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Achene microstructure in *Eriophorum* (Cyperaceae): Taxonomic implications and paleobotanical applications¹

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ABSTRACT

TUCKER, G. C. AND N. G. MILLER (Biological Survey, New York State Museum, The State Education Department, Albany, NY 12230). Achene microstructure in *Eriophorum* (Cyperaceae): Taxonomic implications and paleobotanical applications. Bull. Torrey Bot. Club 117: 266–283, 1990.—Silica bodies in the outer cells of the achene epidermis in 17 species of *Eriophorum* and nine species of *Scirpus*, some of which have been placed in *Eriophorum*, were revealed by sonication and/or acetolysis and examined by scanning electron microscopy. A silica body consists of a basal platform, one or more large elevated protuberances, and sometimes smaller satellite protuberances. Individual species differ in the number of protuberances, the presence/absence of satellites, the texture of the platform, and the occurrence of nodules on the larger protuberances. These features, combined with achene shape and characteristics of the anticlinal walls of the epidermal cells (undulate vs. straight, thick vs. thin, buttressed or not), are expressed in a unique combination for each species. *Scirpus hudsonianus* was examined for geographic and developmental variation in the microstructure of its silica bodies. All samples had similar bodies, characterized by conspicuous nodules on the protuberances and a smooth platform. Nodules were much less evident in immature achenes. Achene epidermal microstructure supports the placement of *S. hudsonianus* in *Scirpus* sect. *Baeothryon* and *S. maximowiczii* in *Scirpus* sect. *Trichophorum*. Achenes of *S. hudsonianus* and *Scirpus cespitosus* share similar silica bodies and other achene features. Achene microstructure of a late-Pleistocene fossil proved to be the same as that in *Scirpus hudsonianus*. Our studies establish the feasibility of identifying all species of *Eriophorum* by utilizing microstructural characteristics of isolated achenes.

Key words: achene morphology, Cyperaceae, *Eriophorum*, Quaternary plant macrofossils, scanning electron microscopy, *Scirpus* sect. *Baeothryon*, *Scirpus* sect. *Trichophorum*, silica bodies, plant systematics.

Removal of the outer periclinal walls of achene epidermal cells of sedges (e.g., *Carex*, *Cyperus*, *Eriophorum*, *Scirpus*, and other genera) reveals silica bodies, the microstructure of which differs in taxonomically important ways (Schuyler 1971; Walter 1975; Denton 1983). A silica body consists of a platform that extends up to or close to the anticlinal walls of a cell and in many sedges one or more conspicuous conical or rounded protuberances projecting from the platform. Additional variation involves the presence of smaller satellite protuberances, nodules on the larger fea-

tures, and buttresses extending from the platform to the anticlinal walls. Comparative studies, employing scanning electron microscopy, have established that silica bodies provide useful characters at various taxonomic levels (Denton 1983; Menapace and Wujek 1986; Tallent and Wujek 1983).

Sedge achenes are common fossils in Quaternary deposits (Miller 1973; Jankovská and Rýbniček 1988), although identifications are rarely taken further than to genus. The discovery of a fossil sedge achene with well preserved epidermal features, including silica bodies, in basal late-Pleistocene silts at Tom Swamp, Petersham, Massachusetts, prompted our investigations into the achene microstructure of *Eriophorum* and *Scirpus* and allowed the fossil to be identified conclusively. The patterns we discovered are diverse, species specific, and useful taxonomically.

Eriophorum, a largely Northern Hemisphere genus (the only exception being disjunct populations of *E. angustifolium* in South Africa; Hul-tén and Fries 1986) has not been monographed

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on a world-wide basis. For this study we assembled specimens of all species of *Eriophorum* treated in the standard North American, European, and Asian floras. We also included *Scirpus hudsonianus* and *S. maximowiczii*, which have been treated as species of *Eriophorum*. We were not able to locate specimens of *E. scabriculum* (Beetle) Raymond, a species considered related to *E. microstachyum* (Raymond 1957), but otherwise our coverage of *Eriophorum* is complete.

Eriophorum and *Scirpus* share many characters, but the numerous, long perianth bristles and oblong achenes (generally widest in the upper one-half) of *Eriophorum* vs. perianth bristles short, six or fewer and achenes broad (generally widest at the middle) in *Scirpus* serve in most cases to distinguish the two genera. Because of the transitional nature of *S. hudsonianus* and *S. maximowiczii* (perianth bristles long, six in number), we also studied achenes of species of *Scirpus* sect. *Baeothryon* Endl., in which *S. hudsonianus* is placed by contemporary taxonomists, as well as species of *S.* sect. *Trichophorum* (Pers.) Darl. and of *Trichophorum* Pers.

Methods. The species included in this study are listed in Appendix A, which also includes information on the voucher specimens examined and a brief description of the geographic distribution of each species.

Achenes were removed from spikelets, freed of perianth bristles, and sonicated and/or acetolyzed to remove the outer periclinal wall of the epidermis. For most species sonication for two hours exposed the silica bodies. However, in some cases (e.g., *Eriophorum scheuchzeri*, *E. latifolium*, species of *Scirpus* sect. *Baeothryon*) it was necessary to place the achenes in acetolysis solution (9 parts acetic anhydride:1 part concentrated sulfuric acid) at room temperature for 3 min, preceded and followed by washes with glacial acetic acid. This treatment was followed by 30 min of sonication. Achenes were put in vials in 70% ethyl alcohol, which were then placed in the water of an ultrasonic cleaner. The cleaned achenes were air dried and affixed to aluminum stubs with double-coated tape. A 7 Å coating of gold-palladium was applied in a sputter coater. For consistency all achenes were observed and photographed at ca. 3000× under SEM, as well as at a lower magnification (32–100×).

In general two achenes from each specimen were processed and examined. For many species two or three plants from different herbarium specimens (i.e., populations) were studied.

The fossil achene was recovered from a sediment sample collected with a Livingstone piston corer during paleoecological studies at Tom Swamp (42°31'N, 72°12'30"W), Massachusetts. The depth of the sample was 9.65–9.72 m. The fossil was removed from a residue of plant debris that remained on a 250 μm-mesh sieve after the smaller inorganic sediments had been flushed away by tap water. A sediment sample between 9.55–9.65 m was radiocarbon dated (Bender *et al.* 1982) at 12,830 ± 120 yr B.P. (WIS-1210), indicating a somewhat greater age for the fossil. Other plant fossils found in the sediments have been described and interpreted by Miller (1987, 1989a, 1989b) and Gaudreau (1986).

Results. Achenes of *Eriophorum* are narrowly to broadly obovoid and moderately to weakly trigonous. In about half the species the style base is persistent (e.g., *E. russeolum* (Fig. 45), *E. scheuchzeri* (Fig. 29)); in the others the style base is visible under high magnification but is greatly reduced in size or absent.

The microstructure of the silica bodies is diverse within *Eriophorum* but consistent for a species. A single, central conical protuberance characterizes most species (e.g., *E. viridi-carinatum*, Fig. 36); two or more protuberances are evident in some (e.g., *E. coreanum*, Fig. 22). In a few (e.g., *E. angustifolium*, Fig. 42) smaller satellite protuberances are associated with larger ones. Nodules are present on the protuberances in some (e.g., *E. crinigerum*, Fig. 20). The platform is smooth (e.g., *E. comosum*, Fig. 52) or minutely roughened (*E. viridi-carinatum*, Fig. 36).

Other microstructural features of the epidermal cells include small buttresses that bridge the silica body and the anticlinal cell walls (e.g., *E. crinigerum*, Fig. 20) and pit-like gaps that are present (*E. tenellum*, Fig. 26) between the buttresses and sometimes appear as holes (*E. coreanum*, Fig. 22). The anticlinal cell walls are undulate in a few of the species (e.g., *E. crinigerum*, Fig. 20) or straight (e.g., *E. coreanum*, Fig. 22).

Achenes and achene epidermal features of 19 species of *Eriophorum* and *Scirpus* are described below in a sequence that groups together species with similar microstructure. We do not intend this arrangement as a phylogenetic scheme, however.

1. *E. crinigerum* (Gray) Beetle. Achenes obovoid, style base persistent; anticlinal walls undulate, buttresses weakly developed, pits absent; silica body with one

- central, nodulose protuberance, satellites absent, platform roughened. Figs. 19, 20.
2. *E. coreanum* Palla. Achenes narrowly obovoid, style base absent or at best a low boss; anticlinal walls straight, with buttresses and conspicuous pit-like gaps; silica bodies mostly with three protuberances, satellites absent, platform slightly roughened. Figs. 21, 22.
 3. *E. gracile* W. D. J. Koch. Achenes obovoid, style base absent; anticlinal walls straight, buttresses weakly developed; silica bodies with one or two large protuberances, nodules present, sometimes forming a ring around the base of a protuberance, satellites present, platform smooth. Figs. 23, 24.
 4. *E. tenellum* Nutt. Achenes narrowly ellipsoid to ellipsoid, style base a low boss, buttresses inconspicuous; silica bodies with one to three large protuberances, satellites present, platform smooth or slightly roughened. Figs. 25, 26.
 5. *E. chamissonis* C. A. Mey. Achenes ellipsoid, style base persistent; anticlinal walls straight and thick, buttresses absent; silica bodies with one central, smooth protuberance, satellites few, platform roughened. Figs. 27, 28.
 6. *E. scheuchzeri* Hoppe. Achenes obovoid, style base persistent; anticlinal walls undulate, buttresses unknown; silica bodies with one or two protuberances, satellites absent, platform roughened. Figs. 29, 30.
 7. *E. spissum* Fern. Achenes broadly obovoid, style base persistent, very short; anticlinal walls straight, thin; silica bodies with one or two, sometimes conical, protuberances, satellites few or none, platform slightly roughened and confluent with the anticlinal walls. Figs. 31, 32.
 8. *E. vaginatum* L. Achenes broadly obovoid, style base persistent, very short; anticlinal walls thin, straight or slightly sinuous; silica bodies with one protuberance, satellites few or none, platform slightly roughened and confluent with the anticlinal walls. Figs. 33, 34.
 9. *E. viridi-carinatum* (Engelm.) Fern. Achenes obovoid, style base persistent; anticlinal walls straight; silica bodies with one central protuberance, satellites none, platform slightly roughened, confluent with the anticlinal walls. Figs. 35, 36.
 10. *E. virginicum* L. Achenes broadly obovoid, style base a low boss; anticlinal walls straight; silica bodies with one, sometimes more, protuberances, nodulose or not, satellites 4-7, prominent, platform bulging, slightly roughened, confluent or not with the anticlinal wall. Figs. 37, 38.
 11. *E. callitrix* Cham. Achenes broadly obovoid, style base absent or very short; anticlinal walls straight or slightly sinuous; silica bodies with one central protuberance, satellites few, platform slightly roughened, confluent with the anticlinal walls. Figs. 39, 40.
 12. *E. angustifolium* Honckeny. Achenes obovoid to ellipsoid, style base absent; anticlinal walls straight, thin; silica bodies with one to five large protuberances and one or more satellites of varying size, sometimes with one or more nodules, platform slightly roughened, confluent with the anticlinal walls. Figs. 41, 42.
 13. *E. opacum* (Bjornstr.) Fern. Achenes obovoid, style base persistent, small; anticlinal walls straight, thin; silica bodies with one low, broadly rounded protuberance, satellites 3-4, platform slightly confluent with the anticlinal walls. Figs. 43, 44.
 14. *E. russeolum* E. Fries. Achenes narrowly obovoid, style base persistent, long; anticlinal walls undulate; silica bodies with one central, weakly nodulose protuberance and from 5-6 satellites, sometimes nearly equalling in size the central protuberance, platform slightly roughened, not confluent with the anticlinal walls. Figs. 45, 46.
 15. *E. latifolium* L. Achenes broadly obovoid, style base persistent, short; anticlinal walls straight; silica bodies with one central protuberance, sometimes bearing a single nodule, satellites none, platform smooth and confluent with anticlinal walls. Figs. 47, 48.
 16. *E. microstachyum* Boeckeler. Achenes narrowly obovoid, style base persistent; anticlinal walls undulate, thin; silica bodies with one small, nodulose central protuberance, satellites none, platform slightly roughened, confluent with anticlinal walls. Figs. 49, 50.
 17. *E. comosum* Wallich. Achenes very narrowly ellipsoid, style base persistent (poorly differentiated from apex of achene); anticlinal walls straight, thin; silica bodies with one conical protuberance ending in

a rounded, slightly nodulose summit, satellites none, platform smooth, extending to anticlinal wall. Figs. 51, 52.

18. *Scirpus hudsonianus* (Michx.) Fern. Achenes obovoid, style base persistent; anticlinal walls of epidermis straight, thin, without buttresses; silica body with one to three nodulose protuberances, satellites present or not, platform smooth or very slightly roughened. Figs. 1-18.
19. *S. maximowiczii* C. B. Clarke. Achenes broadly obovoid, style base persistent; anticlinal walls undulate, buttresses conspicuous; silica bodies with one large central, nodulose protuberance, platform roughened or weakly so. Figs. 53, 54.

VARIATION IN THE ACHENES OF *SCIRPUS HUDSONIANUS*. Achenes from plants collected throughout the nearly continuous circumboreal range of *S. hudsonianus* (Hultén and Fries 1986) are stenotypic in shape and microstructure (Figs. 1, 2, 6-14). The silica bodies have one large, usually central protuberance that is strongly ornamented with rounded or pointed nodules, and from one to four smaller, but similarly ornamented, protuberances. In some cells the smaller protuberances resemble satellites. All of the achenes examined had a persistent style base.

Some conspicuous variation in protuberance ornamentation was noted. In achenes from Vermont and Japan that were flattened and apparently empty, the protuberances were smooth or nearly so. The Japanese samples (Figs. 17, 18) came from different spikelets of the same plant. The achene with well developed nodules was mature (taken from near the base of the spikelet), while the one lacking nodules was a younger achene removed from a position higher in the spikelet. This suggests that the degree of protuberance ornamentation is linked to achene maturation, perhaps reflecting fertilization and normal seed development. Because the Vermont achenes (Figs. 15, 16) were collected in different years, it is not possible to separate possible environmental from developmental effects on nodule expression in these samples.

THE FOSSIL ACHENE. No attempt was made to clean the fossil of adhering debris by sonication or other means because it was fragile. (The achene epidermis fragmented during preparation for SEM study; Fig. 3.) Nevertheless, silica body protuberances (Figs. 4, 5) and their nodulose ornamentation were clearly evident (Fig. 5). One large protuberance is present in most cells, and one or

more smaller protuberances per cell also are visible (Figs. 4, 5).

Discussion. The 19 species examined have unique achene epidermal features that allow individual achenes to be identified to species using a combination of light and scanning electron microscopy. A key to the species employing these features is presented as Appendix B.

We evaluated the expression of silica body microstructure in *Scirpus hudsonianus* and established that representative specimens from throughout the broad range of this species had an essentially consistent pattern. The pattern also was evident in a late-Pleistocene sedge achene recovered from sediments deposited about 12,850 radiocarbon years ago in Massachusetts that we identify as this species. It should be possible to identify isolated fossil achenes of all species of *Eriophorum*, and probably of related genera also, providing that the silica bodies remain intact in achenes during and after deposition and during laboratory processing.

SYSTEMATIC IMPLICATIONS. The species we studied have been placed in the following genera: *Eriophorum*, *Scirpus* (sect. *Baeothryon*), *Trichophorum* Pers., *Eriophorella* Holub, and *Erioscirpus* Palla (Holub 1984; Koyama 1958; Oteng-Yeboah 1974; Schuyler 1971). Some of the species have been assigned to two or three of these genera by various authors, and thus there has been much disagreement about the limits of the genera, and in fact whether some should indeed be recognized.

Achene epidermal microstructure provides no dramatic characters that aid in the delimitation of these genera. However, among the species of *Eriophorum* we studied there are several tendencies in silica body and achene epidermal cell microstructure that are pertinent to questions of generic circumscriptions. Silica bodies having platforms confluent with the anticlinal walls and multiple projections (including satellites) are present in most species of *Eriophorum* having numerous long perianth bristles (i.e., the traditional Northern Hemisphere cotton grasses). The exceptions are *E. latifolium* and *E. viridicarinatum*, in which the silica body has one smooth central projection and no satellites.

Another tendency, evident in species assigned to *Erioscirpus*, is one large, weakly nodulose protuberance per cell and no satellites. The two species of *Erioscirpus* (Oteng-Yeboah 1974) have different types of silica bodies. In *E. microstach-*

yum (Boeckeler) Palla the body platform is confluent with the anticlinal walls, while in *E. comosum* (Wallich) Palla the body platform is delimited, i.e., non-confluent (cf. Figs. 50 and 52). The perianth bristles of these two species are like those of *Eriophorum*, and their silica body microstructure is connected to that of the species of *Eriophorum* with multiple projections through *E. latifolium* and *E. viridi-carinatum*. Although Van der Veken (1965) considered that the embryo of *Eriophorum comosum* is "assez particulier" for the genus and also unlike any of six types present in *Scirpus*, this opinion may relate mostly to the narrowness of the embryo of *E. comosum*, which has by far the narrowest achenes of any species of *Eriophorum* (Fig. 51). For these reasons, we find no compelling evidence to recognize *Erioscirpus*.

Achenes of *Scirpus maximowiczii* (*Eriophorum japonicum* Maxim.), are similar in shape (including the persistent style base) to many species of *Eriophorum*. However, *S. maximowiczii* has only six perianth bristles. These are three to four times longer than the achenes and thus in length approach those of the traditional cotton grasses. However, the achene epidermal microstructure of *S. maximowiczii* (Fig. 54) is similar to that of *Scirpus cyperinus* (L.) Kunth (Fig. 68), and Schuyler (1971) also cited parallels with species of the *S. sylvaticus* group. The similarities include one large, smooth, central protuberance from the silica body platform and strongly undulate anticlinal cell walls. Van der Veken (1965), in an extensive survey of embryos of members of Cyperaceae subf. Cyperoideae, discovered that the embryo of *S. maximowiczii* was most similar to that in species of *Scirpus* sect. *Trichophorum*, which includes *S. cyperinus*. Thus, we exclude *E. japonicum* from *Eriophorum* and treat it as a species of *Scirpus*.

Scirpus hudsonianus often has been treated as a species of *Eriophorum* (*E. alpinum*) because it has white perianth bristles that are much longer than the achenes. We examined achenes of all species of *Scirpus* sect. *Baeothryon* (in which *S. hudsonianus* is generally included), and our results are illustrated in Figs. 55–66. *Scirpus clementis*, *S. clintonii*, *S. verecundus*, *S. pumilus*, and *S. rollandii* have silica bodies with one prominent, central, often weakly nodulose protuberance. The bodies of *S. cespitosus*, in contrast, have one or two low nodulose protuberances from each platform and thus are most similar, among all species of sect. *Baeothryon*, to those of *S. hudsonianus*. Additional characters

that link *S. hudsonianus* and *S. cespitosus* are achene shape, a persistent beaklike style base, and an enlarged achene base. Van der Veken's studies of embryography (1965) established that embryos of *E. alpinum* are like those in species of *Scirpus* sect. *Baeothryon* (*Carex* type) and unlike those of *Eriophorum* (*Fimbristylis* type). Thus there is much evidence for treating *E. alpinum* as a species of *Scirpus*.

Scirpus hudsonianus has been recognized as the sole member of the genus *Eriophorella* Holub (1984). However, as noted above there are a number of similarities between the achenes of *S. hudsonianus* and *S. cespitosus*, indicating that these species can be treated at some level within *Scirpus*.

Trichophorum is currently being used in two senses: as *Scirpus* sect. *Trichophorum* and as a genus for the following species, *Scirpus hudsonianus* (*T. alpinum* (L.) Pers.), *T. cespitosum* (L.) Hartm. (*S. cespitosus*), and *T. pumilum* (Vahl) Schinz & Thell. (*S. pumilus*). Our studies of achene microstructure have revealed no characters that would serve to unify these species under a single generic concept. Salmenkallio and Kukkonen (1989) have proposed conserving the name *Trichophorum*, with *T. alpinum* as the type. We prefer retaining *Trichophorum* as a section of *Scirpus*, with *S. cyperinus* as the type, a usage that can be traced back to Torrey (1836).

The new information on achene epidermal microstructure permits an evaluation of the infra-generic classification of *Eriophorum* in the strict sense (i.e., excluding species we accept as belonging to other genera). Oteng-Yeboah's paper (1974), based in part on the work of Raymond (1954), divided *Eriophorum* in our restricted sense into two subgenera: subg. *Eriophoropsis* (Palla) Raymond (scales brown, spinulose; uppermost sheath with a leaf blade) and subg. *Eriophorum* (scales black, nonspinulose; uppermost sheaths bladeless). Subgenus *Eriophorum* was further divided into two sections, sect. *Eriophorum* (inflorescences a single terminal spikelet) and sect. *Phyllanthela* Anderss. (inflorescences of several, stalked spikelets). Patterns of achene epidermal microstructure do not correlate well with this classification, thereby offering no support for the recognition of these two sections. For example, *E. virginicum* (subg. *Eriophoropsis*) shares a number of achene microstructural features with species of *Eriophorum* subg. *Eriophorum* (cf. Figs. 38 and 44).

Similarities in achene microstructure contribute to understanding relationships between cer-

tain pairs of species that share other characters. *Eriophorum gracile* and *E. tenellum* are similar vegetatively (channelled leaf blades, single involucre bracts) and also have similar silica bodies and anticlinal achene epidermal cell walls (cf. Figs. 24 and 26). *Eriophorum spissum* has been treated as a subspecies of *E. vaginatum*. While the achenes of these cotton grasses are similar in shape, the silica bodies of *E. vaginatum* have numerous satellites and those of *E. spissum* have few or none (cf. Figs. 34 and 32). This difference supports treating them as separate species. *Eriophorum coreanum* has been treated as a subspecies or a variety of *E. gracile* by Hultén (1927) and Koyama (1958), respectively, but the achene microstructure of *E. coreanum* (Fig. 22) differs more from *E. gracile* (Fig. 24) than *E. gracile* does from *E. tenellum* (Fig. 26), thus adding additional support for the recognition of *E. coreanum* as a species.

Finally, our studies have revealed variation in the shape of achenes of *Eriophorum angustifolium* (but not in epidermal microstructure). More investigations of plants from throughout the broad circumboreal range of this cotton grass are needed to evaluate the significance of this variation and its relationship to achene microstructure.

In summary and as confirmed by other workers who have followed up on the pioneering observations of Schuyler (1971), we found that silica body microstructure provides consistent, taxonomically significant patterns that are useful in species delimitation and at other taxonomic levels. These patterns indicate that it should be possible to identify the isolated achenes of species of *Eriophorum* and allied genera, which in addition to vegetative remains, are preserved in Quaternary peats and sometimes in lake sediments.

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Appendix A

Species (synonyms). Distribution.

Eriophorum alpinum, see *Scirpus hudsonianus*.

E. angustifolium Honckeny. Circumboreal.

CANADA. Northwest Territories: Great Slave Lake, Fairchild Point, 17 July 1927, *Raup 360* (GH); Québec: Saguenay Co., Harrington Harbor, 10 Aug. 1939, *Brunel 45* (GH).

E. callitrix Cham. Boreal North America and north-eastern Asia.

CANADA. Newfoundland: Boat Harbor, 19 July 1925, *Fernald et al. 27555* (GH).

E. chamissonis C. A. Mey. (*E. russeolum* subsp. *rufescens* (Anders.) Hyl.). Northeastern Asia, north-western North America.

CANADA. British Columbia: Queen Charlotte Islands, Cumshewa Inlet, 29 June 1957, *Calder et al. 21938* (GH).

E. comosum Wallich. Eastern Asia.

CHINA. Szechuan: Mow Hsien, 27 Sept. 1928, *Fang 5540* (GH).

E. coreanum Palla (*E. gracile* subsp. *coreanum* (Palla) Hultén). Eastern Asia.

JAPAN. Koshiro Prov.: 7 July 1959, *Furuse s.n.* (A).

E. crinigerum (Gray) Beetle. California, Oregon.

USA. California: Siskiyou Co., Taylor Lake, 1 Sept. 1938, *Harris & Leland 5445* (GH).

E. gracile W. D. J. Koch. Circumboreal.

CANADA. Québec: Anticosti Island, Pointe de L'Est, 5 Aug. 1925, *Marie-Victorin et al. 20172* (GH).

USA. New York: Columbia Co., near Harlemlville, 18 June 1933, *McVaugh 1134* (NYS).

E. japonicum, see *Scirpus maximowiczii*.

E. latifolium L. Europe, western Asia.

CZECHOSLOVAKIA. Trebusany: 10 July 1932, *Flora Cechoslovenica Exsiccata 360* (NYS).

E. microstachyum Boeckeler. Himalayan Mountains.

INDIA. Punjab: Dharmkot, 7000', *Stewart 1970* (US).

E. opacum (Bjornstr.) Fern. (*E. brachyantherum* Trautv. & Mey.). Circumpolar.

CANADA. Newfoundland: Big Brook, 15 July 1925, *Fernald & Long 27548* (GH).

E. russeolum E. Fries. Circumpolar.

CANADA. Manitoba: York Factory, 20 July 1949, *Scoggan 5929* (GH).

E. scheuchzeri Hoppe. Circumpolar.

GREENLAND. Anaratok, 21 July 1924, *Robinson 33* (GH).

E. spissum Fern. (*E. vaginatum* subsp. *spissum* (Fern.) Hultén). Boreal North America and northeastern Asia.

CANADA. Newfoundland: Quirpon Island, 7 Aug. 1925, *Fernald & Long 27560* (GH); Québec: Pontiac Co., Cawood Twp., *Pinder-Moss s.n.* (NYS).

E. tenellum Nutt. Northeastern North America.

USA. New York: Franklin Co., Derrick, 31 July 1918, *Johnson 1517* (NYS).

E. vaginatum L. Boreal Eurasia and northwestern North America.

CZECHOSLOVAKIA. Trebusany, 10 July 1932, *Flora Cechoslovenica Exsiccata 361* (NYS).

AUSTRIA. Tyrol: Schwarzsee, 6 June 1975, *Fritze s.n.* (NYS).

E. virginicum L. Temperate and boreal eastern North America.

CANADA. Ontario: Dundas Co., near Elma, 9 Oct. 1935, *House 23364* (NYS).

USA. Maine: York Co., York, 25 Aug. 1896, *Bicknell 1012* (NYS); Rhode Island: Washington Co., Hopkinton, Ell Pond, 8 Sept. 1985, *Tucker 3175A* (NYS); South Carolina: Darlington Co., near Hartsville, 12 July 1920, *Norton s.n.* (NYS).

E. viridi-carinatum (Engelm.) Fern. Boreal North America.

CANADA. Québec: Anticosti Island, Rivière la Loutre, 5 Aug. 1926, *Marie-Victorin & Rolland-Germain 24502* (GH).

Scirpus cespitosus L. Circumboreal.

CANADA. Québec: Iles de la Madeleine, Ile-du-Hâvre-au-Ber, 15 July 1919, *Marie-Victorin & Rolland-Germain 9359* (NYS); Rivière George, 5 Aug. 1947, *Rousseau 818* (NYS).

USA. New York: Genesee Co., Bergen Swamp, 20 July 1938, *Muenschler 21237* (NYS); North Carolina: Mitchell Co., Roan Mtn., 16 July 1891, *Small & Heller 287* (NYS).

S. clementis M. E. Jones. California.

USA. California: Mono Co., Hall Area, 29 Aug. 1938, *Keck 5002* (GH).

S. clintonii Gray. Northeastern North America.

USA. New York: Warren Co., The Glen, 11 June 1980, *Yanuck & Platt s.n.* (NYS).

S. cyperinus (L.) Kunth. Temperate eastern North America.

USA. New York: Ontario Co., near Naples, 5 Oct. 1941, *Clausen 5414* (NYS).

S. hudsonianus (Michx.) Fern. (*Eriophorum alpinum* L.). Circumboreal.

CANADA. Newfoundland: Millertown, 19 July 1930, *Jansson s.n.* (GH); near Holyrood, "1928," *Ayre s.n.* (GH); Québec: Magdalen Islands, Grindstone, 17 July 1912, *Fernald et al. 6966* (GH); Saskatchewan: near Prince Albert, July 1896, *Macoun 16383* (GH).

USA. Maine: Aroostook Co., Crystal, 11 July 1946, *Ogden & Chamberlain 2616* (NYS); Massachusetts: Hampden Co., Wilbraham, 5 June 1928, *Clark & Seymour 641* (GH); Michigan: Alger Co., Shingleton, 14 Aug. 1934, *Hermann 6398* (GH); Vermont: Caledonia Co., Wheelock, 14 June 1982, *Boufford & Conant 22954* (A); Orange Co., Topsham, 7 July 1984, *Boufford & Wood 23707* (NEBC).

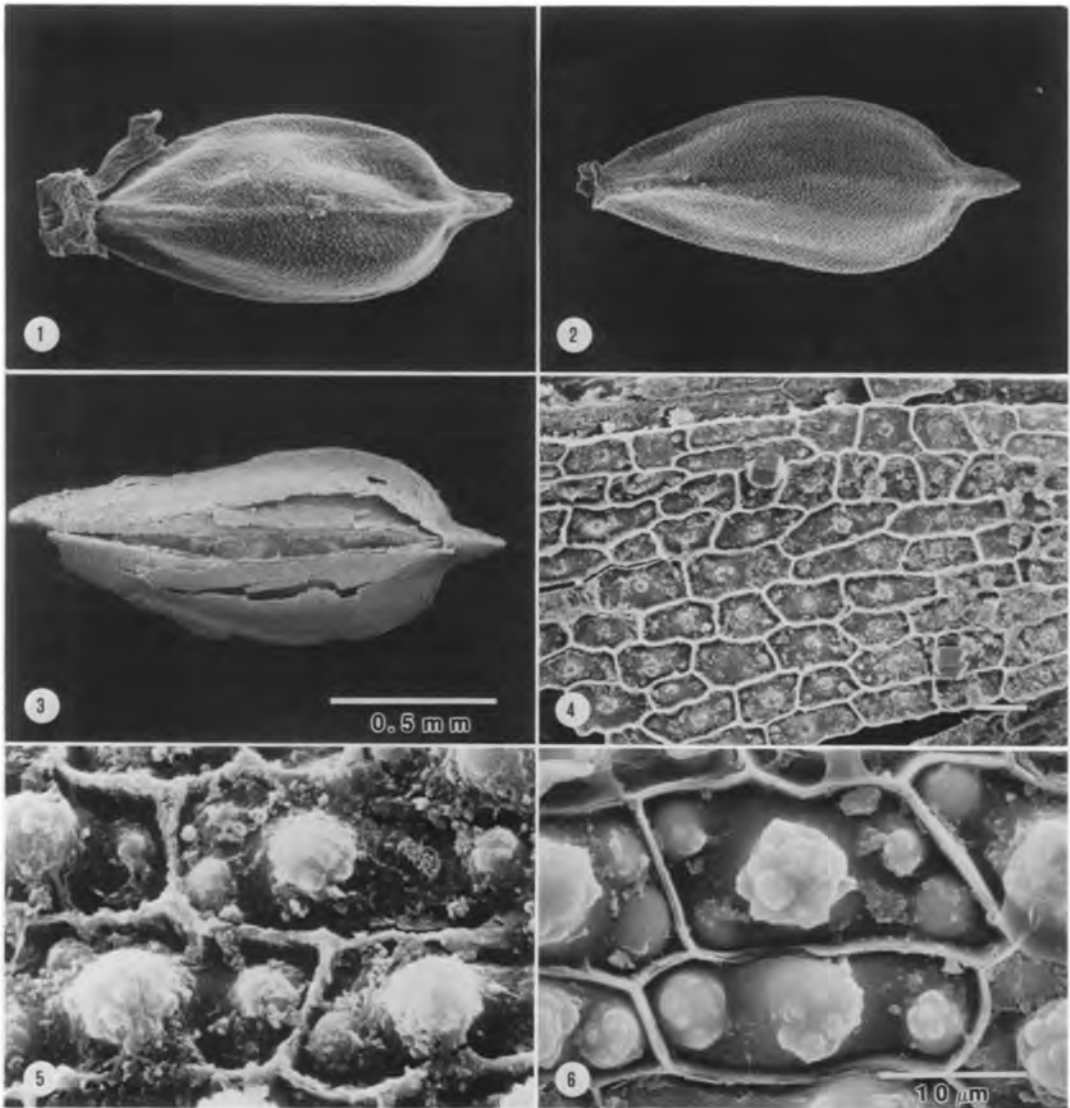
JAPAN. Hokkaido: Akkoshi in Kushiro, 4 July 1953, *Togasi 947* (A).

- SWEDEN. Rockelkjalan, 6 July 1901, *Ringselle s.n.* (GH).
- S. maximowiczii* C. B. Clarke. (*Eriophorum japonicum*). Eastern Asia.
- U.S.S.R. Magadanskaya Oblast, Tschukotka Peninsula, 18 Aug. 1967, *Petrovsky 5613* (A).
- JAPAN. Gumma Pref., Mount Shibutsu, 19 July 1946, *Suzuki 86* (GH).
- S. pumilus* Vahl. Boreal Eurasia.
- U.S.S.R. Siberia: Prov. Semipalatinsk, 21 May 1920, *Simonova & Batueva s.n.* (GH).
- S. rollandii* Fernald. Southeastern Canada.
- CANADA. Québec: Anticosti Island, 19 Aug. 1926, *Marie-Victorin & Rolland-Germain 25784* (GH).
- S. verecundus* Fern. Northeastern North America.
- USA. New York: Dutchess Co., Stissing Mountain, 26 May 1963, *Smith et al. 35476* (NYS).

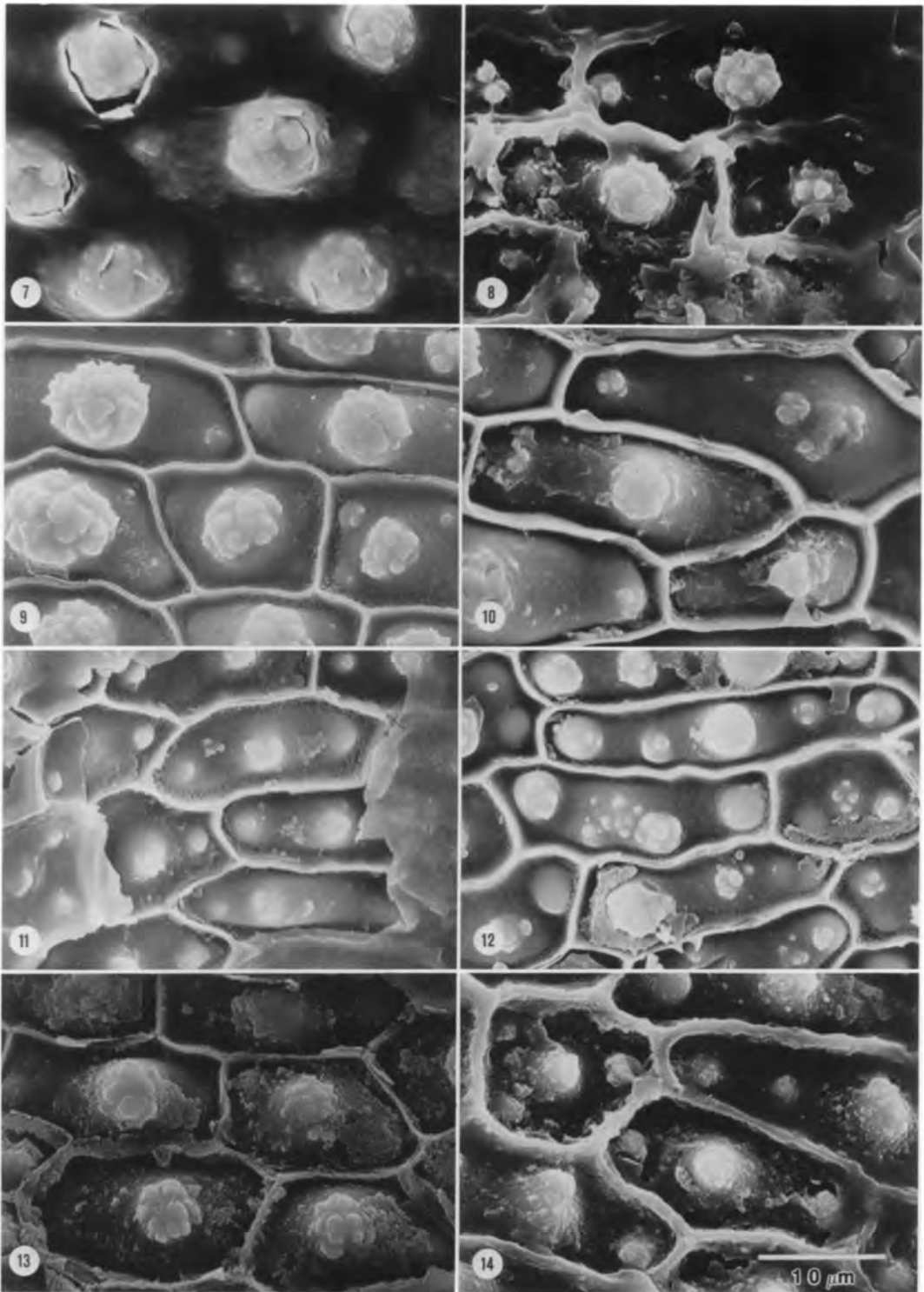
Appendix B

Key to species of *Eriophorum* sensu lato using achene characters as revealed by scanning electron microscopy.

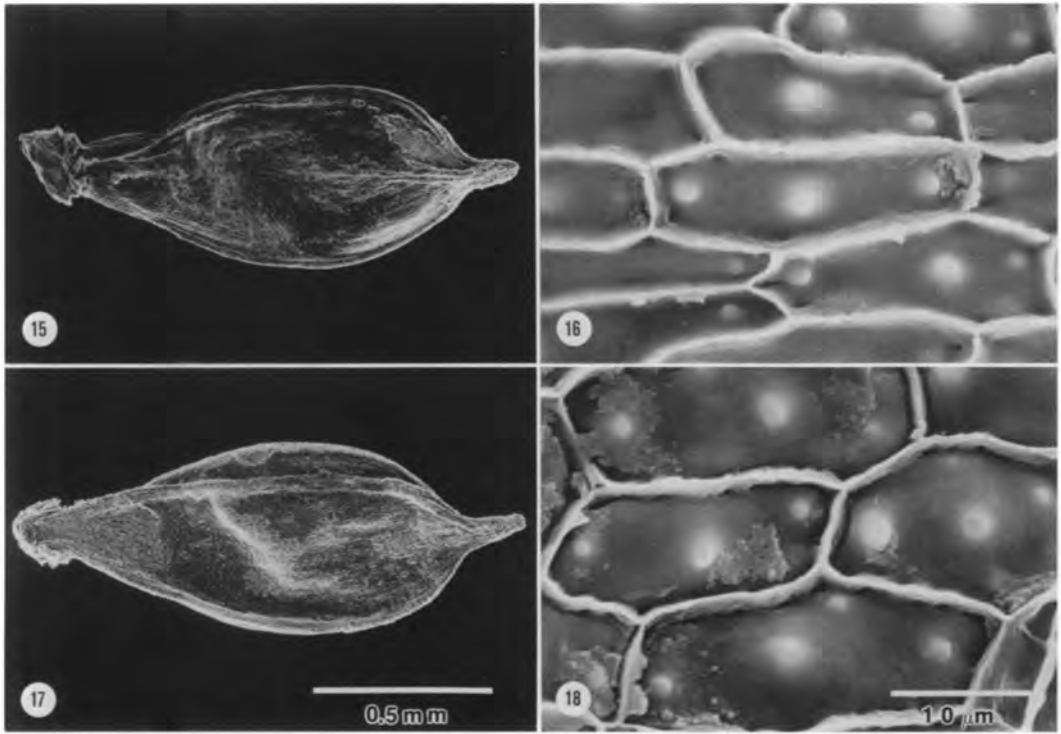
1. Style base persistent, beak-like, conspicuously longer than wide at low magnification
 2. Nodules present on central protuberance
 3. Anticlinal walls linear *E. alpinum*.
 3. Anticlinal walls undulate
 4. Anticlinal walls pitted *E. crinigerum*.
 4. Anticlinal walls without pits *E. microstachyum*.
 2. Nodules absent on central protuberance
 5. Satellites present
 6. Anticlinal walls thick (ca. 4 μ m) *E. chamissonis*.
 6. Anticlinal walls thin (ca. 1 μ m)
 7. Anticlinal walls linear *E. virginicum*.
 7. Anticlinal walls undulate *E. russeolum*.
 5. Satellites absent
 8. Platform roughened *E. viridi-carinatum*.
 8. Platform smooth
 9. Achene very narrowly ellipsoidal, not flattened *E. comosum*.
 9. Achene obovoid, flattened *E. scheuchzeri*.
1. Style base not persistent or small, inconspicuous at low magnification
 10. Satellites present or central protuberances 2 or more
 11. Platform roughened
 12. Anticlinal walls pitted *E. coreanum*.
 12. Anticlinal walls without pits
 13. Achene about 3 times longer than wide
 14. Satellites much smaller than the single central protuberance *E. opacum*.
 14. Satellites slightly smaller than the several central protuberances *E. angustifolium*.
 13. Achene about 2 times longer than wide
 15. Central protuberance about $\frac{1}{2}$ as wide as smallest dimension of epidermal cell *E. spissum*.
 15. Central protuberance about $\frac{1}{4}$ as wide as smallest dimension of epidermal cell *E. callitrix*.
 11. Platform smooth
 16. Anticlinal walls undulate, nodules arranged in a ring on central protuberance *E. gracile*.
 16. Anticlinal walls linear, nodules few, scattered on central protuberance *E. tenellum*.
 10. Satellites absent
 17. Anticlinal walls undulate and pitted; nodules present *E. maximowiczii*.
 17. Anticlinal walls straight and smooth; nodules absent.
 18. Platform smooth *E. latifolium*.
 18. Platform rough *E. vaginatum*.



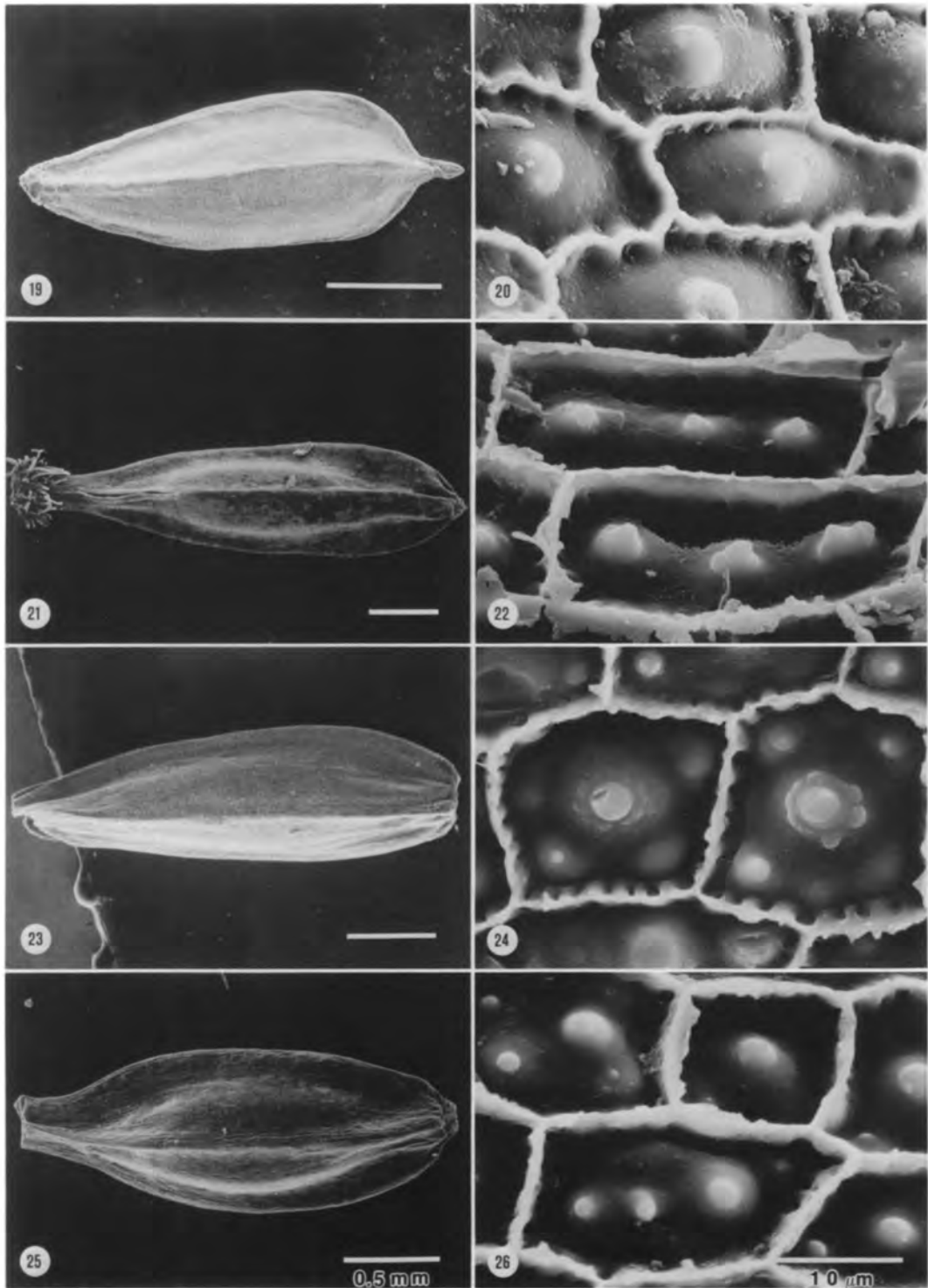
Figs. 1-6. Achenes of *Scirpus hudsonianus* (*Eriophorum alpinum*). — 1. from Quebec (sonicated). — 2. from Maine (sonicated). — 3. late-Pleistocene fossil achene from Massachusetts. — 4, 5. achene epidermis of fossil, low and high magnifications; 6. epidermis of achene from Newfoundland. (Scale bars: 1-3 = 0.5 mm; 4-6 = 10 μ m.)



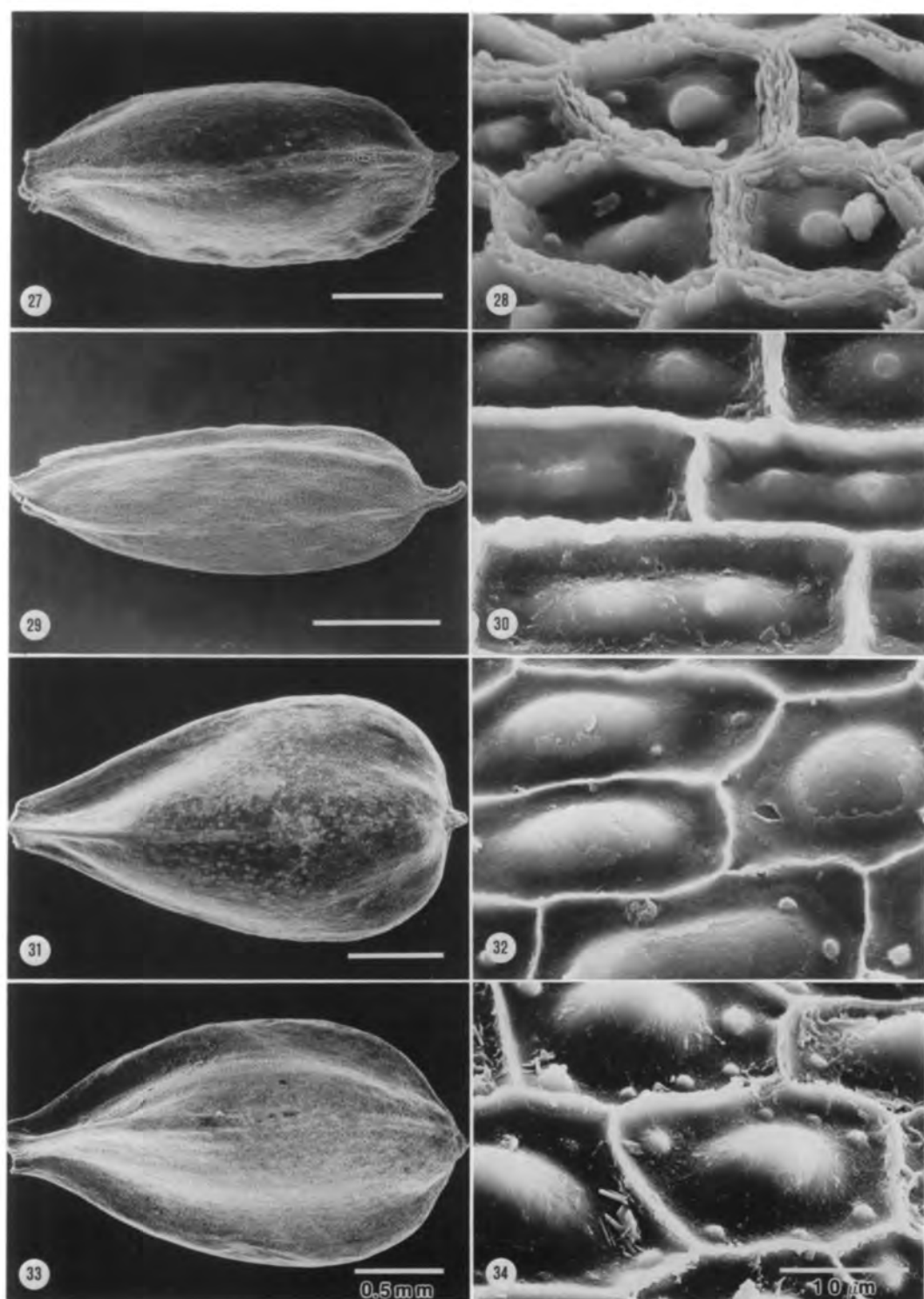
Figs. 7-14. Achenes of *Scirpus hudsonianus* (*Eriophorum alpinum*) (cont.). — 7. from Massachusetts (untreated). — 8. from Vermont, *Boufford & Wood 23707* (acetolyzed). — 9. from Maine (sonicated). — 10. from Québec (sonicated). — 11. from Michigan (sonicated). — 12. from Saskatchewan (sonicated). — 13. from Japan (sonicated). — 14. from Sweden (sonicated). (Scale bar: = 10 μm .)



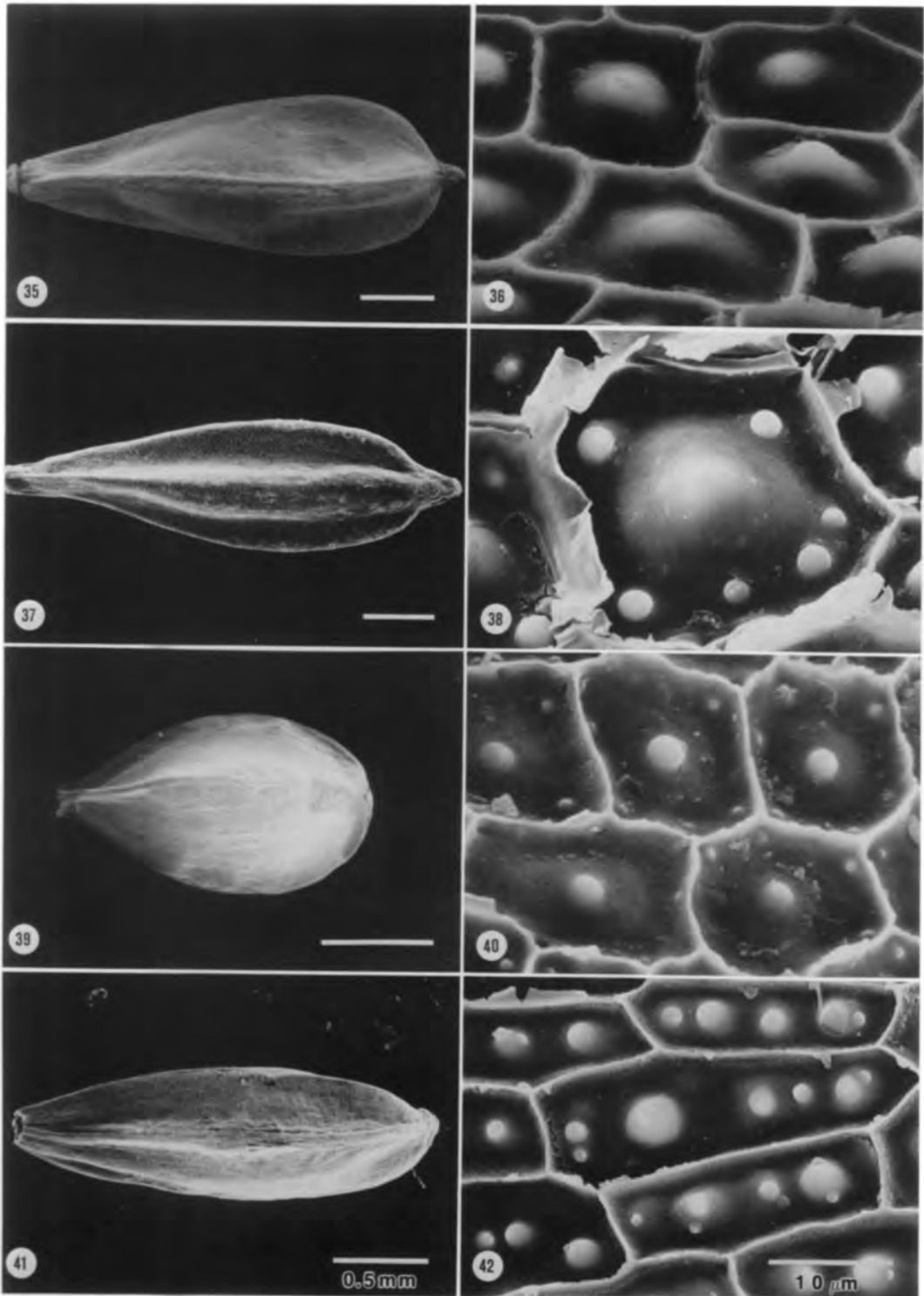
Figs. 15–18. Immature achenes of *Scirpus hudsonianus* (*Eriophorum alpinum*). — 15, 16. from Vermont, Boufford & Conant 22954 (sonicated). — 17, 18. from Japan (sonicated). (Scale bars: 15, 17 = 0.5 mm; 16, 18 = 10 μm .)



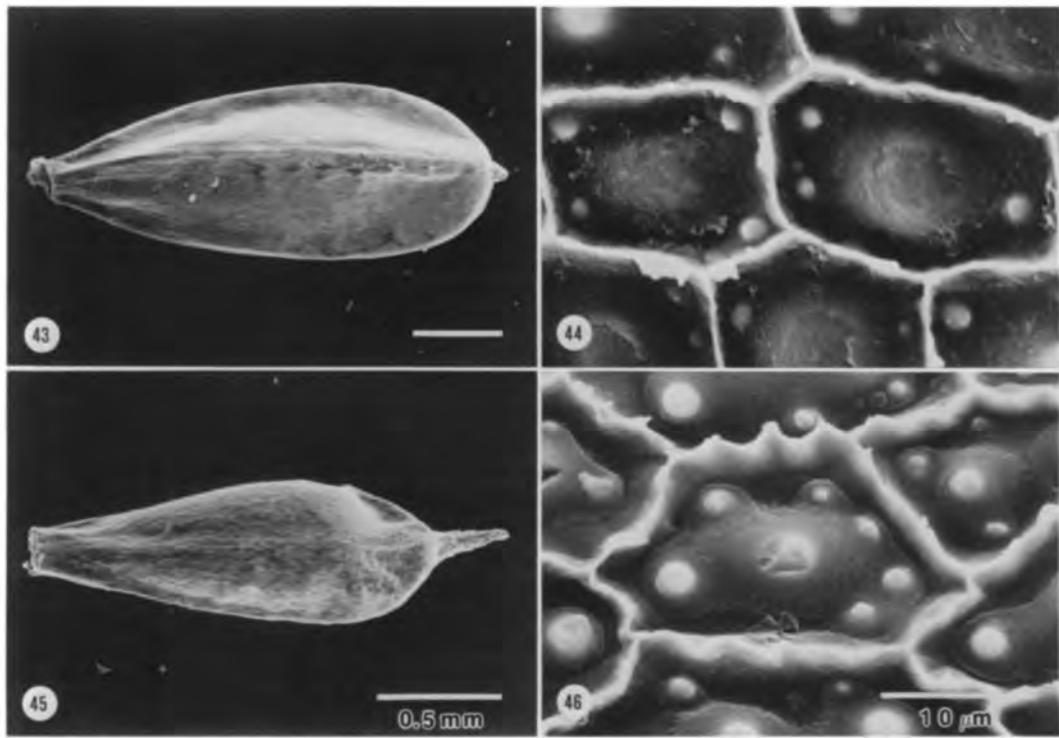
Figs. 19–26. Achenes of species of *Eriophorum*. — 19, 20. *E. crinigerum* from California (sonicated). — 21, 22. *E. coreanum* from Japan (sonicated). — 23, 24. *E. gracile* from New York (sonicated). — 25, 26. *E. tenellum* from New York (sonicated). (Scale bars: 19, 21, 23, 25 = 0.5 mm; 20, 22, 24, 26 = 10 μ m.)



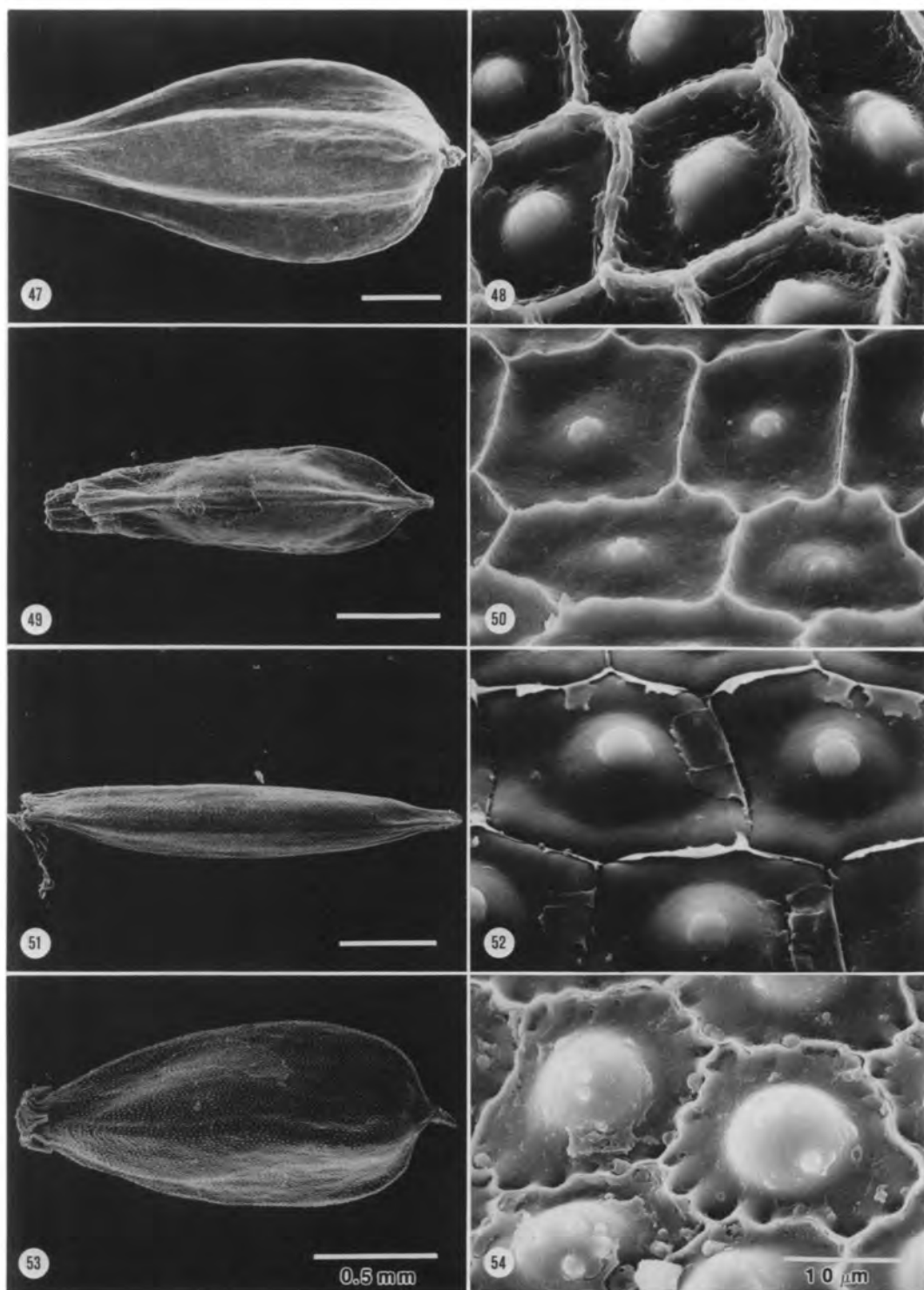
Figs. 27–34. Achenes of species of *Eriophorum* (cont.). — 27, 28. *E. chamissonis* from British Columbia (sonicated). — 29, 30. *E. scheuchzeri* from Greenland (acetolyzed and sonicated). — 31, 32. *E. spissum* from Québec (sonicated). — 33, 34. *E. vaginatum* from Austria (acetolyzed and sonicated). (Scale bars: 27, 29, 31, 33 = 0.5 mm; 28, 30, 32, 34 = 10 μ m.)



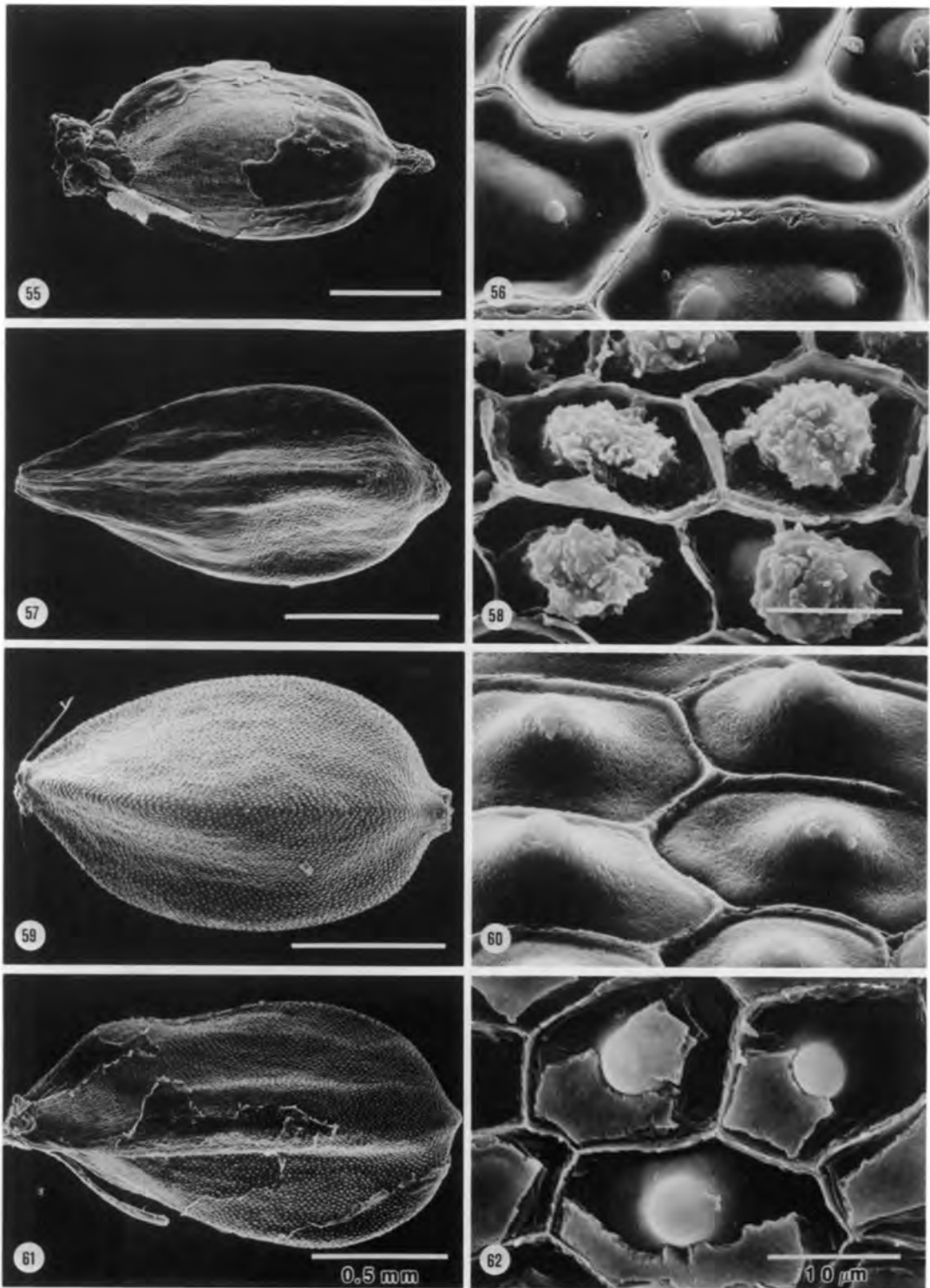
Figs. 35–42. Achenes of species of *Eriophorum* (cont.). — 35, 36. *E. viridi-carinatum* from Québec (sonicated). — 37, 38. *E. virginicum* from South Carolina (sonicated). — 39, 40. *E. callitrix* from Newfoundland (sonicated). — 41, 42. *E. angustifolium* from Northwest Territories, Canada (sonicated). (Scale bars: 35, 37, 39, 41 = 0.5 mm; 36, 38, 40, 42 = 10 μ m.)



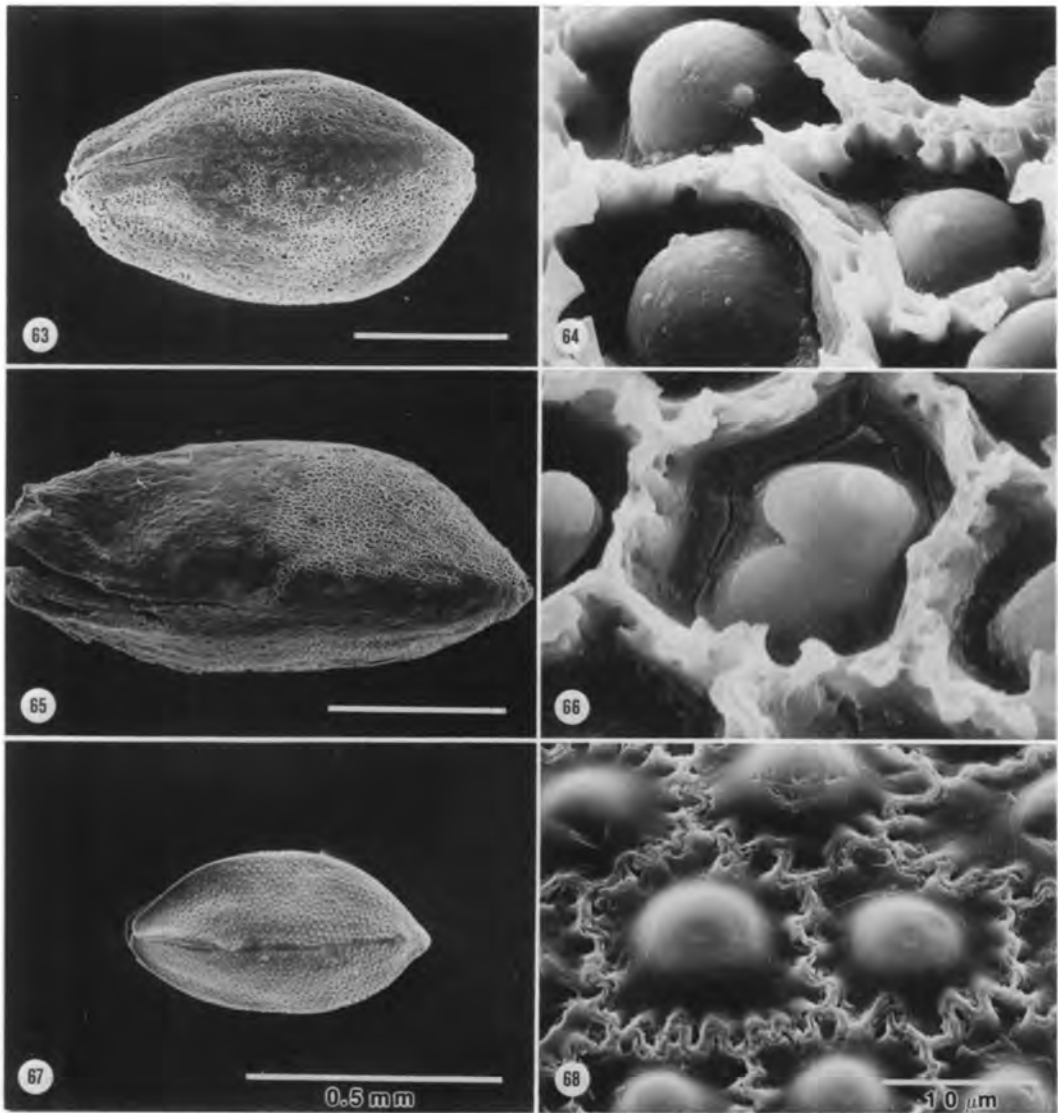
Figs. 43–46. Achenes of species of *Eriophorum* (cont.). — 43, 44. *E. opacum* from Newfoundland (sonicated). — 45, 46. *E. russeolum* from Manitoba (sonicated). (Scale bars: 43, 45 = 0.5 mm; 44, 46 = 10 μm.)



Figs. 47–54. Achenes of species of *Eriophorum* (concl.) and *Scirpus maximowiczii*. — 47, 48. *E. latifolium* from Czechoslovakia (acetolyzed and sonicated). — 49, 50. *E. microstachyum* from India (sonicated). — 51, 52. *E. comosum* from China (sonicated). — 53, 54. *S. maximowiczii* from Japan (sonicated). (Scale bars: 47, 49, 51, 53 = 0.5 mm; 48, 50, 52, 54 = 10 μ m.)



Figs. 55–62. Achenes of species of *Scirpus* sect. *Baeothryon*. — 55, 56. *S. cespitosus* from Québec, *Rousseau 818* (sonicated). — 57, 58. *S. clementis* from California (sonicated). — 59, 60. *S. clintonii* from New York (sonicated). — 61, 62. *S. verecundus* from New York (sonicated). (Scale bars: 55, 57, 59, 61 = 0.5 mm; 56, 58, 60, 62 = 10 μ m.)



Figs. 63–68. Achenes of species of *Scirpus* sect. *Baeothryon* (concl.) and *S. cyperinus* (sect. *Trichophorum*). — 63, 64. *S. pumilus* from U.S.S.R. (acetolyzed and sonicated). — 65, 66. *S. rollandii* from Québec (acetolyzed and sonicated). — 67, 68. of *S. cyperinus* from New York (sonicated). (Scale bars: 63, 65, 67 = 0.5 mm; 64, 66, 68 = 10 μ m.)