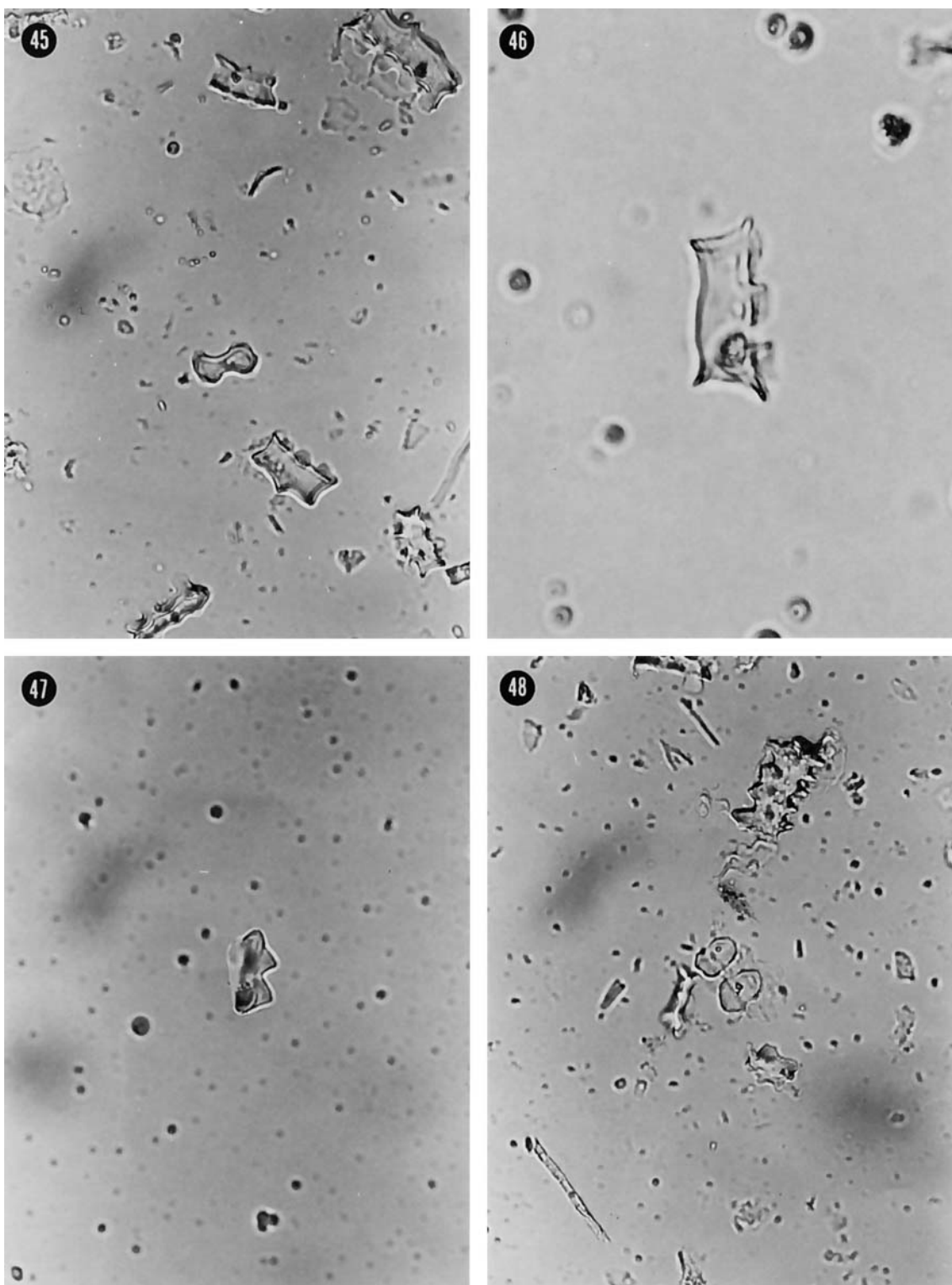
FIGURES 45–48.—45, Top and bottom, irregular, complex short-cell phytoliths from *Olyra latifolia*. These phytoliths are characteristic of the tribe Olyreae. The phytolith in the center is a bilobate (×200). 46, An irregular, complex short-cell phytolith from *Pariana campestris* (×400). 47, A Variant 3 bilobate phytolith from *Arberella dressleri*. The phytolith is partially turned, revealing aspects of both of its faces (×400). 48, Center, two Variant 8 bilobates from *Olyra latifolia* (×400).
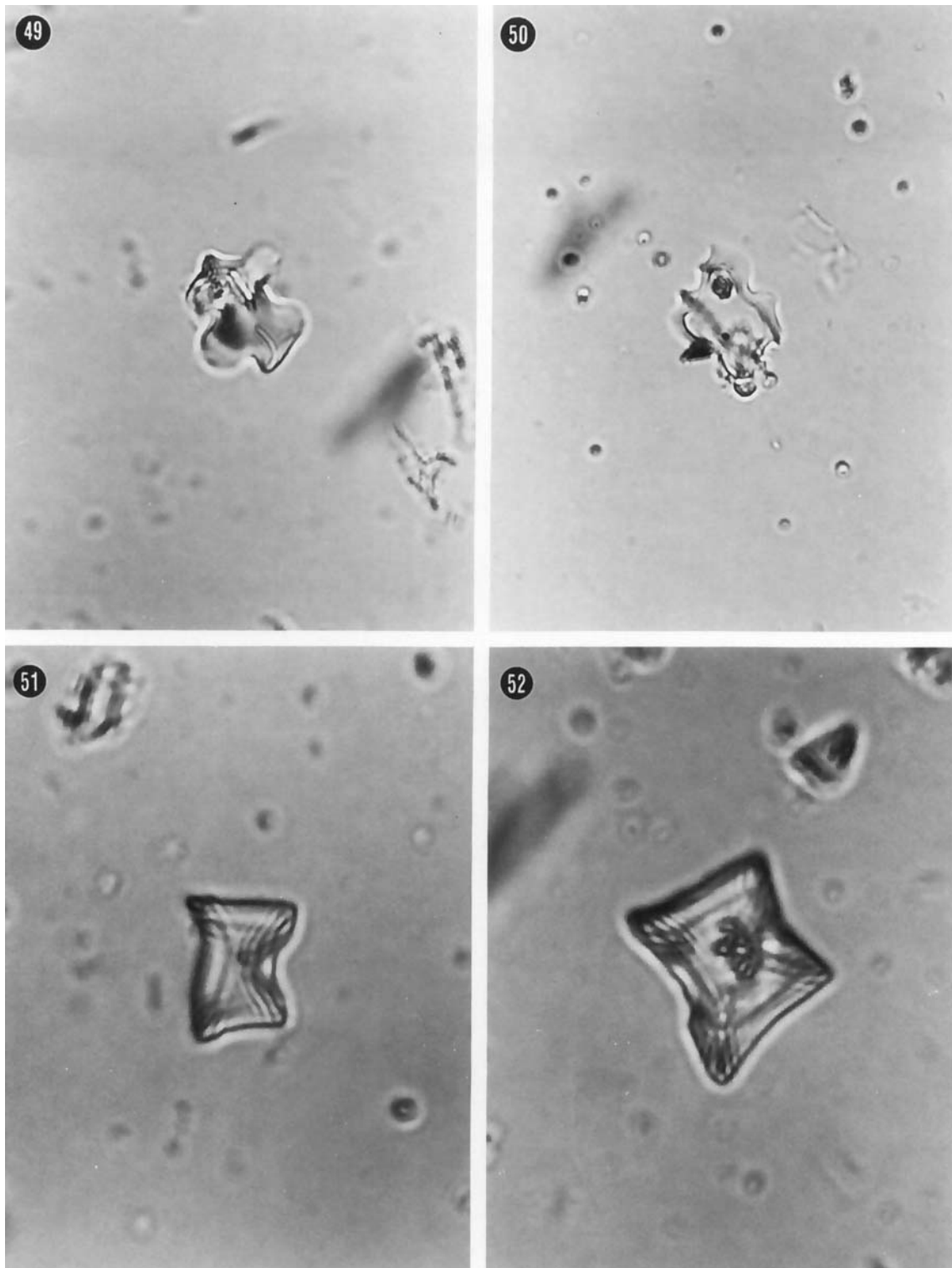
FIGURES 49–52.—49, A thick, cross-shaped phytolith with a concave face from *Otatea fimbriata* (×400). Most cross-shaped phytoliths from this species have only three indentations. 50, A cross-shaped phytolith from *Chusquea pittieri* with serrated short axes, three indentations, and a concave face (×400). This phytolith is not as thick as is usual in the genus. 51, A phytolith from *Arundinella confinis* marked by considerable width and the presence of one slightly concave and one somewhat sloping edge (×400). 52, A phytolith from *Arundinella confinis* marked by considerable width and the presence of one somewhat concave and one somewhat sloping edge (×400).
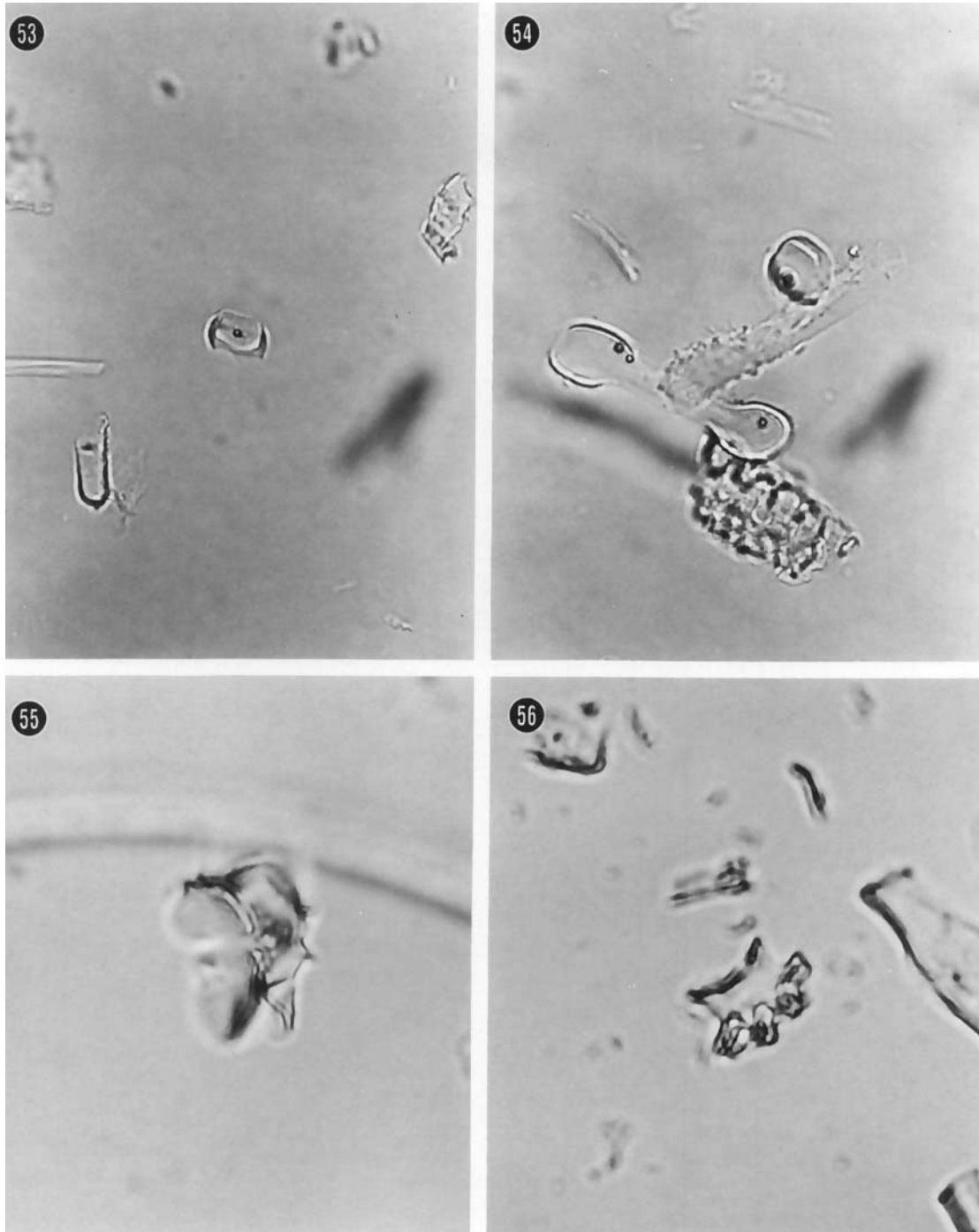
FIGURES 53–56.—53, A rondeloid/saddeloid phytolith from the inflorescence of *Aristida recurrata.* As the name implies, it exhibits features characteristic both of phytoliths in the Pooideae and Chloridoideae (×400). 54, Top, a rondeloid/saddeloid phytolith from *Aristida orizaliensis.* Also present is a bilobate (×400). 55, A unique type of cross-shaped phytolith, from *Polypogon elongatus,* in which one side of the phytolith has a saddle- or bilobate-like structure that extends only about two-thirds the length of the longer, cross-shaped side. It is also very wide. The phytolith is slightly turned, thus both faces may be seen (×400). Bilobates from this grass also carry the same features. 56, A phytolith from *Aegopogon cenchroides* (×400).
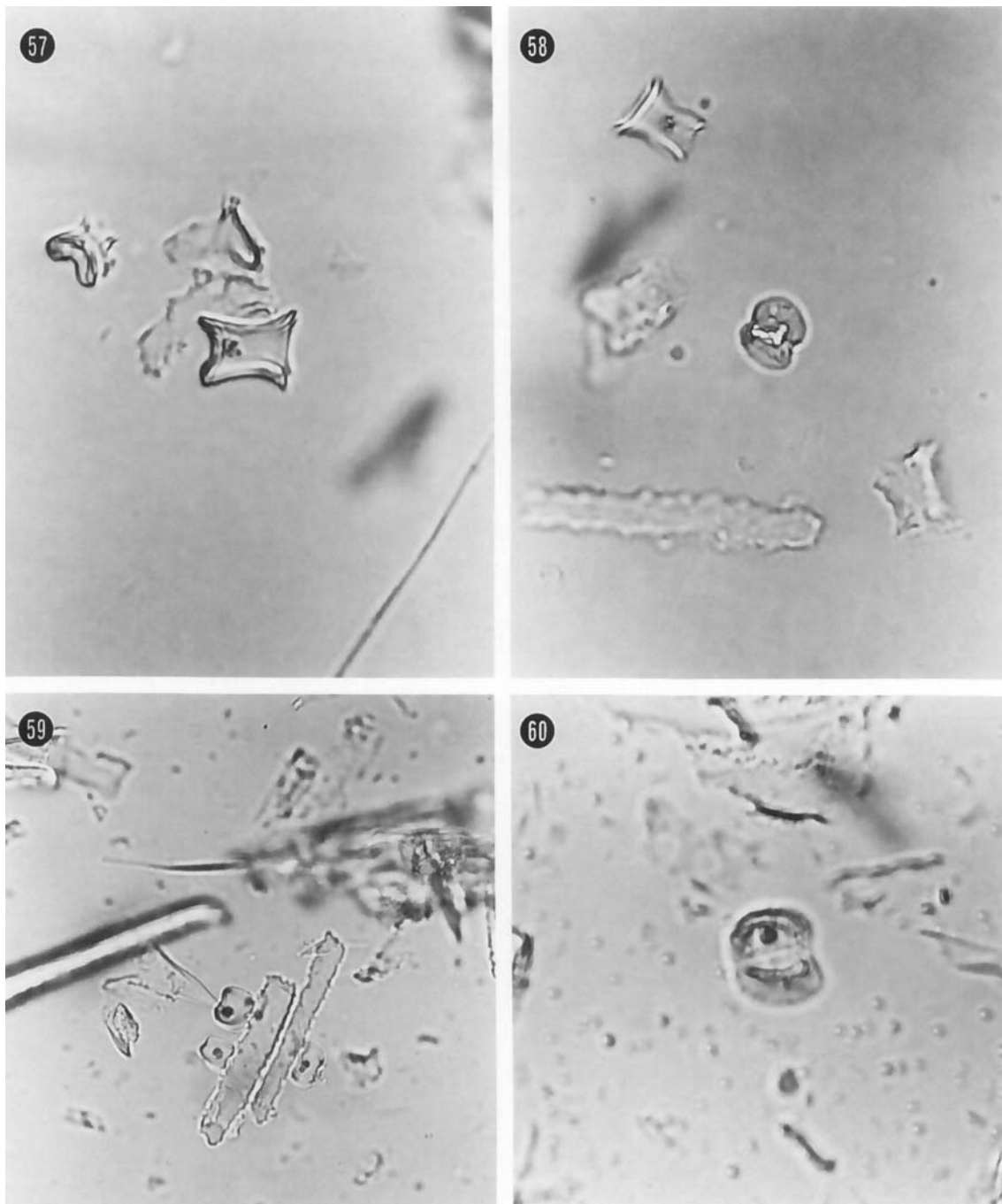
FIGURES 57–60.—57, A phytolith typically produced in the leaves of *Gynerium sagittatum* (×400). 58, Center, a bilobate from the inflorescence of *Guadua latifolia* (×400). 59, Center, bilobates from the inflorescence of *Chusquea longifolia*. They are attached to two elongated phytoliths (×200). 60, A tall saddle from *Phragmites australis* (×400).
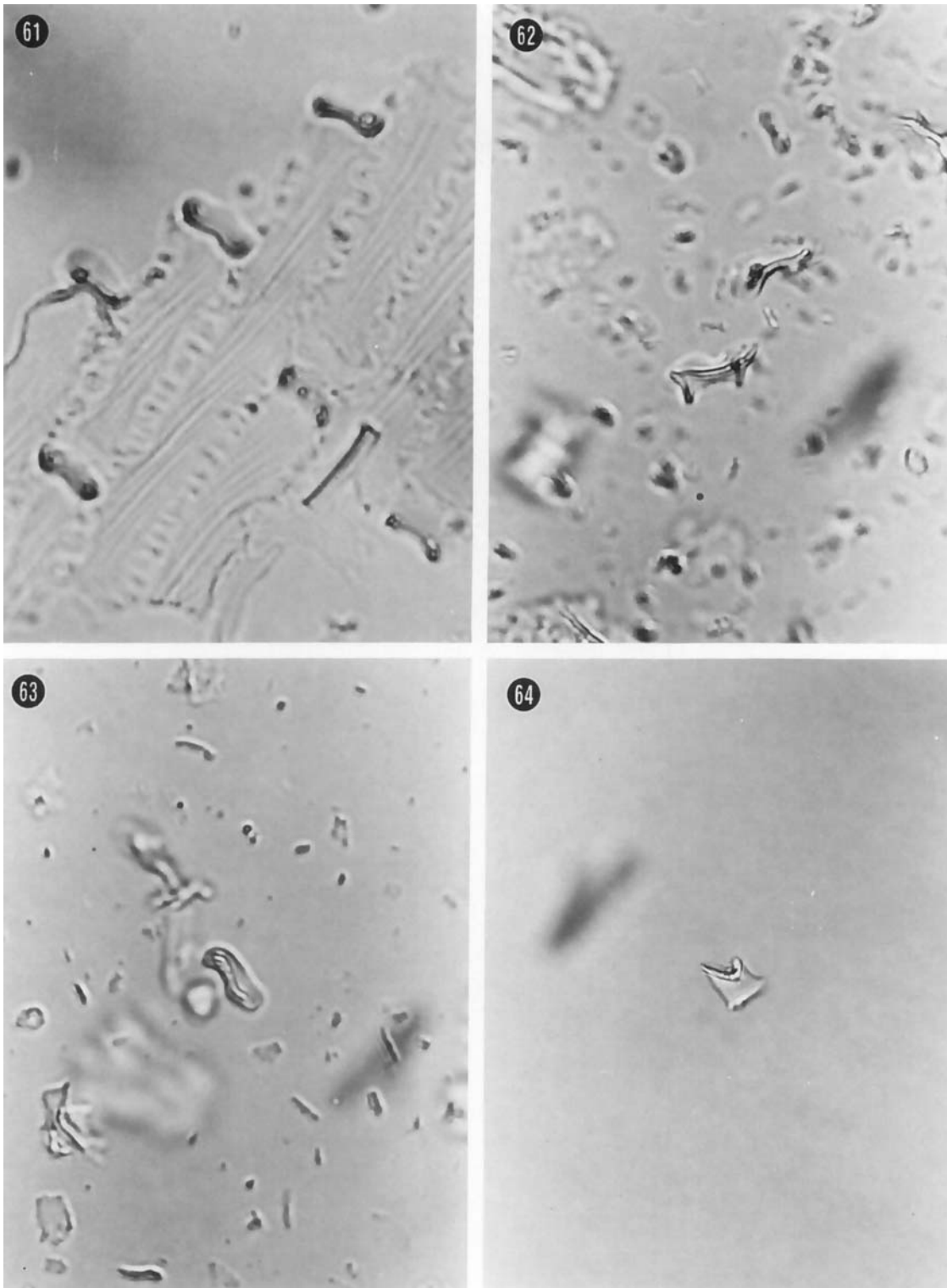
FIGURES 61–64.—61, Narrow elliptate phytoliths from *Guadua latifolia* still enclosed in tissue (×400). 62, Narrow elliptate phytoliths from *Guadua angustifolia* removed from tissue (×400). 63, A narrow elliptate phytolith from *Gynerium sagittatum* (×400). 64, An odd silica body from the culm of *Aristida ternipes* (×400).
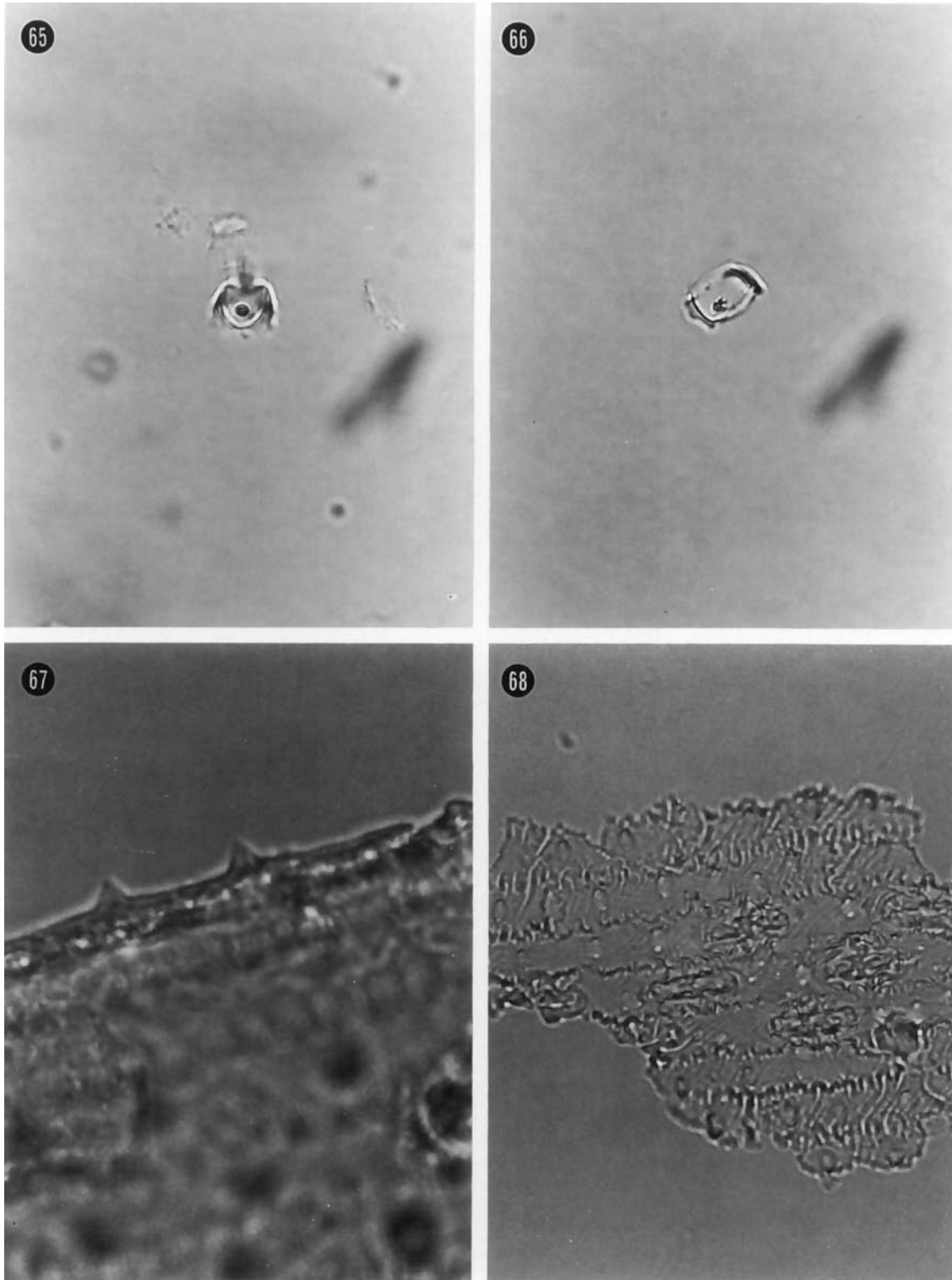
FIGURES 65–68.—65, An odd silica body with saddle tendencies from the culm of *Aristida orizaliensis* (×400). 66, An unusual silica body from the inflorescence of *Aristida orizaliensis* (×400). 67, Top, conical siliceous bodies emerging from the leaf epidermis of *Elytrostachys clanisera* (×400). 68, Two-peaked conical siliceous bodies in epidermis from *Elytrostachys clanisera* (×200).
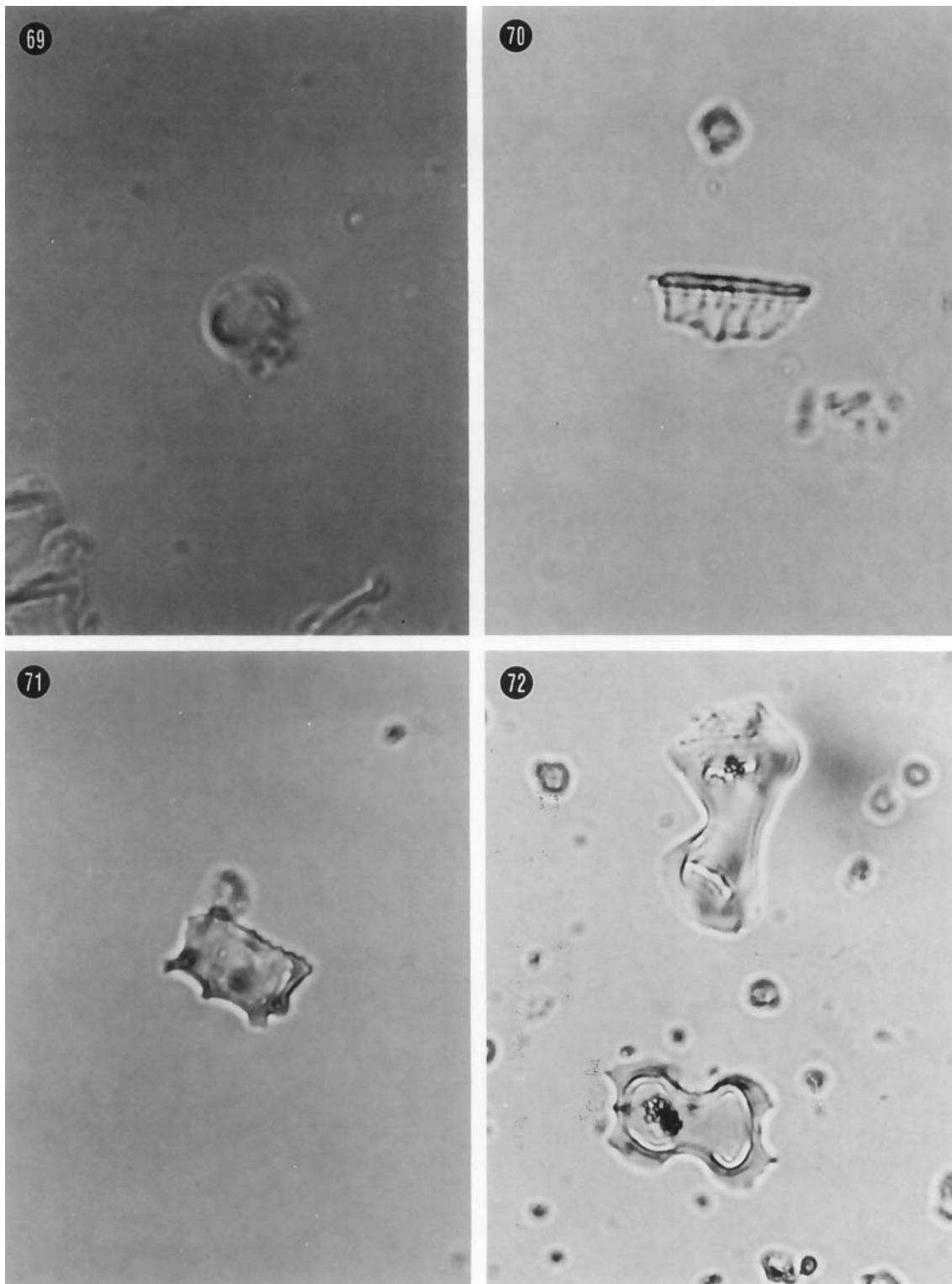
FIGURES 69–72.—69, A two-peaked conical siliceous body from *Actinocladum merticulatum* (×400). 70, A genus-specific epidermal-cell phytolith from the fruitcase of *Tripsacum lanceolatum* (×400). 71, A teosinte-specific epidermal-cell phytolith from the fruitcase of Balsas teosinte (*Zea mays* ssp. *parviglumis* var. *parviglumis*) (×400). 72, Top, a *Chusquea*-body phytolith as it would appear in leaf tissue. Below is a *Chusquea*-type bilobate (×400).
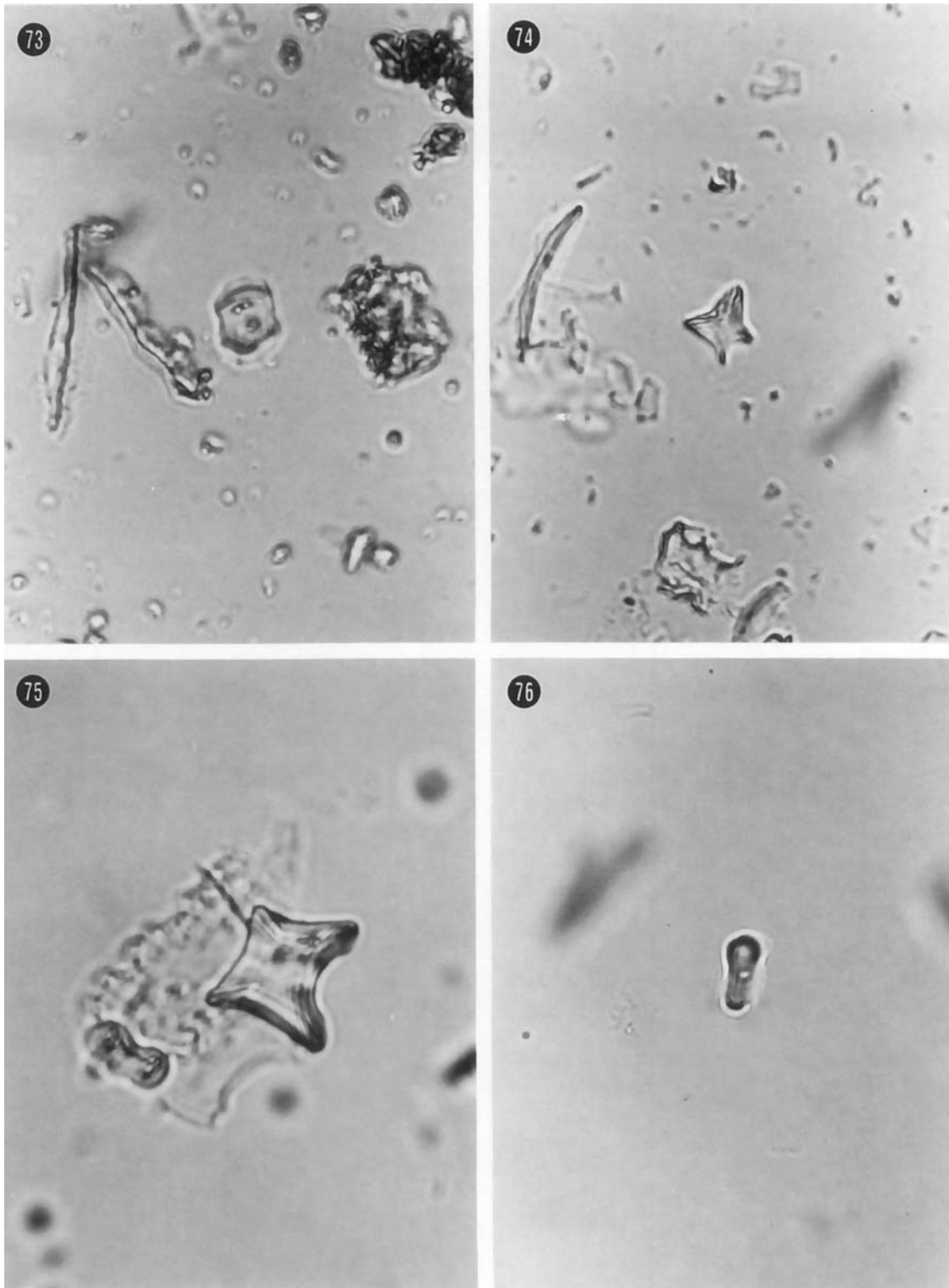
FIGURES 73–76.—73, A tall saddle from *Isachne arundinaceae* (×400). 74, A typical phytolith from *Gynerium saggitatum* (×400). 75, Right, a thick, collapsed saddle from *Guadua amplexifolia* (×400). 76, A phytolith with both saddle and bilobate characteristics from *Guadua amplexifolia* (×400).