

A CONTRIBUTION TO THE TAXONOMY OF
BOLBOSCHOENUS (CYPERACEAE),
WITH PARTICULAR REFERENCE TO
FRUIT MORPHOLOGY
AND THE AFRICAN SPECIES

Volume 2
FIGURES & TABLES

Jane Beatrice Mary Browning

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Note 2. Type specimens are indicated by the use of bold typeface and the inclusion of author names.

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Figure 1.

Bolboschoenus maritimus (Entity 1), Lubke 93 (NU).

Scanning electron micrographs of fruit.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section;

D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 50 μm .

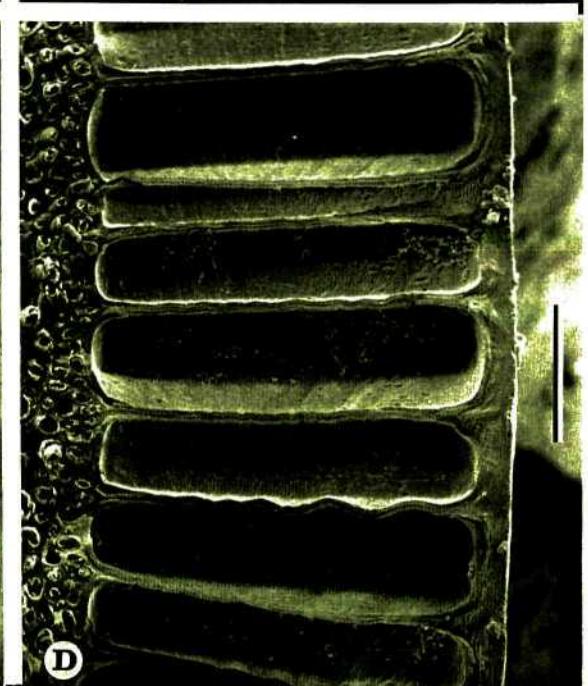
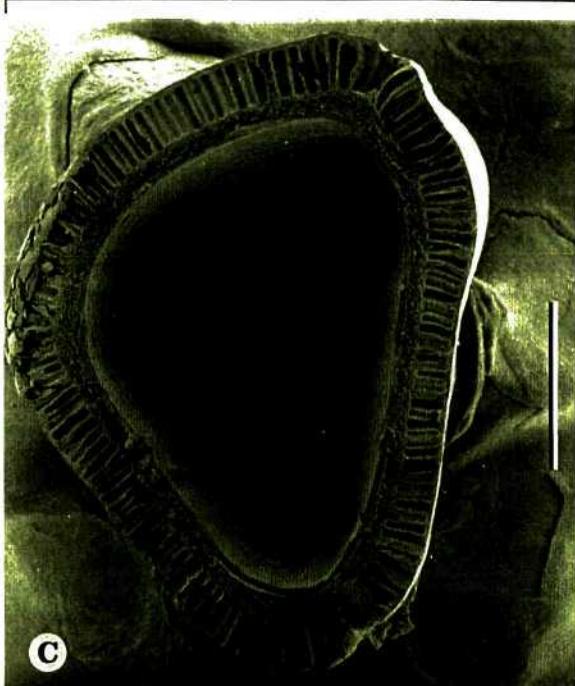
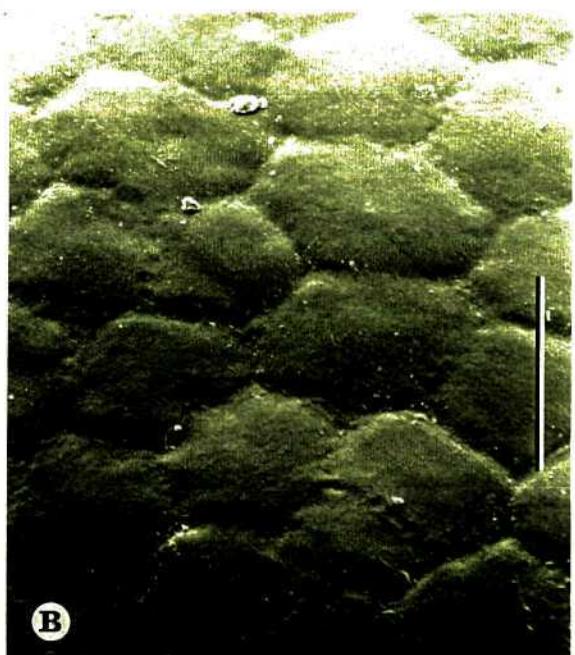
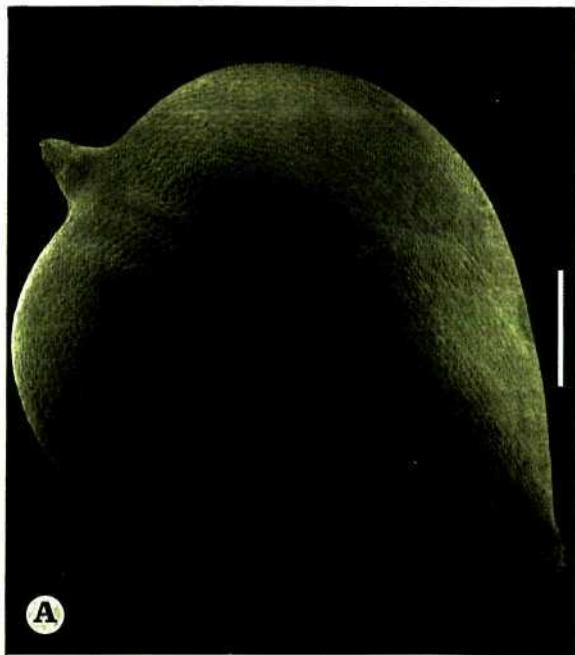


Figure 2.

Bolboschoenus maritimus (Entity 2), *de Beer & Yalala 4* (NU).

Scanning electron micrographs of fruits.

A, nut in outline with abaxial surface uppermost, perianth bristles persistent; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 50 μm .

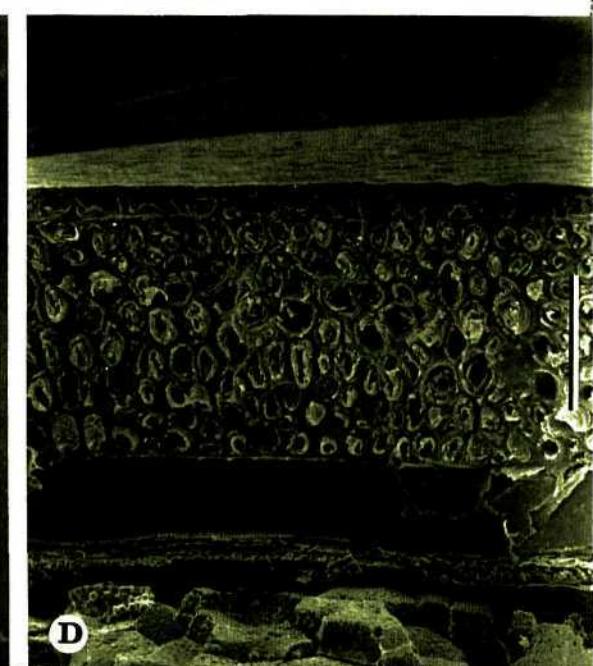
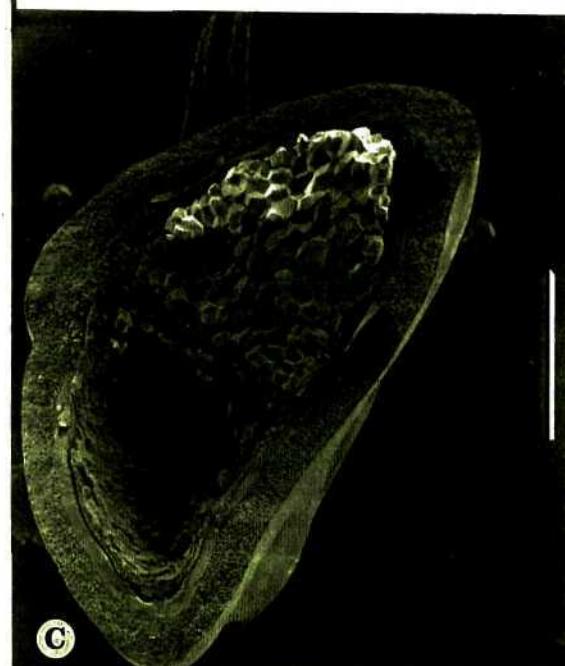
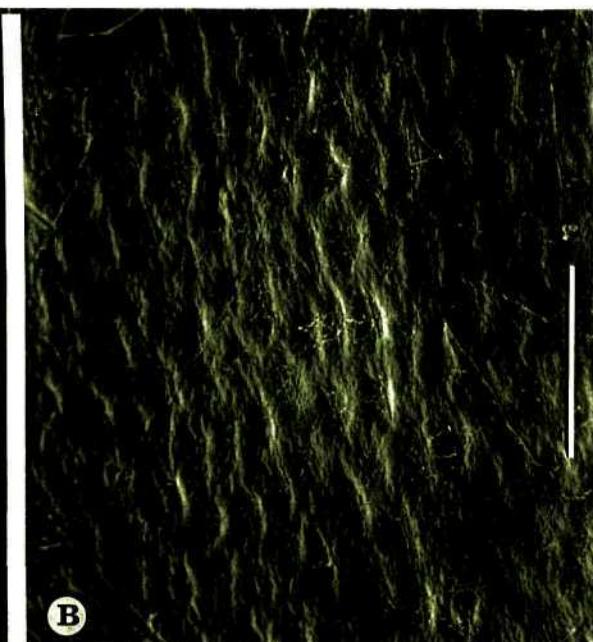
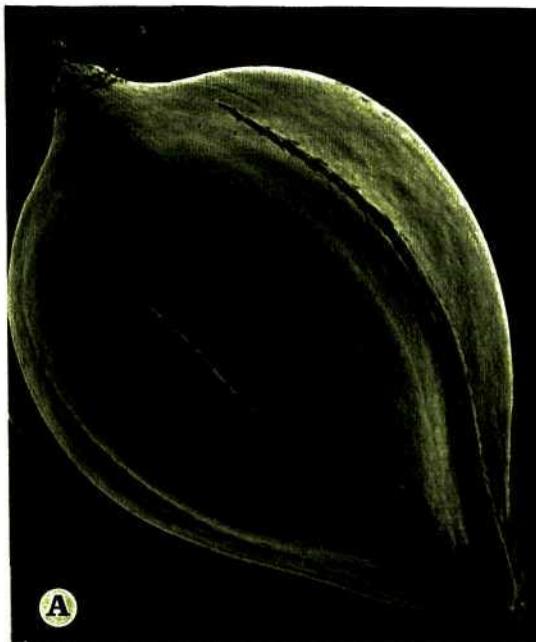


Figure 3.

Bolboschoenus nobilis, Giess 9564 (WIND).

Scanning electron micrographs of fruits.

A, nut in outline; B, surface topography; C, exocarp with outer periclinal walls peeled away; D, pericarp in transverse section. Scale bars: A = 500 μm ; B, C, D = 50 μm .

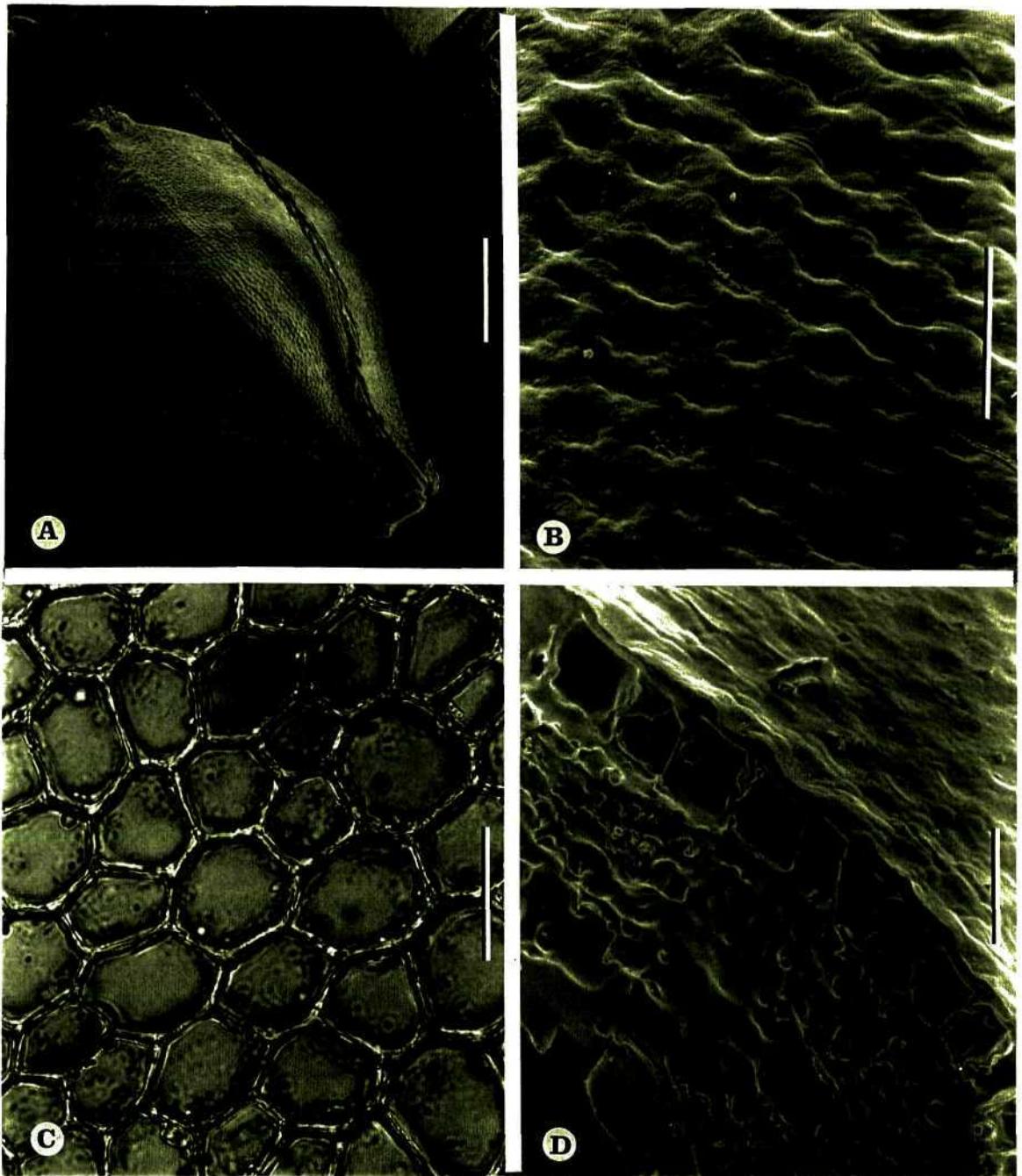


Figure 4.

Bolboschoenus nobilis, Story 5873 (PRE).

Scanning electron micrographs of pericarp.

A, surface topography; B. after removal of outer periclinal walls of exocarp cells (note silica bodies). Scale bars: A, B = 50 μm .

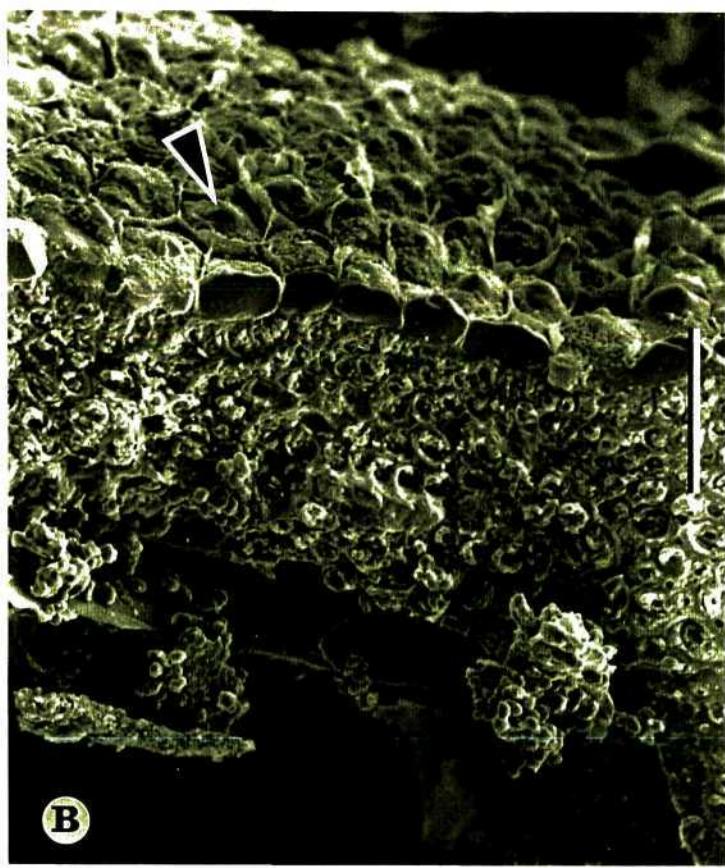
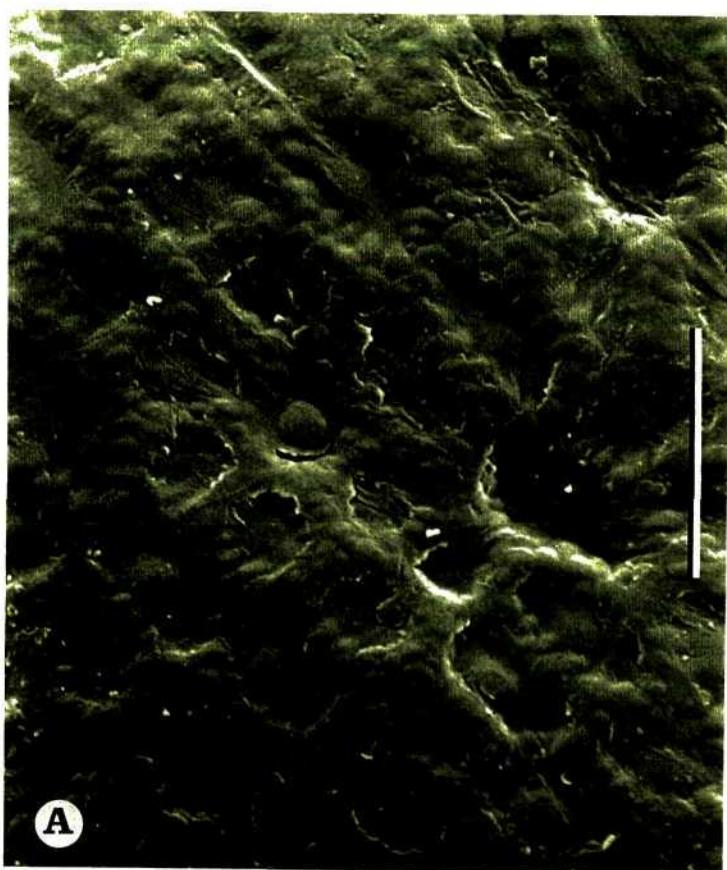


Figure 5.

Diagrams of embryos of *Bolboschoenus maritimus*: Entity 1 (A, A1) [Lubke 93 (NH)]; Entity 2 (C, C1) [Faure H638 (PRE)]; *B. nobilis* (B, B1) [Giess 14698 (WIND)]. A--C, median longitudinal view; A1--C1, surface of cotyledon from above. x = coleoptile lip. Scale bar: 100 μm .

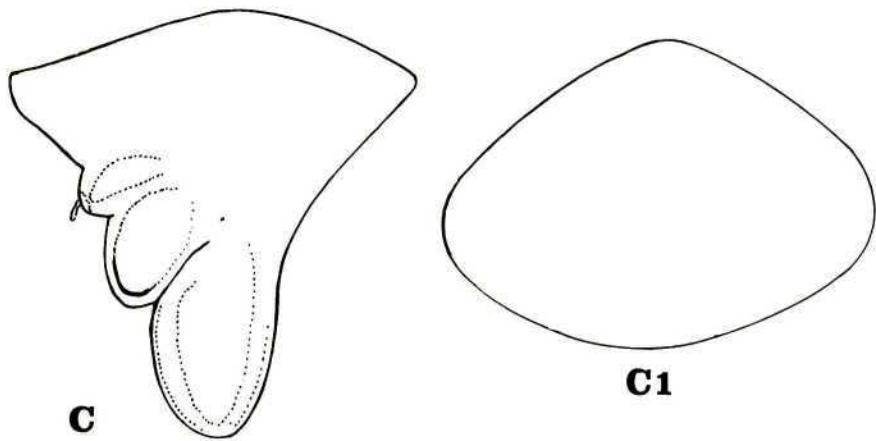
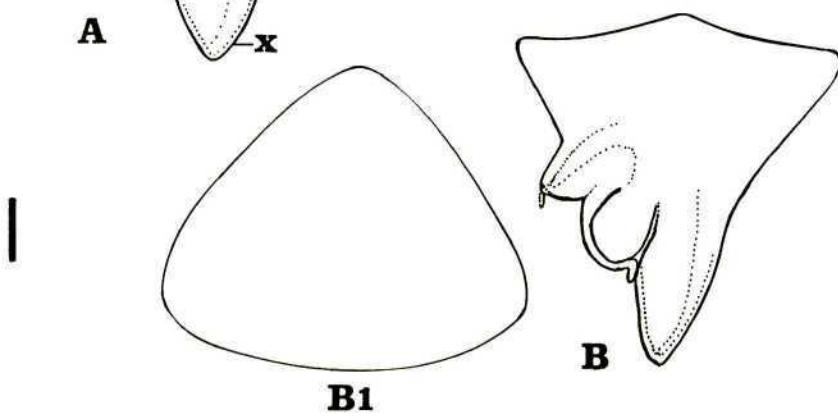
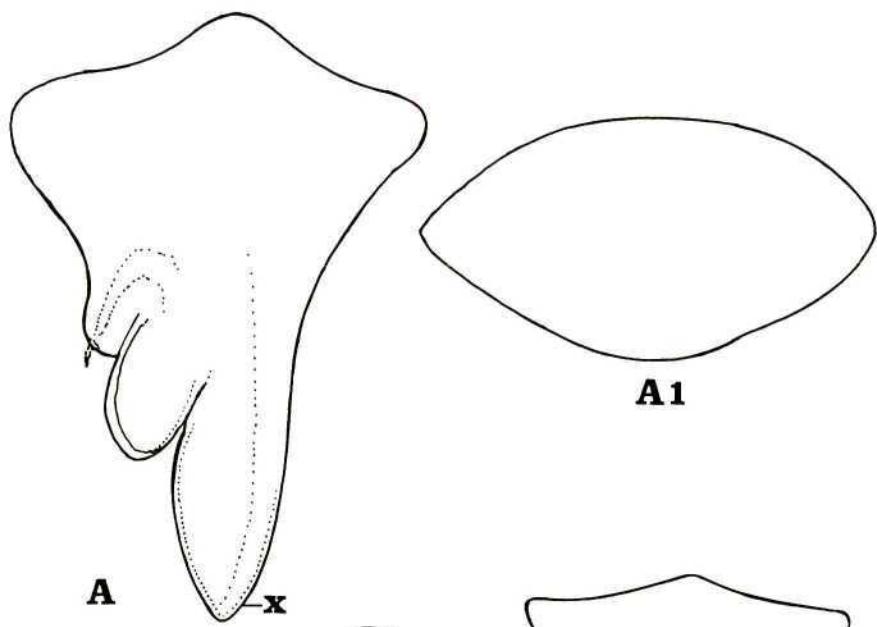


Figure 6.

Map of Verlorenvlei showing sampling and collecting sites.

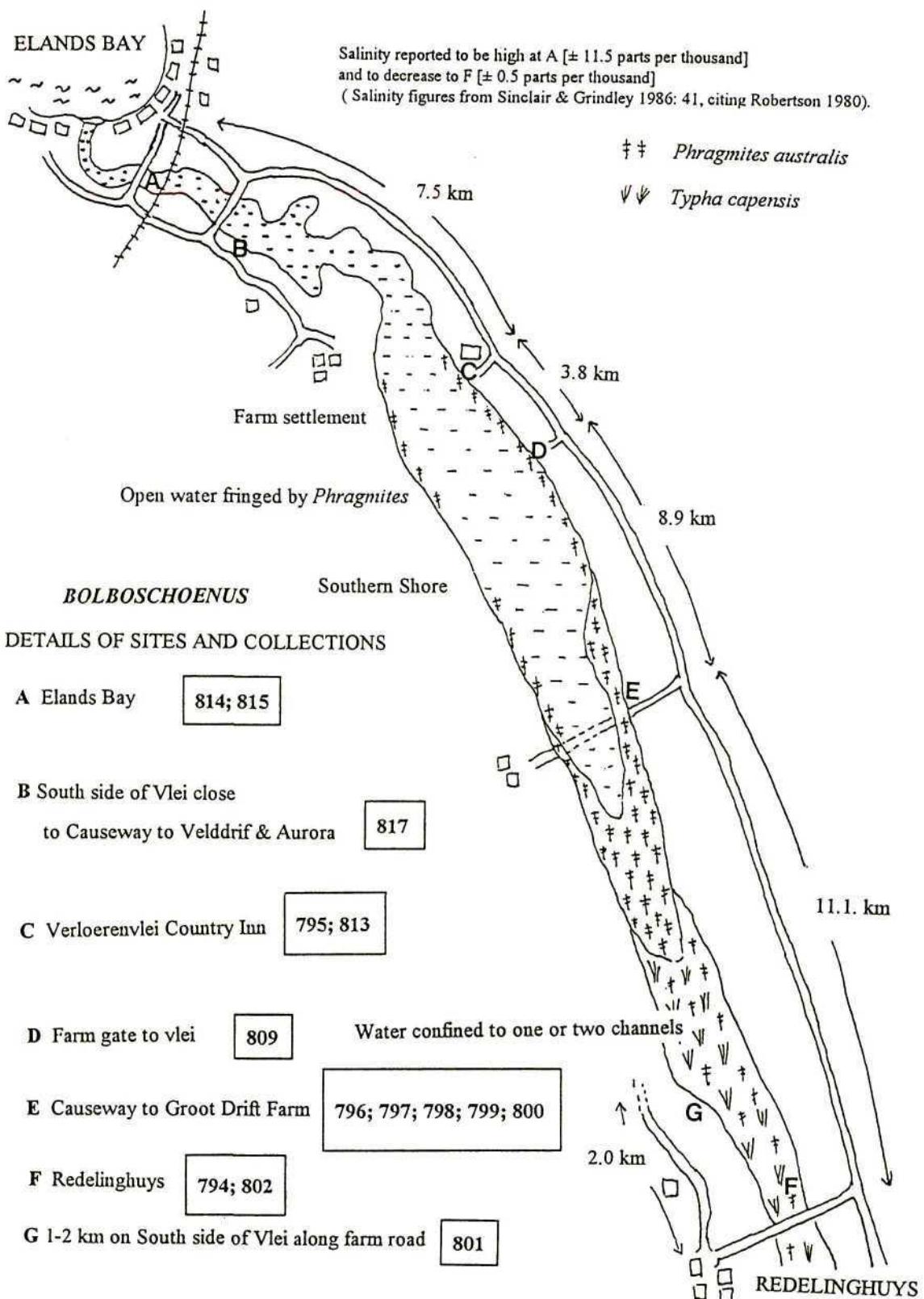


Figure 7.

Verlorenvlei: coastal site with *Bolboschoenus maritimus s.l.* in foreground on wet sand.

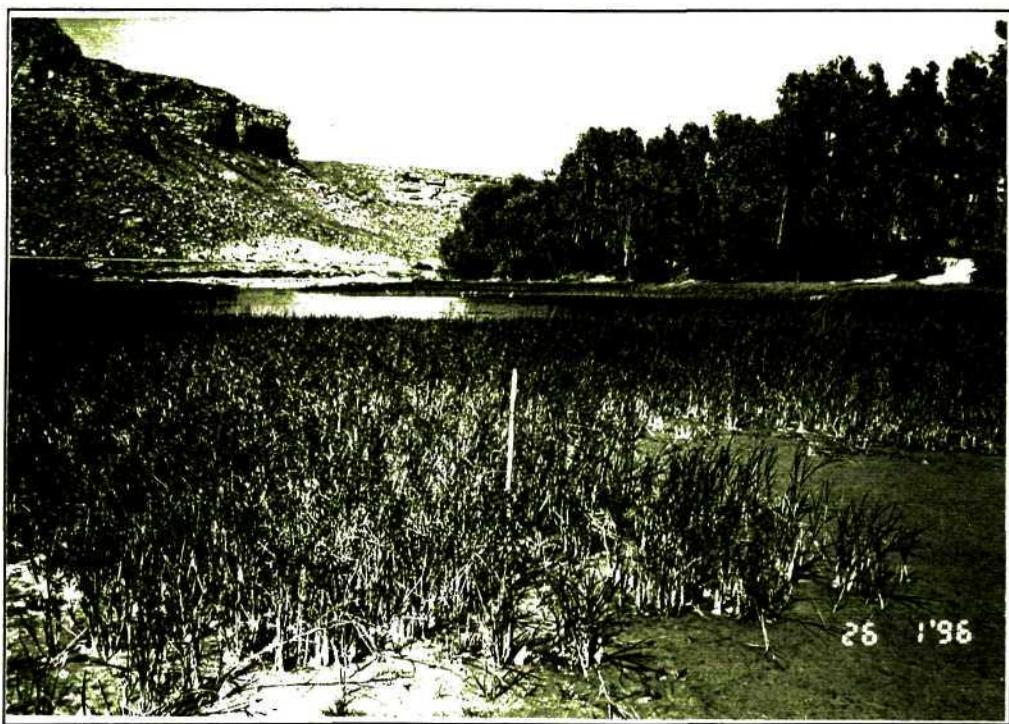


Figure 8.

Verlorenvlei: inland site with *Bolboschoenus maritimus s.l.* protected from predation by a fence.

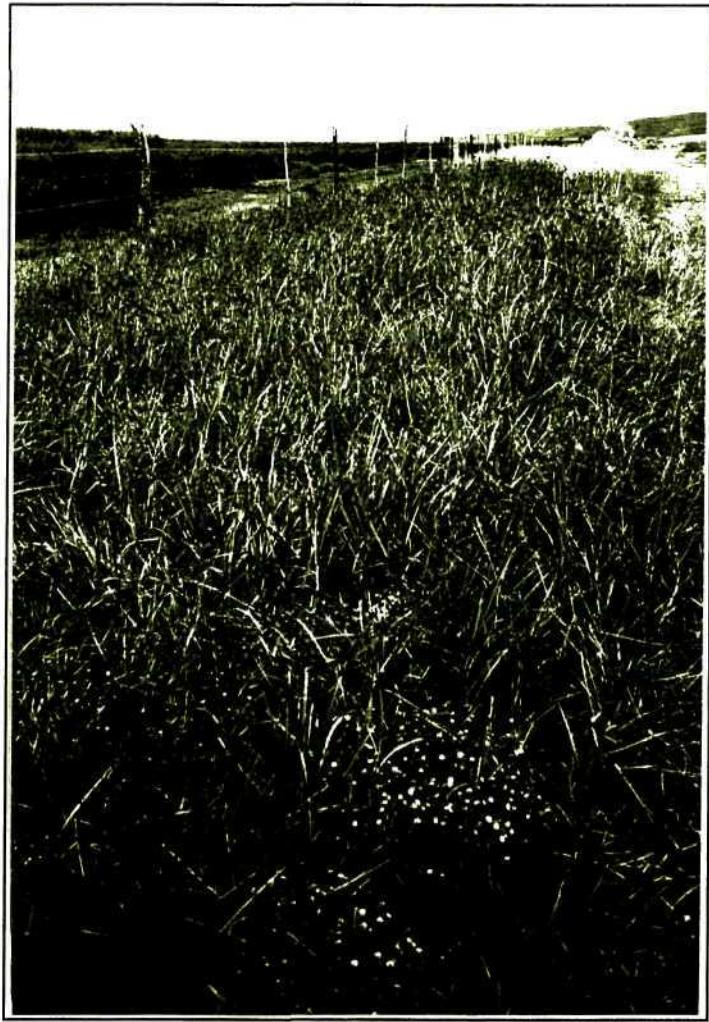


Figure 9.

Bolboschoenus maritimus s.l.: spikelet silhouettes. A--C, coastal inflorescences; D--I, inland inflorescences. Scale bar = 10 mm.

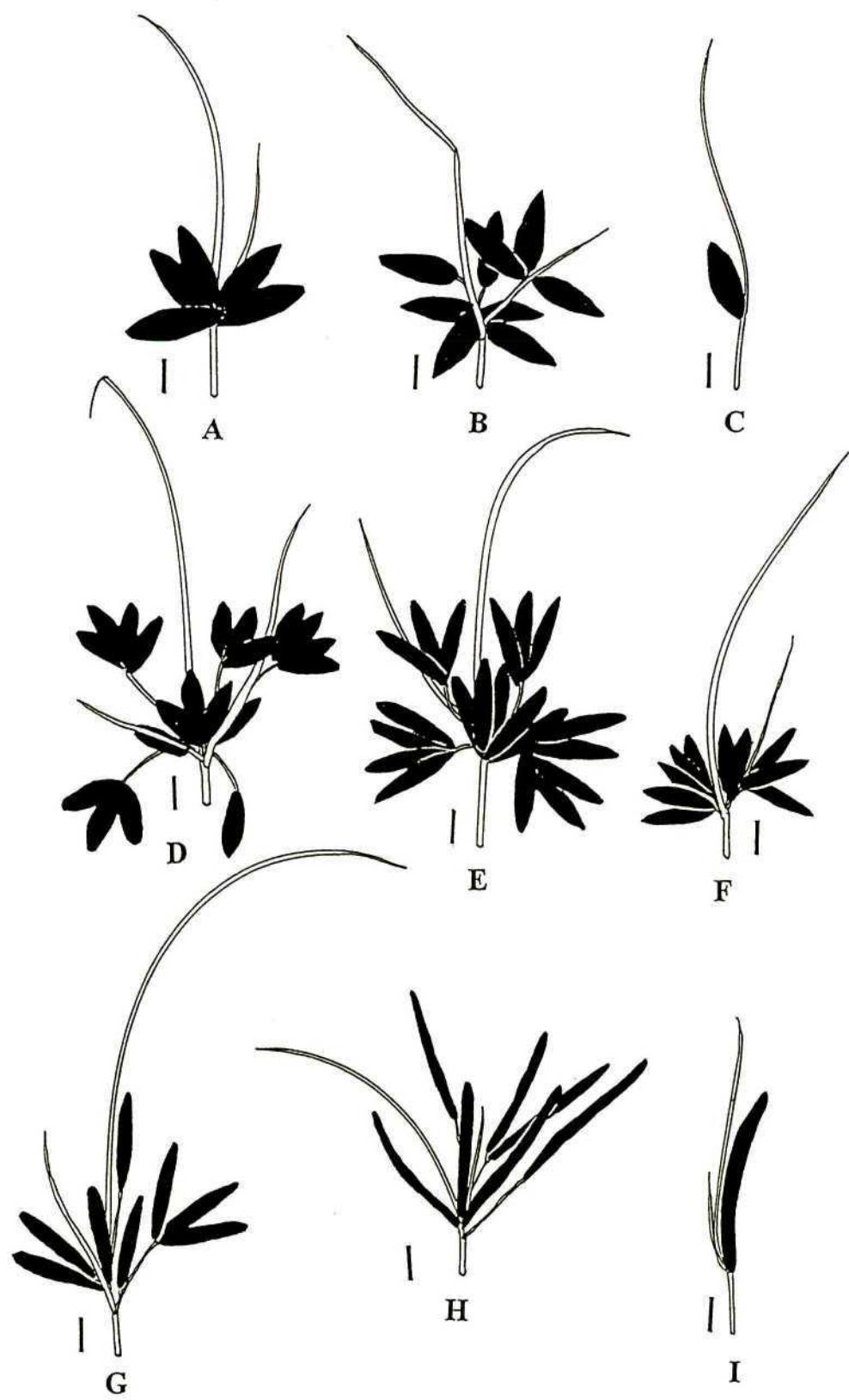
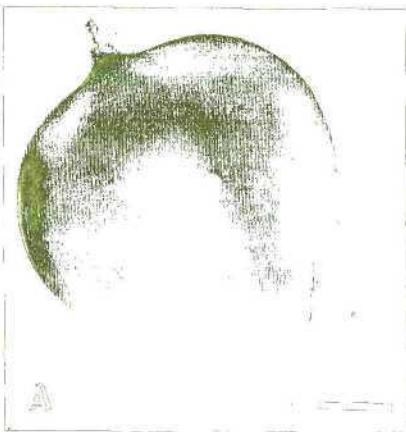


Figure 10.

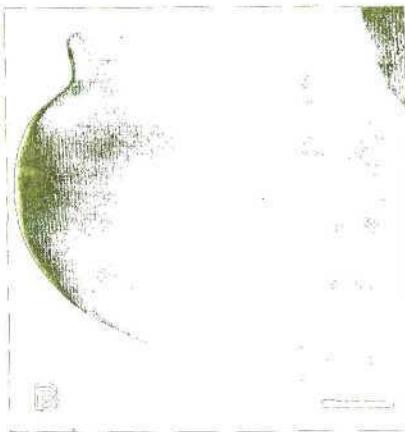
Bolboschoenus maritimus s.l.: coastal, site A, Browning 814.

Scanning electron micrographs of fruits.

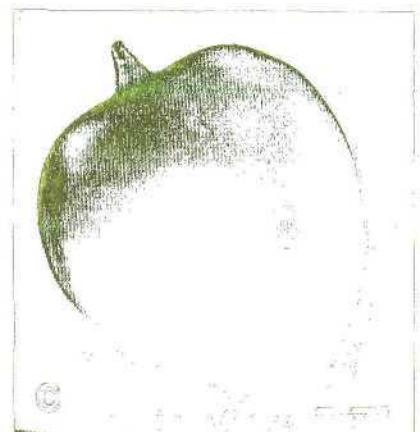
A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).



A



B



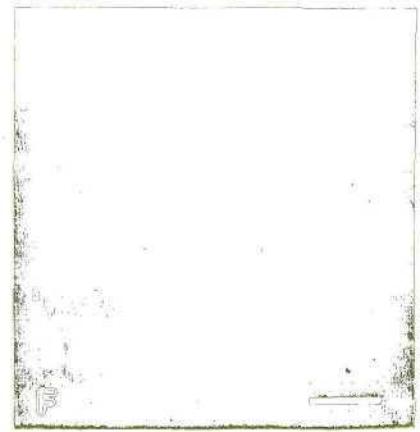
C



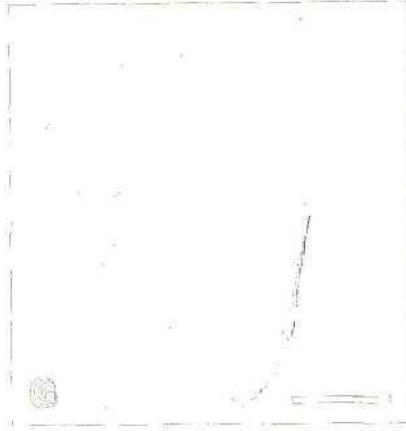
D



E



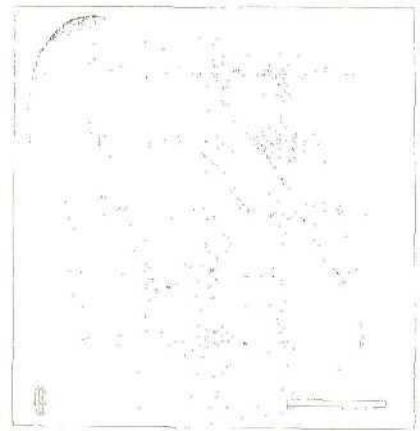
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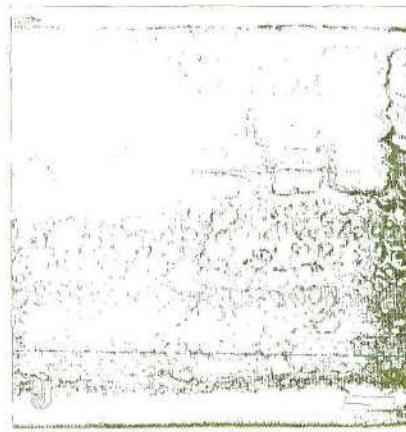
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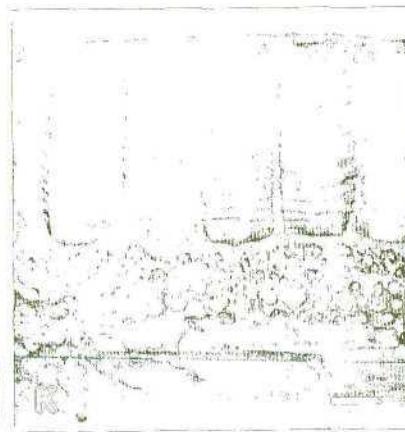
H



I



J



K

Figure 11.

Bolboschoenus maritimus s.l.: coastal, site A, *Browning 815*.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

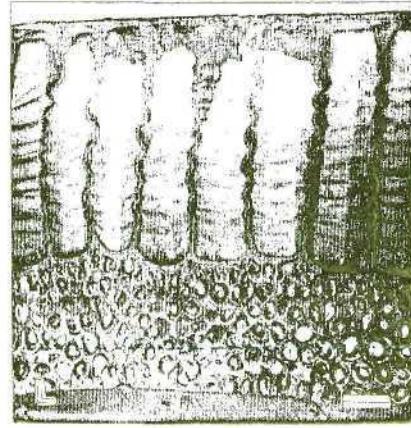
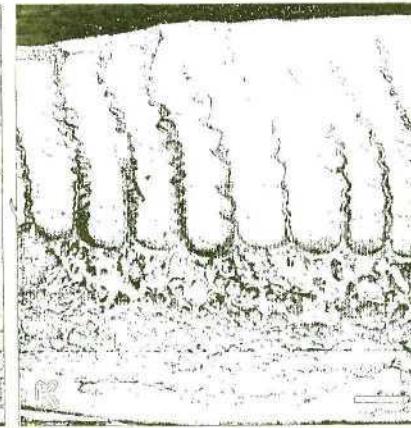
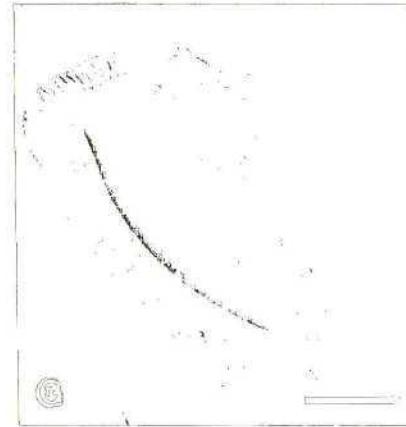
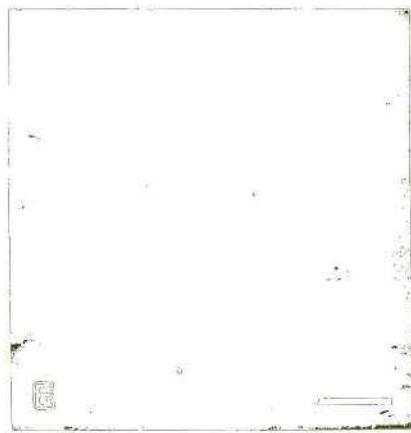
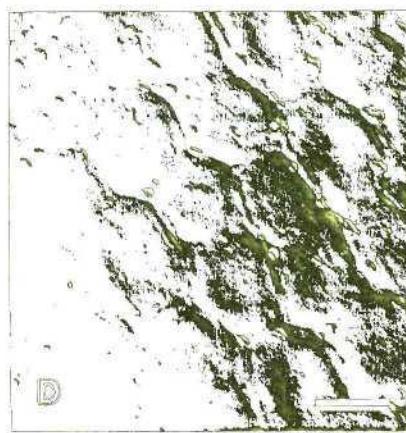
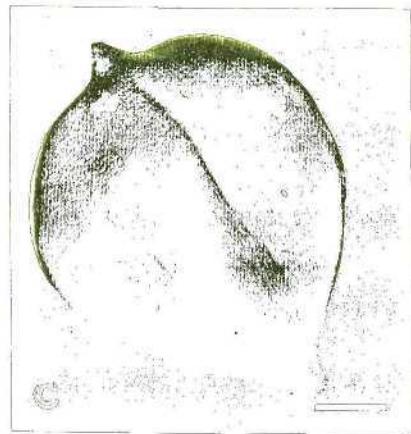
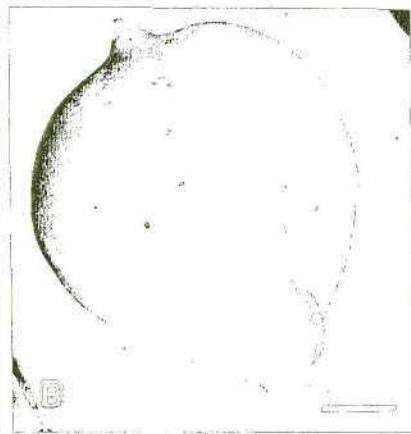
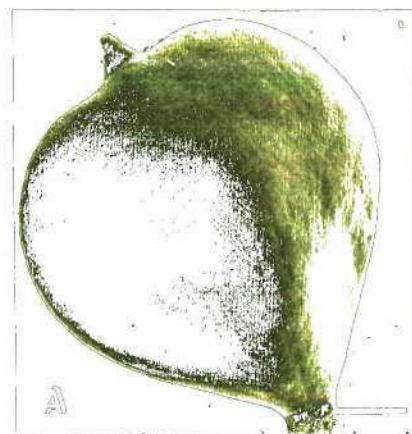


Figure 12.

Bolboschoenus maritimus s.l.: coastal, site B, Browning 817.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

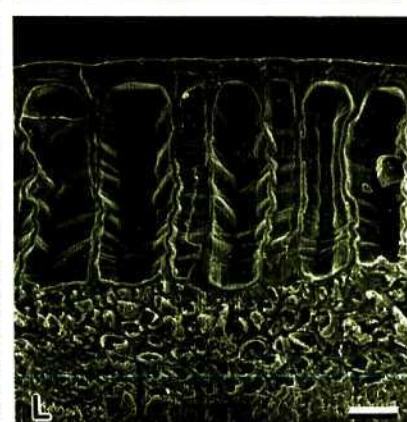
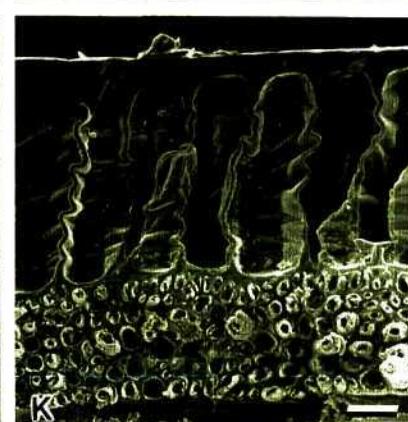
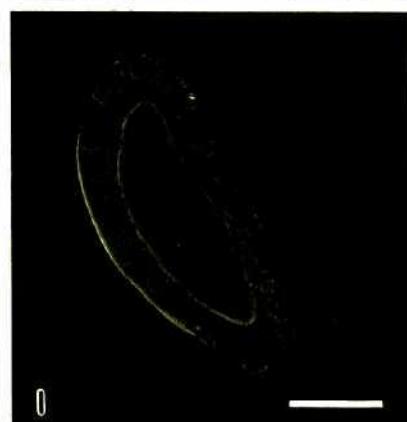
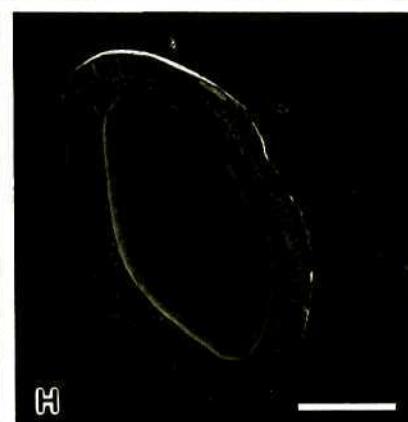
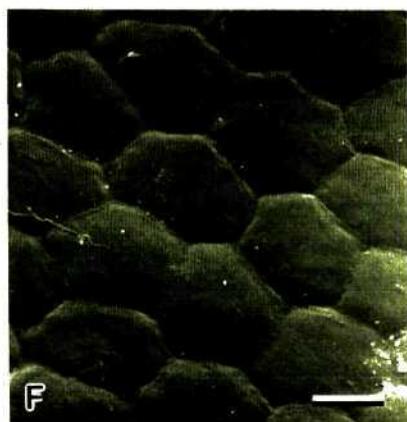
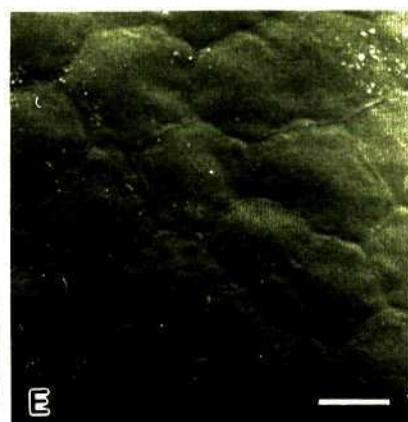
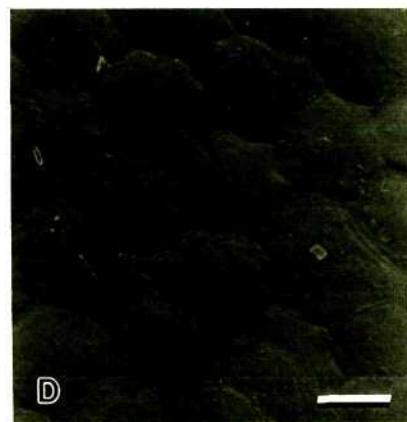
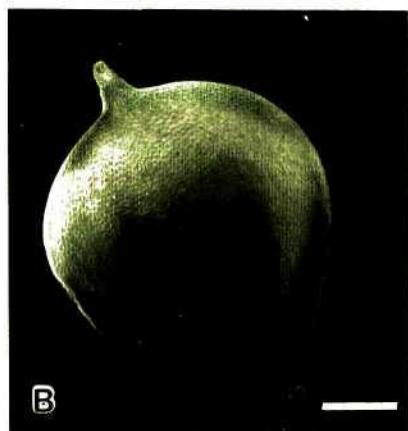
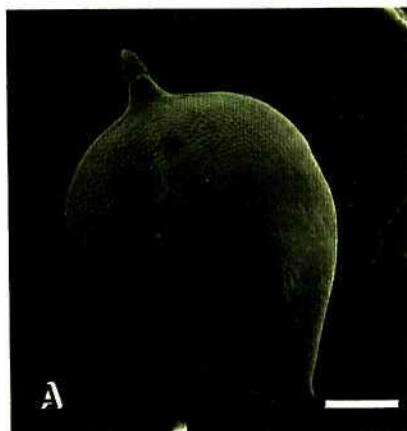


Figure 13.

Bolboschoenus maritimus s.l.: coastal, site C, *Browning* 795.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

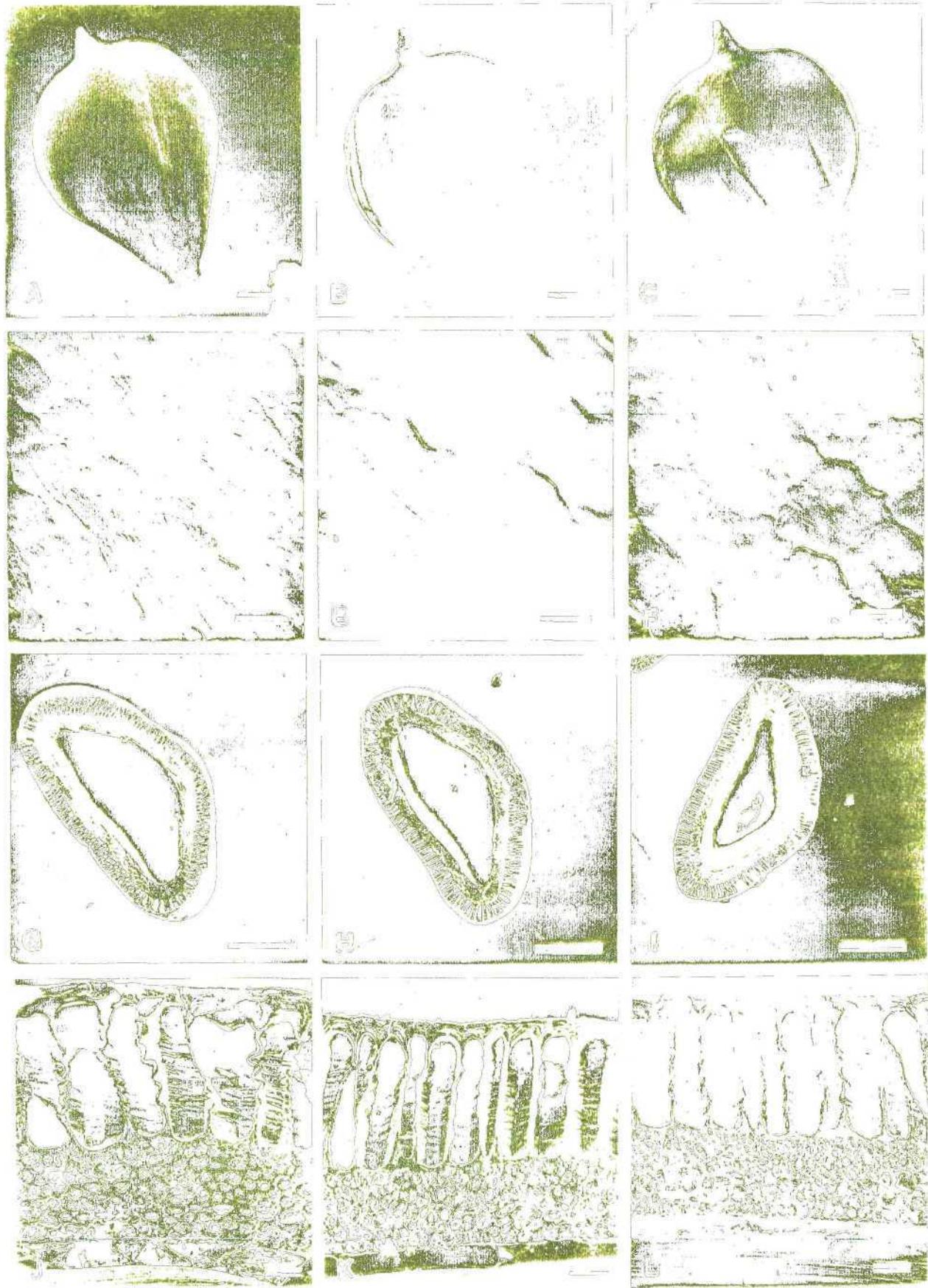


Figure 14.

Bolboschoenus maritimus s.l.: inland, site D, *Browning 809*.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

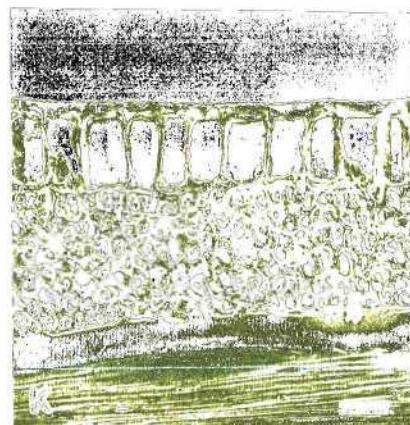
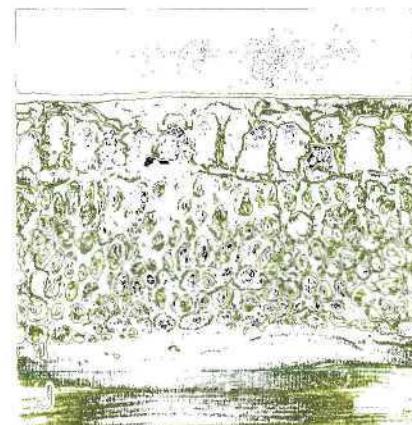
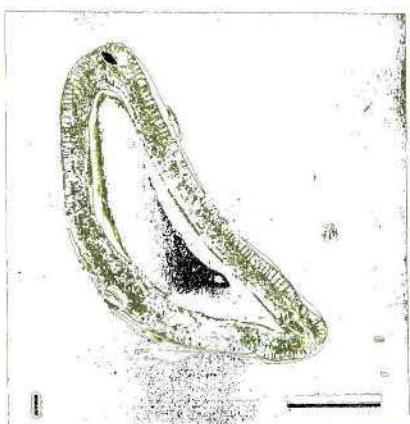
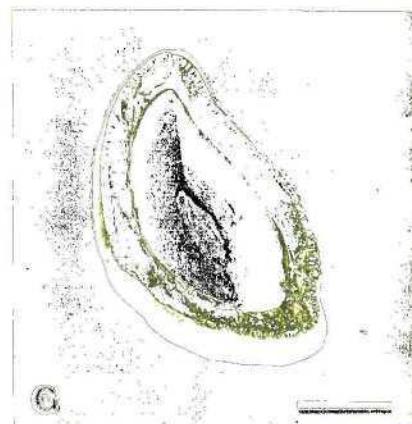
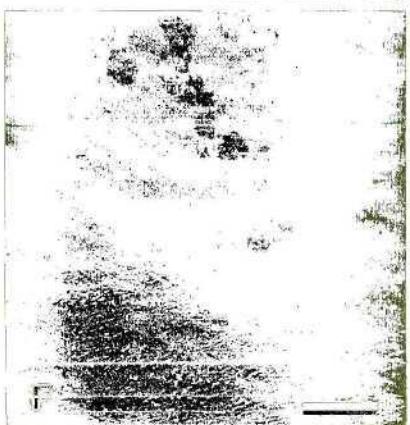
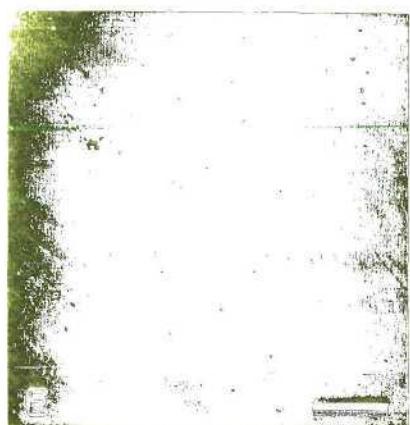
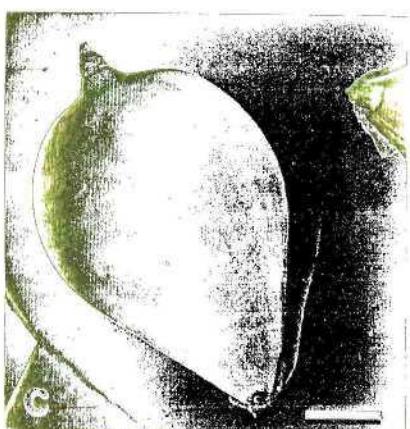
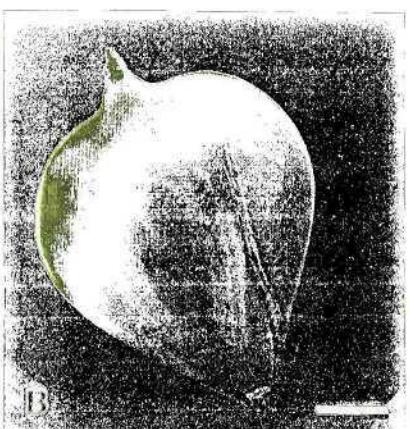
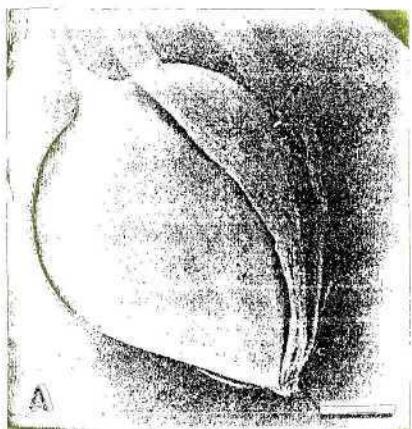


Figure 15.

Bolboschoenus maritimus s.l.: inland, site E, *Browning* 796.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

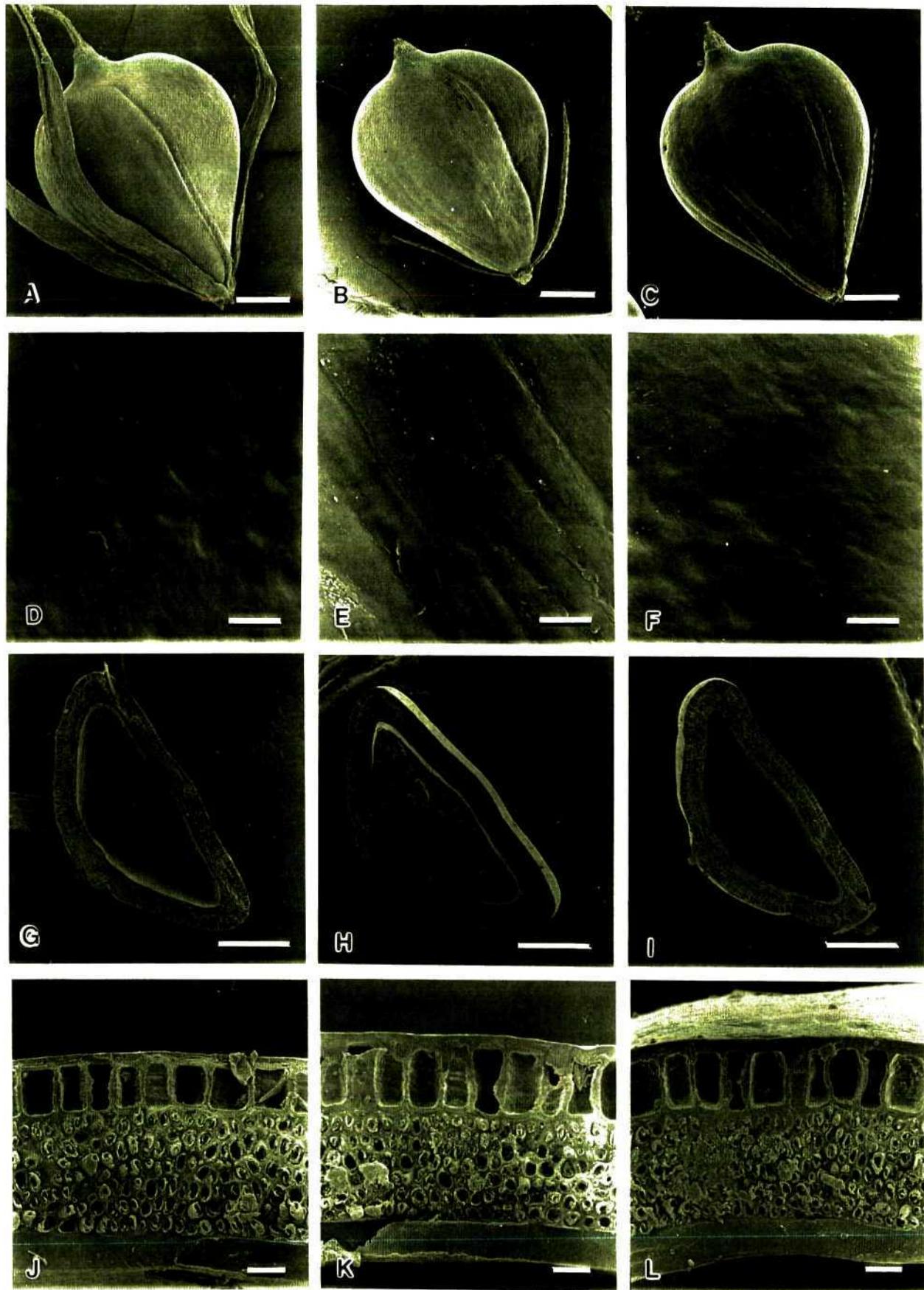


Figure 16.

Bolboschoenus maritimus s.l.: inland, site E, *Browning 800*.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

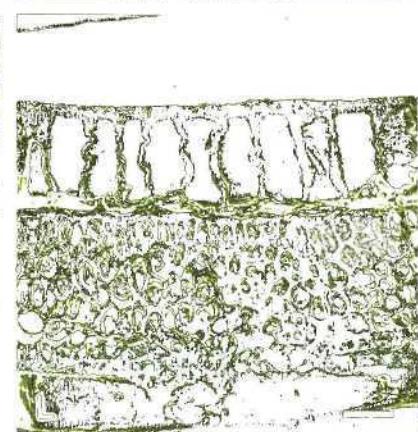
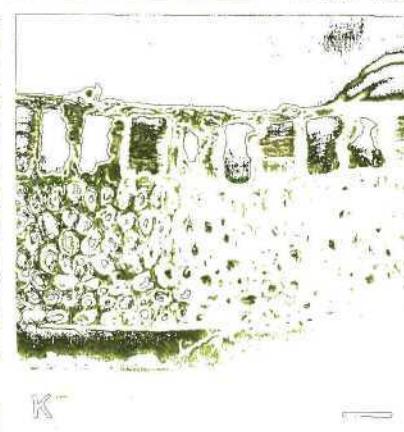
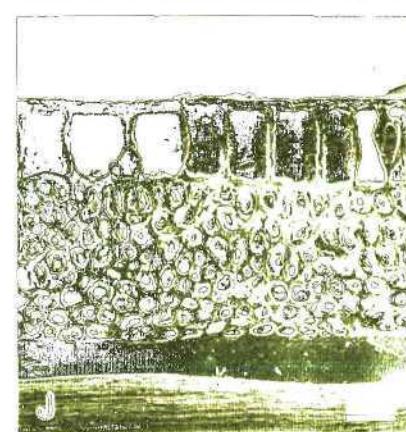
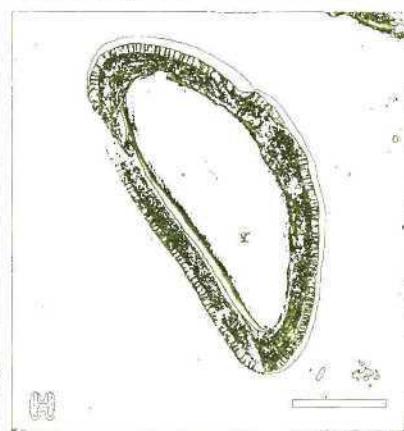
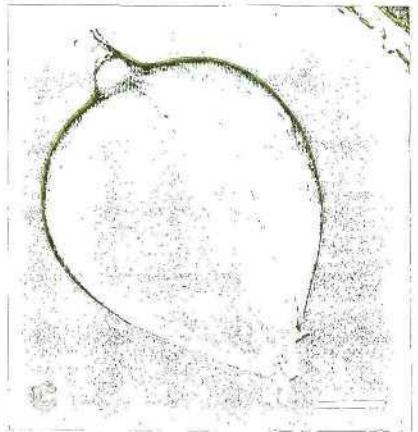
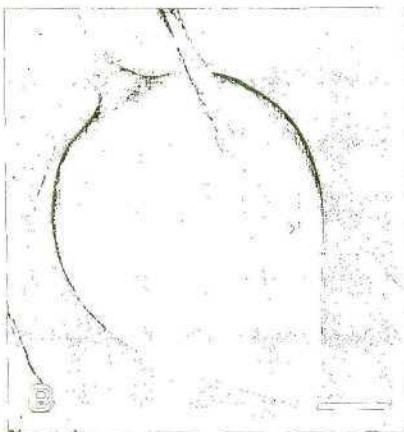
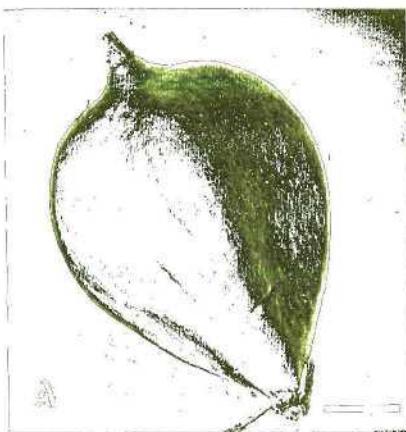


Figure 17.

Bolboschoenus maritimus s.l.: inland, site F, *Browning 802*.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial view (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section (with or without endosperm) (scale bar = 500 μm); J--L, detail of pericarp in transverse section (scale bar = 25 μm).

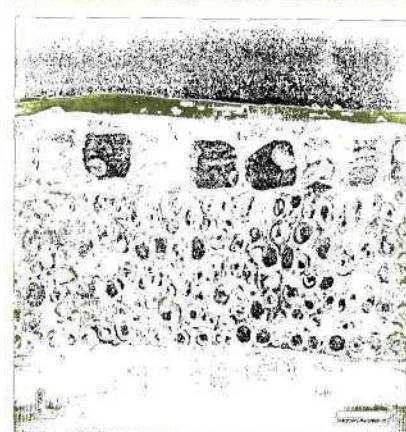
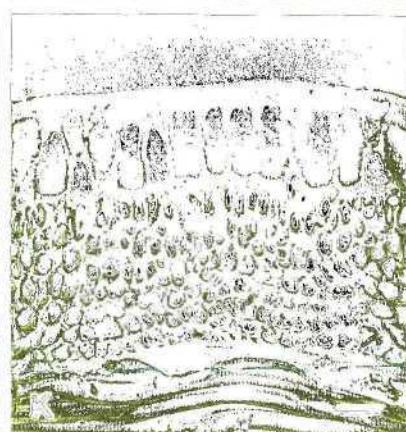
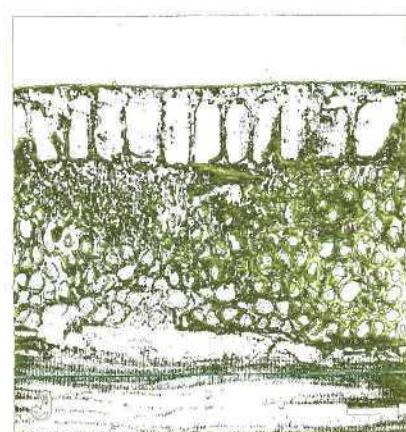
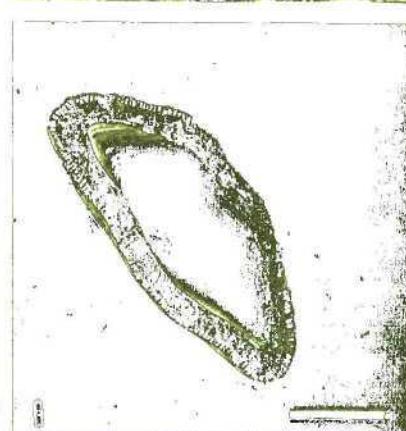
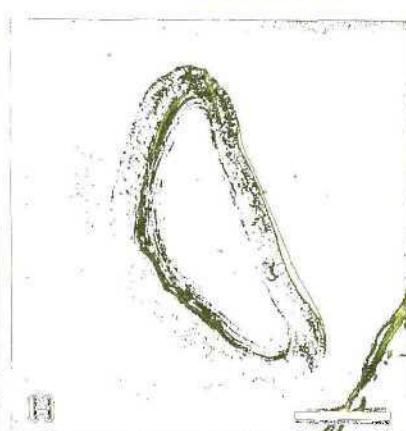
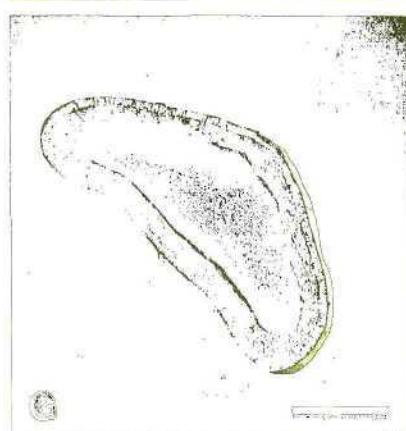
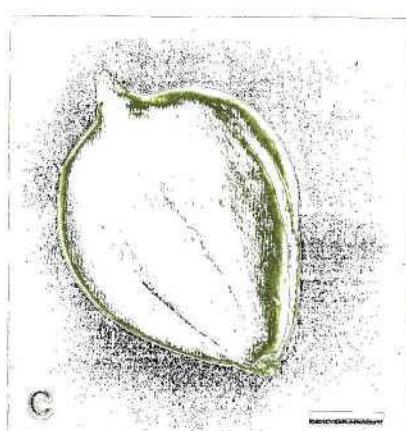
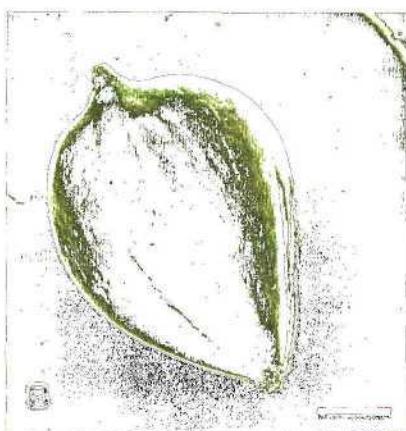
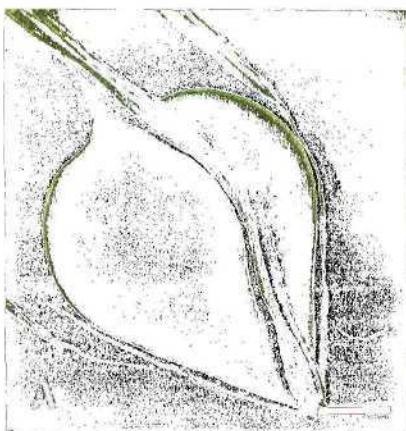
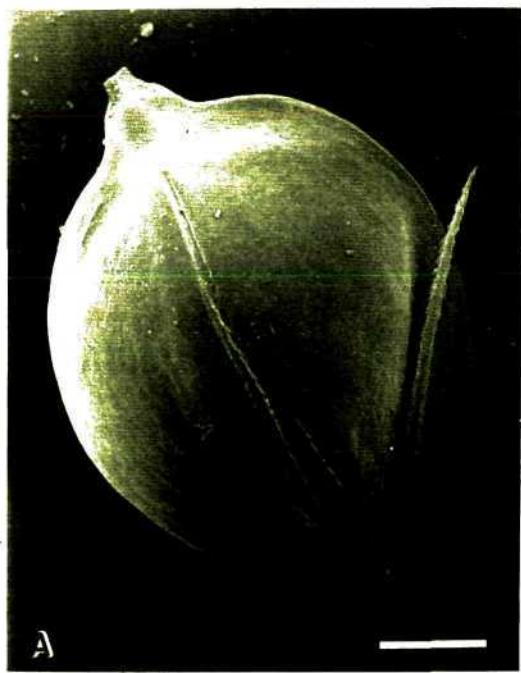


Figure 18.

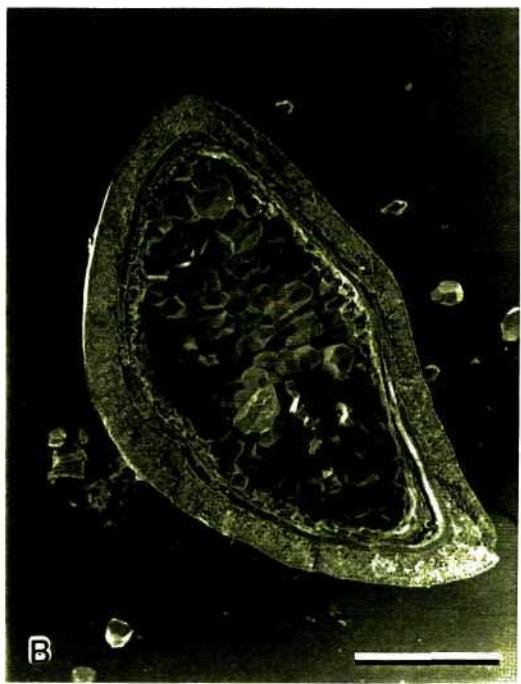
Bolboschoenus glaucus, Torre 8345 (LISC).

Scanning electron micrographs of fruit.

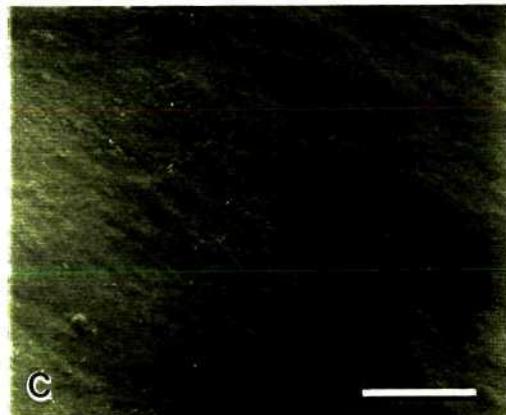
A, nut in outline; B, nut in transverse section; C, surface topography; D, pericarp in transverse section (1, exocarp, 2, mesocarp, 3, endocarp); E, silica body in exocarp cell (arrow). Scale bars: A, B = 500 μm ; C, D = 25 μm ; E = 10 μm .



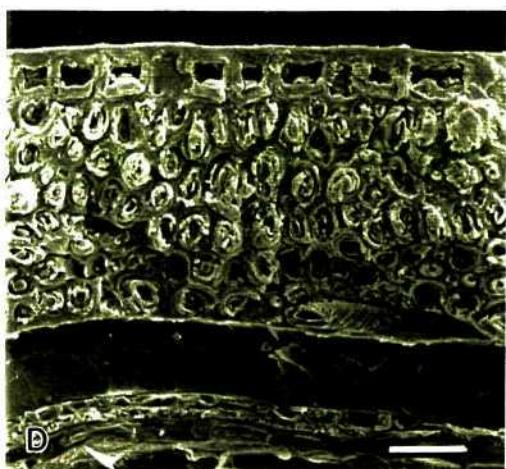
A



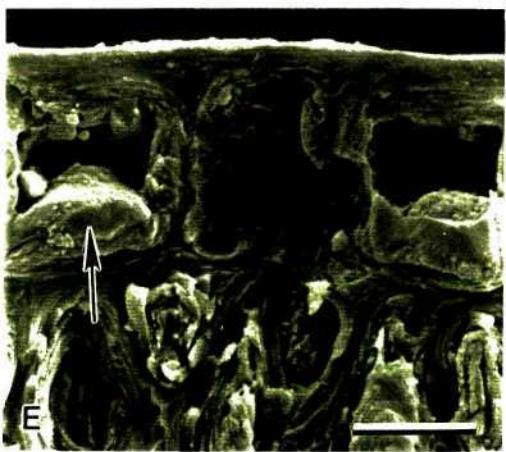
B



C



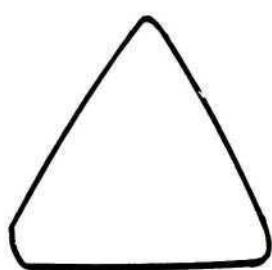
D



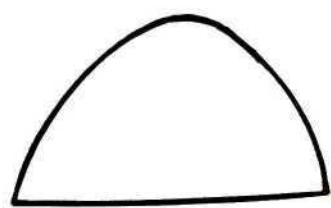
E

Figure 19.

Diagrams of nut shapes in transverse section. A-- D trigonous; E-G lenticular. A, sharply triangular; B, obtusely trigonous, abaxial angle exceeding 90° ; C, subtrigonous; D, trigonous with abaxial faces concave; E, lenticular with both faces convex; F, lenticular with both faces flat; G, lenticular with both faces concave.



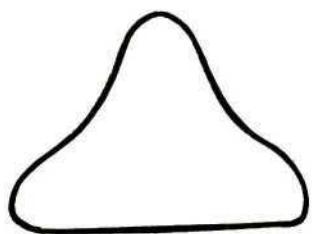
A



B



C



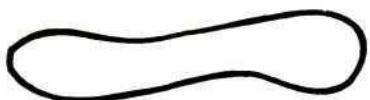
D



E



F



G

Figure 20.

Scirpus nobilis Ridley, in Trans. Linn. Soc. ser. 2, Bot., 2: 159 (1884).

Scanning electron micrographs of fruits of **holotype**: *Welwitsch* 6975 (BM !), Angola, Mossamedes, Maiombo river, Oct. 1859.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. nobilis* (Ridley) P. Goetghebeur & D.A. Simpson.

Place and date of publication: Kew Bull., 46 (1): 173 (1991).

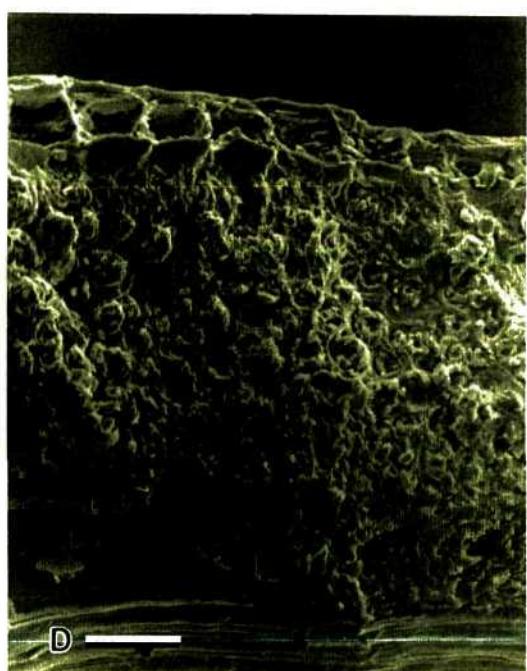
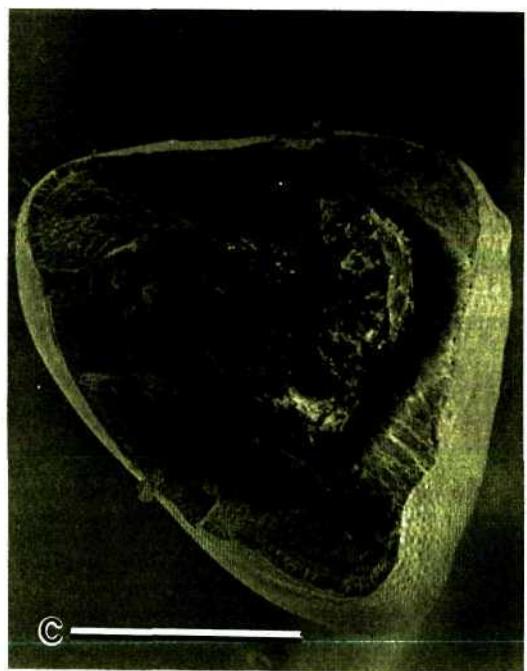
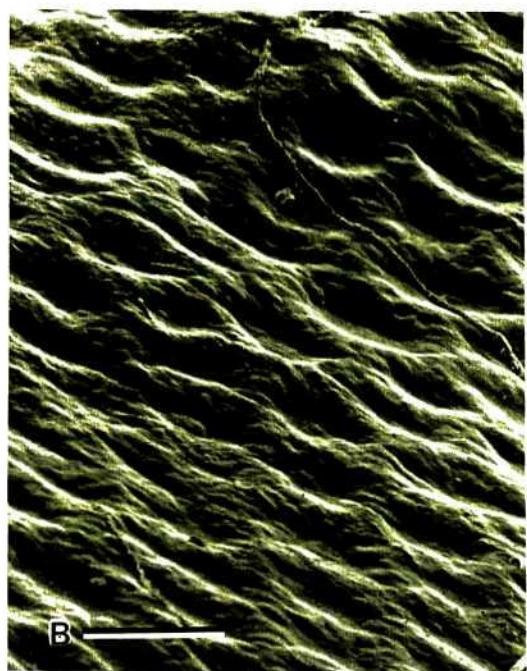
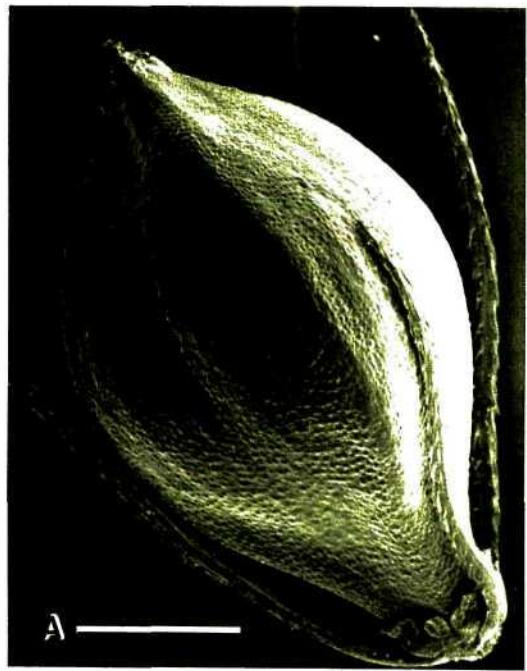


Figure 21.

Scirpus laeteflorens C.B. Clarke, Clarke (Cyperaceae) in Dur. & Schinz, Conspect. Fl. Afr. V: 625 (1894) *nomen nudum*; Clarke (Cyperaceae) in Thiselton-Dyer Fl. Trop. Afr. ed. 2.: 456 (1902) (descr.).

Scanning electron micrographs of fruit of **syntype**: *Chapman & Baines s.n.* (K!), South West Africa, without further locality.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. nobilis* (Ridley) P. Goetghebeur & D.A. Simpson.

Place and date of publication: Kew Bull., 46 (1): 173 (1991).

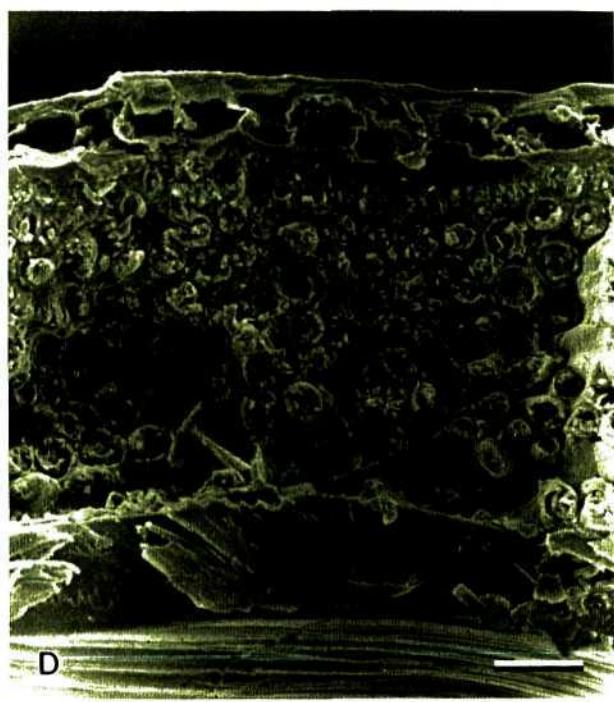
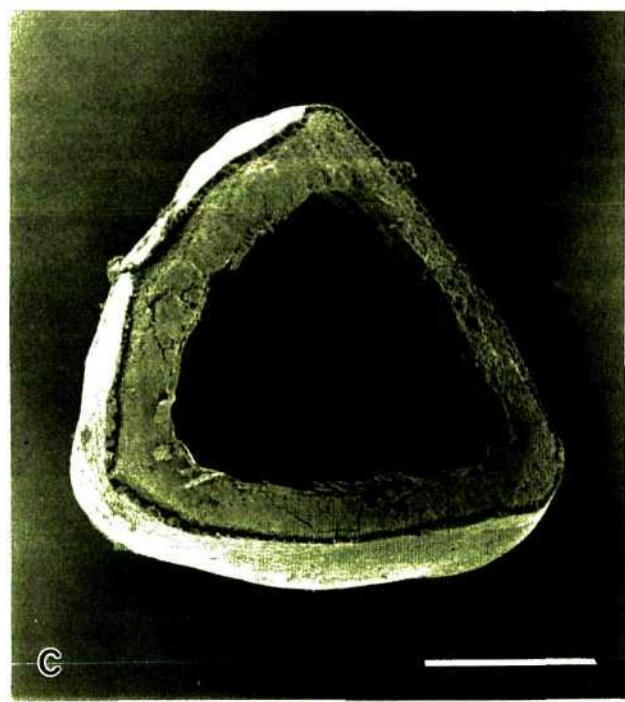
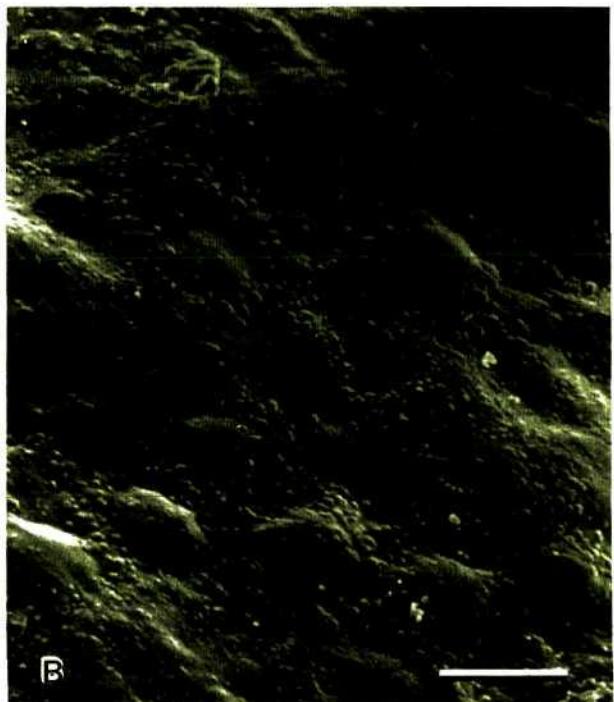
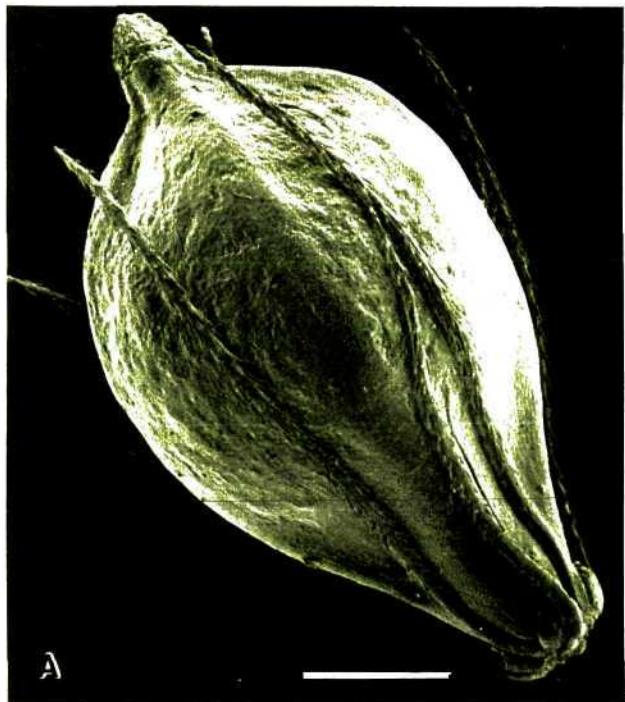


Figure 22.

Isolepis grandispica Steudel, Syn. Pl. Cyp: 318 (1855).

Scanning electron micrographs of fruit of **isotype**: Herbarium *Perrottet nr. 838* (P!), Senegal, without further locality.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. grandispicus* (Steudel) K. Lewejohann & W. Lobin

Place and date of publication: Courier Forschungsinst. Senckenberg 52: 267 (1982).

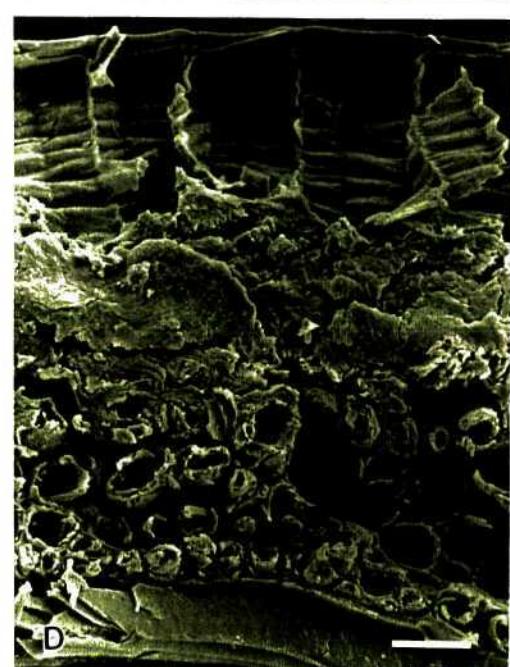
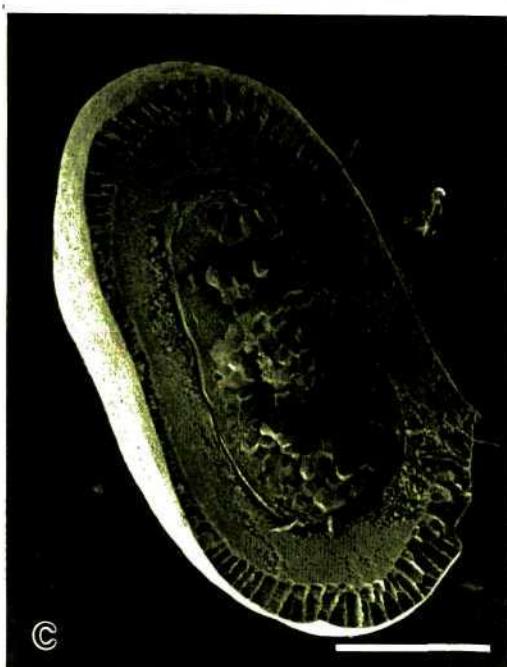
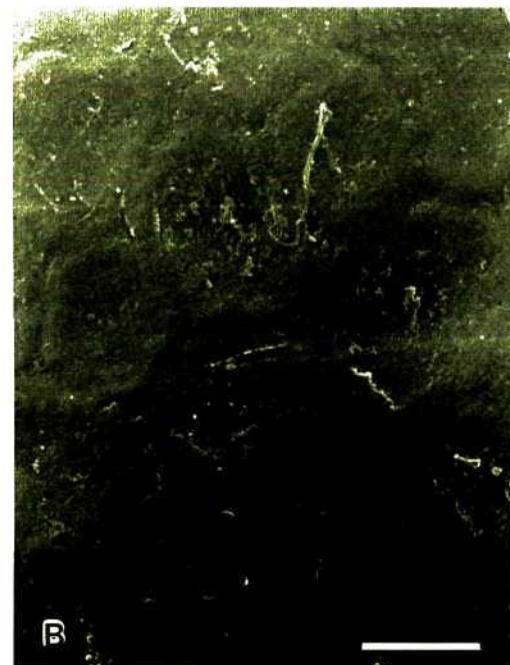
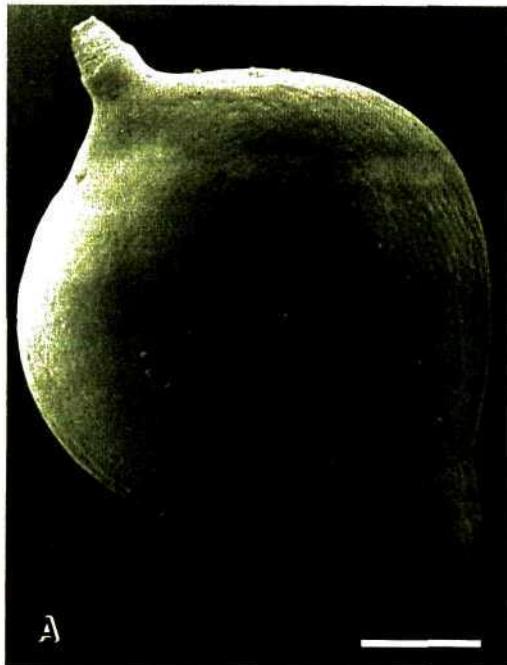


Figure 23.

Bolboschoenus grandispicus (Steudel) K. Lewejohann & W. Lobin

Scanning electron micrographs of fruit of another specimen from Senegal: *Berhaut 1021* (P).
A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section;
D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

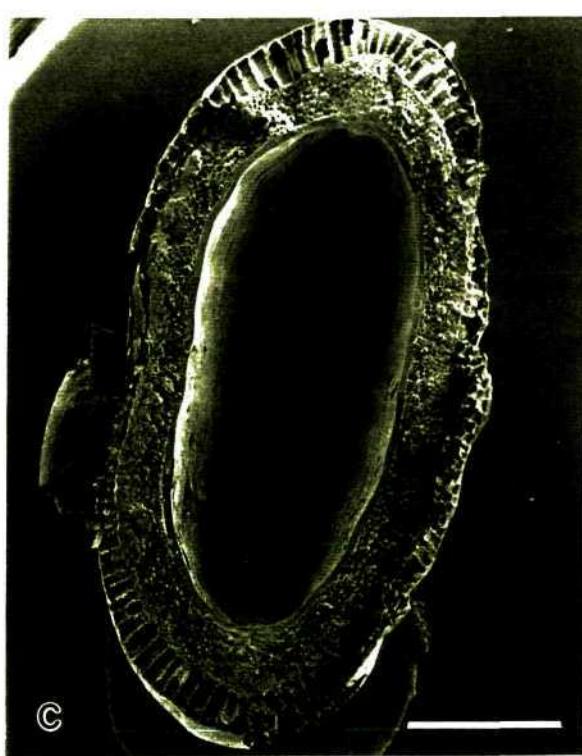
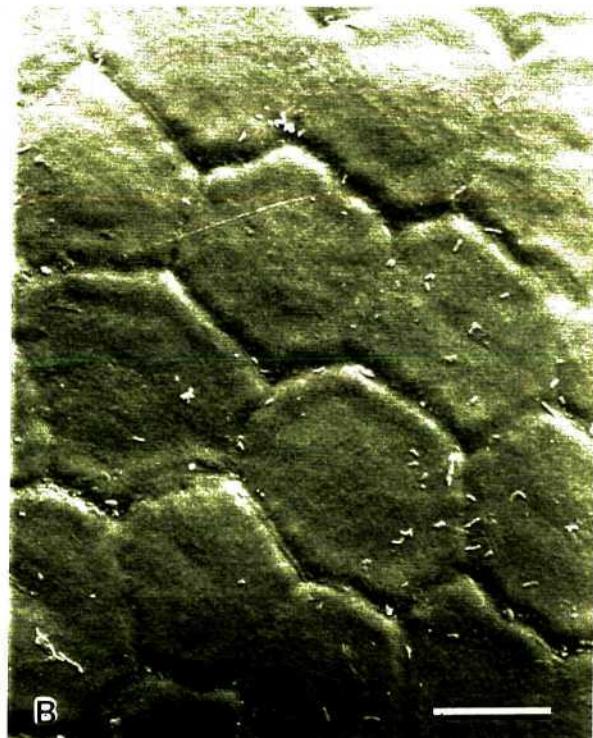


Figure 24.

Scirpus tridentatus Roxburgh, Hort. Beng. 81 (1814), *nomen nudum*, Fl. Ind., ed. Carey & Wall., i: 228 (1820); Fl. Ind., ed. Carey, i: 225 (1832).

Scanning electron micrographs of fruit of **holotype**: Herb. Roxb. no. ? 419. (K !).

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. glaucus* (Lamarck) S.G. Smith.

Place and date of publication: Novon 5: 101 (1995).

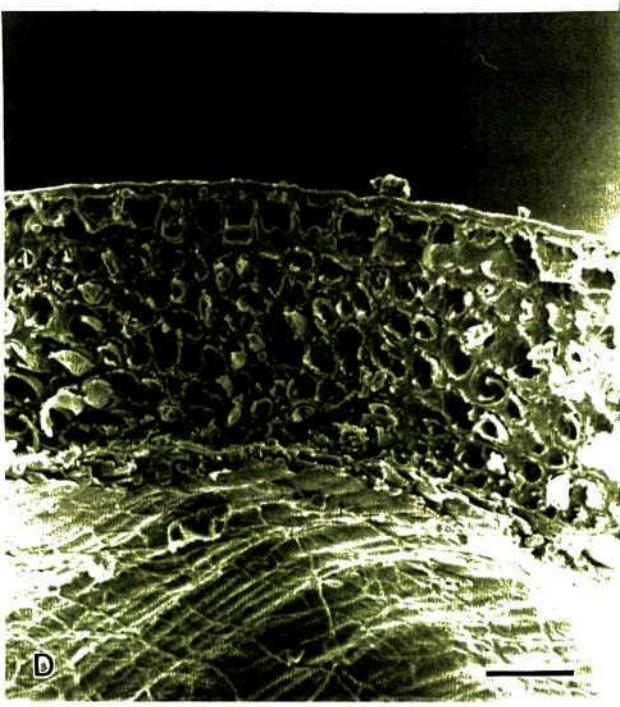
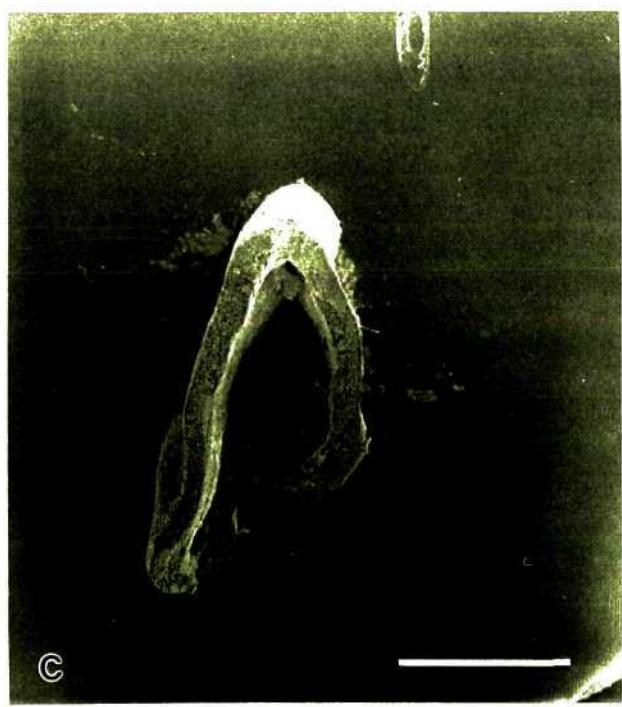
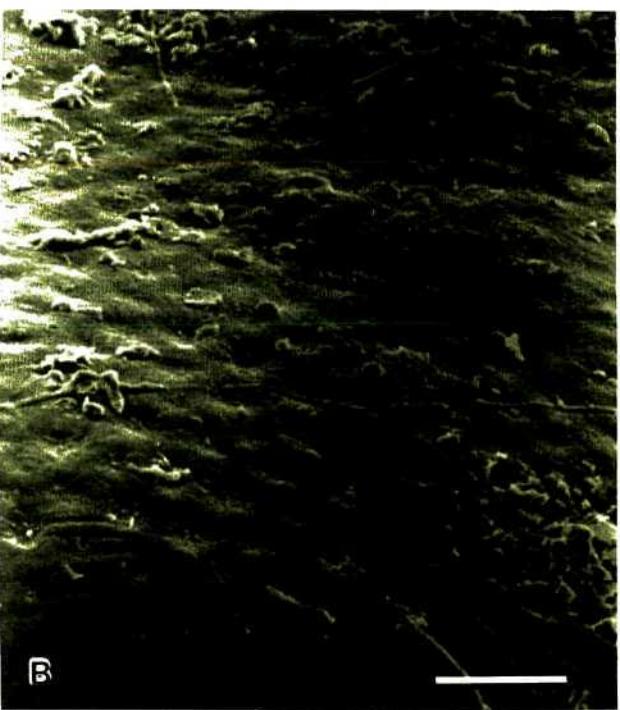
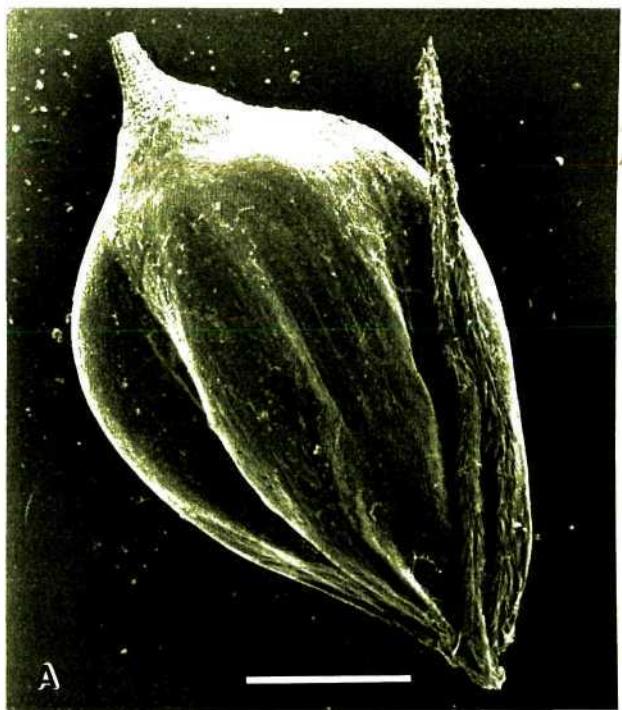


Figure 25.

Scirpus tuberosus Desfontaines, Fl. Atlant. 1: 50 (1798).

Scanning electron micrographs of fruit of **holotype**: *Desfontaines s.n.* in ‘Herbier de la Flore Atlantique’ (P, photo!), ‘in locubus propre La Calla’.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. maritimus* (L.) Palla

Place and date of publication: In Koch, synops. Deutsch. Schweiz. Fl. ed. 3, 3: 2532. (1905).

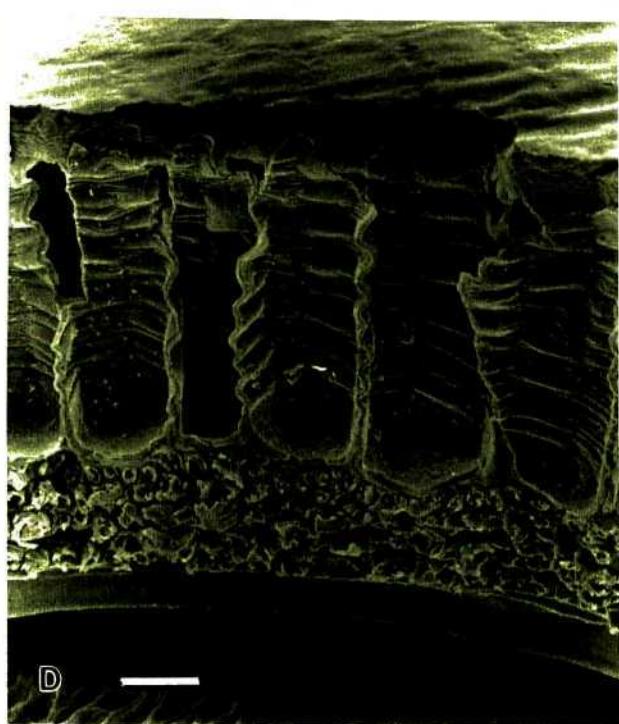
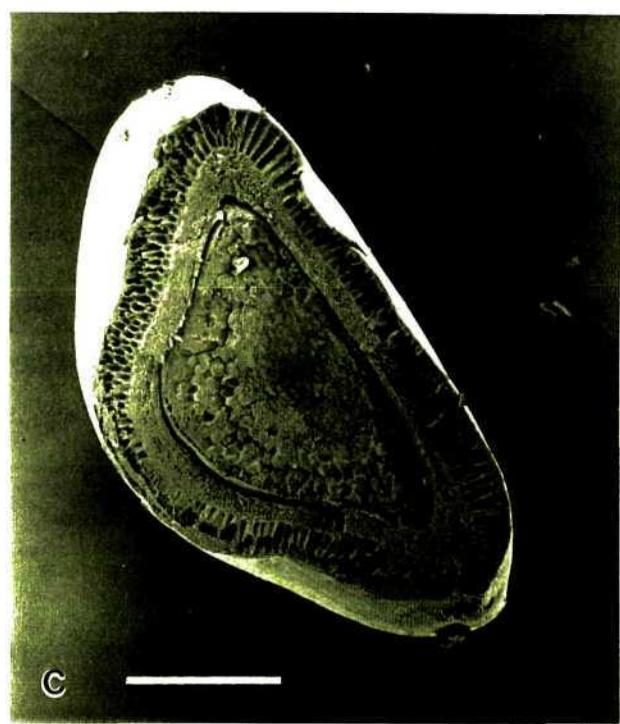
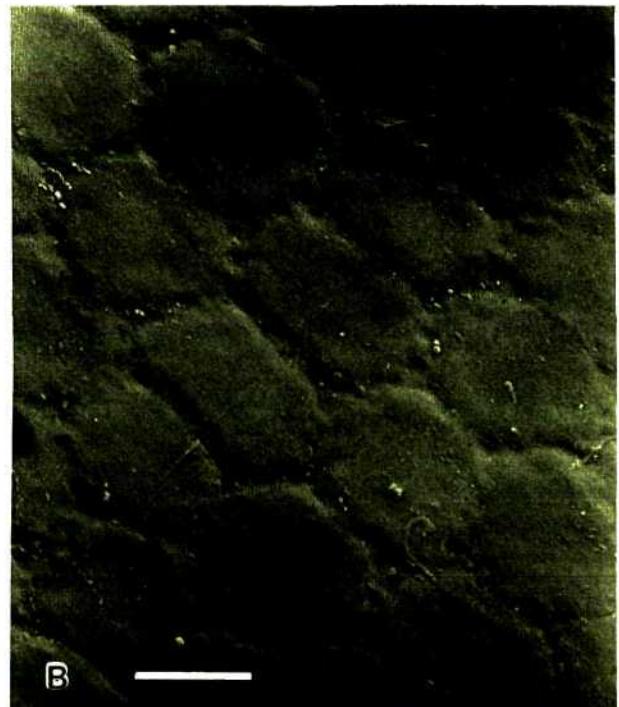
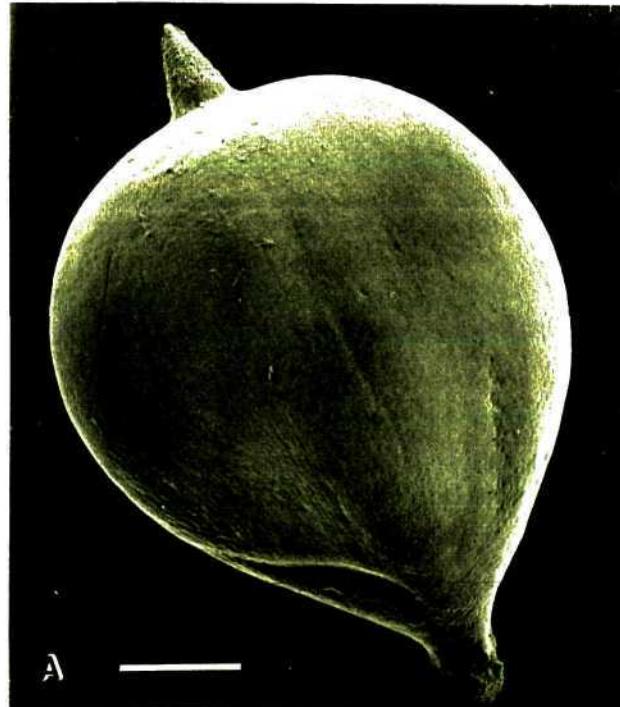


Figure 26.

Bolboschoenus glaucus, Smith & Taylor 3134 (NY).

Scanning electron micrographs of fruit.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bar, A = 500 μm ; B = 25 μm ; C = 400 μm ; D = 40 μm .

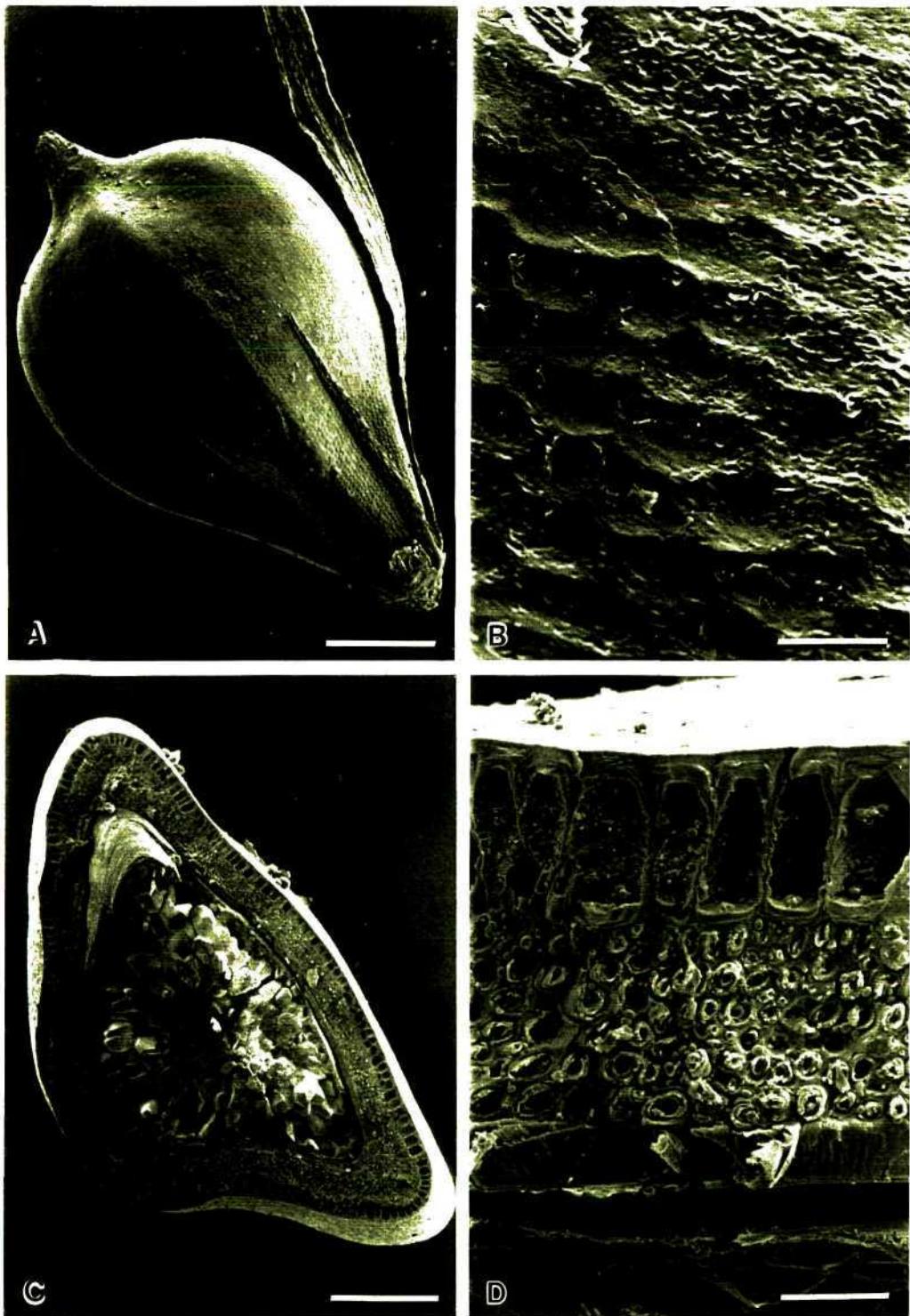


Figure 27.

Scirpus maritimus L. β ? . *fluviatilis* Torrey, Ann. Lyceum Nat. Hist. New York 3: 324 (1826).

Scanning electron micrographs of fruit of **lectotype**: *Dr. Baldwin s.n.* (NY 7158, photostat!), U.S.A., Banks of the Missouri, July 6, 1819.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. fluviatilis* (Torr.) Soják

Place and date of publication: Čas. Nář. Muz. (Prague), 141 (1-2): 62 (1972).

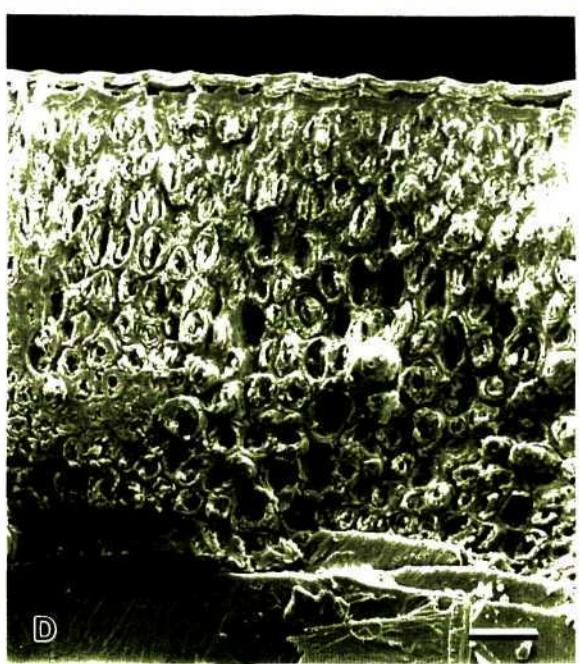
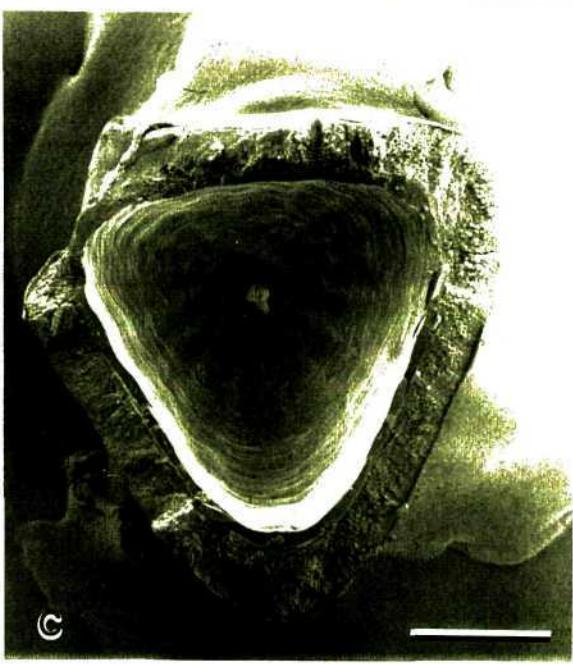
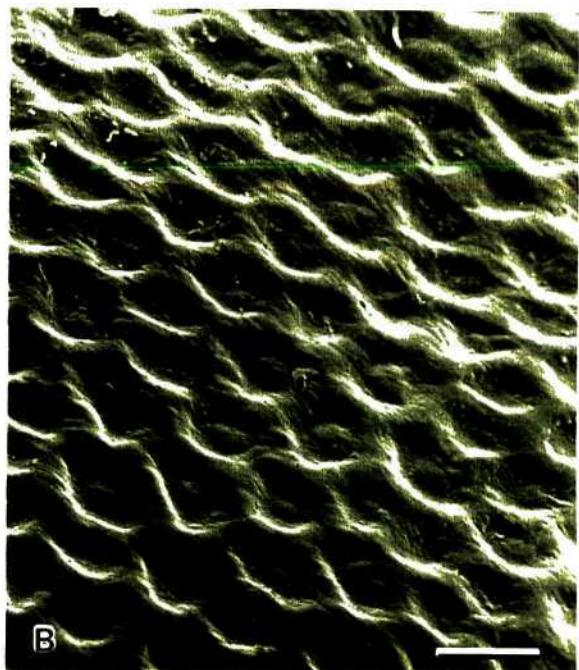
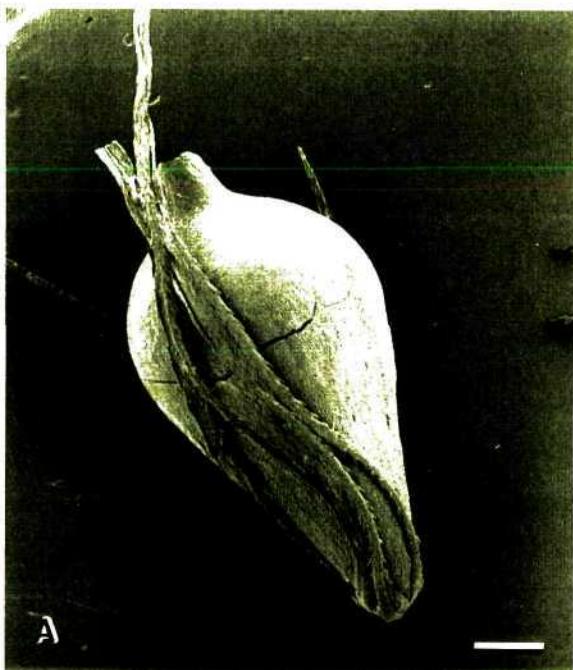


Figure 28.

Scirpus maritimus L. var. *macrostachyos* Michaux, Fl. Bor. Amer. 1: 32 (1803).

Inflorescence of **lectotype**, selected by Schuyler, published by J. Ewan (1979). *Herbarium Michaux s.n.(P)*, N. America, Carolina, in salt marsh.

Name under *Bolboschoenus*: *B. robustus* (Pursh) Soják

Place and date of publication: Čas. Nár. Mus. Odd. Přír. 141: 63 (1972).

* Note: the spelling of the epithet used by Michaux has varied with different authors, namely:

macrostachys Clarke, det. label, 1887; see Vol. 1 pg. 54 of present text;

macrostachya Cook (1947: 567); see Vol. 1 pg. 56 of present text.



10 mm

Figure 29.

Scirpus fernaldii Bicknell, Torreya 1: 96 (1901).

Scanning electron micrographs of pericarp of **holotype**: *E.P. Bicknell s.n.* (NY 5883), Mt. Desert [Island], Maine, Aug. 20 1898.

A, pericarp surface; B, pericarp in transverse section; C, pericarp in longitudinal section. Scale bars A--C = 25 μ m.

Name under *Bolboschoenus*: *B. fernaldii* (Bicknell) Soó

Place and date of publication: Acta. Bot. Acad. Sci. Hung., 16 (3-4): 368 (1970, publ. 1971).

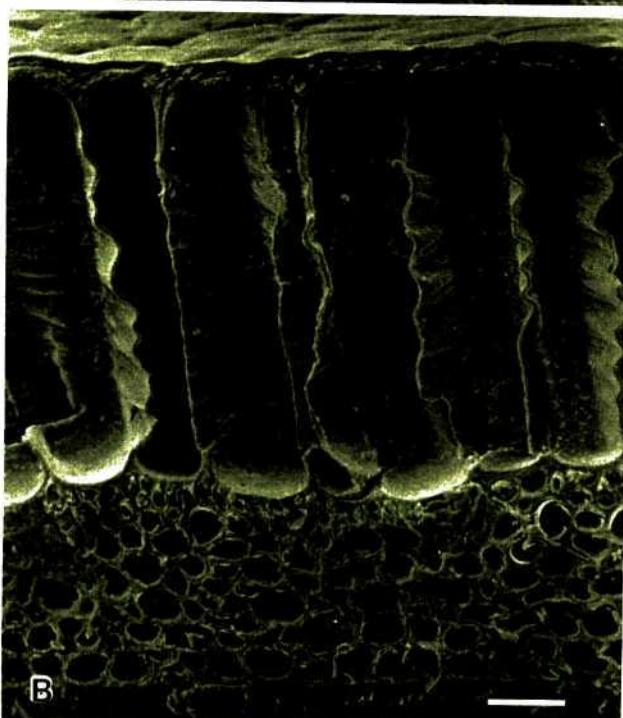
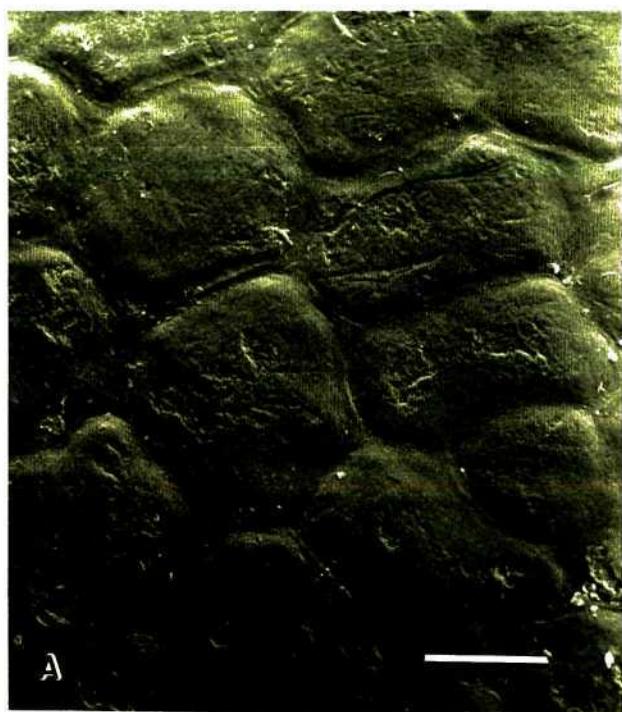


Figure 30.

Scirpus paludosus A. Nelson, Bull. Torrey Bot. Club 26: 5 (1899).

Scanning electron micrographs of fruit of **holotype**: *Nelson* 3874, (RM), Granger, July 30, 1897. A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. maritimus* (L.) Palla subsp. *paludosus* (A. Nelson) T. Koyama

Place and date of publication: Acta Phytotax. Geobot. 31: 148 (1980).

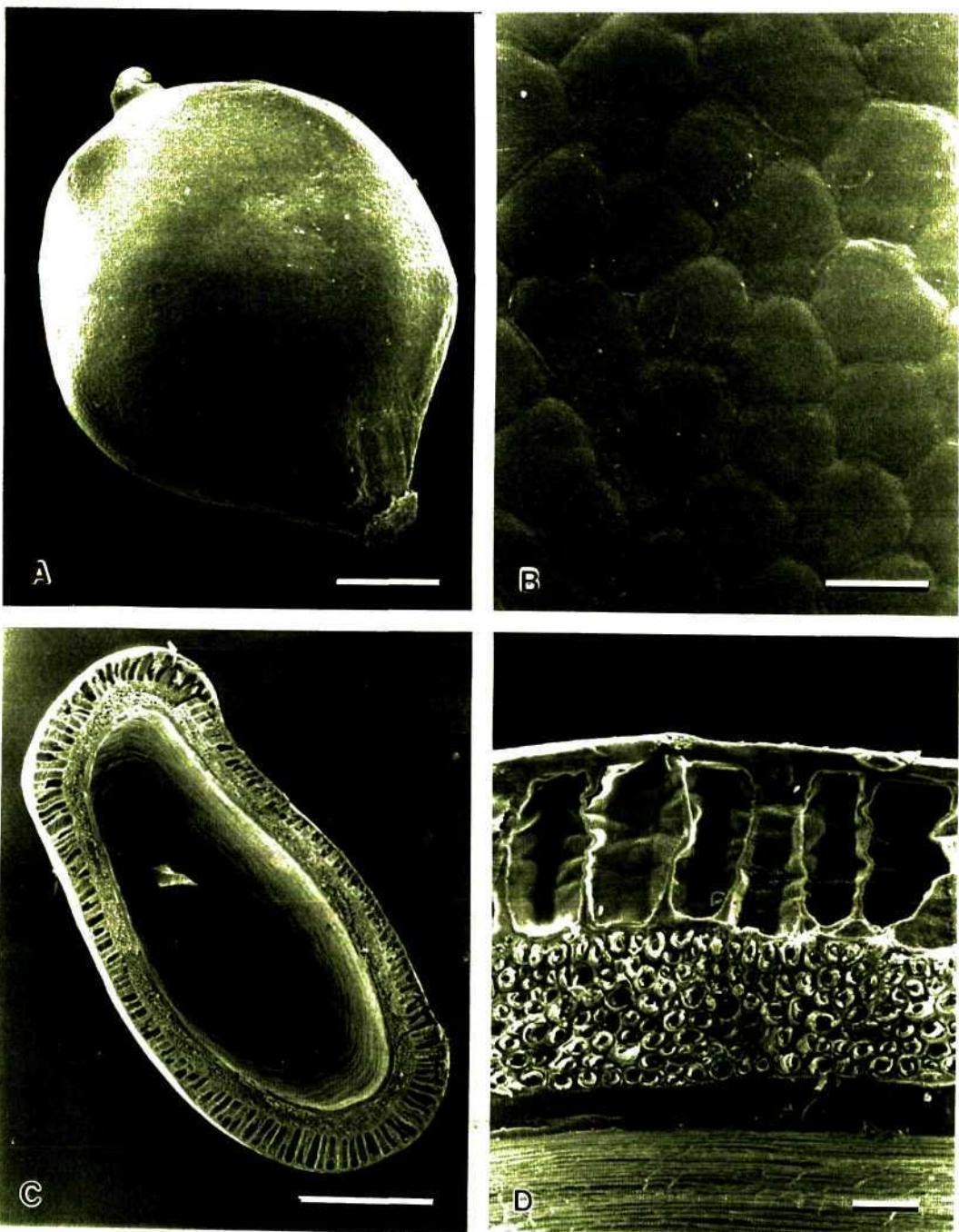


Figure 31.

Bolboschoenus maritimus (L.) Palla subsp. *paludosus* (A. Nelson) T. Koyama, Wiggins & Gillespie 3970 (MICH).

Scanning electron micrographs of fruit.

A, nut in transverse section; B, surface topography; C, pericarp in transverse section; D, exocarp in transverse section, angle of nut. Scale bars: A, = 500 μm ; B, C, D = 25 μm .

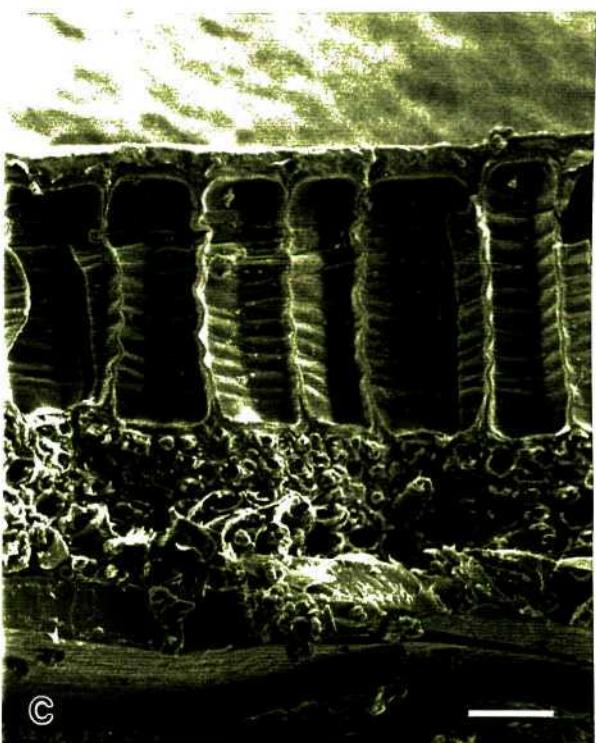
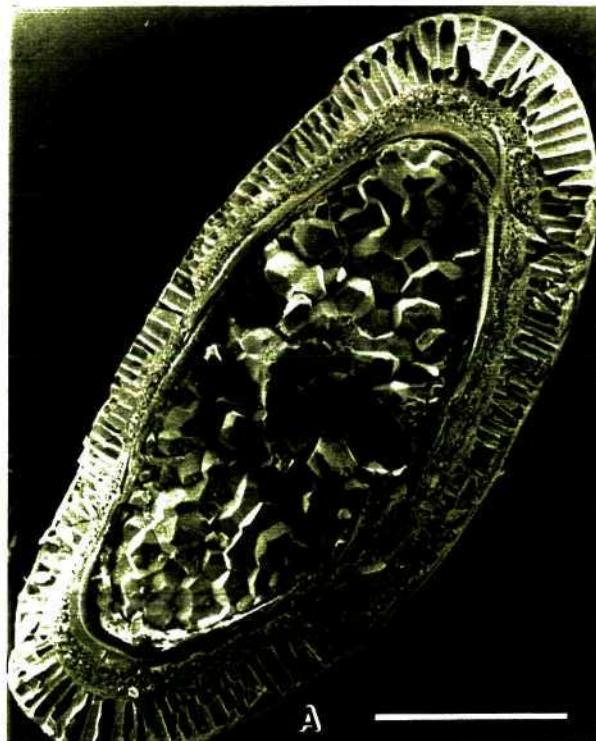


Figure 32.

Scirpus novae-angliae Britton, Britton & Brown, Illus. Fl. n. U.S. 3: 509. 1898.

Scanning electron micrographs of fruit of **isotype**: *Eames, s.n.* (NY5884), Fairfield, Conn., 19 July 1896.

A, nut (broken) in outline, abaxial surface uppermost; B, surface topography; C, pericarp in longitudinal section. Scale bars: A = 500 μm ; B, C = 25 μm .

Name under *Bolboschoenus*: *B. novae-angliae* (Britton) S.G. Smith

Place and date of publication: *Brittonia* 47 (4): 434 (1995).

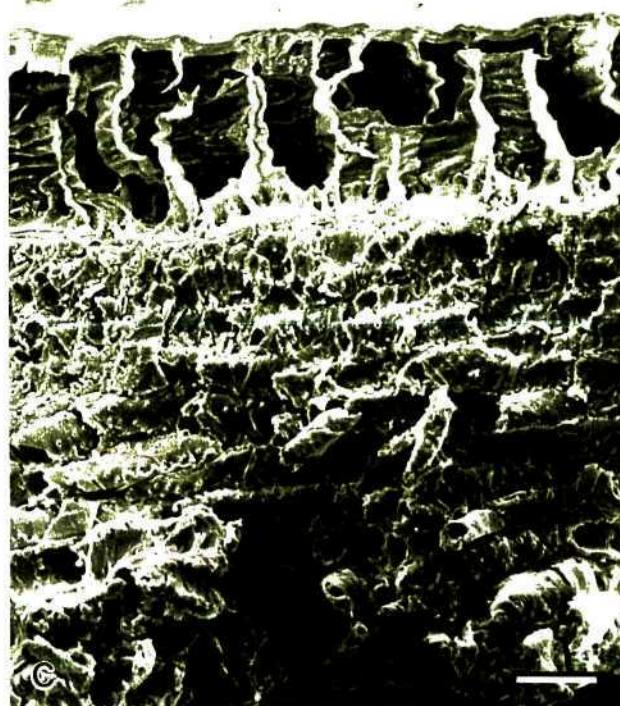
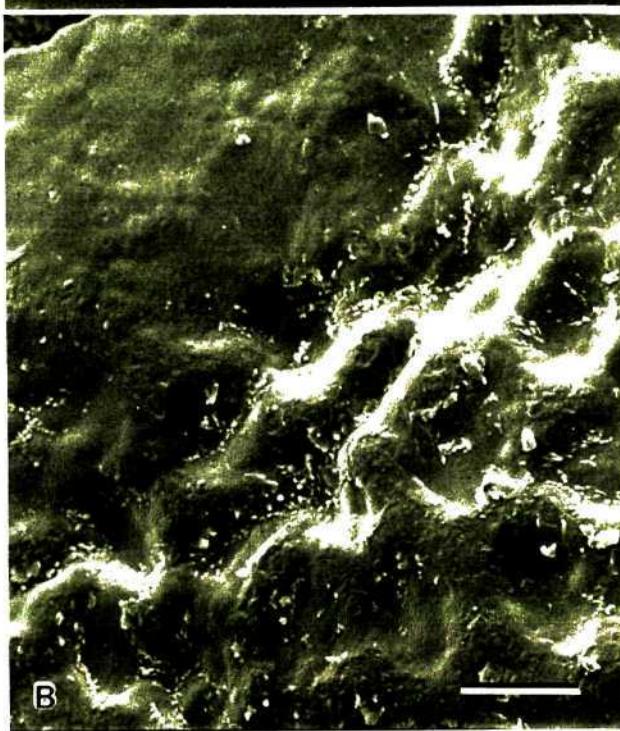
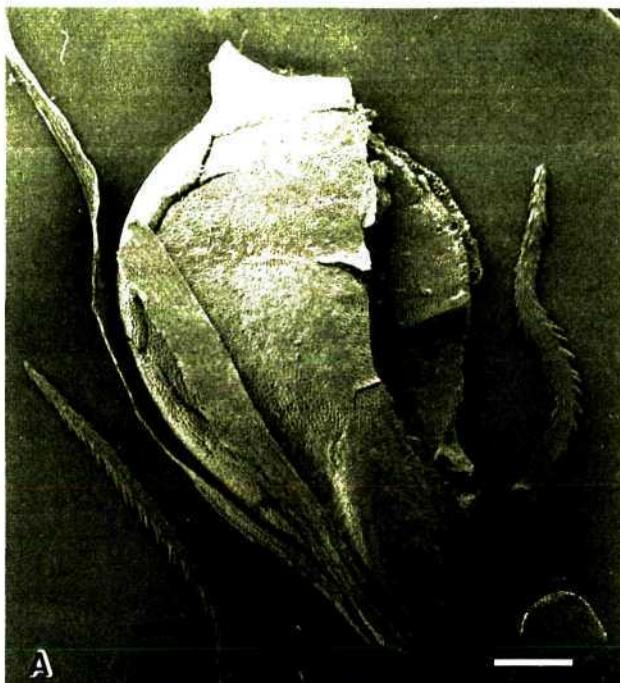


Figure 33.

Scirpus novae-angliae Britton, Britton & Brown, Illus. Fl. n. U.S. 3: 509. 1898.

Scanning electron micrographs of fruit of **isotype**: *Eames, s.n.* (NY5881), Fairfield, Conn., 19 July 1896

A, nut (broken) in outline, adaxial surface uppermost; B, surface topography; C, pericarp in longitudinal section; D, silica bodies on inner pericinal walls of exocarp cells (outer pericinal walls removed). Scale bars: A, = 500 μm ; B, C, D = 25 μm .

Name under *Bolboschoenus*: *B. novae-angliae* (Britton) S.G. Smith

Place and date of publication: Brittonia 47 (4): 434 (1995).

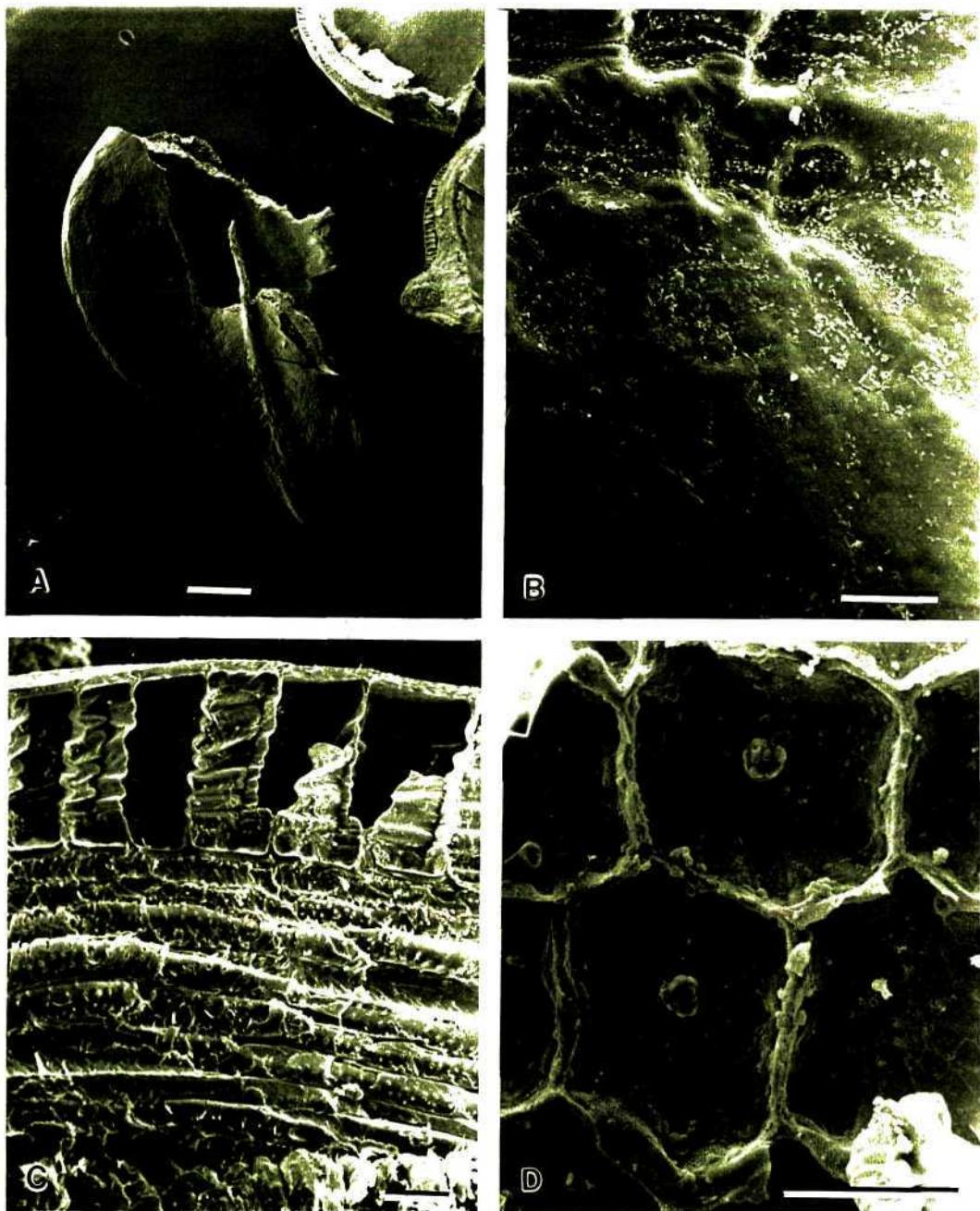


Figure 34.

Silica bodies in exocarp cells of nuts of two Australian specimens. A. *Bolboschoenus fluviatilis*, Skinner s.n. (NE); B, *B. medianus*, Lepschi 1598 (CANB, NU). Scale bar = 10 μm .

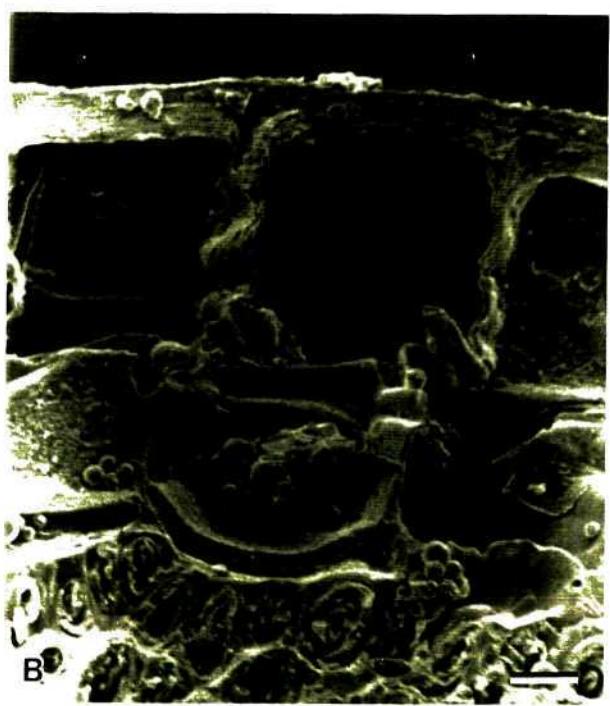
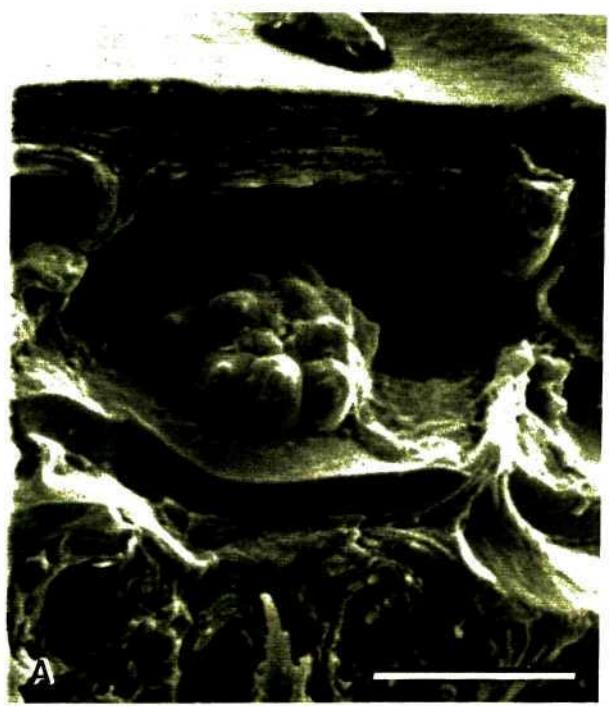


Figure 35.

Bolboschoenus maritimus subsp. *paludosus*, O. Degener 31.113 (K).

Scanning electron micrographs of nuts.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section;

D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

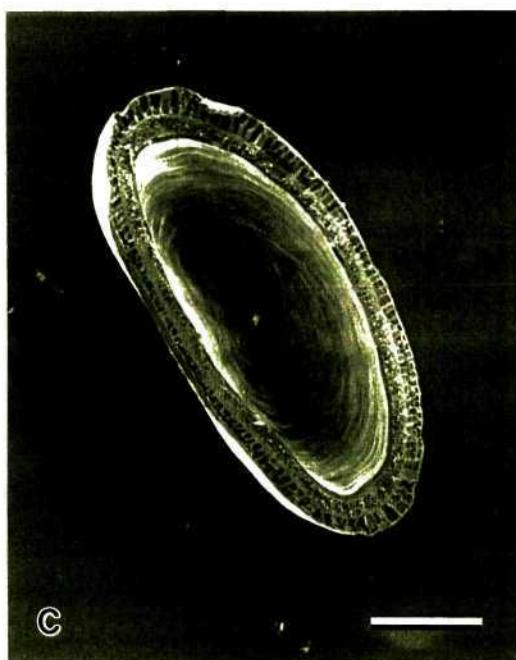
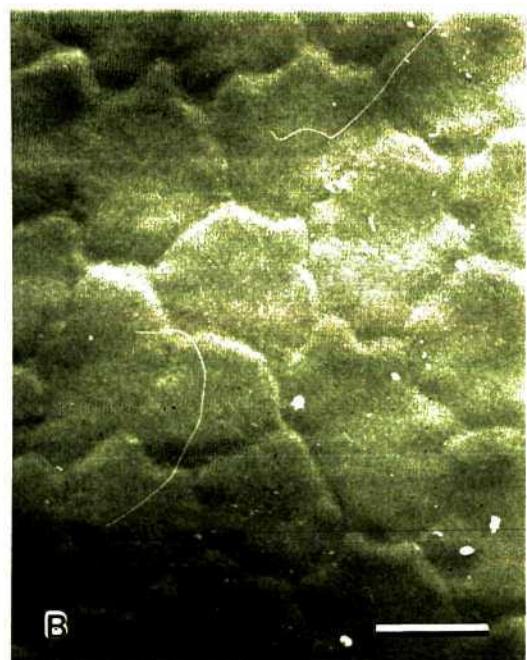


Figure 36.

Bolboschoenus maritimus subsp. *paludosus*, H.L. Mason 1580 (K).

Scanning electron micrographs of nuts.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section;

D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

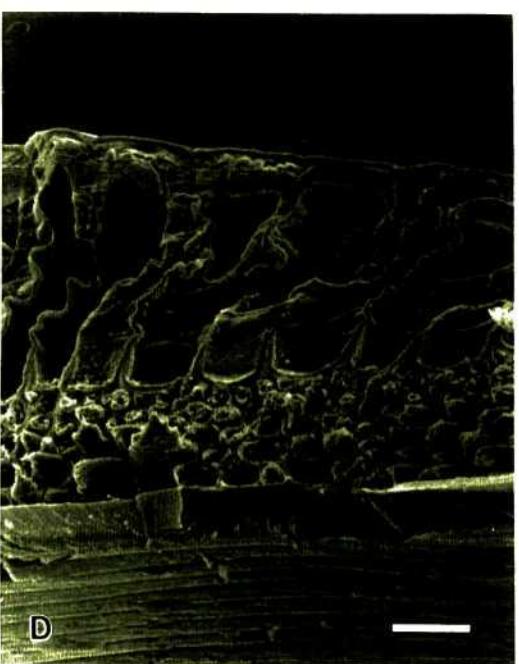
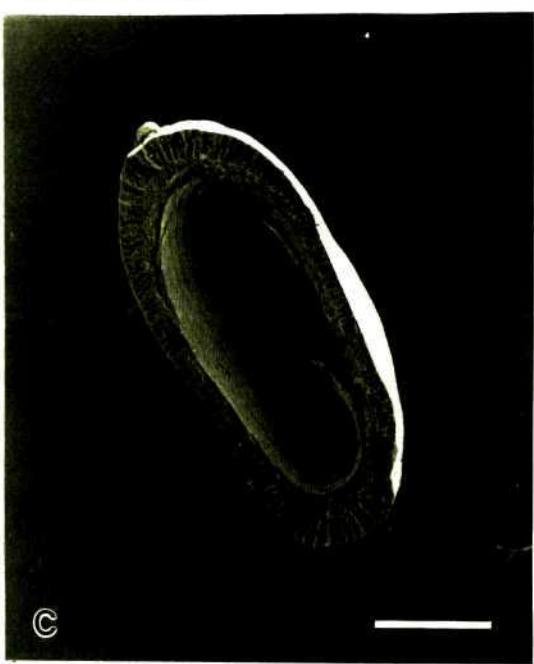
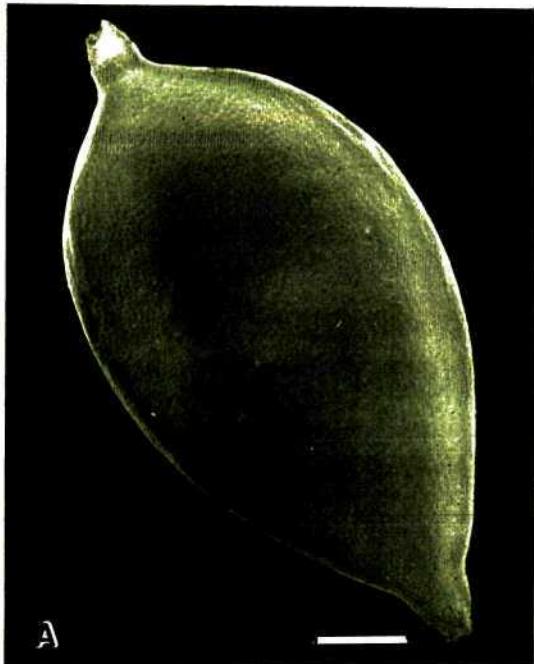


Figure 37.

Bolboschoenus, North American species. A--D, *B. fluviatilis*, Smith & Smith 8505 (WIS); E--H, *B. robustus*, Ewan 17566 (NO); I--L, *B. novae-angliae*, Schuyler 4417 (PH).

Scanning electron micrographs of fruits.

A, E, I, nuts in outline, abaxial surfaces uppermost; B, F, J, surface topography; C, G, K, nuts in transverse section; D, H, L, pericarps in transverse section. Scale bars A, C, E, G, I, K = 500 μm ; B, D, F, H, J, L = 25 μm .

Note the pericarp construction of *B. novae-angliae* which exhibits features intermediate between the pericarp construction of *B. fluviatilis* and *B. robustus*, in surface topography and in the ratio of exocarp depth to mesocarp depth..

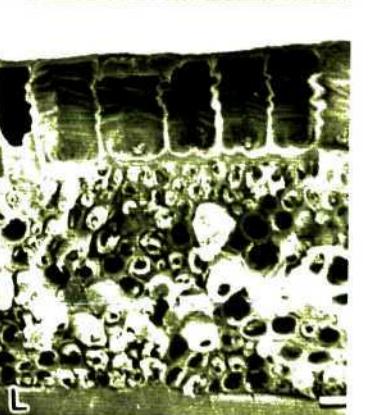
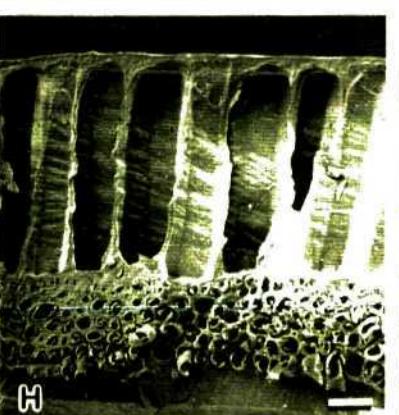
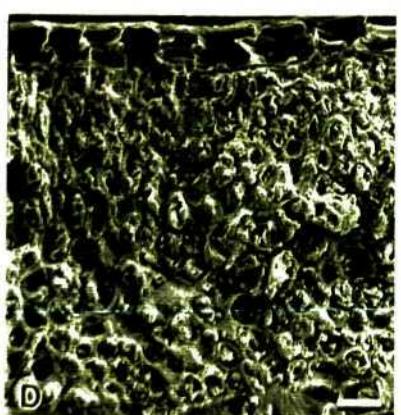
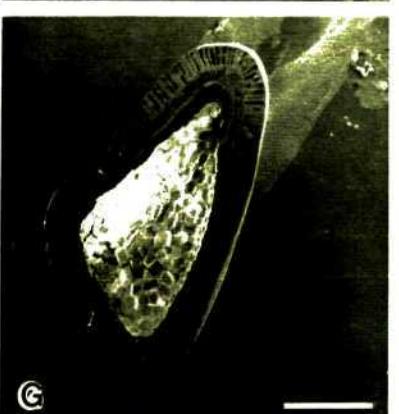
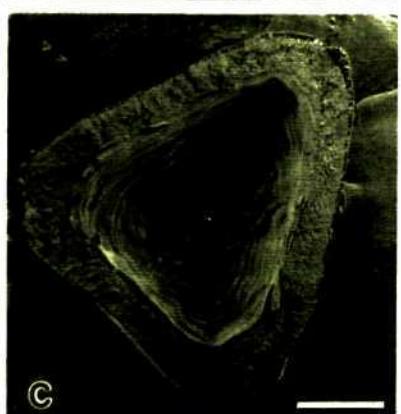
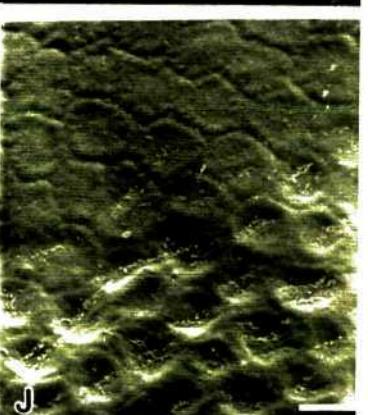
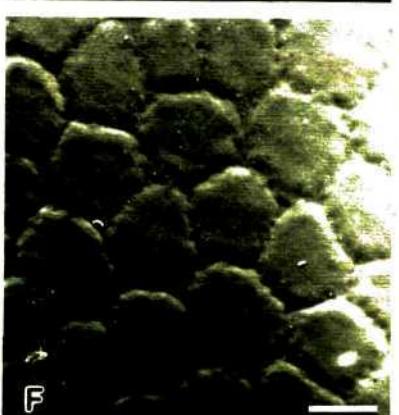
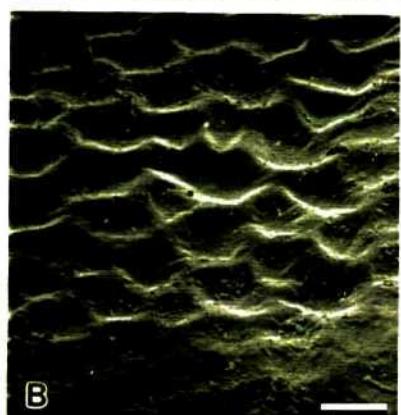
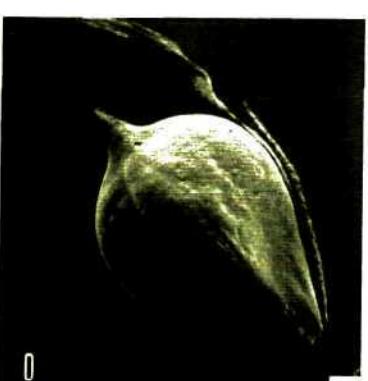
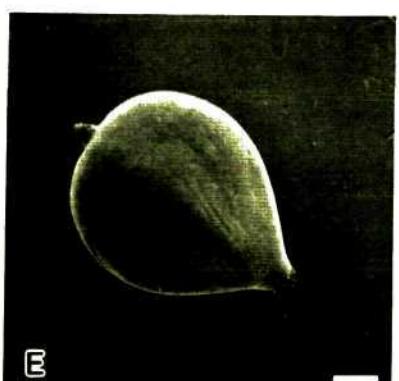
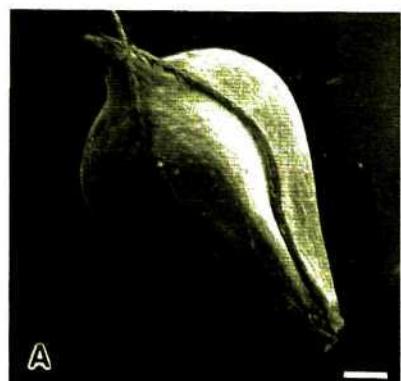


Figure 38.

Australian species of *Bolboschoenus*: colours of nuts. A, *B. caldwellii*, Wilson 7576 (NSW); B, Blake 23073 (NSW); C, *B. medianus*, Wilson 8612 (NSW); D, *B. fluvialis*, Beaglehole 70665 (NSW). Scale bar = 1mm.

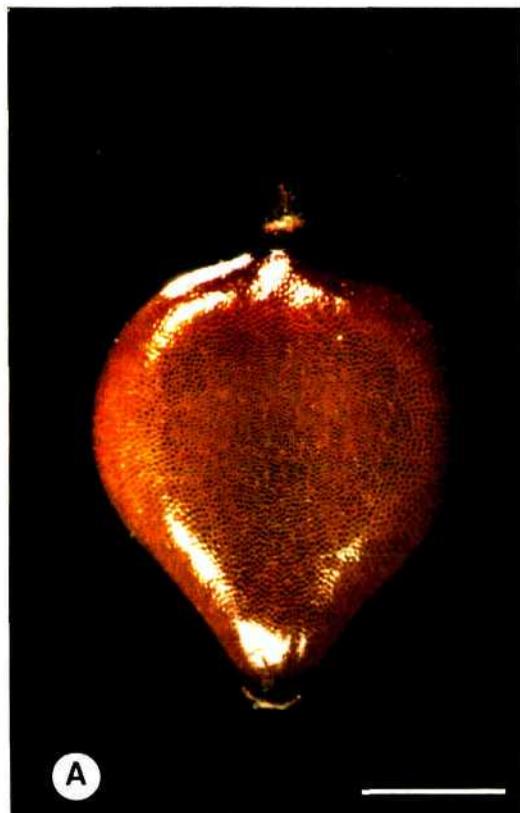


Figure 39.

Scirpus pervaeridis V.J. Cook, Trans. & Proc. Roy. Soc. New Zealand 76: 570, pl. 56, fig. 1 (1947).

Scanning electron micrographs of fruit of **isotype** :V.J. Cook 534 (AK 59189 !), New Zealand, Vicinity Port Waikato. Holotype retained in Cook's private herbarium.

A, nut in outline, abaxial surface uppermost, perigonial bristles persistent; B, surface topography; C, nut in transverse section, endosperm removed; D, pericarp in transverse section showing exocarp with silica deposits (top), mesocarp (middle) and endocarp (bottom). Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. fluviatilis* (Torr.) Soják

Place and date of publication: Čas. Nár. Muz. (Prague), 141 (1-2): 62 (1972).

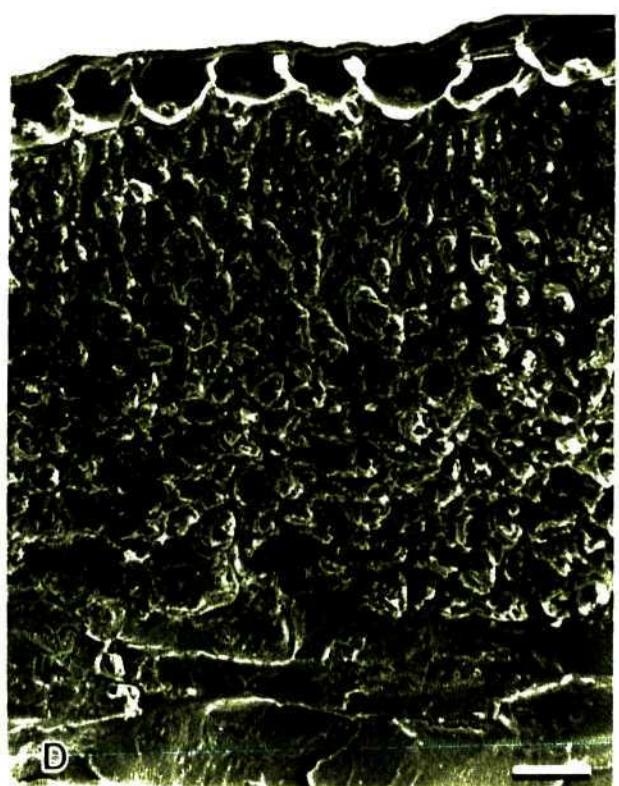
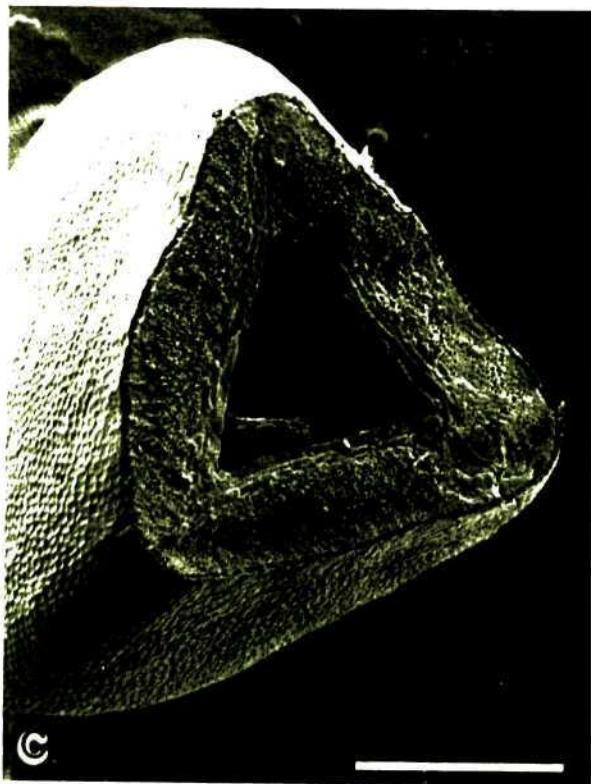
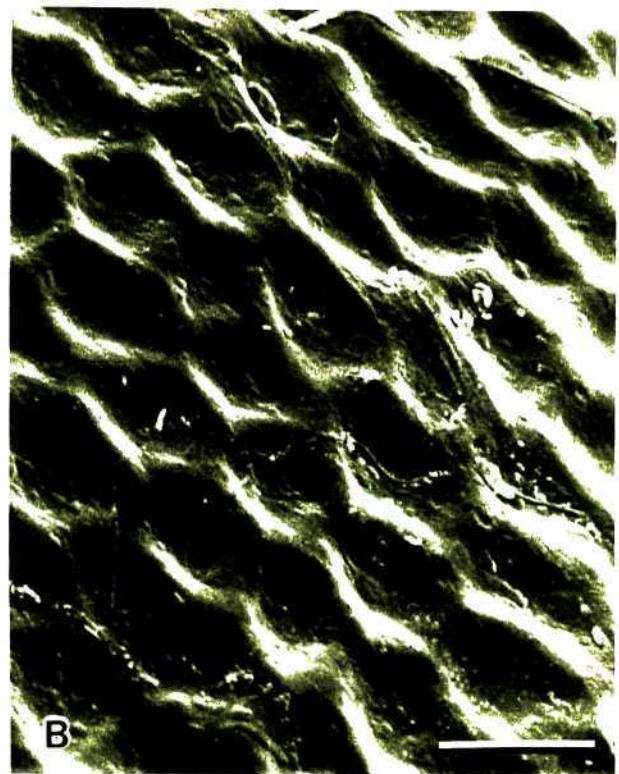
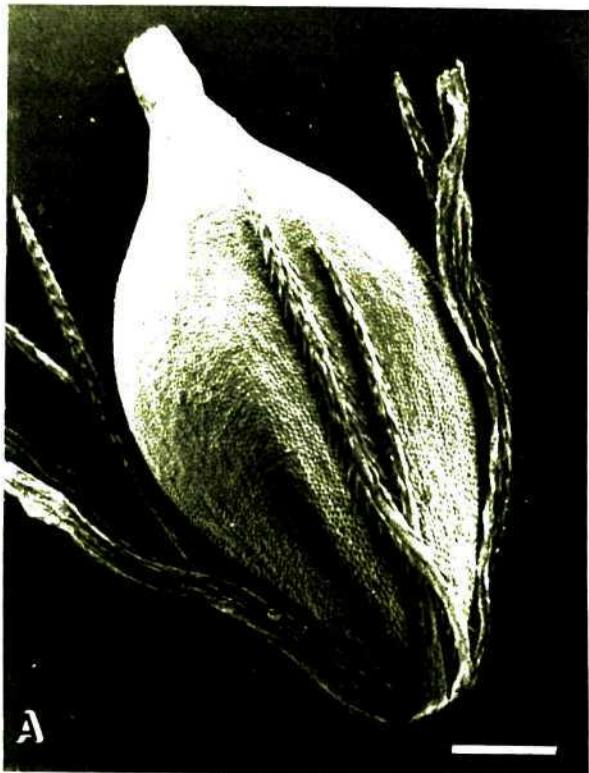


Figure 40.

Scirpus caldwellii V.J. Cook, Trans. & Proc. Roy. Soc. New Zealand 76: 568, pl. 56, fig. 3 (1947)

Scanning electron micrographs of fruit of **isotype**: *V.J. Cook* 542 (AK 59206 !), New Zealand, Waitakaruru. Thames Estuary. Holotype retained in Cook's private herbarium.

A, nut, perigonal bristles fallen; B, surface topography; C, nut in transverse section, endosperm in situ; D, pericarp in transverse section showing exocarp fragmented (top) and mesocarp (bottom); endocarp not represented. Scale bars A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. caldwellii* (V.J. Cook) Soják

Place and date of publication: Čas. Nár. Muz. (Prague), 141 (1-2): 62 (1972).

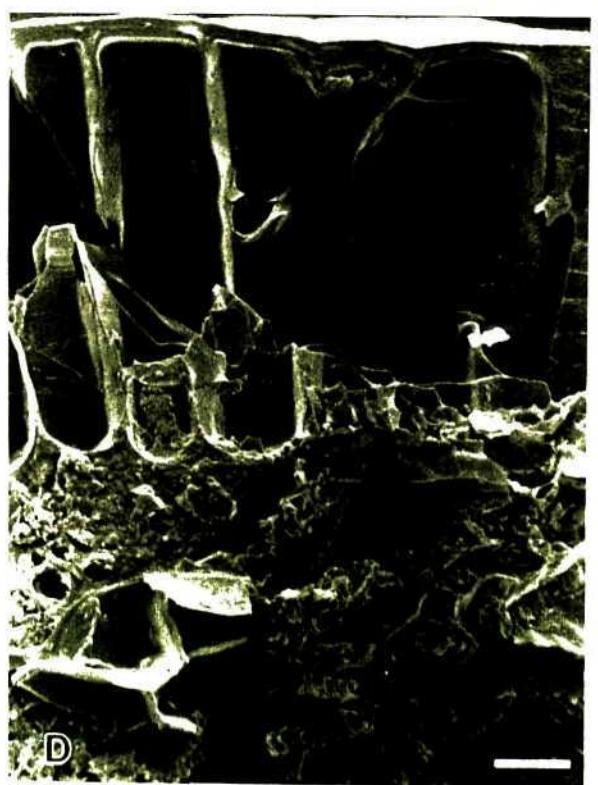
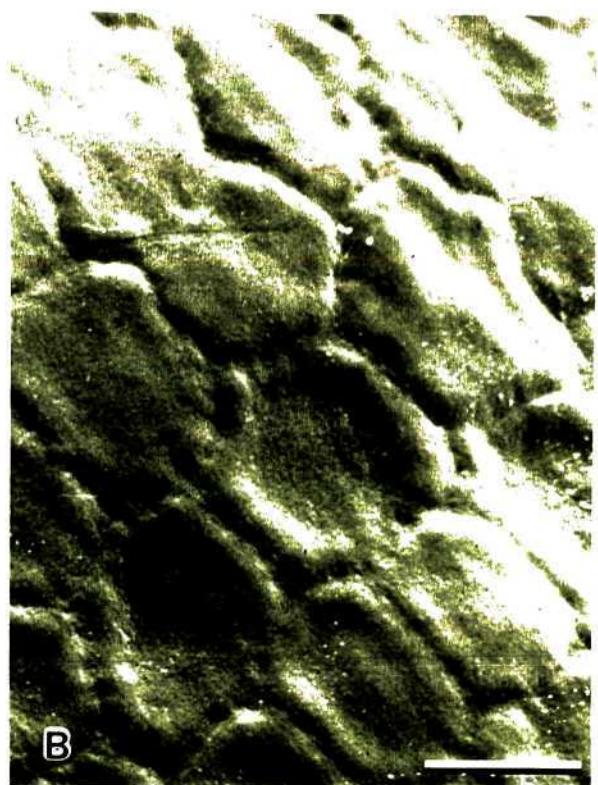


Figure 41.

Scirpus medianus V.J. Cook, Trans. & Proc. Roy. Soc. New Zealand 76: 569, pl. 56, fig. 2 (1947).

Scanning electron micrographs of fruit of **isotype**: *V.J. Cook 463* (AK 61798 !), New Zealand, Vicinity Thames. Holotype retained in Cook's private herbarium.

A, nut, some perigonial bristles persistent; B, surface topography; C, nut in transverse section, endosperm removed; D, pericarp in transverse section showing exocarp (top), mesocarp (middle) endocarp (bottom). Scale bars A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. medianus* (V.J. Cook) Soják

Place and date of publication: Čas. Nár. Muz. (Prague), 141 (1-2): 63 (1972).



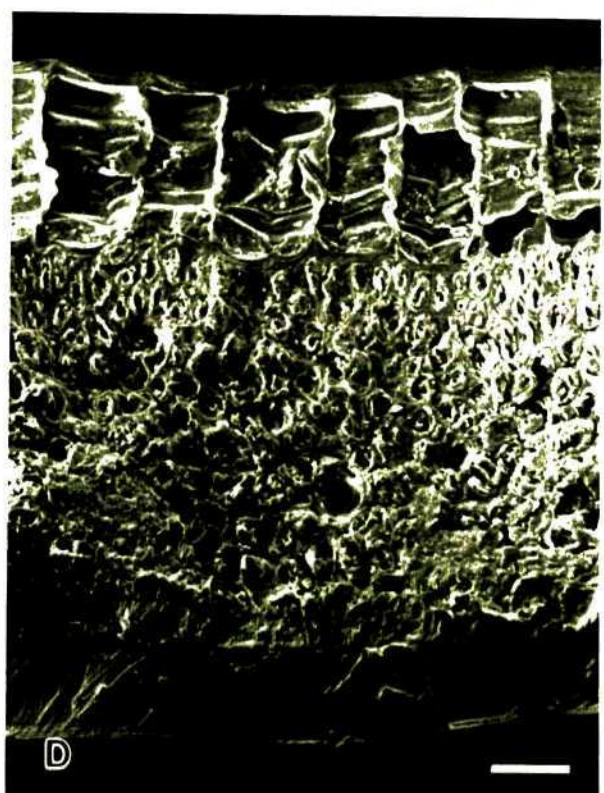
A



B



C



D

Figure 42.

Bolboschoenus medianus, Lepschi 1598 (CANB, NU).

Scanning electron micrographs of lenticular and trigonous nuts from within the same spikelet. A, lenticular nut in outline, abaxial surface uppermost; E, trigonous nut in outline, abaxial surface uppermost; B, F, surface topography; C, G, nuts in transverse section; D, H, pericarps in transverse section. . Scale bars A, E, C, G = 500 μm ; B, F, D, H = 25 μm .

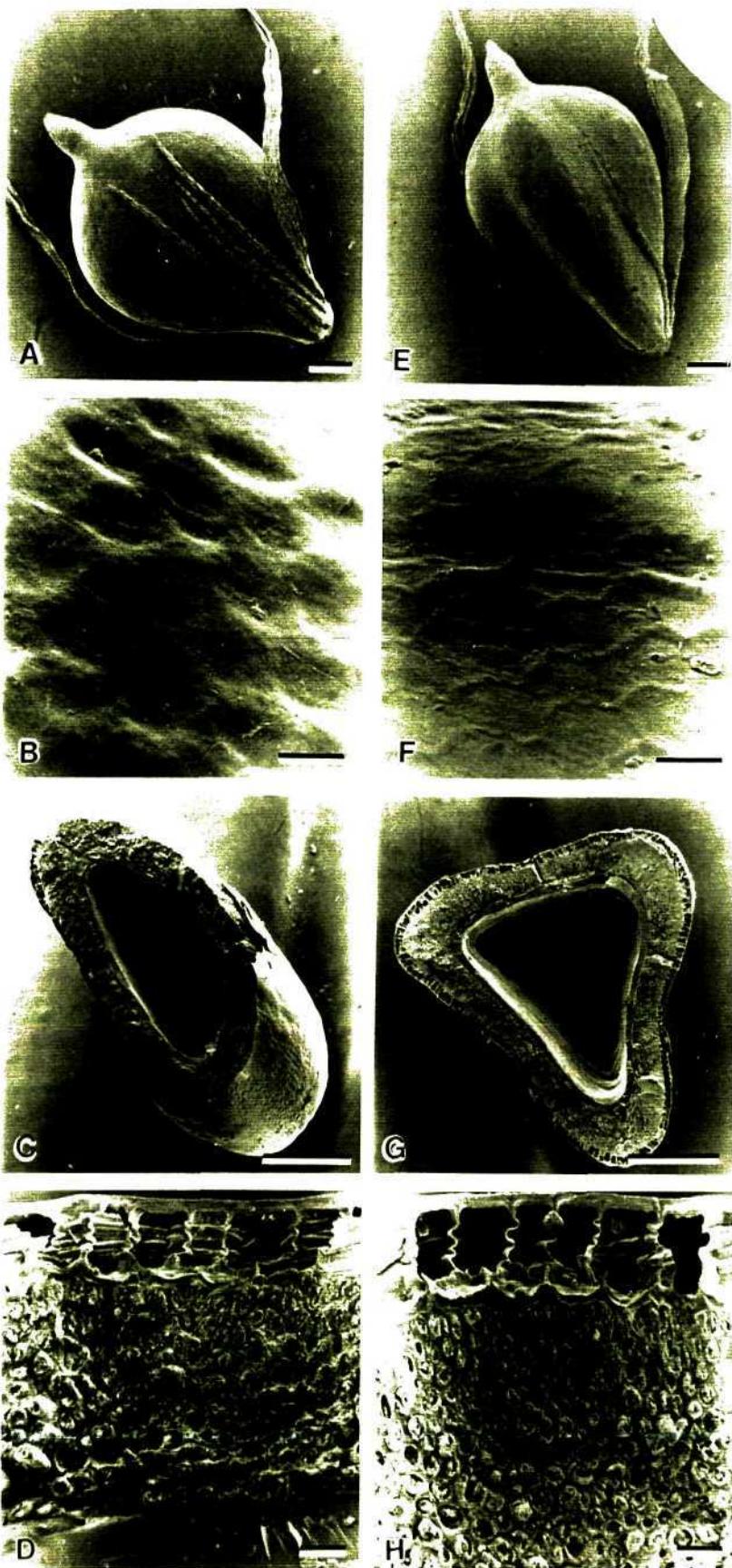


Figure 43.

Bolboschoenus glaucus, Healy & Hamlin 50/70 (K) (Duplicate of 82080 CHR). Scanning electron micrographs of fruit.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Note the pericarp construction of this specimen differs from that of typical *B. glaucus* in that the exocarp cells are slightly radially elongated.

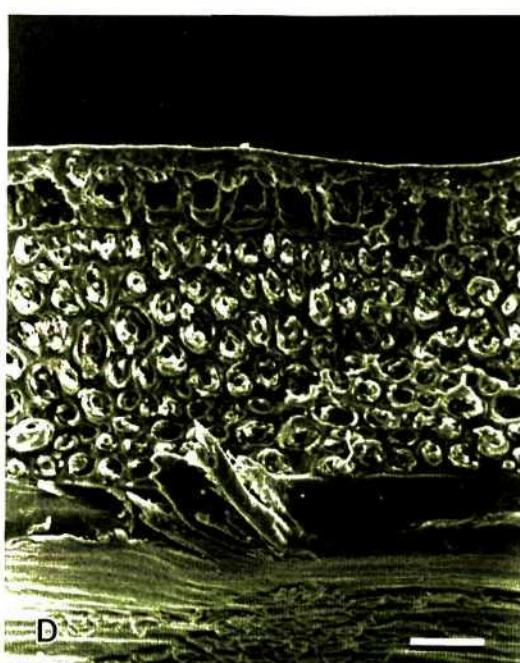
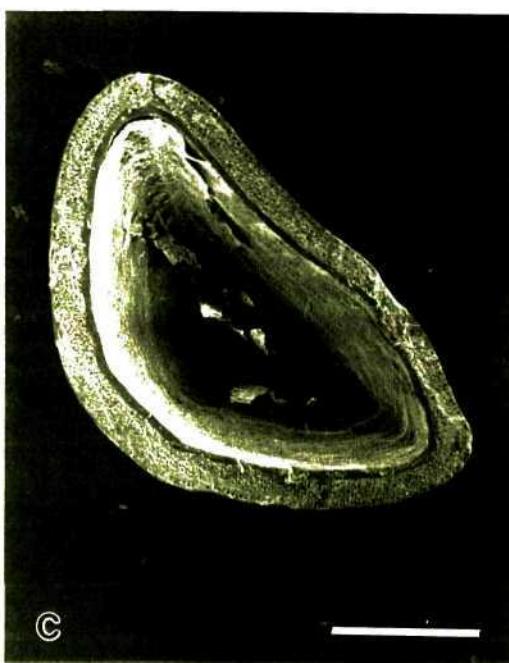
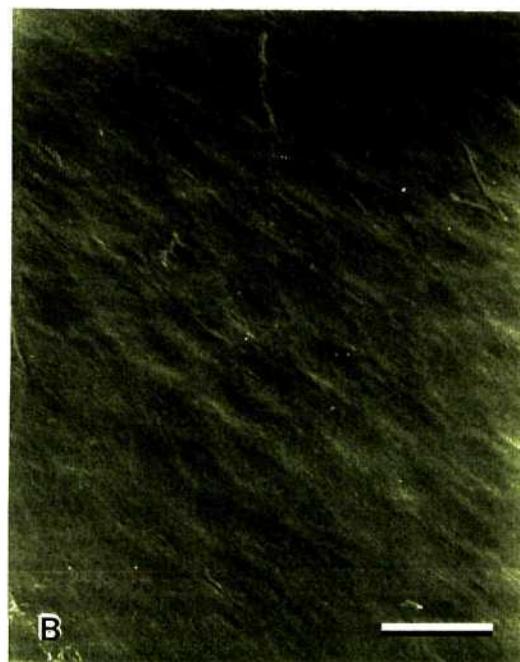
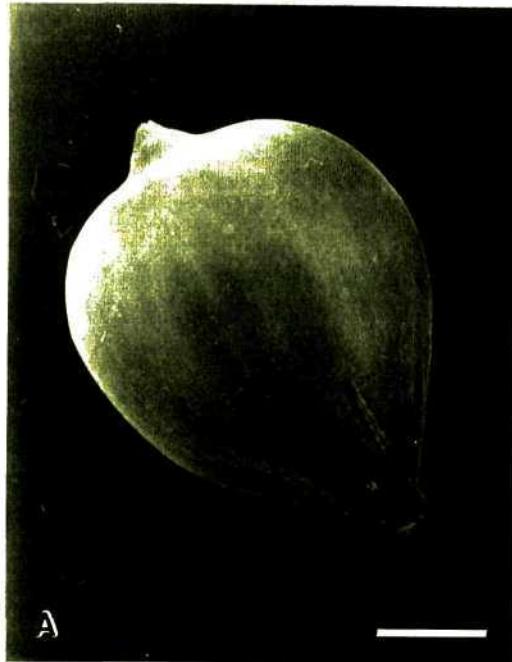


Figure 44.

Scirpus maritimus, LINN 71.44 (BM).

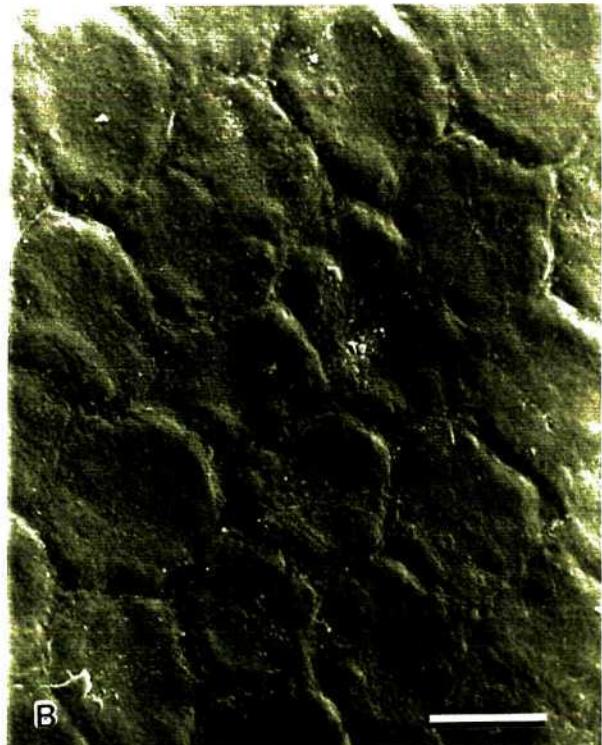
Scanning electron micrographs of fruits.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section;

D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .



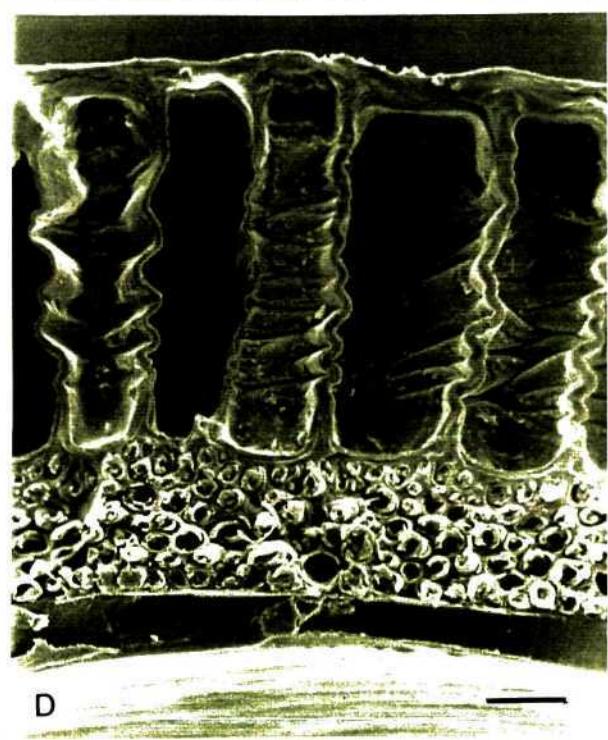
A



B



C



D

Figure 45.

Scirpus maritimus L., Sp. Pl. 1: 75. 1753.

Scanning electron micrographs of fruit of proposed **neolectotype**: *Orjan Nilsson* 9515 (H), Sweden; E. Uppland (Roslagen), par. Börstill, 2 km W Kallö near Husbacka. *

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. maritimus* (L.) Palla

Place and date of publication: In Koch, synops. Deutsch. Schweiz. Fl. ed. 3, 3: 2532. (1905).

Note: the lectotype of *Scirpus maritimus* L., selected by T. Koyama (1962: 932), U.S.A., Virginia, *John Clayton* 570 (LINN 71.43) is a specimen of (*Scirpus robustus* Pursh) = *Bolboschoenus robustus* (Pursh) Soják.

*Subsequent to submission of this thesis the apparently original Linnaean specimen from Roslagen has been located in the Celsius Herbarium at UPS.

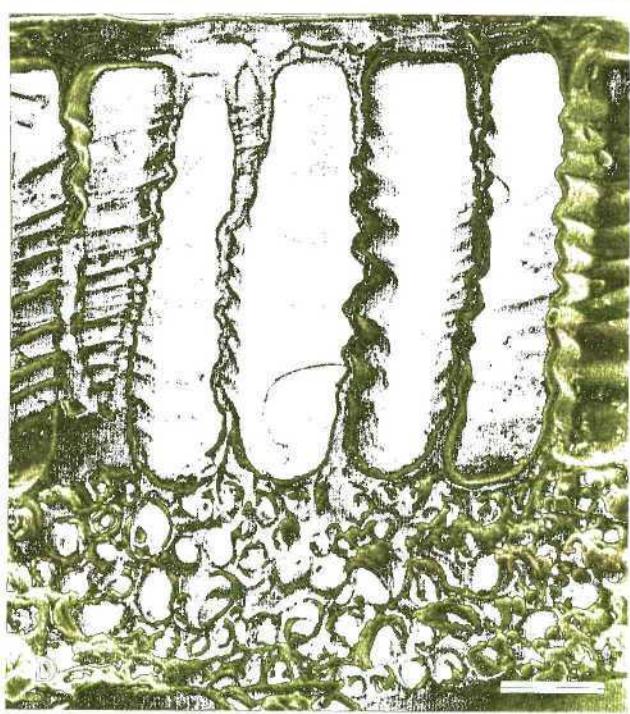
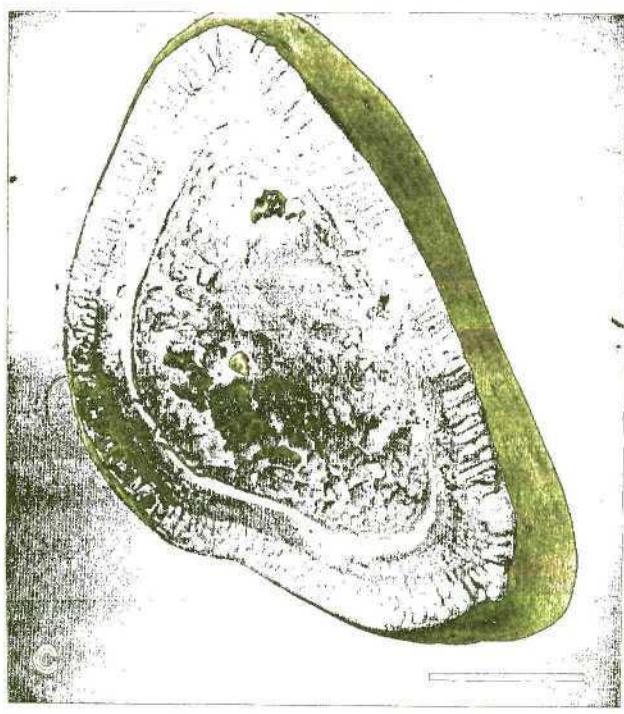
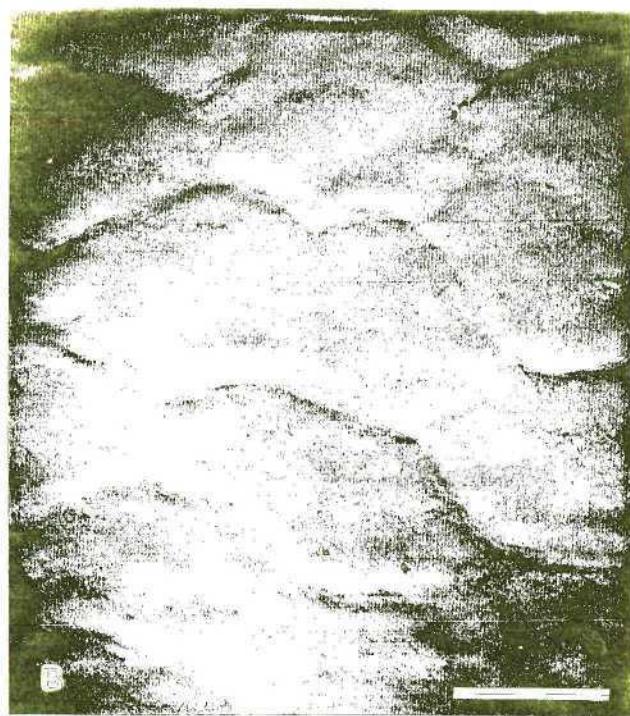
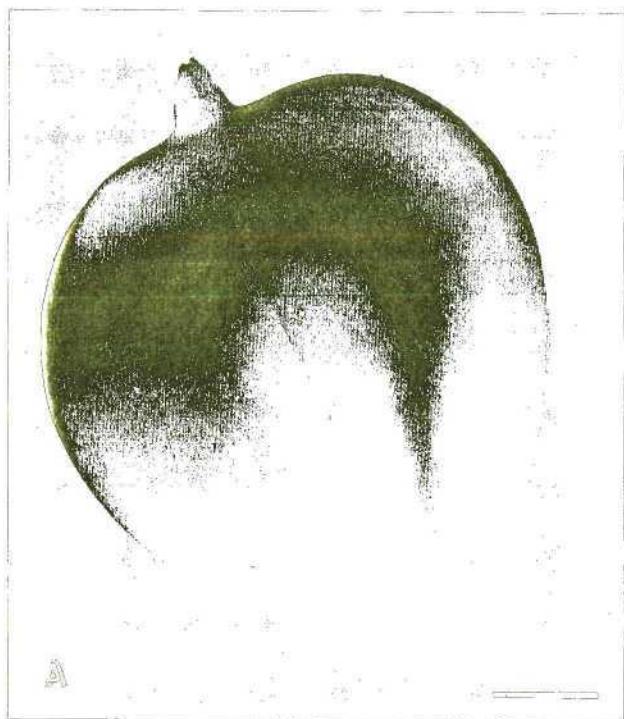


Figure 46.

Bolboschoenus maritimus, Groningen West E2.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial surfaces uppermost (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section, (scale bar = 500 μm); J--L, pericarps in transverse section (scale bar = 25 μm).

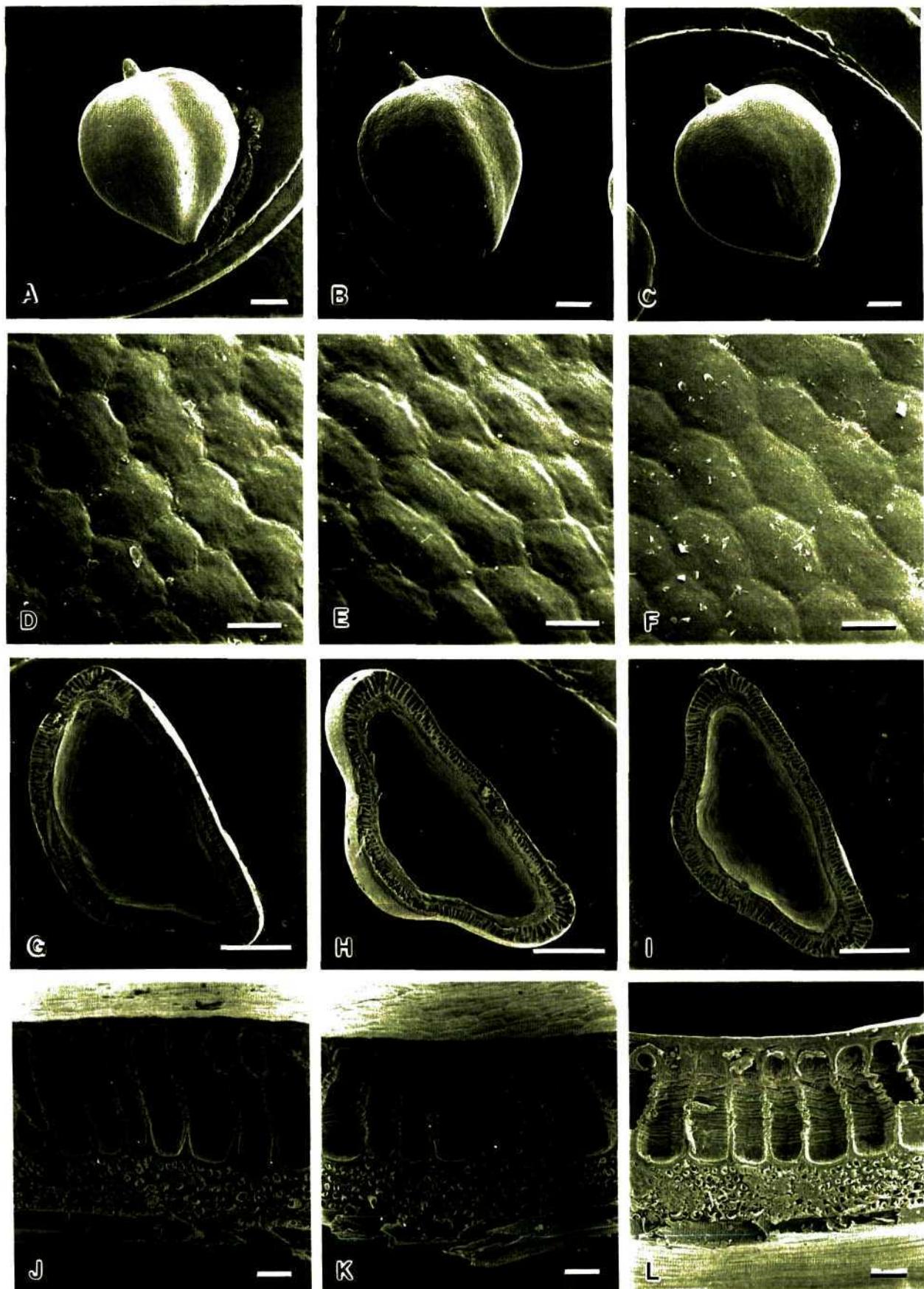


Figure 47.

Bolboschoenus maritimus, Haringvliet H4.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial surfaces uppermost (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section, (scale bar = 500 μm); J--L, pericarps in transverse section (scale bar = 25 μm).

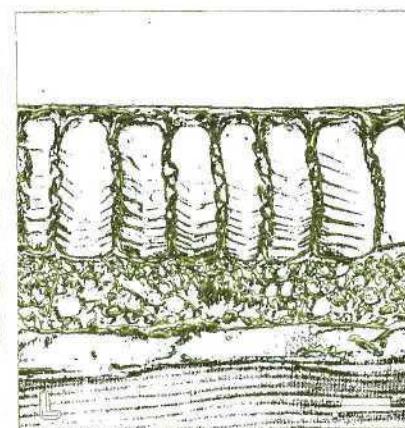
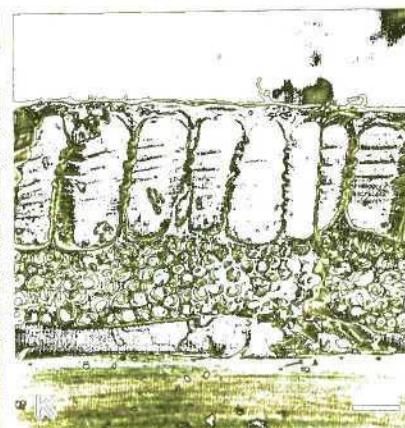
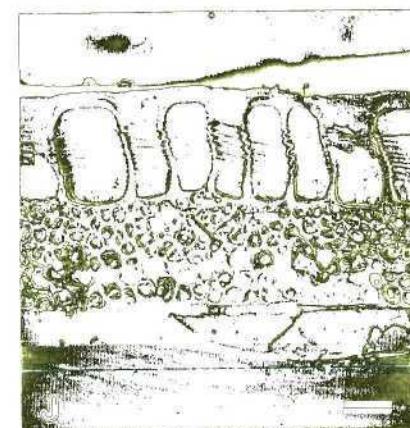
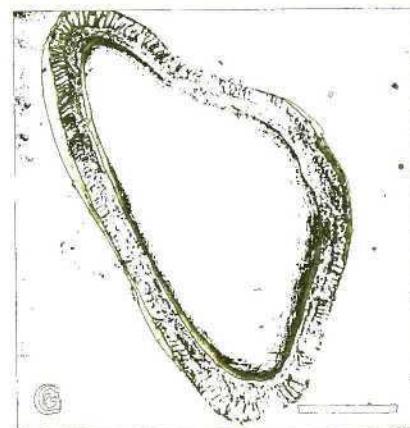
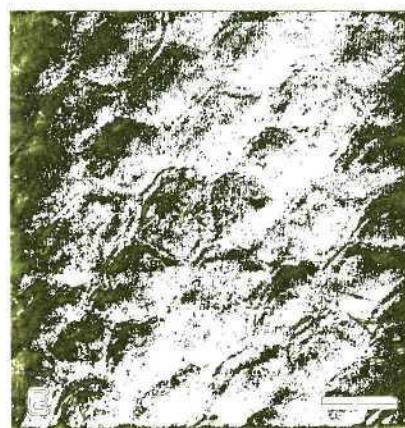


Figure 48.

Bolboschoenus maritimus, Punt van Reide R7.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial surfaces uppermost (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section, (scale bar = 500 μm); J--L, pericarps in transverse section (scale bar = 25 μm).

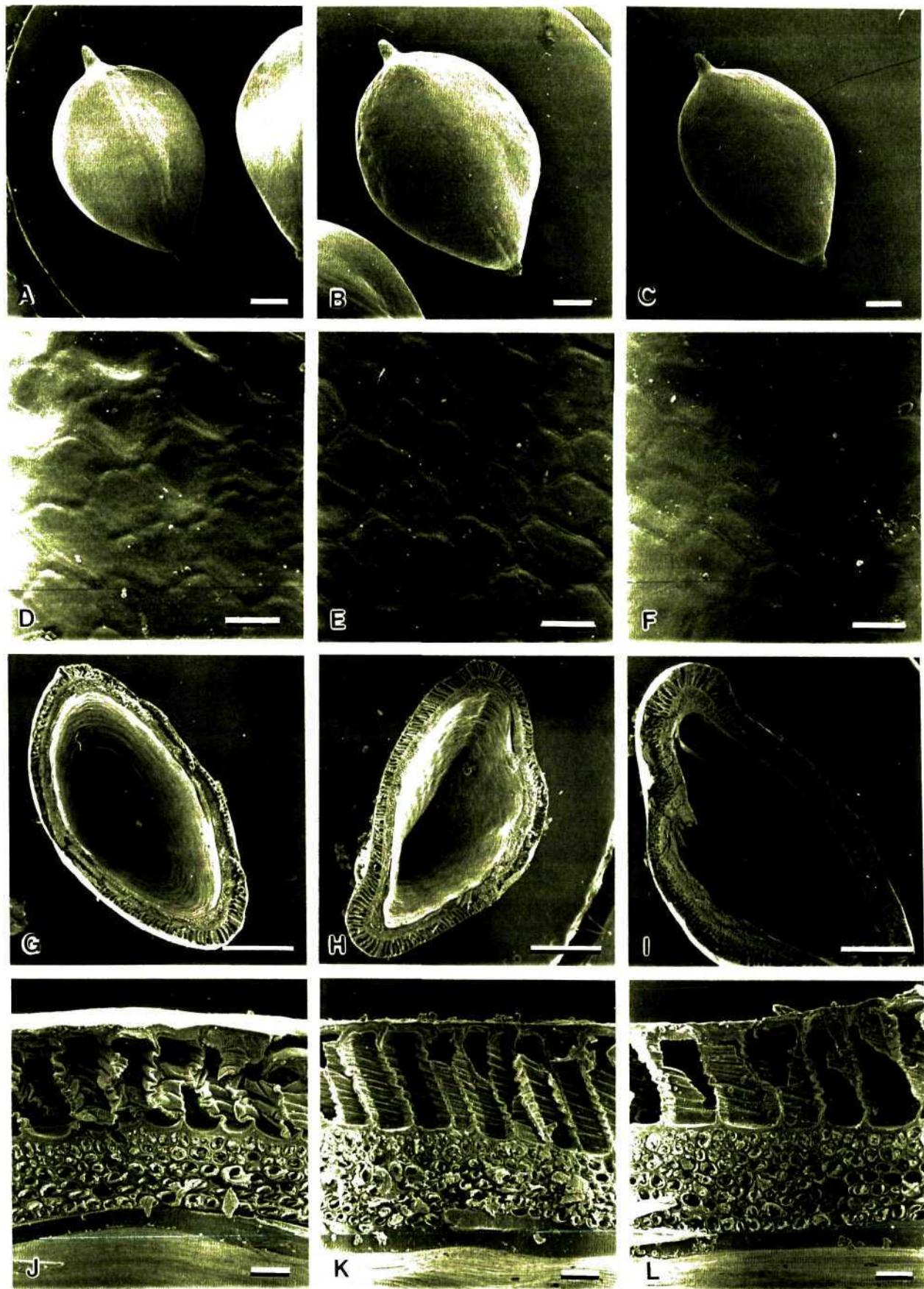


Figure 49.

Bolboschoenus maritimus, Biesbosch.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial surfaces uppermost (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section, (scale bar = 500 μm); J--L, pericarps in transverse section (scale bar = 25 μm).

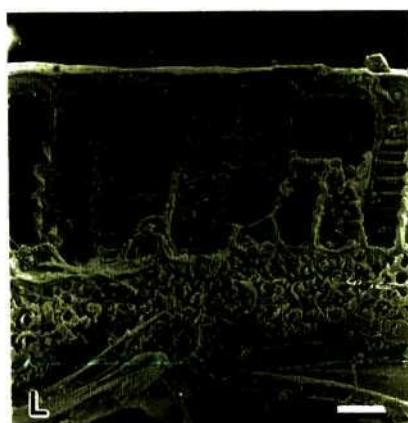
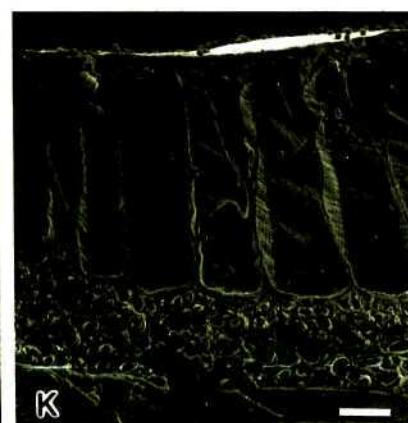
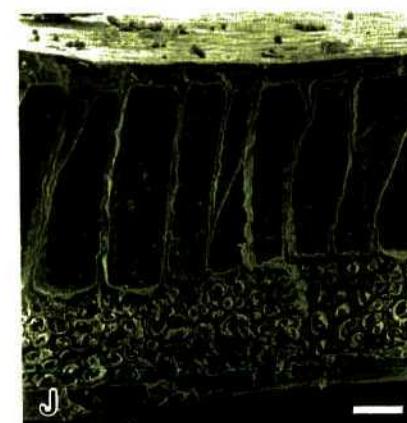
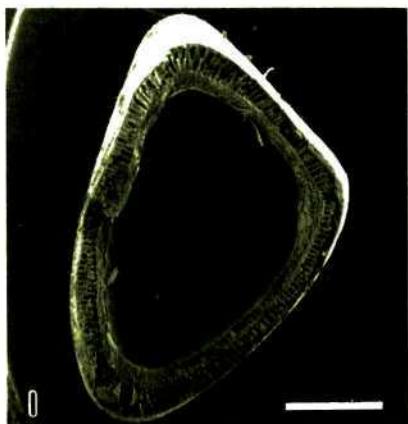
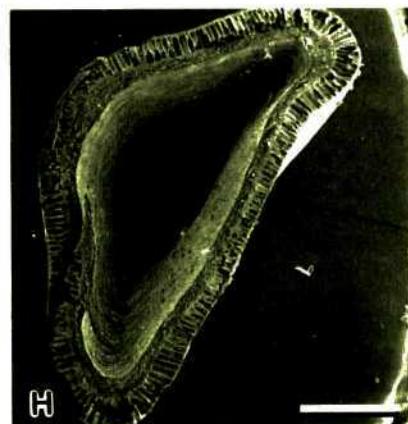
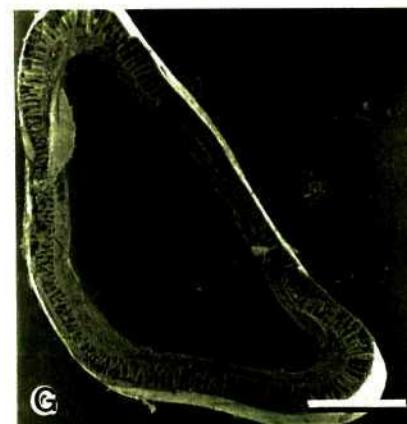
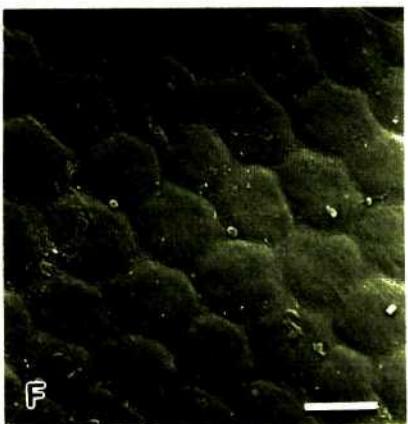
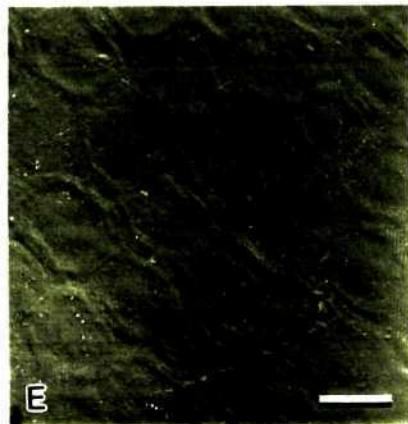
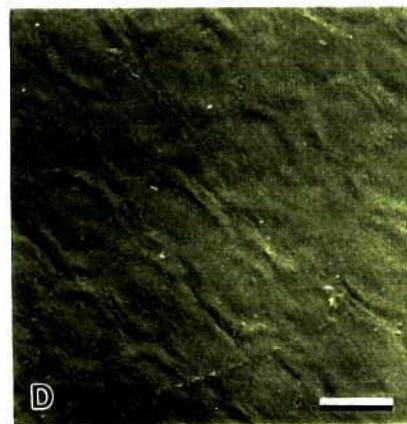
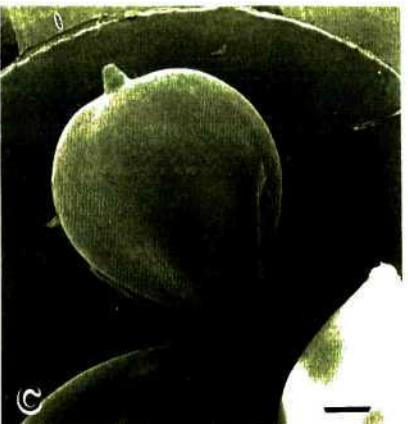
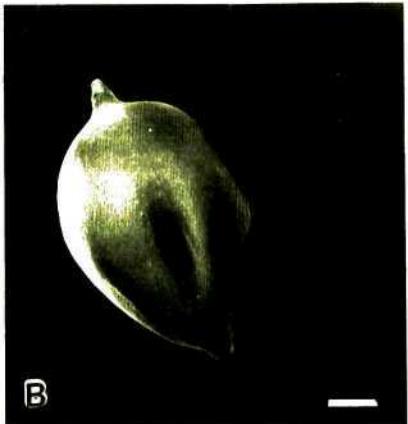
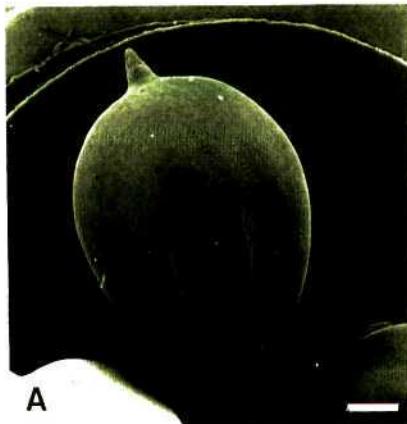


Figure 50.

Bolboschoenus maritimus, Maastrict.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial surfaces uppermost (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section, (scale bar = 500 μm); J--L, pericarps in transverse section (scale bar = 25 μm).

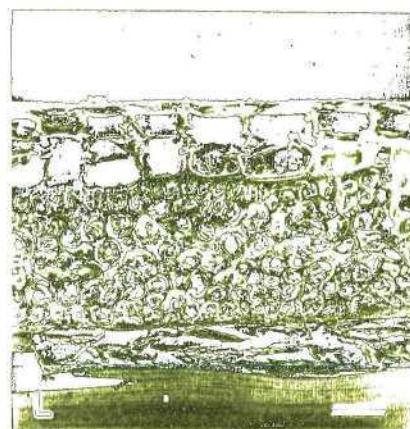
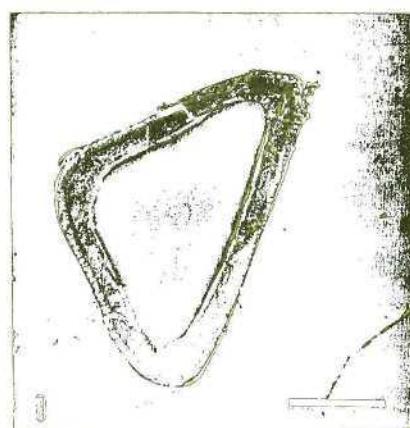
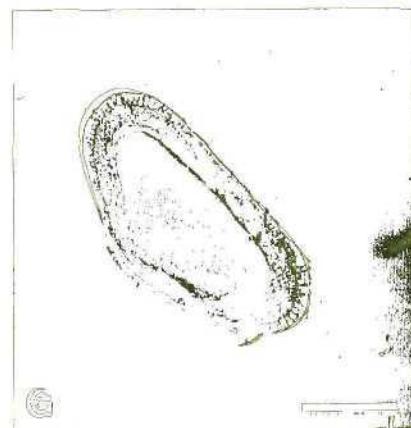
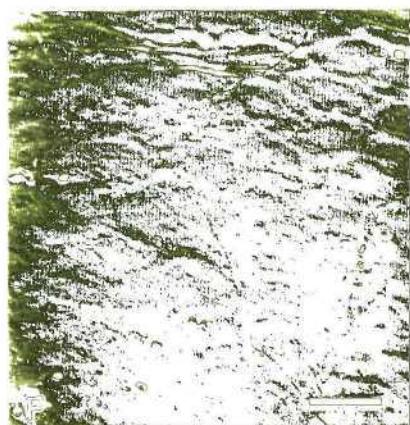
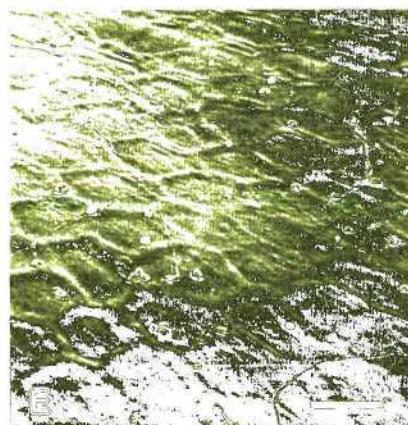
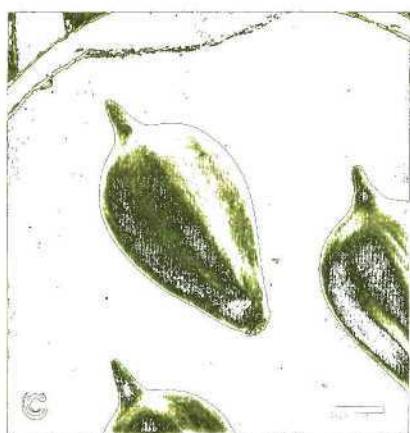


Figure 51.

Bolboschoenus maritimus, Schoonhoven L1.

Scanning electron micrographs of fruits.

A--C, nuts in outline, abaxial surfaces uppermost (scale bar = 500 μm); D--F, surface topography (scale bar = 25 μm); G--I, nuts in transverse section, (scale bar = 500 μm); J--L, pericarps in transverse section (scale bar = 25 μm).

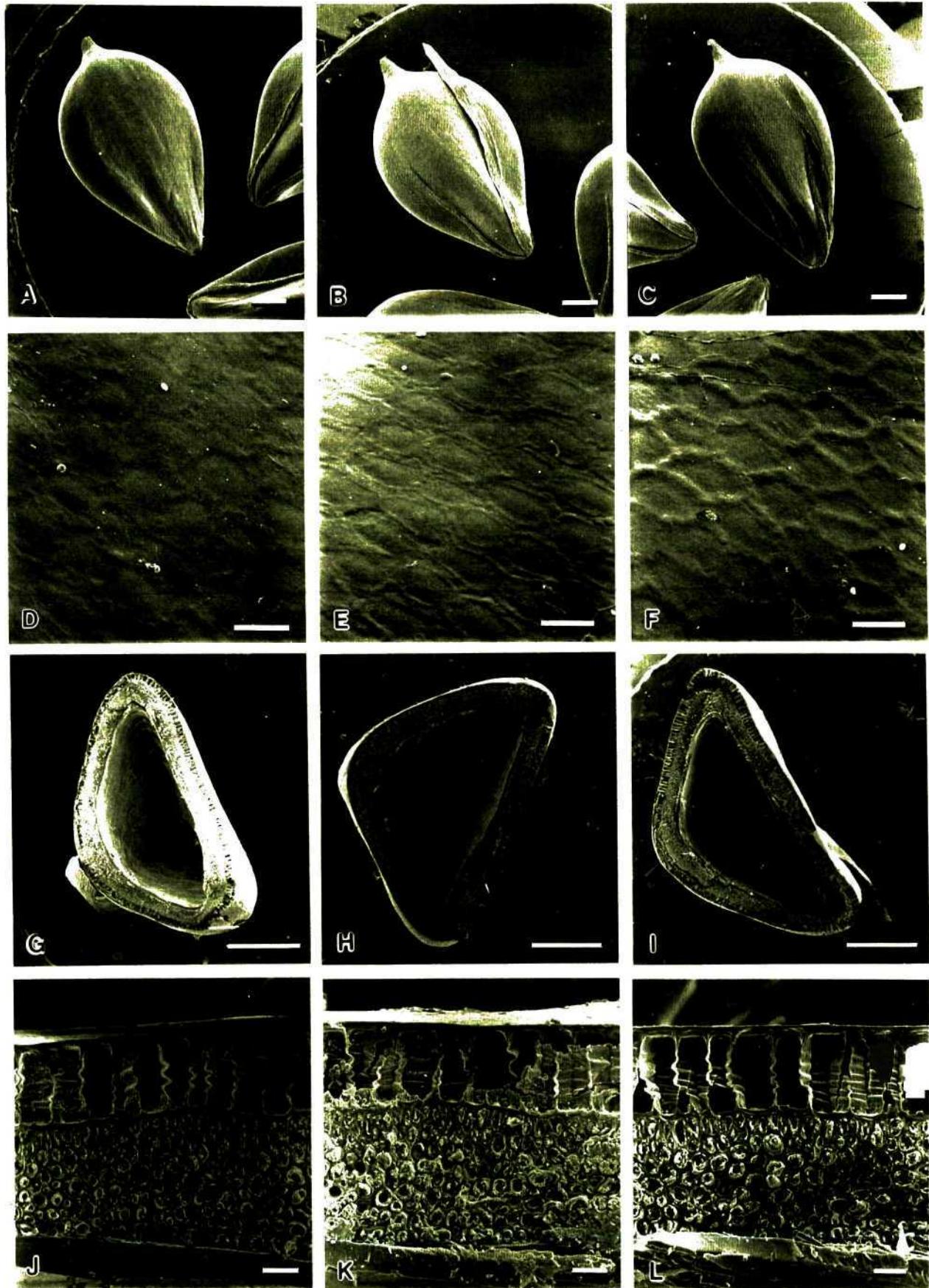


Figure 52.

Scirpus affinis Roth: In Roemer & Schultes, Syst. veg II (1817), p. 140.

Scanning electron micrographs of fruit of **neotype** (selected Norlindh 1972: 404) *Stocks, Law etc., s.n.(C)*, India orientalis. Malabar, Concan etc. Regio. Trop.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

Name under *Bolboschoenus*: *B. affinis* (Roth) Drobow

Place and date of publication: In Trav. Mus. bot. Acad. Pétersb. 16: 139 (1916).

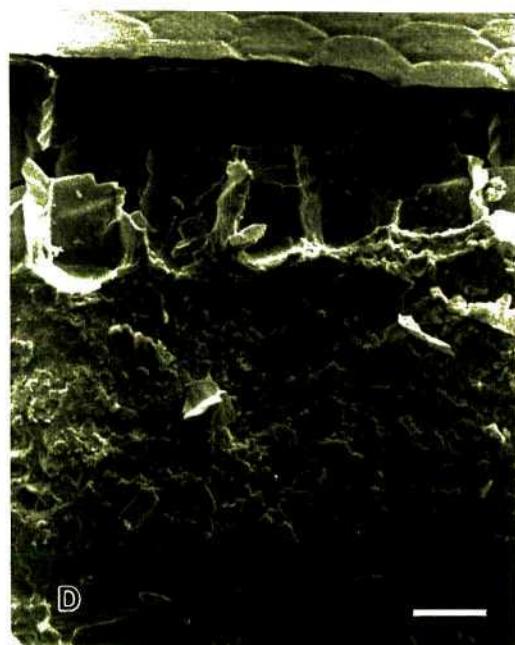
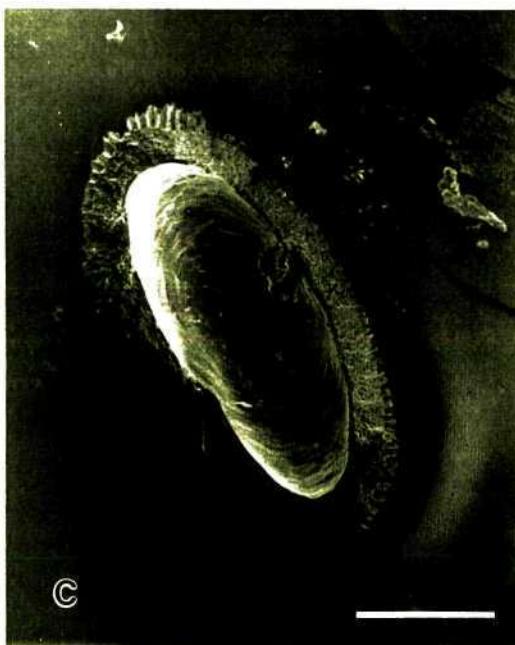
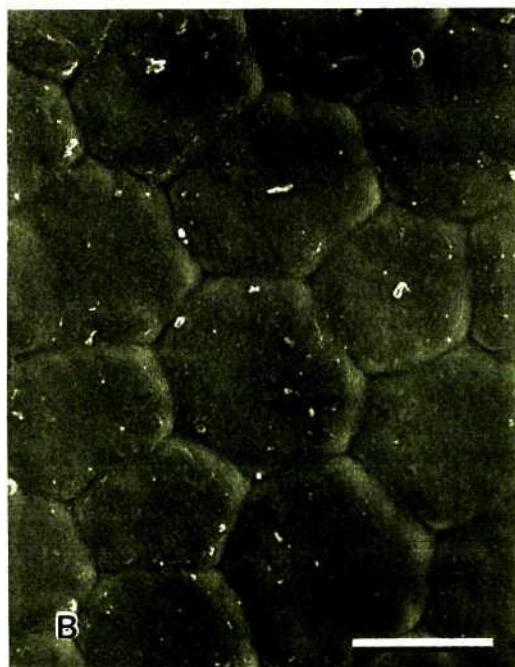
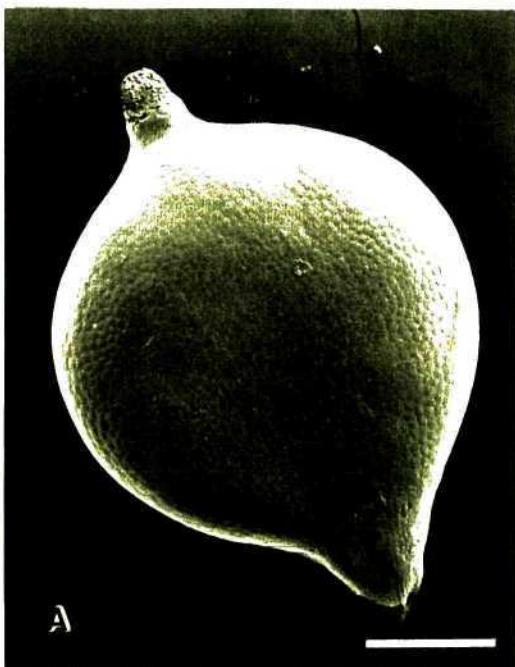


Figure 53.

Bolboschoenus affinis, Kukkonen 12727 (H).

Scanning electron micrographs of fruit.

A, nut in outline, abaxial surface uppermost; B, nut in transverse section; C, surface topography towards angle of nut; D, surface topography, abaxial surface; E, pericarp in transverse section at angle of nut; F, pericarp in transverse section, abaxial surface. Scale bars: A, B = 500 μm ; C--F = 25 μm .

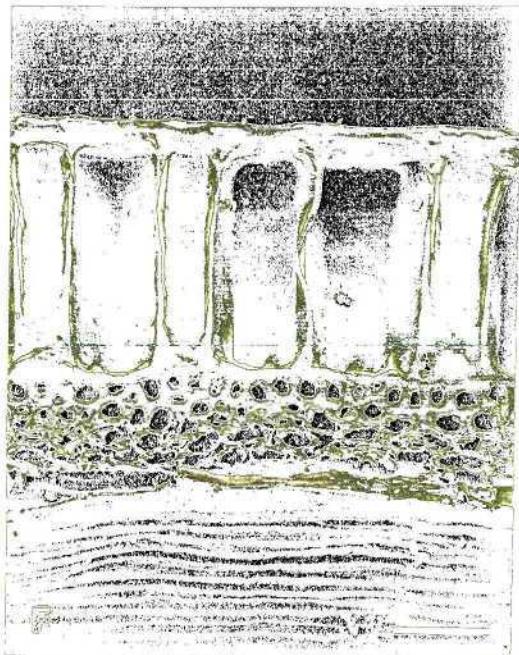
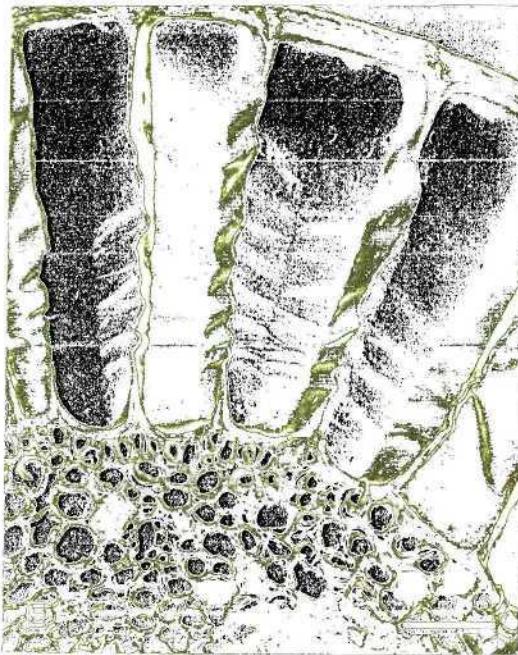
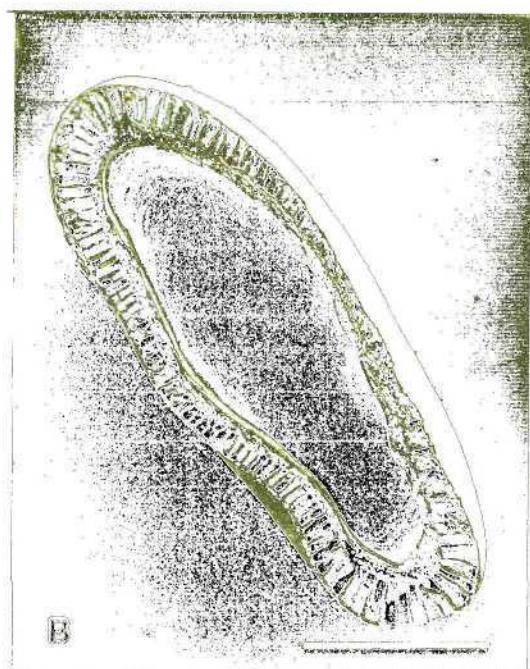
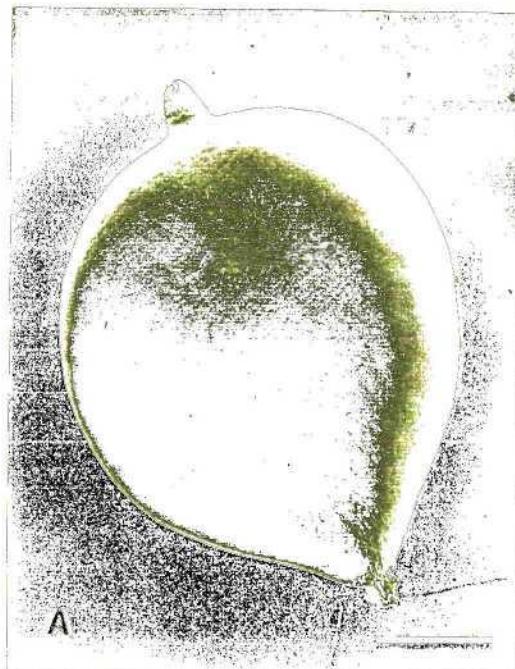


Figure 54.

B. maritimus s.l. x yagara :putative hybrids.

Scanning electron micrographs of fruits showing features of pericarp anatomy suggestive of intermediacy between putative parents.

A--D, *Charles Firket s.n.* (WIS); note variable surface topography in B, and radially elongated exocarp cells and wide mesocarp in D.

E--L, *F. Schuhwerk 86/490* (NY); note trigonous and lenticular nuts in same clone (G, K); also variable surface topography (F, J).

A, E, I, nuts in outline, abaxial surfaces uppermost; B, F, J, surface topography; C, G, K, nuts in transverse section; D, H, L, pericarps in transverse section. Scale bars: A, C, E, G, I, K = 500 μm ; B, D, F, H, J, L = 25 μm .

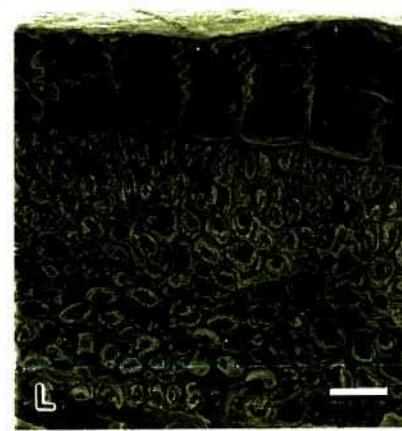
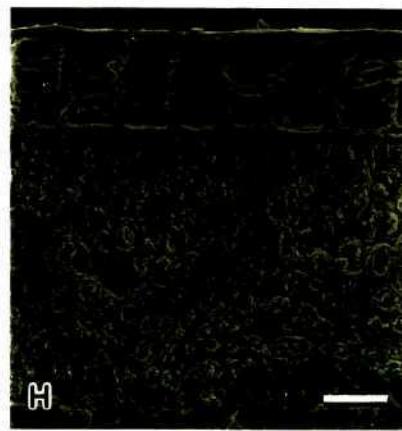
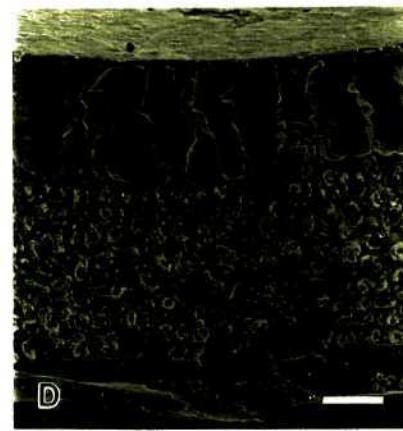
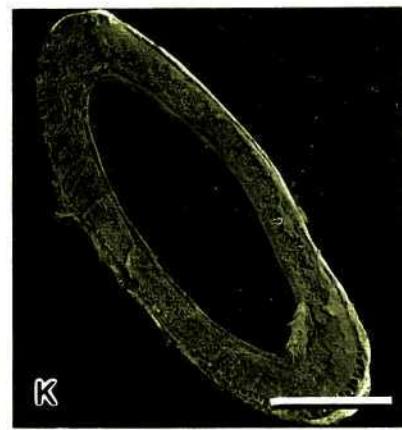
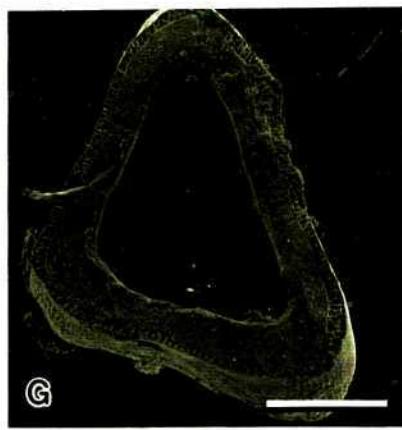
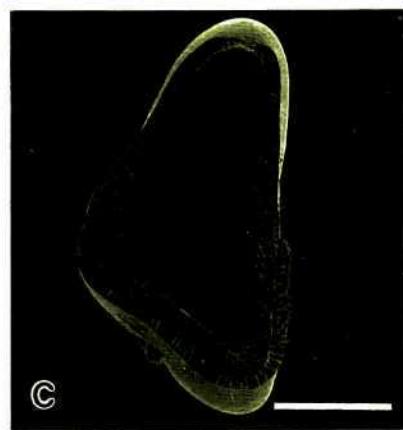
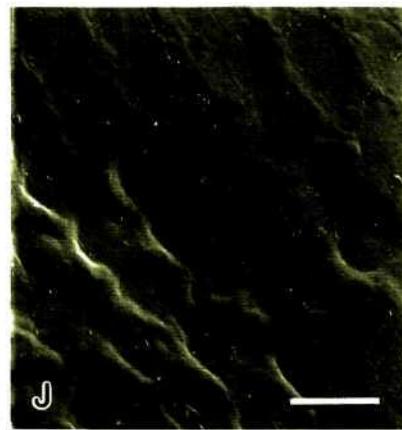
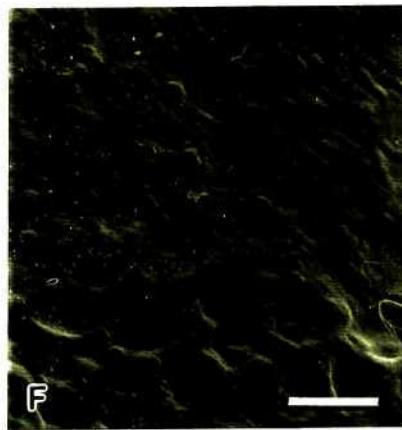
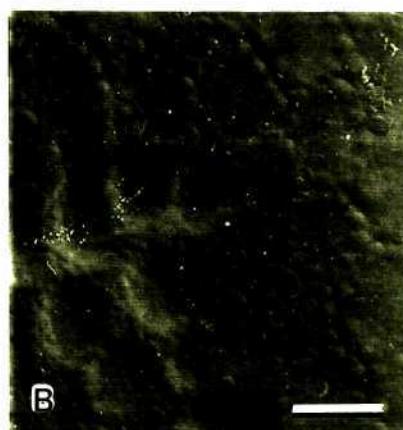
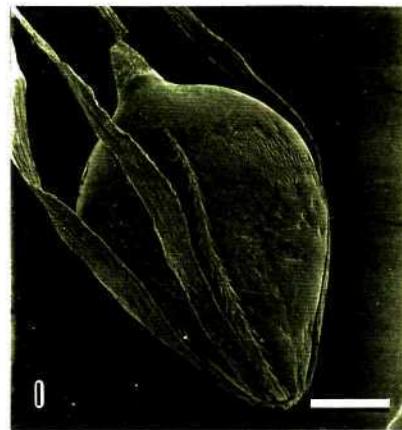
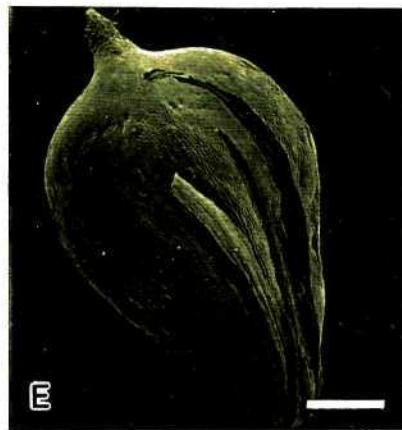
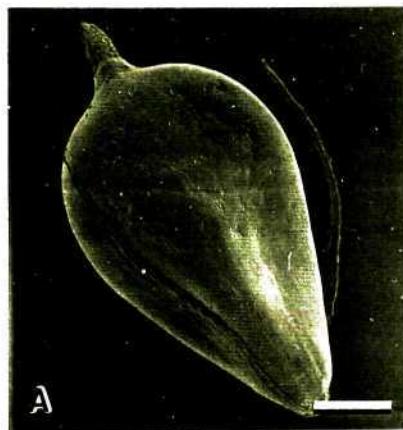


Figure 55.

Bolboschoenus planiculmis, Koyama (?) 3197 (NY) ex Herb. T. Koyama, det. T. Koyama.

Scanning electron micrographs of fruit.

A, nut in outline, abaxial surface uppermost; B, surface topography; C, nut in transverse section; D, pericarp in transverse section. Scale bars: A, C = 500 μm ; B, D = 25 μm .

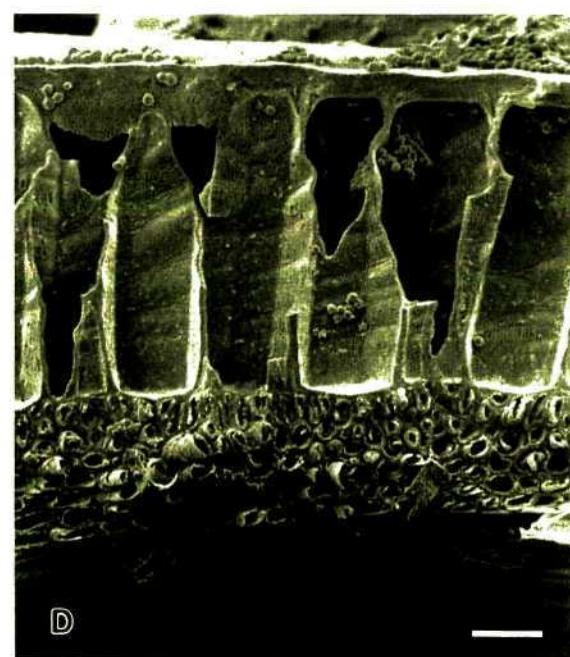
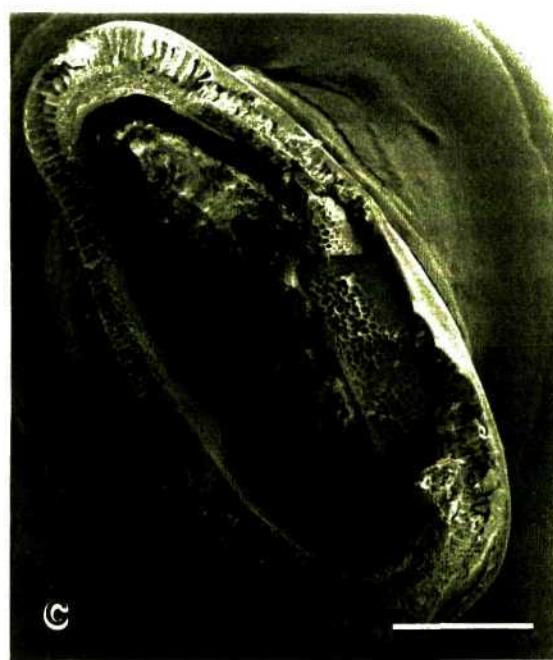
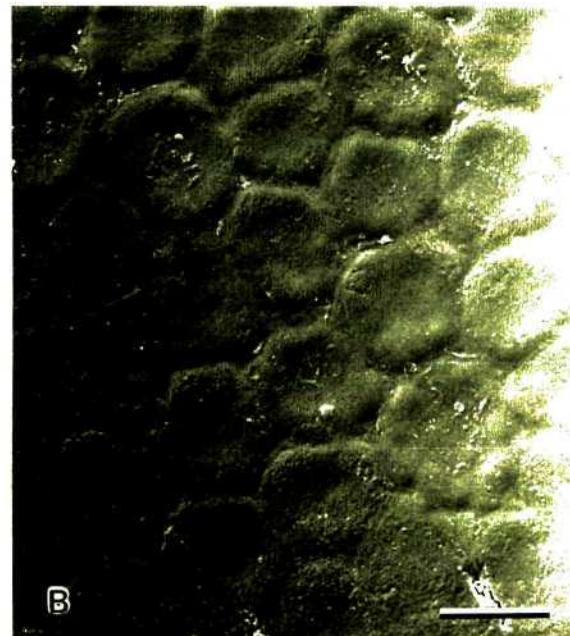
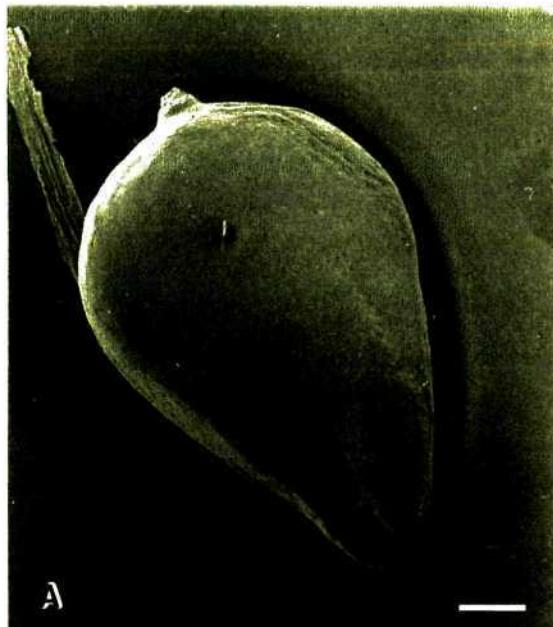
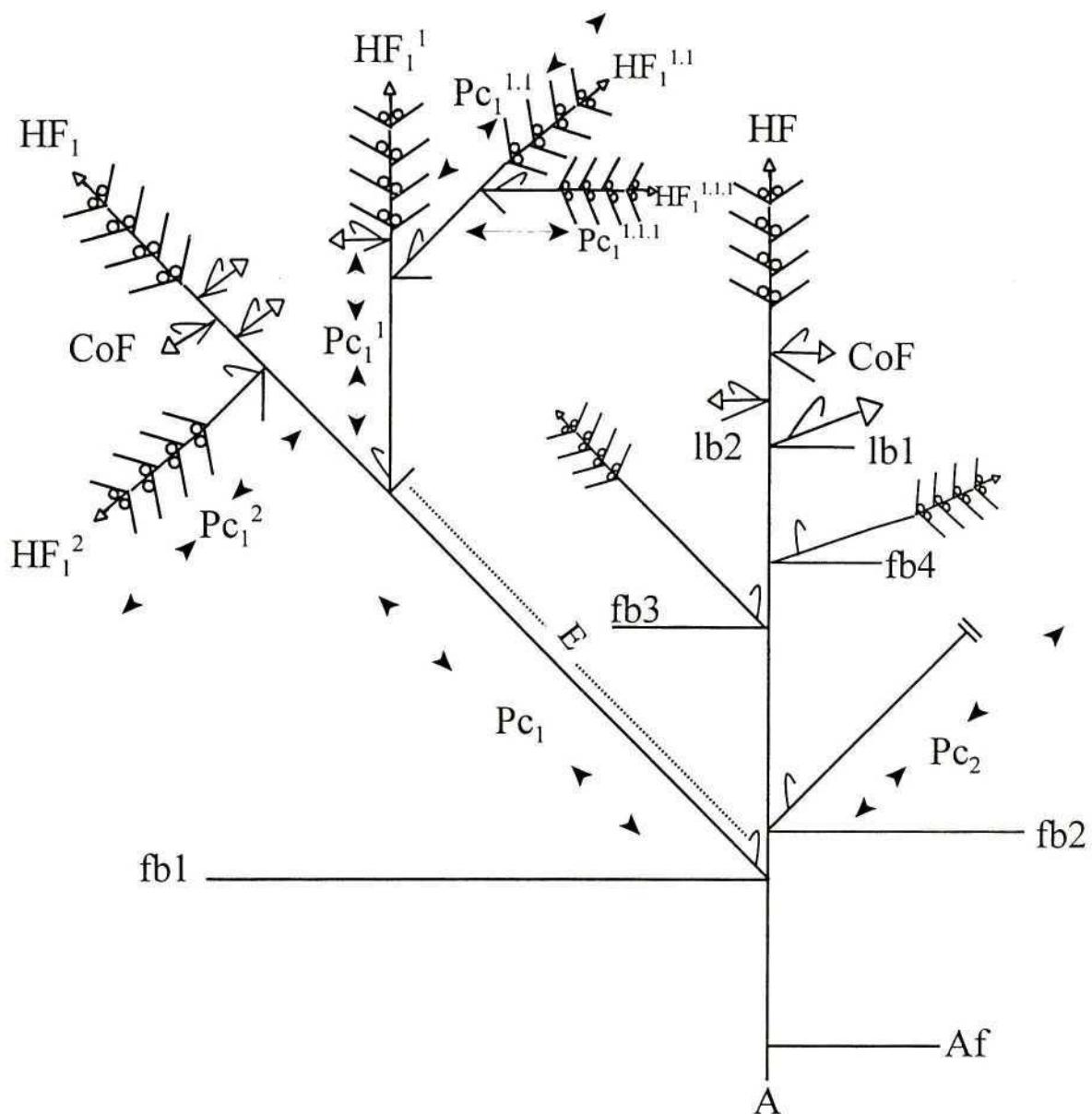


Figure 56.

Bolboschoenus: inflorescence structure: a diagrammatic, representation of a portion of the most complex construction encountered with branching of first to fourth orders. Note that for the purpose of simplification : 1. only four paracladia arising from the main culm axis have been shown; 2. the number of coflorescences arising from the main axis has been reduced to three; 3. paracladium 2 has been severed; it has a construction comparable with that of paracladium 1; 4. paracladia 3 and 4 from the main axis (not numbered in diagram) have been reduced in complexity.



A = culm axis

Af = uppermost culm leaf

fb₁, fb₂, fb₃ etc = foliaceous bracts

lb₁, lb₂ etc = laminar bracts

HF = main, terminal, central partial fluorescence

HF₁ = main fluorescence of paracladium 1

PC₁ = paracladium 1 (first order branch)

PC₂ = paracladium 2 (first order branch)

PC₁¹ = paracladium (second order branch)

PC₁^{1.1} = paracladium (third order branch)

PC₁^{1.1.1} = paracladium (fourth order branch)

CoF = spikelet, prophyll + subtending bract

E = epipodium (= ray or peduncle)

△ = spikelet bud

○ = potential or developed bisexual floret

Figure 57.

Bolboschoenus: graphic representations of inflorescence morphology for use with glossary.

T1, *B. glaucus*: proximal part of main axis of inflorescence showing one foliose and two laminar bracts, three epipodia (severed) and associated pulvinate cladoprophylls.

Note epipodia lie at right angles to main axis (usual in *B. glaucus*).

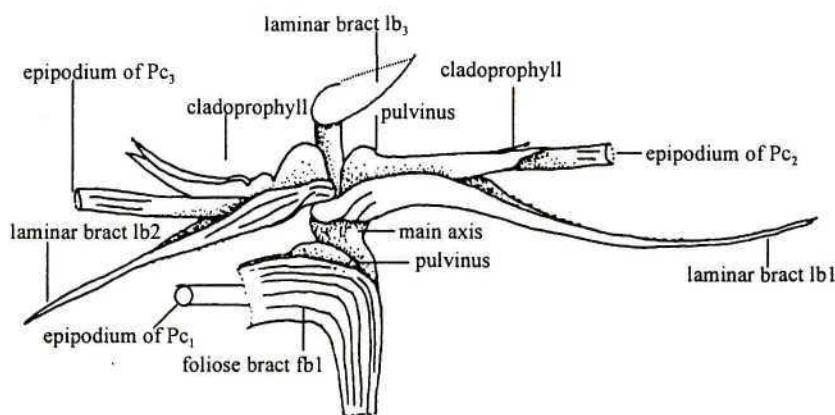
T2, *B. glaucus*: partial lateral florescence of paracladium, showing main florescence HF and two coflorescences (one removed) with associated glumaceous bracts and prophylls.

T3, *B. glaucus*: paracladium showing cladoprophyll, epipodium, main florescence and one coflorescence.

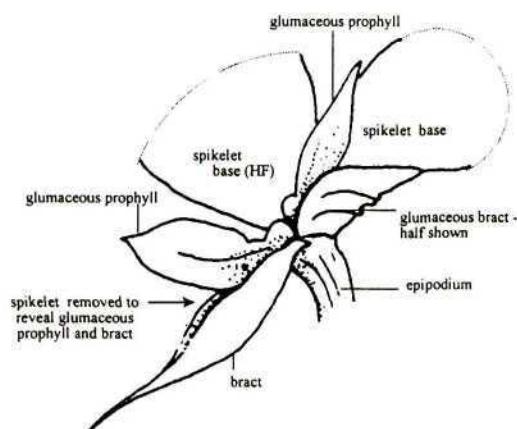
T4, *B. maritimus*: inflorescence consisting of main florescence HF, one coflorescence with laminar bract and prophyll and one paracladium with cladoprophyll and epipodium. Note angle of epipodium = less than right angle (usual in *B. maritimus s.s.*).

T5, *B. maritimus*: paracladium bearing one spikelet; glumaceous bract turned back to reveal axillary bud with recognisable prophyll.

Drawings not to scale.



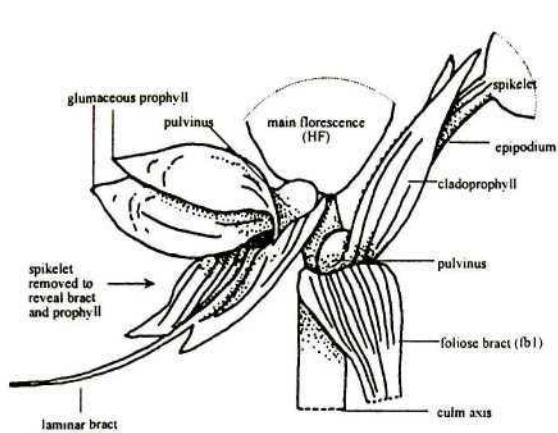
T1



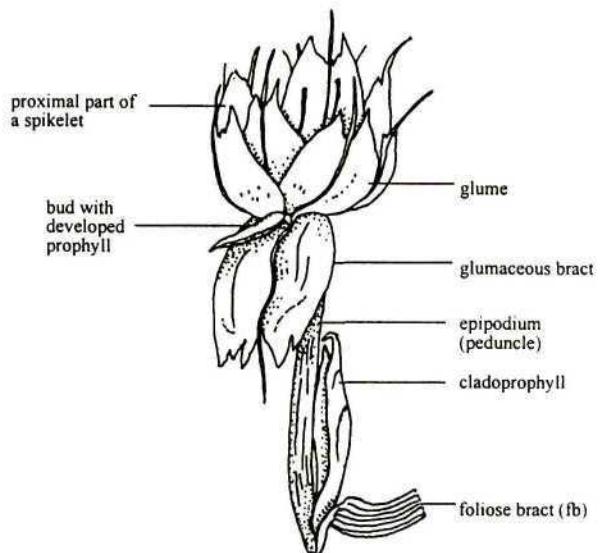
T2



T3



T4



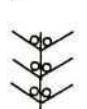
T5

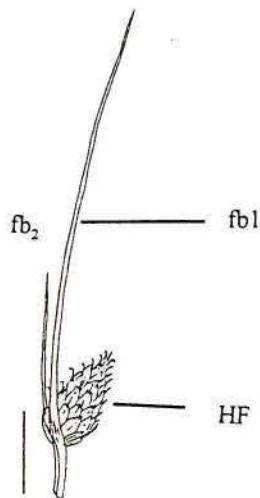
Figure 58.

Bolboschoenus maritimus s.s.: inflorescence of one spikelet.

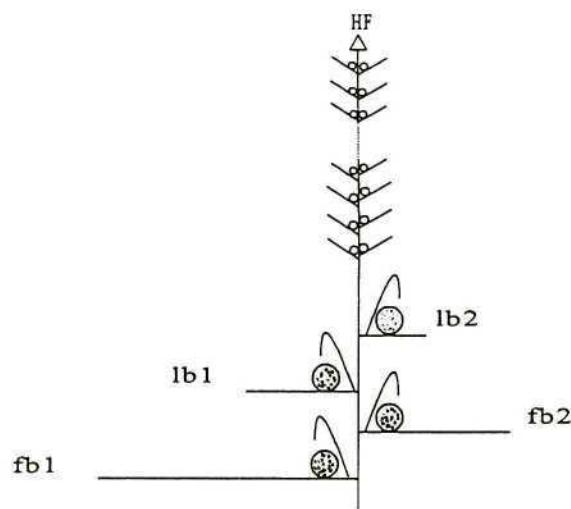
A₁ - in lateral view; A₂ - diagrammatic representation of dissection of this.

A₁, Browning 814 (NU). Scale bar = 20 mm.

- bract
- fb = foliose bract
- lb = laminar bract
- branch bud
- △ spikelet bud
- / glume
-  part of spikelet
- ↑ prophyll
- floret
- abortive floret
-  HF = main florescence
CoF = coflorescence



A₁

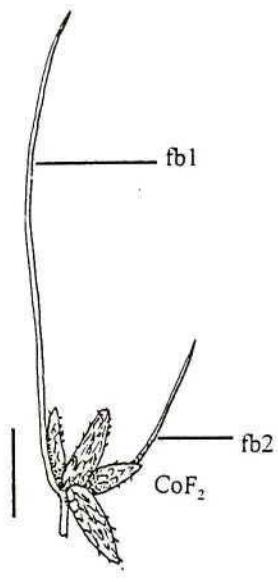


A₂

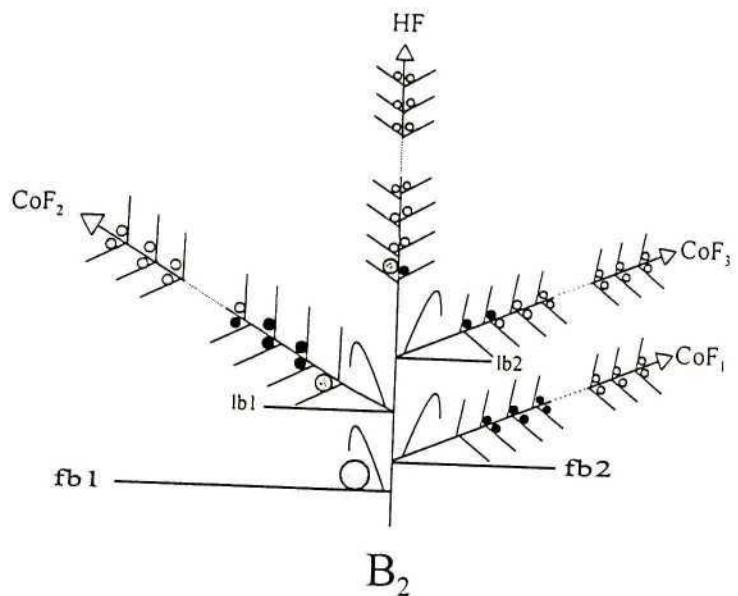
Figure 59.

Bolboschoenus maritimus s.s.: inflorescences representative of contracted heads; B_1 , of four spikelets; C_1 , of two spikelets; D_1 , of three spikelets; B_2 , C_2 , D_2 , diagrammatic representations of dissections of these. B_1 , *Browning 815 (NU)*; C_1 , D_1 , *Browning 814 (NU)*. Scale bar = 20 mm.

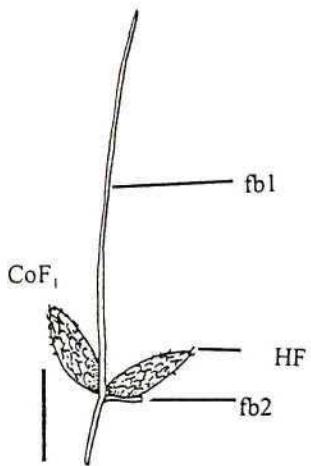
- bract
- fb = foliose bract
- lb = laminar bract
- branch bud
- △ spikelet bud
- / glume
-  part of spikelet
- ↑ prophyll
- floret
- abortive floret
-  CoF = coflorescence
- HF = main florescence



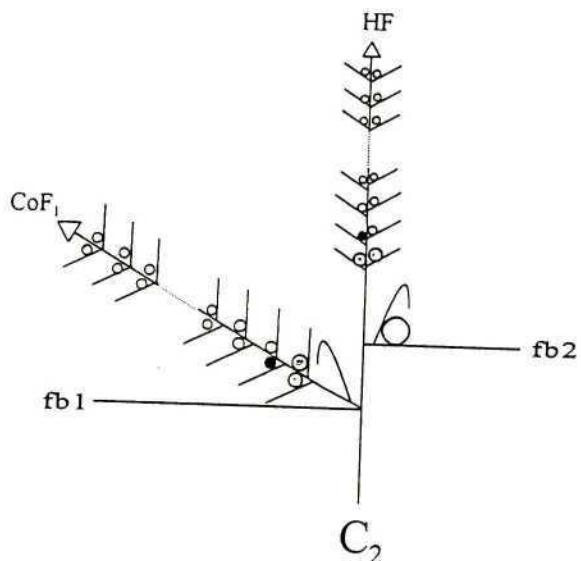
B₁



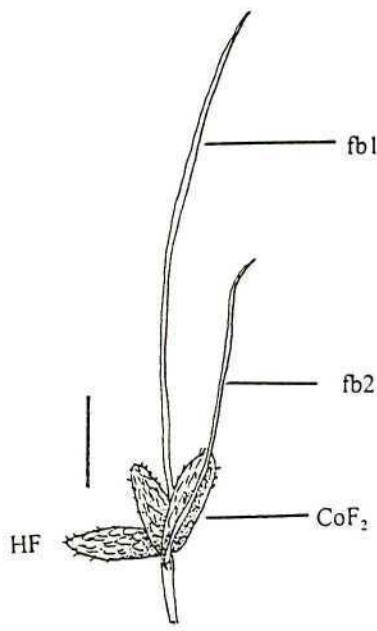
B₂



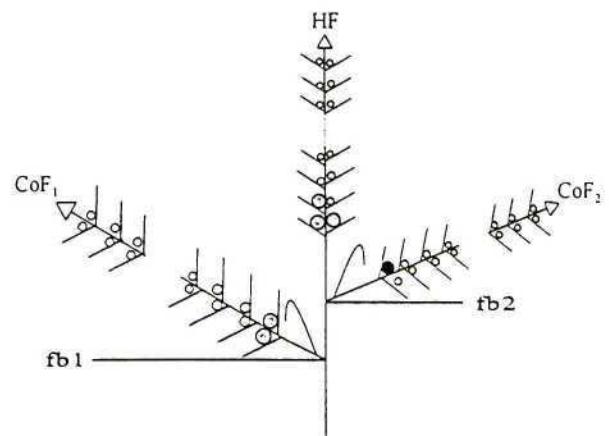
C₁



C₂



D₁

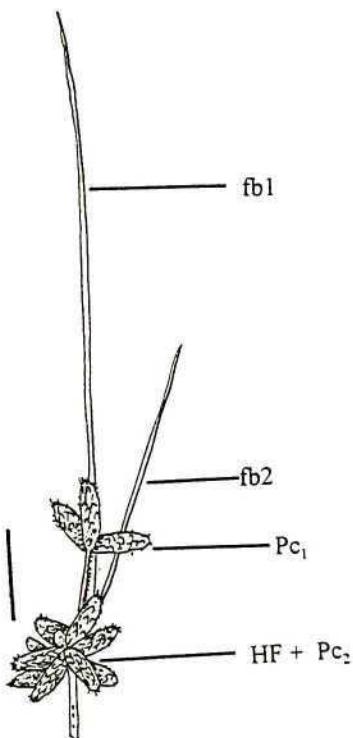


D₂

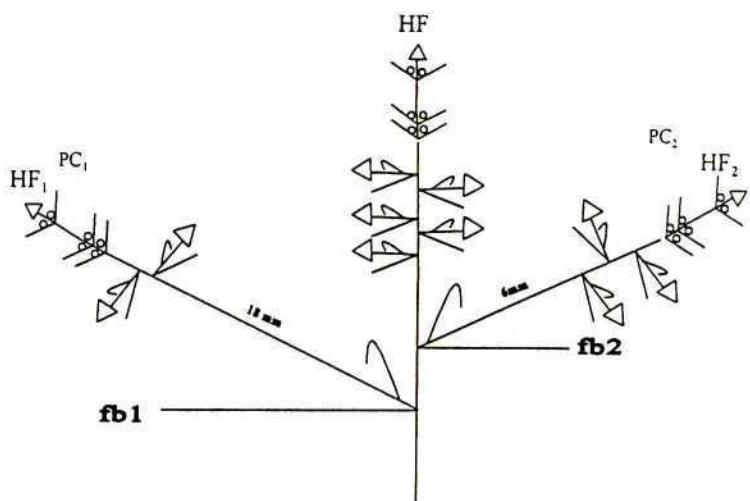
Figure 60.

Bolboschoenus maritimus s.s.: inflorescence representative of the few-rayed anhelodium; E₁, example with two rays (short ray obscured); E₂, diagrammatic representation of dissection of this. E₁, Browning 817 (NU). Scale bar = 20 mm.

- bract
- fb = foliose bract
- lb = laminar bract
- branch bud
- △ spikelet bud
- / glume
-  part of spikelet
- Pc₁, Pc₂ = paracladia
of main axis
- ⌞ prophyll
- floret
- abortive floret
-  CoF = coflorescence
- HF = main florescence



E₁

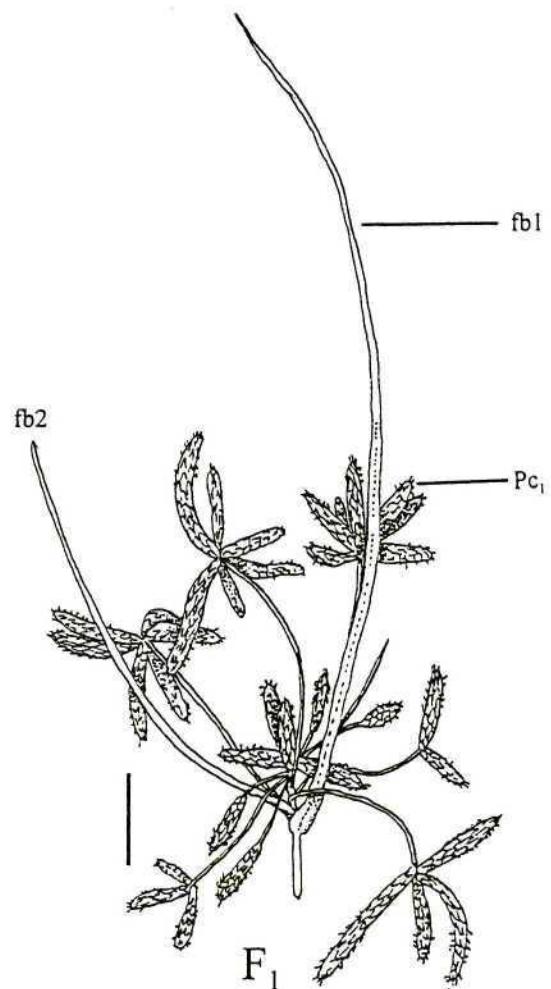


E₂

Figure 61.

Bolboschoenus glaucus: inflorescence representative of the many-rayed anthelodium; F_1 , example with ten rays; F_2 , diagrammatic representation of dissection of this. F_1 , Johnson s.n. (NU) Senegal, West Africa. Scale bar = 20 mm.

- bract
- fb = foliose bract
- lb = laminar bract
- branch bud
- △ spikelet bud
- / glume
-  part of spikelet
- Pc₁, Pc₂ etc. = paracladia
of main axis
- ⌞ prophyll (cladopropyl or
glumaceous)
- floret
- abortive floret
-  CoF = coflorescence
- HF = main florescence



F₁

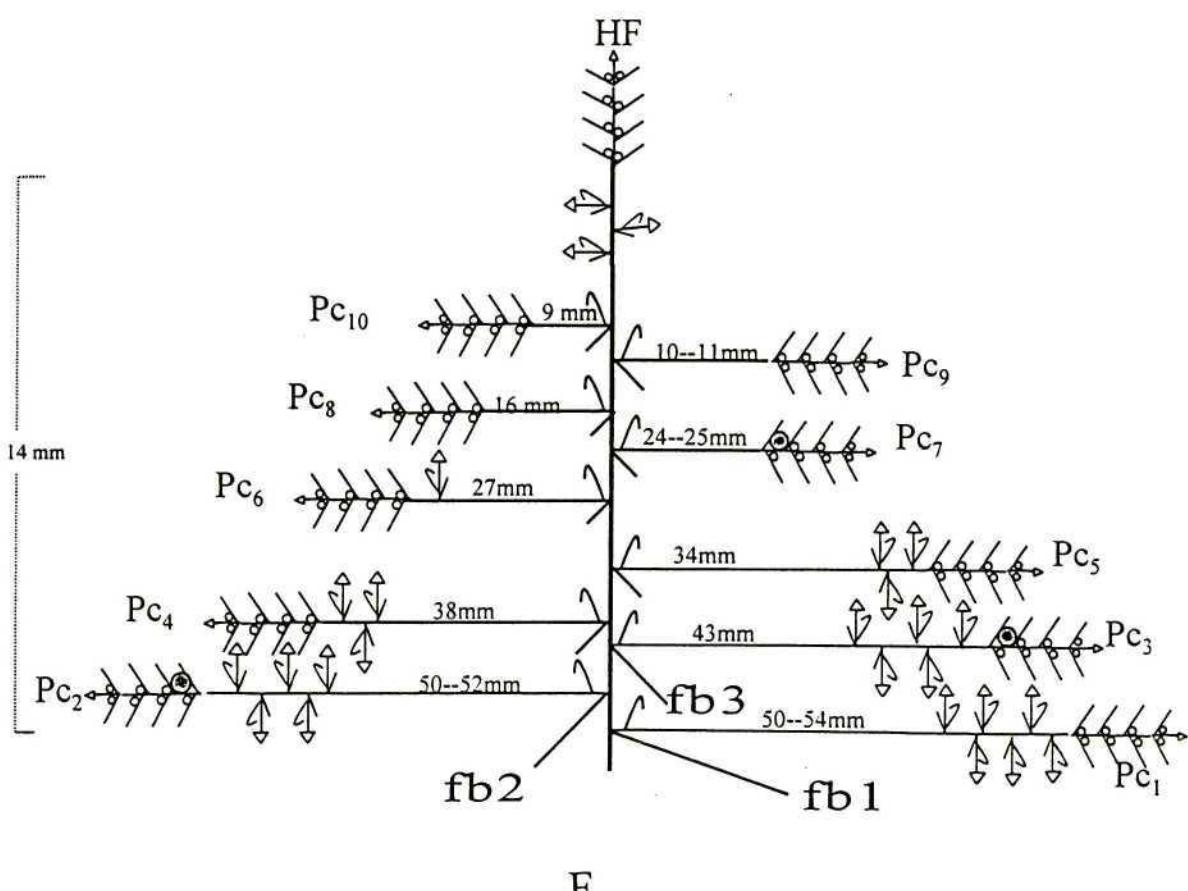
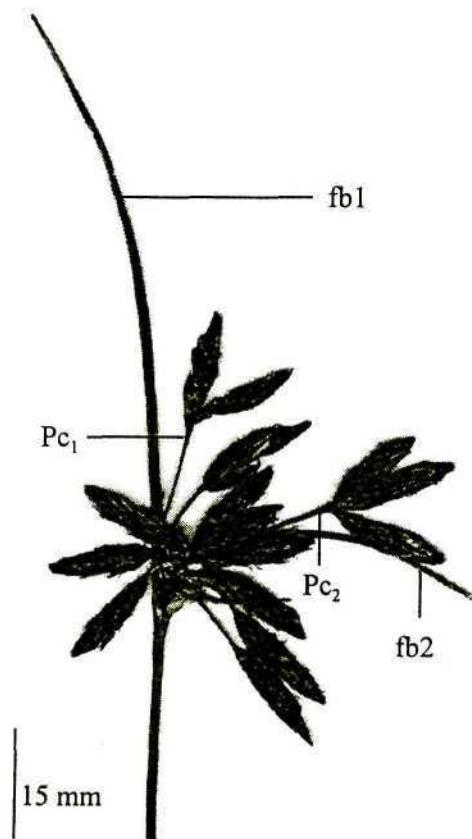


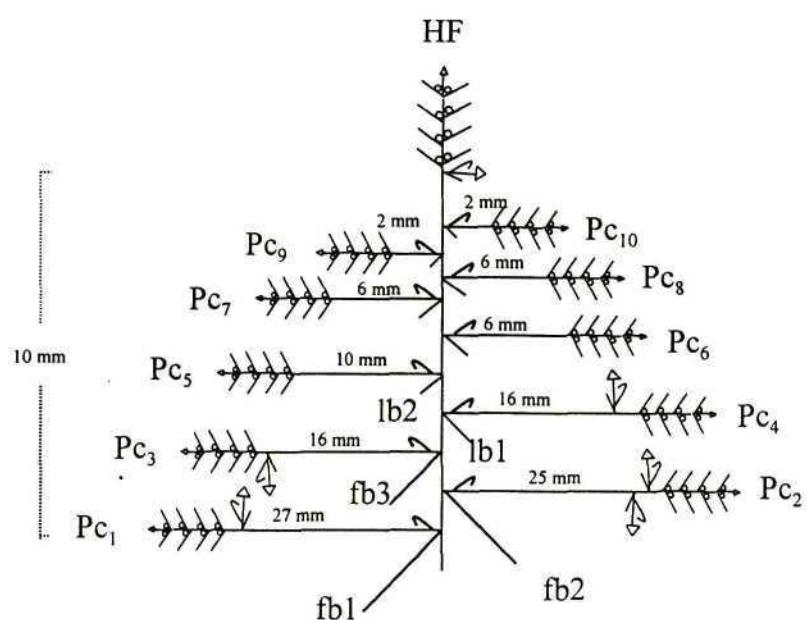
Figure 62.

Bolboschoenus glaucus: inflorescence representative of the many-rayed anthelodium; G₁, example with ten rays; G₂, diagrammatic representation of dissection of this. G₁, C.J. Ward 14201 (NU) KwaZulu/Natal, South Africa.

- bract
- fb = foliose bract
- lb = laminar bract
- branch bud
- △ spikelet bud
- / glume
-  part of spikelet
- Pc₁, Pc₂ etc. = paracladia
of main axis
- ↑ prophyll (cladopropophyll or
glumaceous)
- floret
- abortive floret
-  CoF = coflorescence
- HF = main florescence



G₁

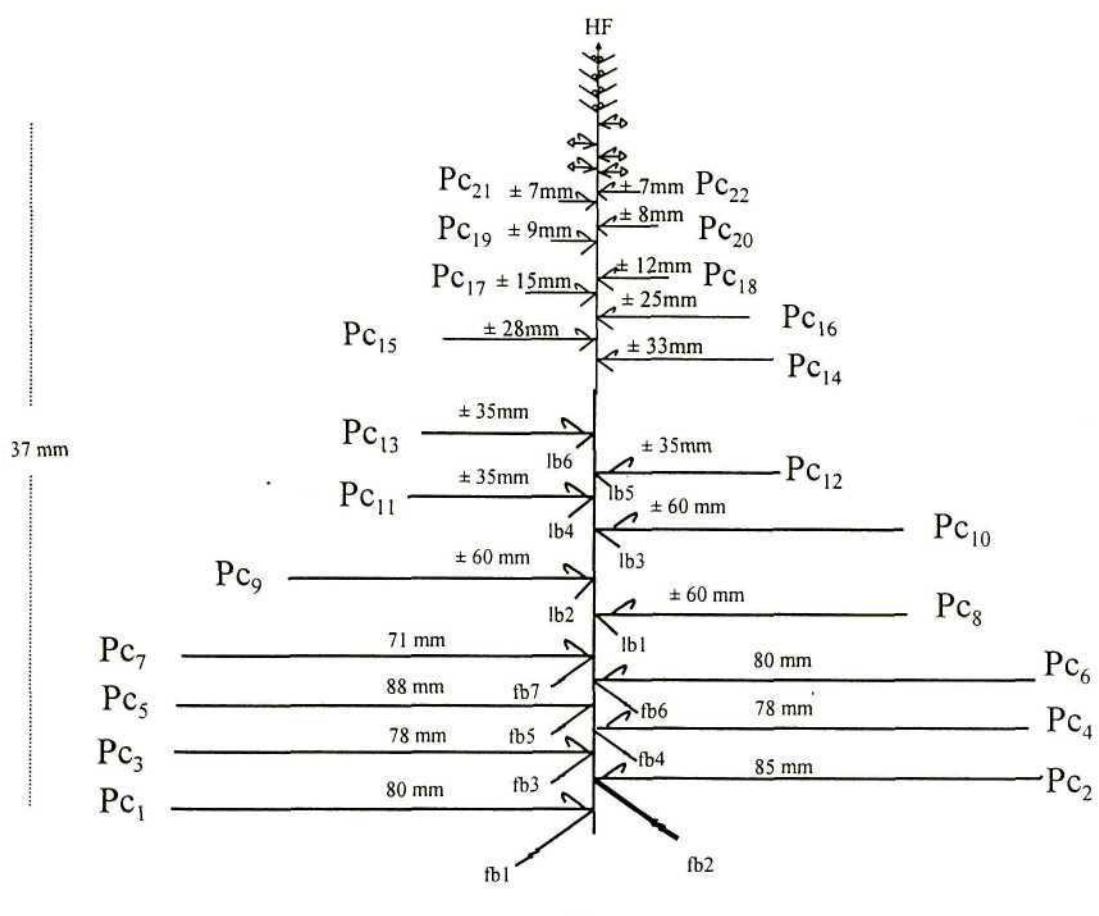
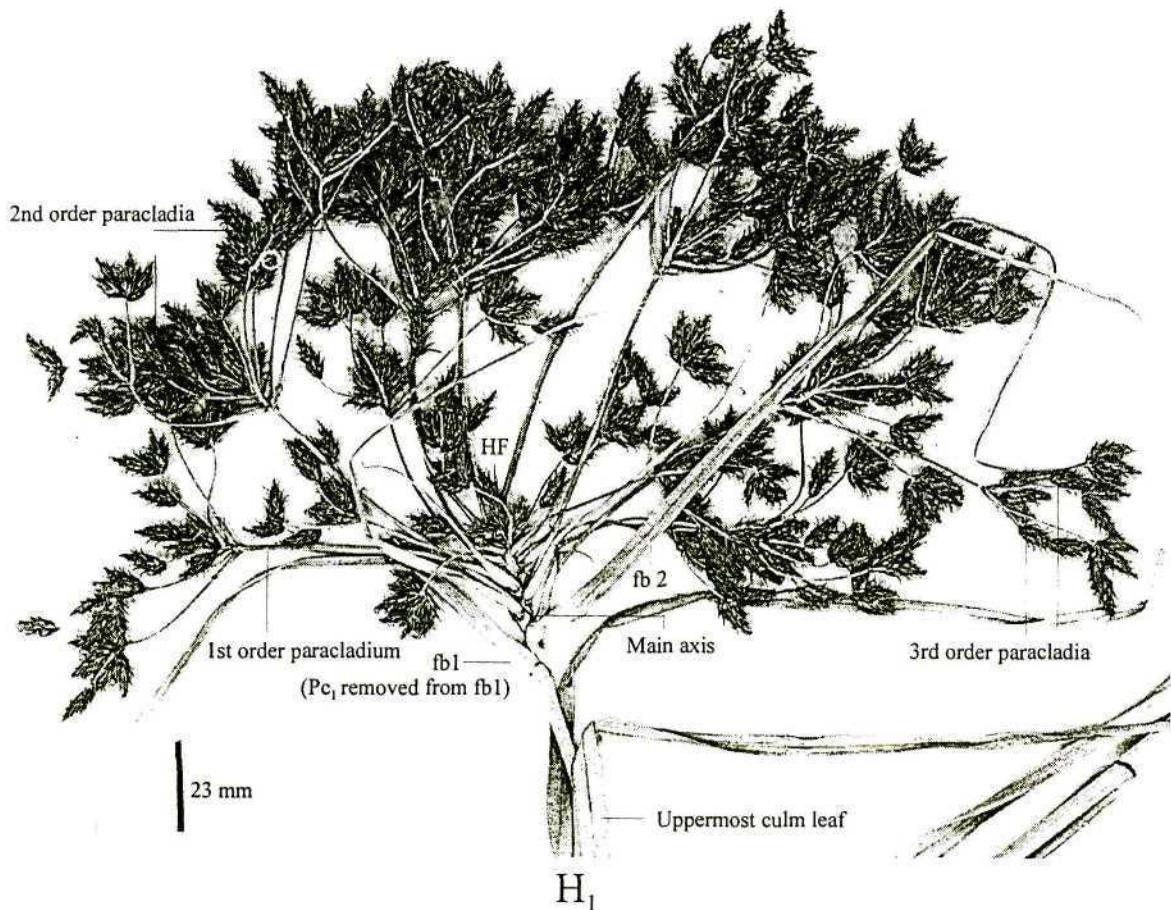


G₂

Figure 63.

Bolboschoenus nobilis: inflorescence representative of the compound anhelodium; H₁, example (lowest paracladium removed to permit better positioning); H₂, diagrammatic representation of main axis of this example showing first order paracladia in sequence (Pc₁--Pc₂₂) followed by five coflorescences (CoF) and main florescence (HF). The coflorescences and main florescence collectively constitute the short, compact cluster central in the synflorescence. This cluster appears sessile terminating the main axis. H₁, C.J. Ward 13245 (NU).

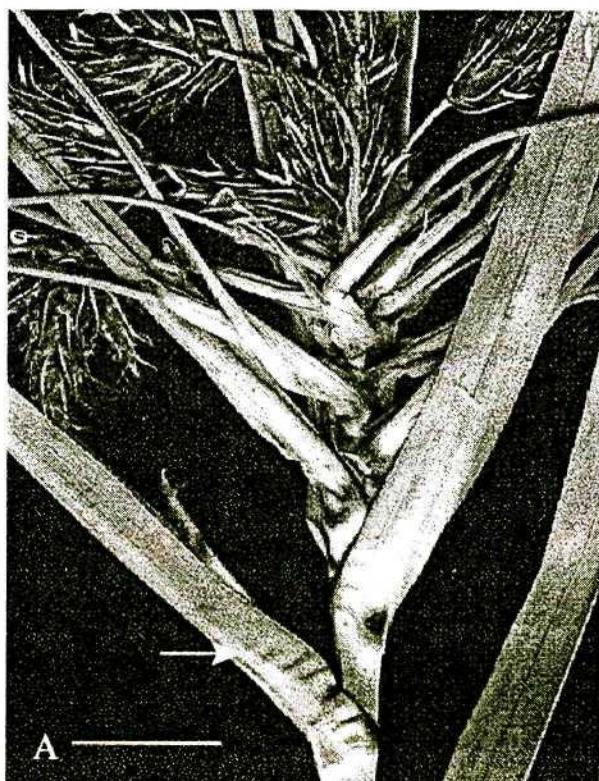
- bract
- fb = foliose bract
- lb = laminar bract
- △ spikelet bud
- / glume
-  part of spikelet
- Pc₁--Pc₂₂ = paracladia of main axis
- ↑ prophyll
- floret
- abortive floret
-  CoF = coflorescence
- HF = main florescence



H₂

Figure 64.

Bolboschoenus nobilis: inflorescence representative of the compound anhelodium; H₃, main axis enlarged to show spirality and parts in greater detail; note cladoprophyll within first foliar bract (arrowed); H₄, partial florescence of one first order paracladium after glumes had abscised naturally; note bracts, cladoprophylls, and presence of second order paracladium on uppermost centrally placed first order paracladium. H₃, H₄, C.J. Ward 13245 (NU). Scale bar = 10 mm.



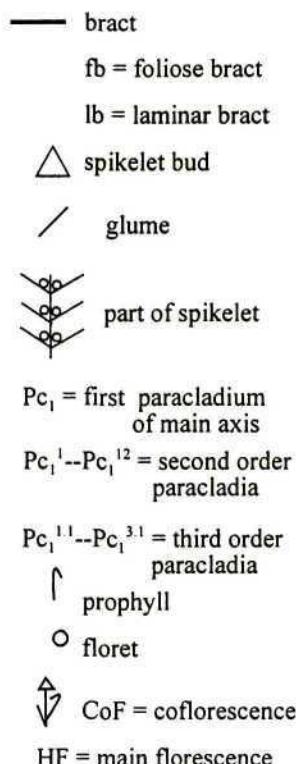
H₃

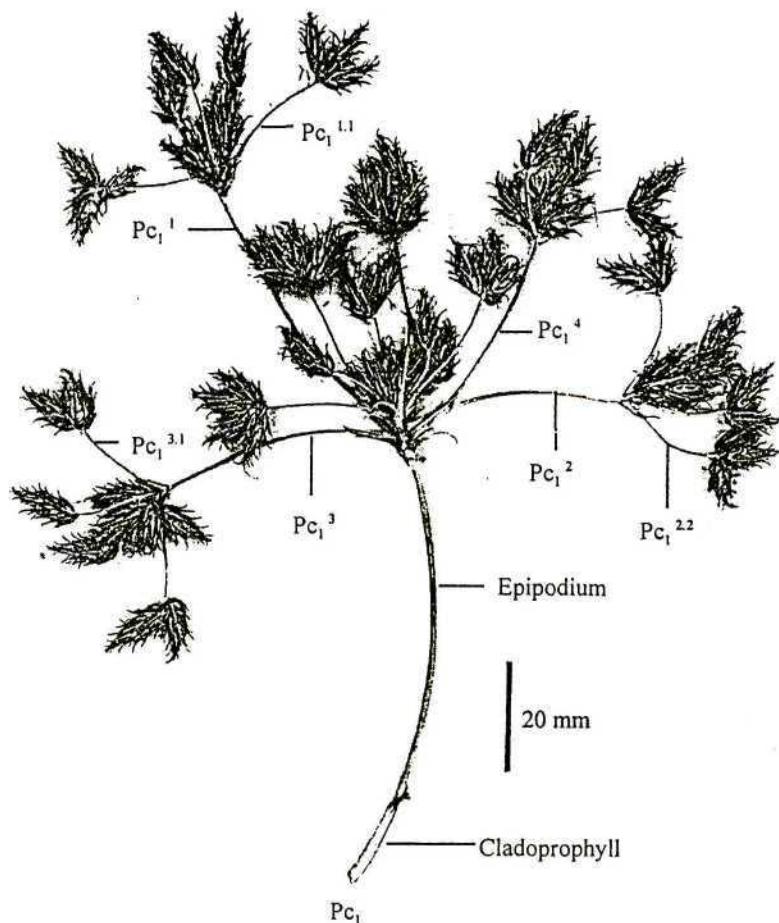


H₄

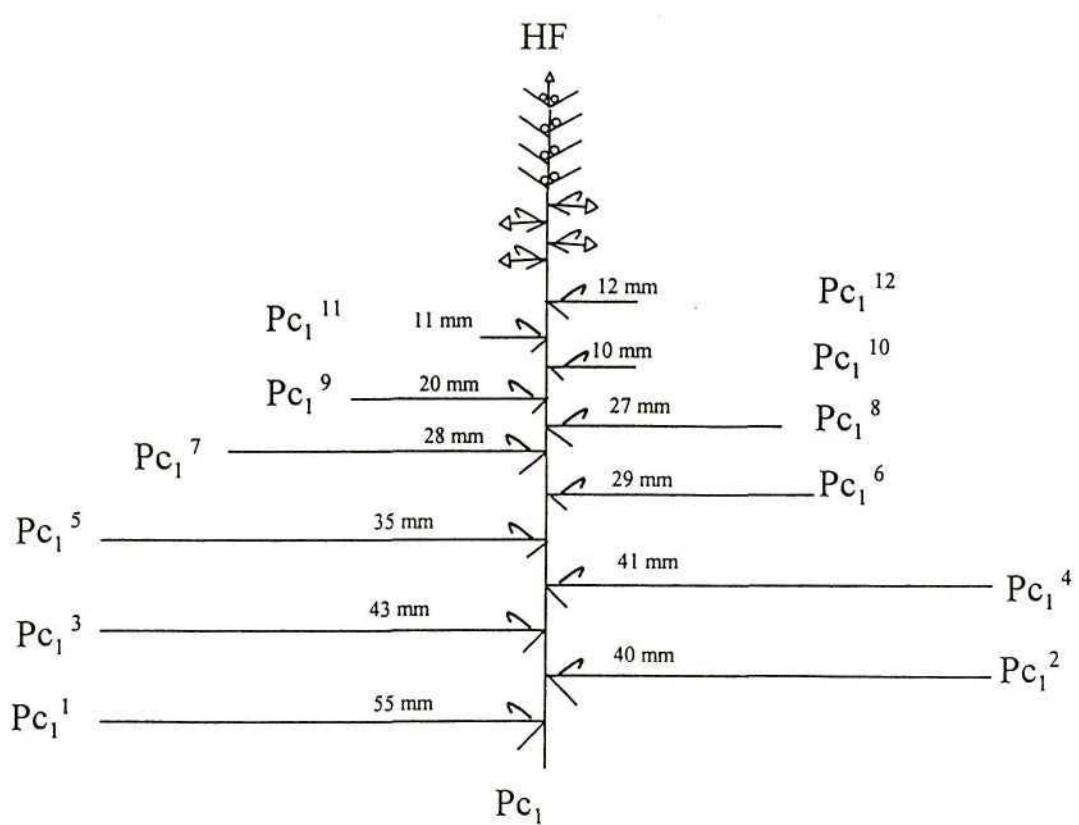
Figure 65.

Bolboschoenus nobilis: inflorescence representative of the compound anhelodium; H₅, structure of first order paracladium (Pc₁) removed from synflorescence (remainder shown in H₁, Figure 63). H₆, diagrammatic representation of dissection of this. H₅, C.J. Ward 13245 (NU).





H_5

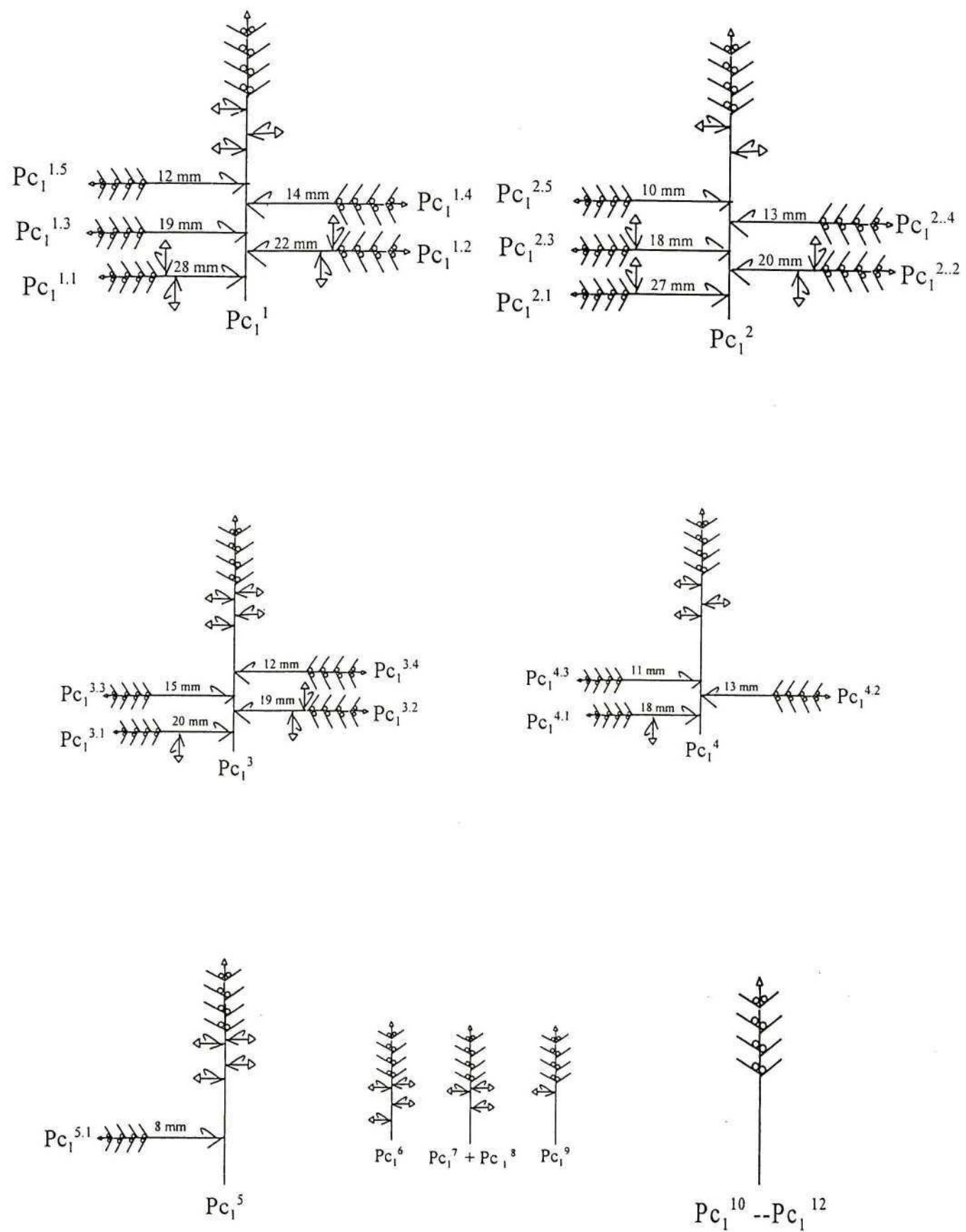


H_6

Figure 66.

Bolboschoenus nobilis: inflorescence representative of the compound anthelodium; H₇, diagrammatic representations of dissections of second order paracladia (Pc_1^1 -- Pc_1^{12}): note that Pc_1^6 -- Pc_1^{12} , show no development of third order branches and Pc_1^{10} -- Pc_1^{12} , lack third order branches and coflorescences. H₇, C.J. Ward 13245 (NU).

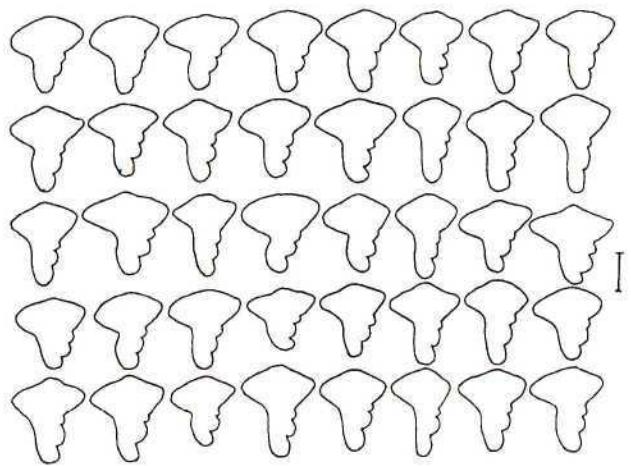
- bract
- fb = foliose bract
- lb = laminar bract
- △ spikelet bud
- / glume
-  part of spikelet
- Pc_1^1 = second order paracladia
- Pc_1^{11} = third order paracladia
- ↑ prophyll (cladoprophyll + glumaceous)
- floret
-  CoF = coflorescence
- HF = main florescence



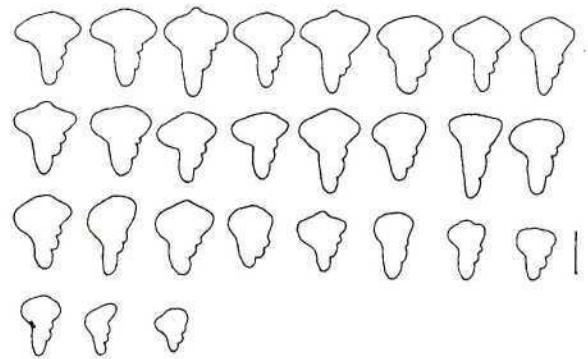
H₇

Figure 67.

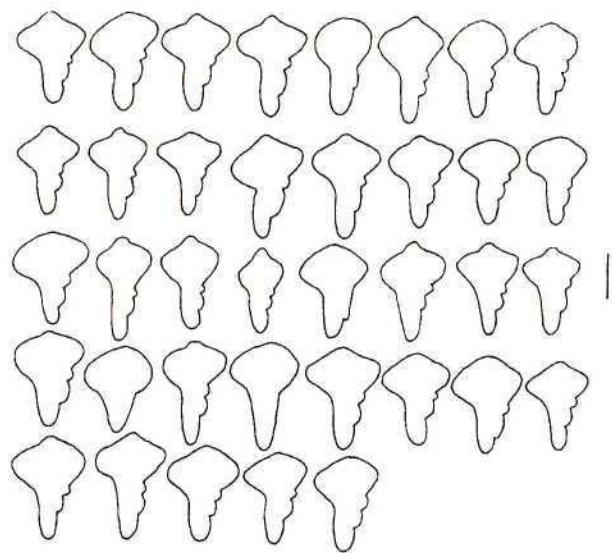
Bolboschoenus maritimus s. l.: southern Africa. Embryo profiles. A, Namibia, C.J. Ward 12575; B, Cape, coastal Verlorenvlei, Browning 814--817, 795; C, Cape, inland Verlorenvlei, Browning 796, 800, 802, 809; D, Cape, Nieuwoudtville, C.J. Ward 13973.(All NU). Scale bar = 0.5 mm.



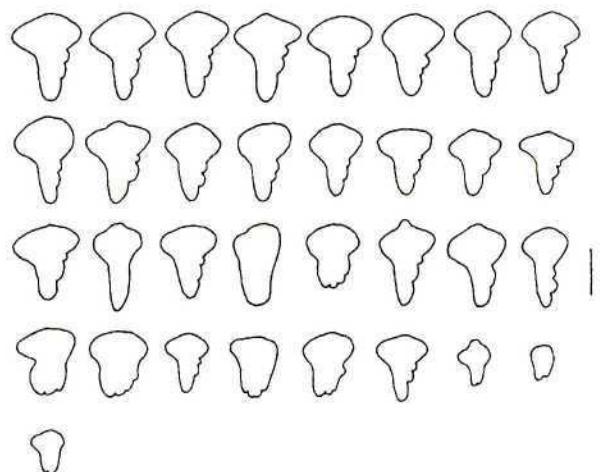
A



C



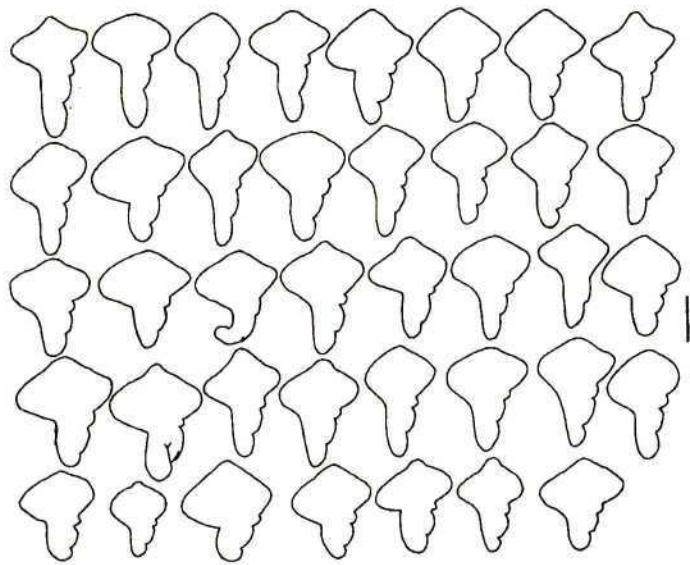
B



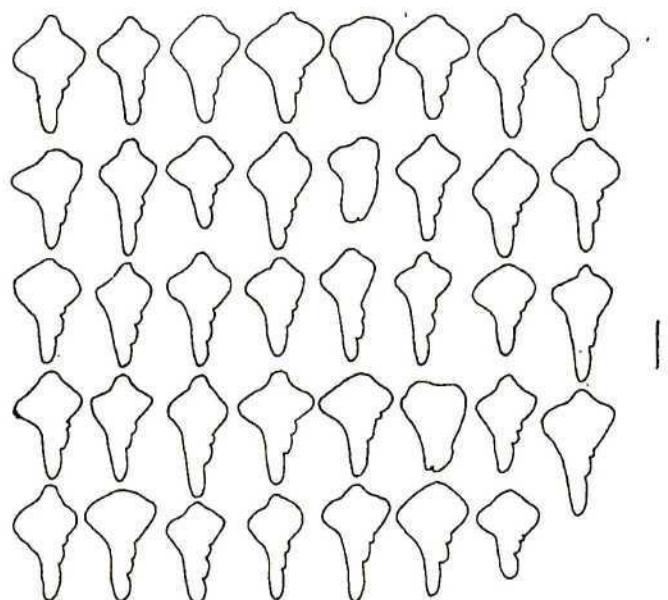
D

Figure 68.

Bolboschoenus maritimus s. l.: The Netherlands. Embryo profiles. E, Reide, *Robertus-Koster s.n.*, Aug. 1996; F, Schoonhoven, *Robertus-Koster s.n.*, Aug. 1996 (both NU). Scale bar = 0.5 mm.



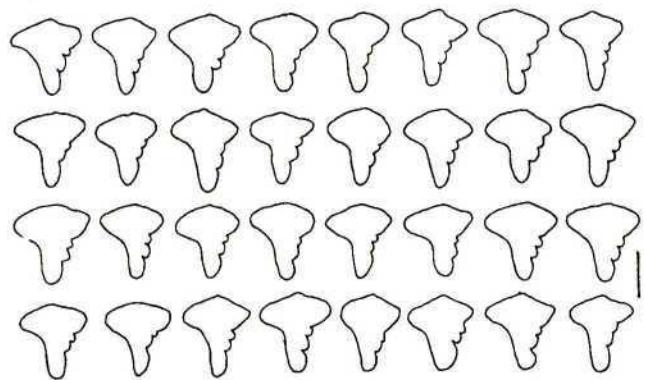
E



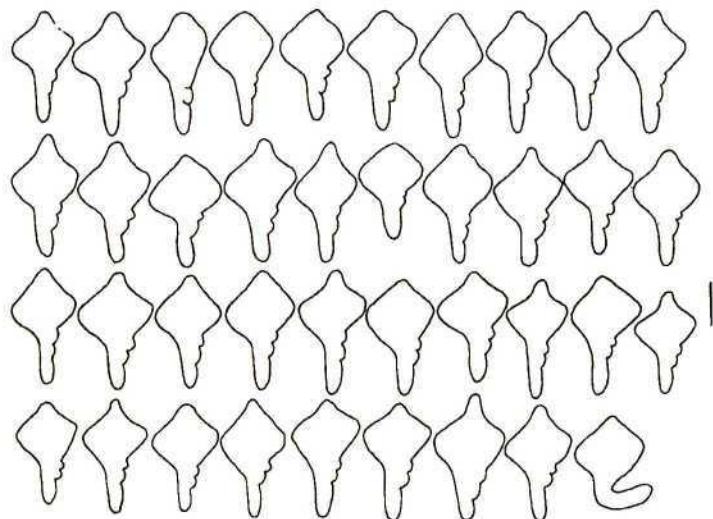
F

Figure 69.

Bolboschoenus species: West Africa and America. Embryo profiles. G, Senegal, *B. glaucus*, Johnson s.n. (NU); H, America, Wisconsin, *B. fluvialis*, G. Smith 8620 (NU, WIS). Scale bar = 0.5 mm.



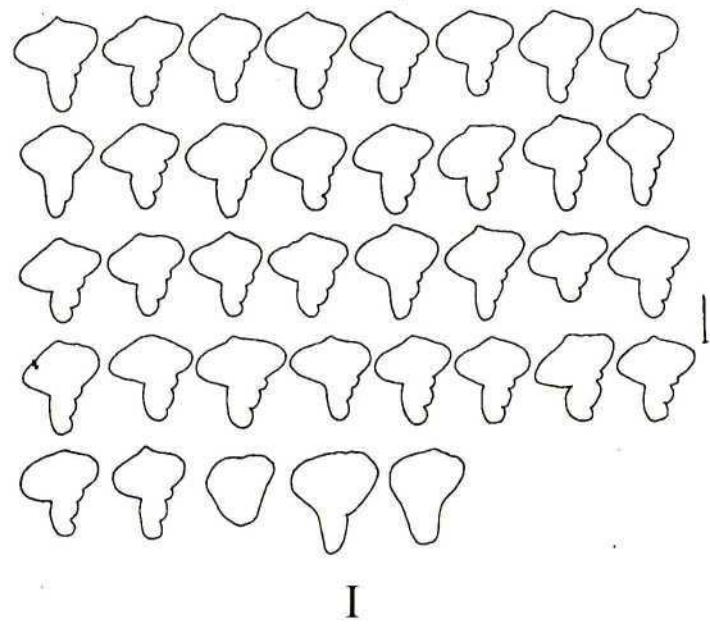
G



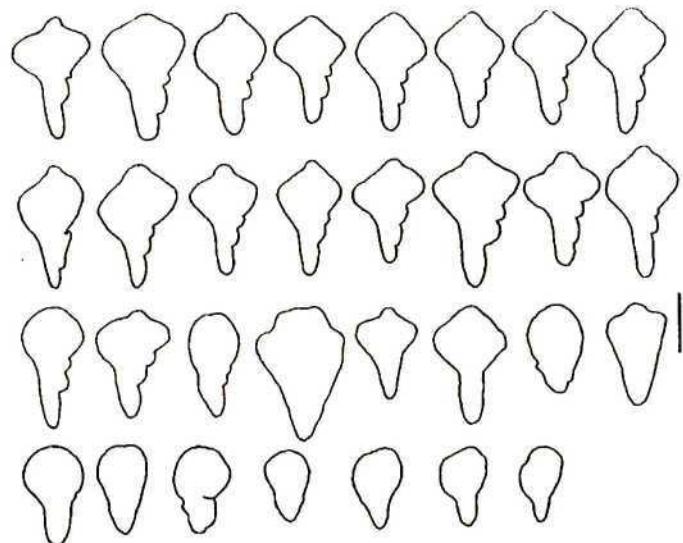
H

Figure 70.

Bolboschoenus species: Australia. Embryo profiles. I, Perth, *B. caldwellii*, Lepschi & Lally 1758; J, New South Wales, *B. medianus*, Lepschi 1598, 1604 (all NU). Scale bar = 0.5 mm.



I



J

Figure 71.

Bolboschoenus species, Australia and southern Africa. Photographs of embryo in optical, sagittal section. A--E, *B. medianus*; F, *B. maritimus s.l.* A, B, *Lepisci* 1598 (CANB, NU); C, D, *Lepisci* 1604 (CANB, NU); E, M & B. Gray 4002A (NE); F, C.J. Ward 12575 (NU). Scale bar = 200 μm .

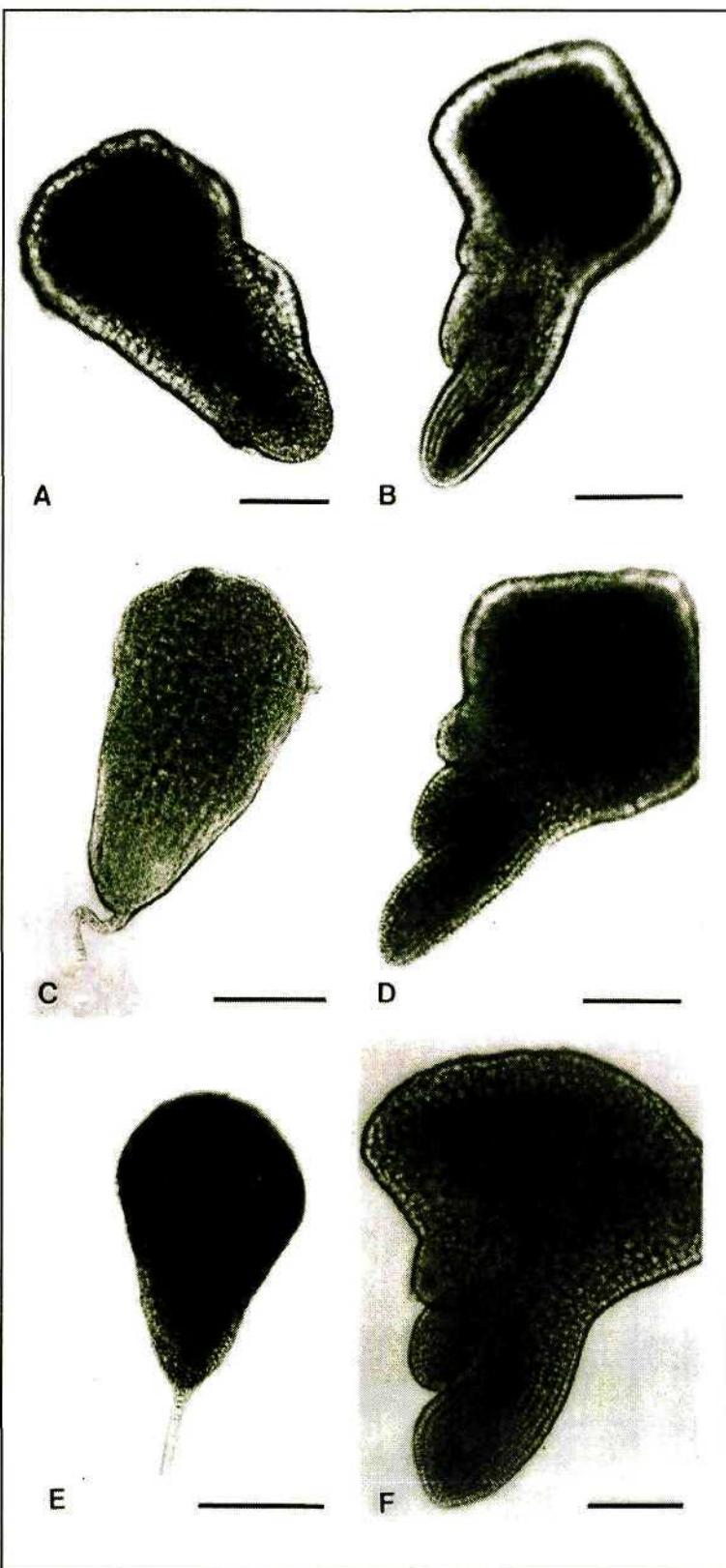


Figure 72.

Isolepis grandispica Steudel

Type: Herbarium Perrottet nr. 838, Senegal (holotype P !)

Bolboschoenus grandispicus (Steudel) K. Lewejohann & W. Lobjin

Scale bar = 20 mm. (Photograph: R.B. Roth)



Ruboriorum grandipetiolatum (Steud.) E. Leyssaigne & W. Lohm.
Drawing April, 1927.

HERB. MUS. PARIS.

herbarium
E. Leyssaigne
R. Lohm.
he R. S.



Straw.—Plante graminac.



Figure 73.

Bolboschoenus nobilis rhizome. Upper photograph: external features of youngest portion showing uniseriate arrangement of culms (two severed, one with leaves just expanding), fragmenting leaf sheaths, scale leaves, adventitious roots and latest culm (shoot bud). Lower photograph: A, B, internal features of portions of two rhizomes showing variation in shape and extent of thickening of culm bases. Scale bar = 30 mm. (Photographs: R.B. Roth)

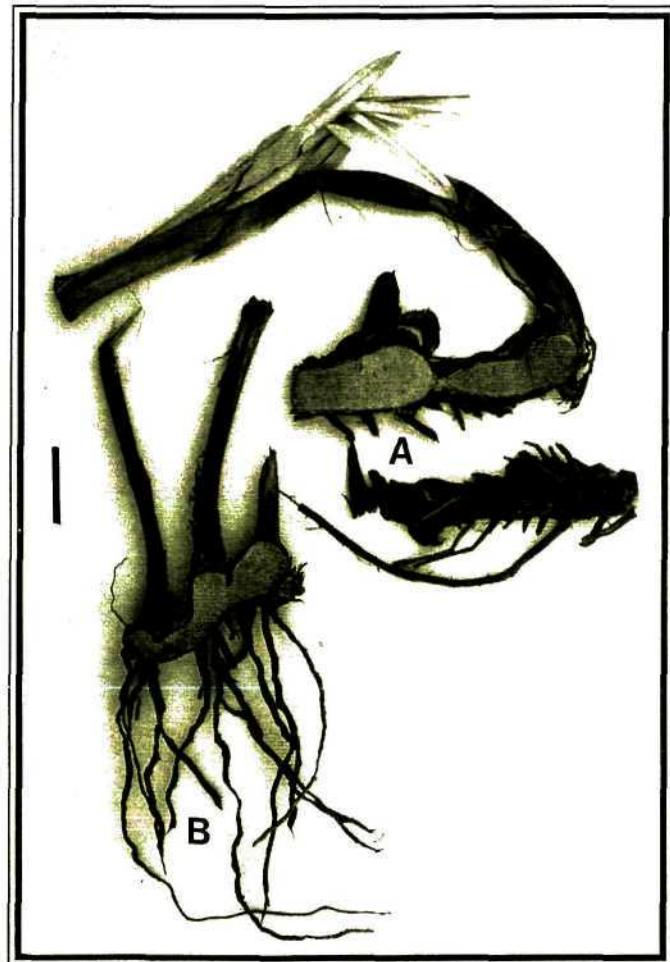
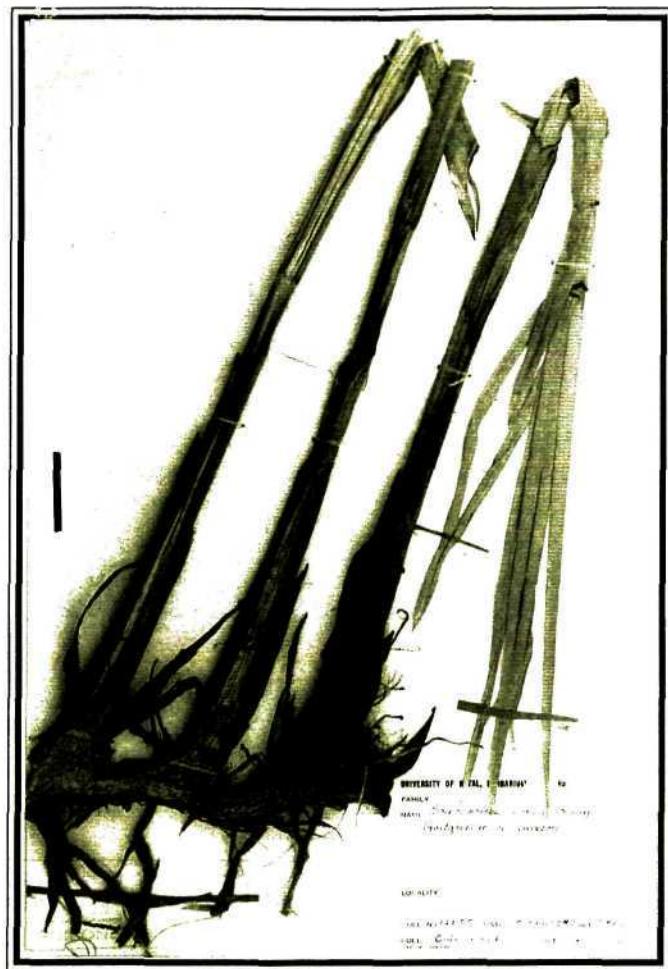


Figure 74.

Bolboschoenus rhizomes: A, *B. glaucus*, C.J. Ward 1707; B, *B. maritimus* s.s., Browning 927 (both NU). Scale bar = 30 mm. (Photographs: R.B. Roth)

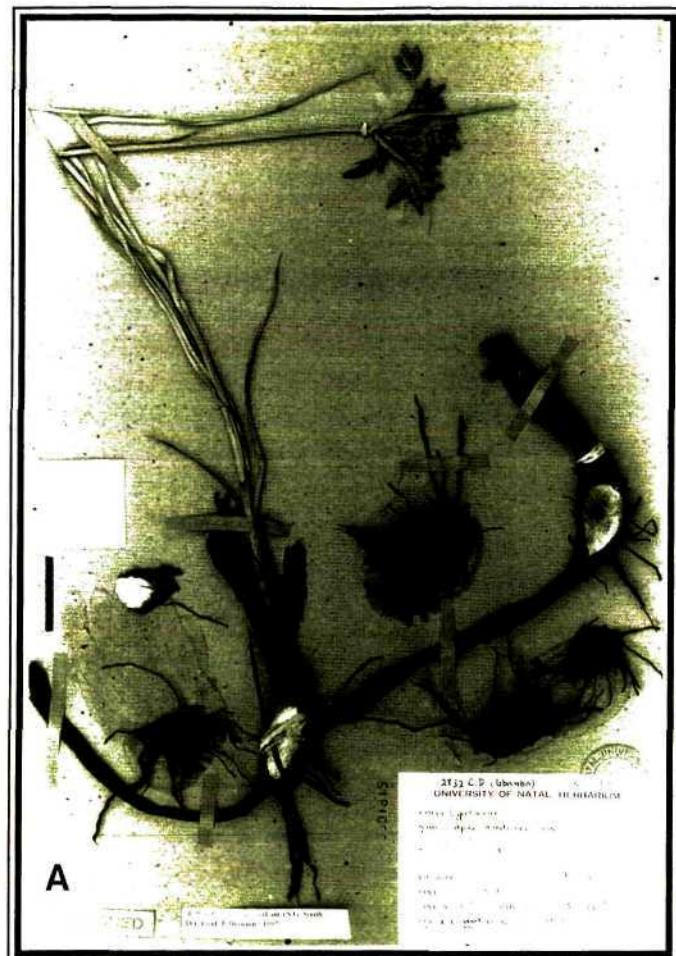


Figure 75.

Bolboschoenus : plan of general areas of distribution of species in Africa and Madagascar.

Note: the precise overall distribution of *B. glaucus* within a country is difficult to assess. For the purpose of this map, presence of the species has been recorded by shading of the **whole** country whether there are records of one or of many collections: an exception to this is Zambia, where only the southernmost zone has been shaded, because no records are known for elsewhere in that country.

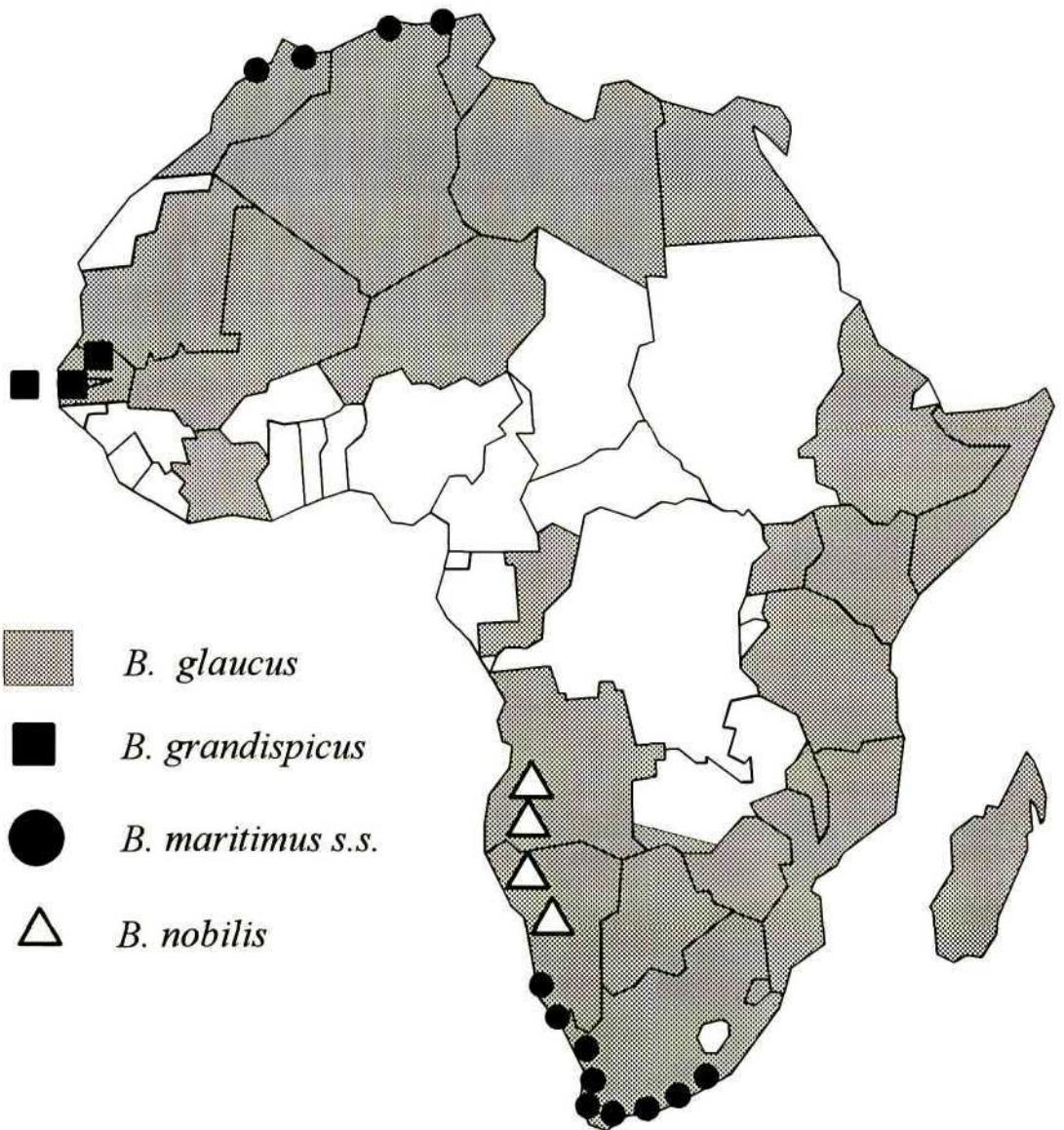


Figure 76.

Bolboschoenus: known distribution of species in southern Africa.

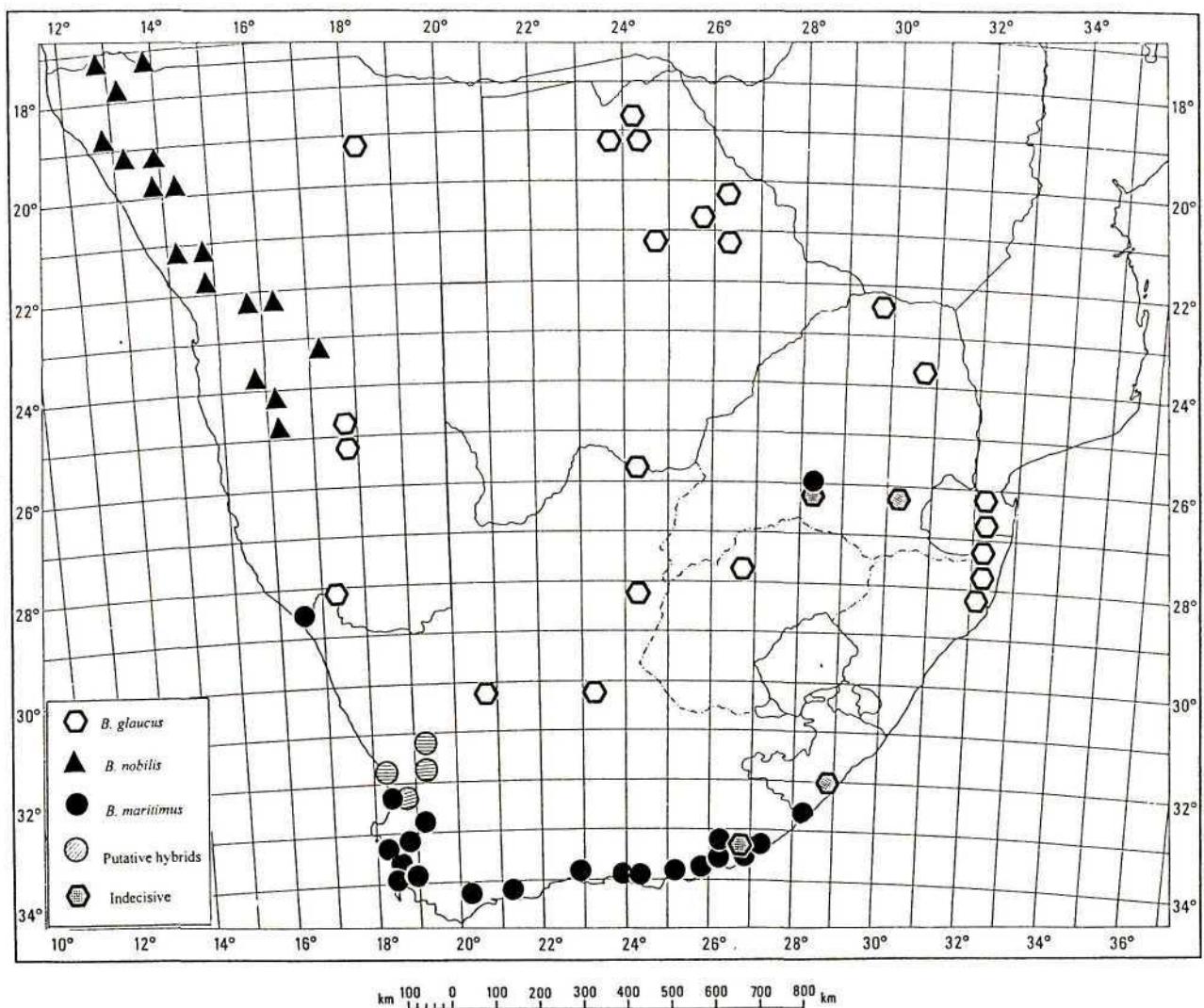


Figure 77.

Bolboschoenus nobilis. C.J. Ward 13245 (NU).

Top: mature inflorescence.

Centre: plants in natural habitat.

Bottom: plants in dried watercourse amongst Brandberg Mountains, Namibia.

(Photographs: C.J. Ward)



Figure 78.

Bolboschoenus glaucus. C.J. Ward 13781 (NU).

Top: inflorescence, showing elongate lowest bract.

Centre: inflorescence enlarged.

Bottom: plants natural in water course of Lower Mzinene River,
KwaZulu/Natal. (Photographs: C.J. Ward)



Figure 79.

Bolboschoenus glaucus. C.J. Ward 13862 (NU).

Top: inflorescence: note the long, narrow spikelets.

Centre: several inflorescences all with long, narrow spikelets.

Bottom: plants natural along margins of water course near confluence of Fish (Vis) and Orange Rivers, Namibia. (Photographs: C.J. Ward)



Figure 80.

Bolboschoenus maritimus s.s. C.J. Ward 13922 and 13929 (NU).

Top: inflorescence.

Centre: plants bearing inflorescences at Morgan's Bay, Cape Province.

Bottom: creeping rhizomes intermingled with grass (narrower leaves). S. side of estuary, Morgan's Bay. (Photographs: C.J. Ward)



Figure 81.

Bolboschoenus fluviatilis (A, C, D) and *B. yagara* (B): fruits from a range of localities showing variation. A, America, *Smith, G. 8620* (NU, WIS); B, Asia, *Paulenko 2791* (M); C, Australia, *Apeo Pty. Ltd., NSW 77413* (NSW); D, Australia, *Beauglehole 70665* (NSW). Scale bar = 1 mm.

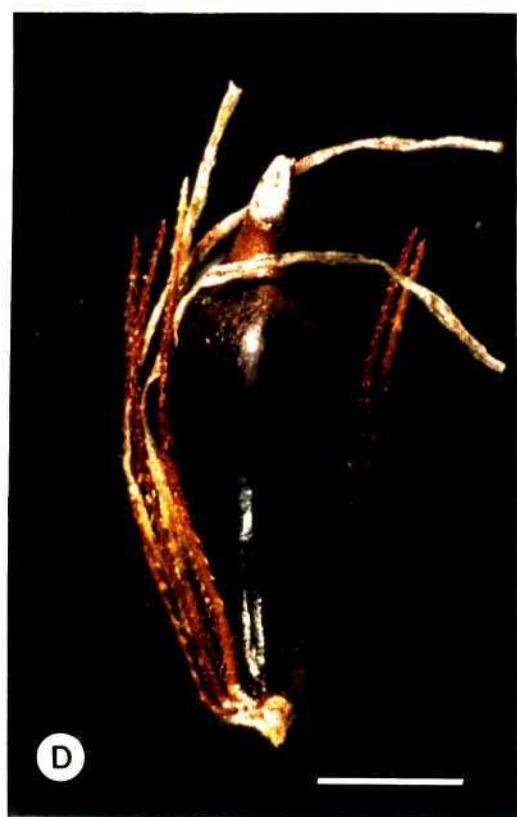
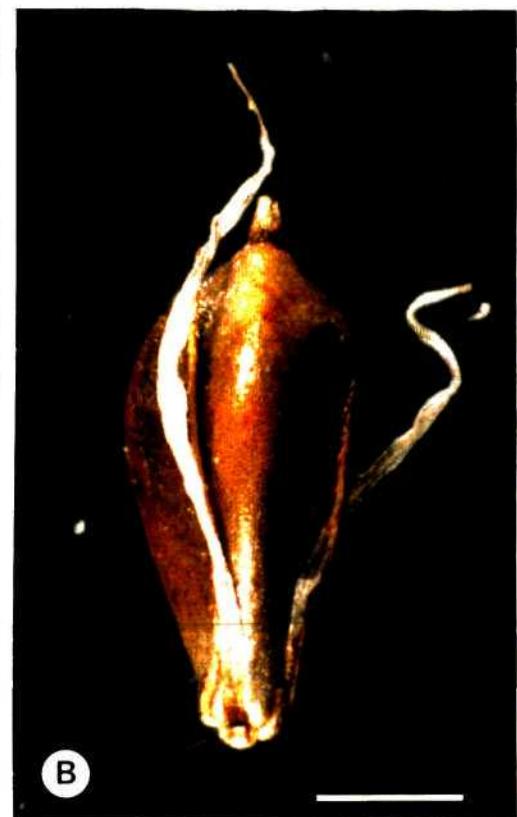


Figure 82.

Bolboschoenus:groupings of more important world species based on characters of nut morphology, pericarp anatomy, style branch number and persistence, or not, of perianth bristles and the known world distribution of these species.

SPECIES

STYLE BRANCH
NUMBER

OUTLINE SHAPE

NUT

TRANSVERSE SECTION EXOCARP CELL

Two-branched styles

B. affinis (Roth) Drobow
B. caldwellii (V.J. Cook) Soják
B. grandispicus (Steud.) K. Lewejohann & W. Lobin
B. paludosus (A. Nelson) Soó
B. planiculmis (F. Schmidt) T.V. Egorova
Scirpus biconcavus Ohwi

Two- and three-branched styles

B. maritimus (L.) Palla s.s.
B. robustus (Pursh) Soják

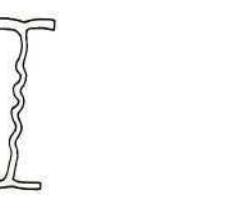
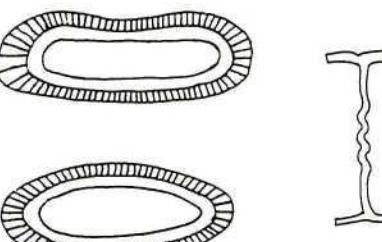
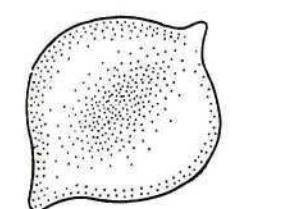
B. medianus (V.J. Cook) Soják
B. novae-angliae (Britton) S.G. Smith

Three-branched styles

B. fluvialis (Torr.) Soják
B. yagara (Ohwi) A.E. Kozhevnikov

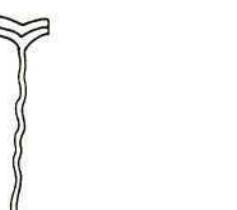
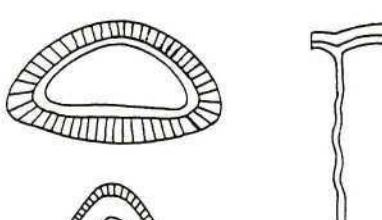
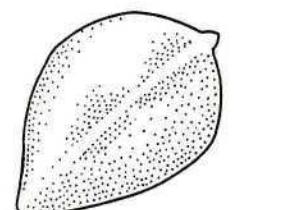
B. nobilis (Ridl.) Goetghebeur & D.A. Simpson
B. glaucus (Lam.) S.G. Smith

2



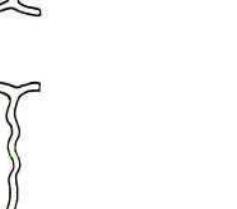
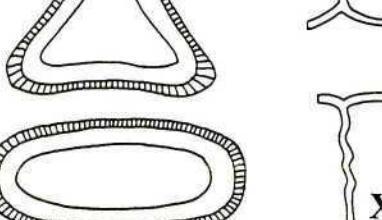
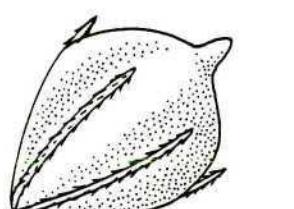
Taxa with two-branched styles

2

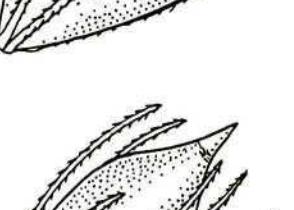


and

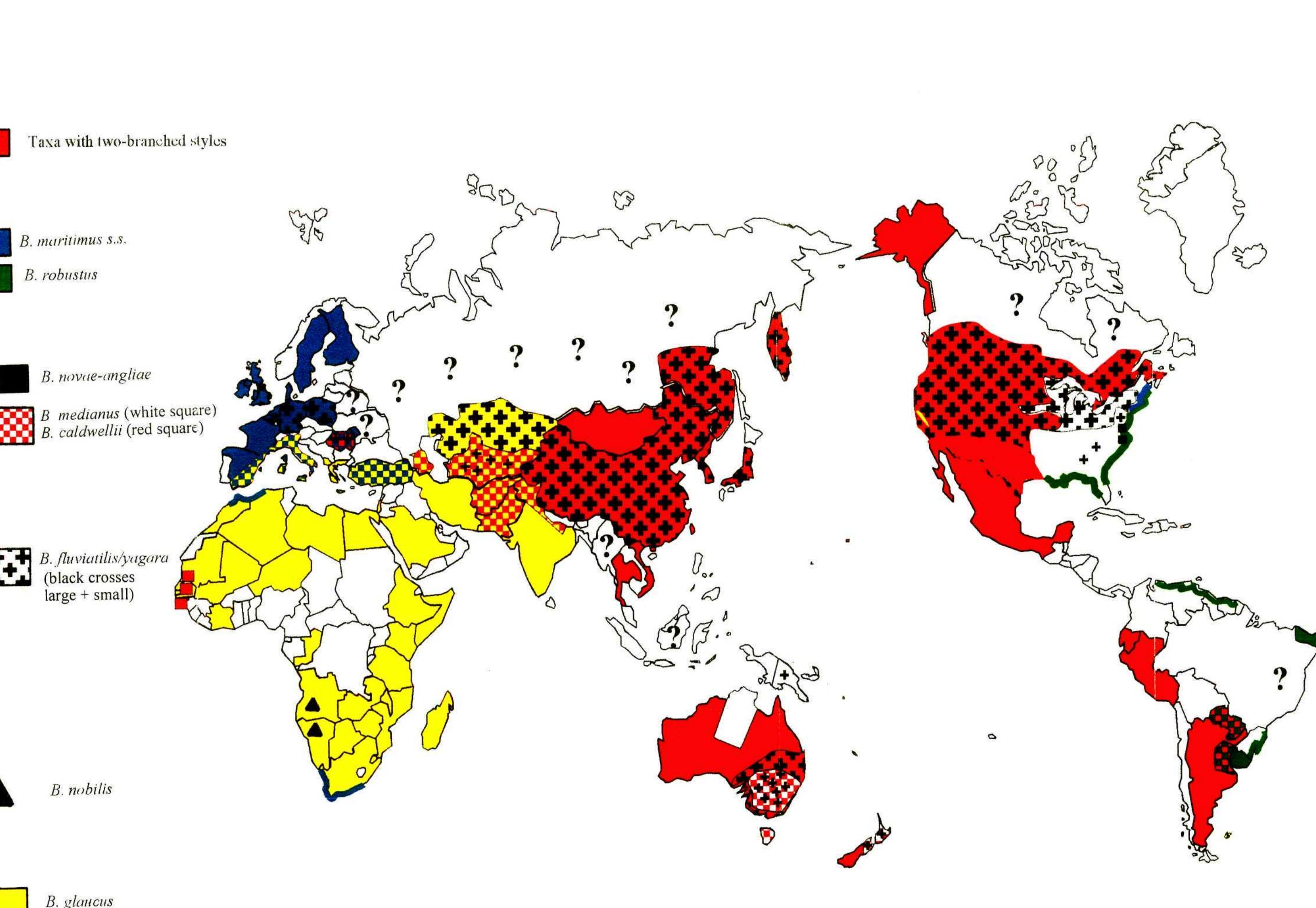
3

*B. maritimus* s.s.*B. robustus*

3

*B. novae-angliae**B. medianus* (white square)
B. caldwellii (red square)*B. fluvialis/yagara*
(large + small)*B. nobilis**B. glaucus*

(Silica indicated by X)



TABLES

Table 1.

Bolboschoenus nobilis and *B. maritimus* : characters useful in distinction [after Goetghebeur & D.A. Simpson, (1991)]

Character	<i>B. nobilis</i>	<i>B. maritimus</i>
Contralaminar portion of sheath apex	Shallowly concave, with a narrow membranous band and dark brownish margin; nerves sharply angled round sheath apex.	Deeply cleft, the cleft membranous, red-dotted, margin ± hyaline, rarely coloured; nerves gently angled round sheath apex.
Inflorescence	Much branched, with 100-200 spikelets.	Sparingly branched, with up to 50 spikelets.
Achene [Fruit]	Dark grey-green, spotted or blotched with black, rarely all black; surface irregular, somewhat shining, with scattered, minute, distinctly raised, blackish papillae.	Mid grey-green to dark brown, without spotting or blotching; surface smooth, distinctly shining, without raised papillae.
Anthers, at or after anthesis	Less than or equalling 2 mm long, crest red brown, more than 0.5 mm long.	Less than or equalling 3 mm long, crest pale, less than 0.25 mm long.

Table 2.

Bolboschoenus nobilis and *B. maritimus* : addenda to Table 1, derived from study of southern African specimens

	<i>B. nobilis</i>	<i>B. maritimus</i>
Fruit	1.3--1.7 mm wide; sharply 3-angled; surface markings irregular.	1.9--2.4 mm wide; bluntly 3-angled, abaxial angle poorly defined; occasionally black in colour; surface markings almost regular; small, raised blackish papillae occasional, not obtrusive.
Perianth (hypogynous bristles)	Strong, persistent.	Softer, caducous to poorly persistent.
Spikelet length (at stage of post anthesis of lowest quarter of florets)	Less than 10 mm.	Exceeding 10 mm.

Table 3.

Bolboschoenus: features of mature fruits representative of *B. maritimus* (Entity 1), *B. maritimus* (Entity 2) and *B. nobilis*

	Entity 1	Entity 2	<i>B. nobilis</i>
Nut shape (Figs 1A, 2A, 3A)	obovate, tapering to a narrow base (maximum:base width 7--9:1)	obovate to obovate-elliptic, tapering to a medium base (maximum:base width 6:1)	ovate-elliptic to elliptic, tapering to a medium base (maximum:base width 3--5:1)
Nut length	3.0--3.4 mm	2.4--3.3 mm	2.3--2.8 mm
Nut width	1.9--2.4 mm	1.8--2.2 mm	1.3--1.7 mm
Pericarp epidermal cells (surface view x 600; Figs 1B, 2B, 3B, 4A)	isodiametric 5--6--7 sided; walls not raised, cell size medium	longitudinally--oblong, obscurely 5--6--7 sided, walls raised, central zone depressed, cell size small	isodiametric to longitudinally- oblong, 5--6--7 sided; walls raised, central zone depressed, cell size medium
Exocarp in t.s. (Figs 1C, 2C, 3D, 4B)	1-layered; cells radially elongate (oblong) depth:width 4:1	1-layered; cells not radially elongate (transversely oblong) depth:width 1:3	1-layered; cells not radially elongate (almost square) depth:width 2:3
Response to 24 hrs. soaking	outermost periclinal exocarp walls not detachable; pericarp softened; became compressible	outermost periclinal exocarp walls not detachable; pericarp firm, incompressible	outermost periclinal exocarp walls easily detachable as a sheet of tissue; pericarp firm, incompressible
Reflection of light from nut surface (x20)	highly reflective, sparkling, light particulate	reflective, the light giving a somewhat shining polished effect, not particulate	poorly reflective, slightly polished to dull, light not particulate

Table 4.

Bolboschoenus maritimus Entity 1, Entity 2 and *B. nobilis*: size differences in embryos, based on measurement of samples from two different plants. (measurements in mm).

	Entity 1	Entity 2	<i>B. nobilis</i>
length (extremes)	0.88--1.0	0.5--0.75	0.5--0.55
width (extremes)	0.68--0.78	0.55--0.8	0.52--0.63

Table 5.

Bolboschoenus maritimus s.l., Verlorenvlei: spikelet number per inflorescence (range; mode = m); number of rays per inflorescence (range; mode = m); lengths of rays (range in mm) for four collections from each of three coastal and three inland sites (each sample = nine inflorescences; total for each of coastal and inland sites = 36 inflorescences).

Coastal sites	Collection number	Spikelet no. range (mode = m)	Rays per inflorescence range (mode = m)	Ray lengths range in mm
A	814	1--7 m 5	0--2 m 0	5--12
A	815	5--8(-13) m 6	0--3 m 1	8--15
B	817	5--11(-14) m 6	1--3 m 1	3--12
C	795	4--11 m 6	0--1 m 0	1--3
Extremes		(1-)5--6(-14)	0--3	1--15
Inland sites				
D	809	(1-)4--12(15) m 6	0--6 m 2	10--25
E	796	(9-)11--26(-40) m 18	3--6 m 4	15--35
E	800	(9-)12--21 m 3	1--3 m 3	5--14
F	802	6--26 [no mode]	2--8 m 3	10--35
Extremes		(1-)6--18(-40)	0--8	5--35

Table 6.

Bolboschoenus maritimus s.l., Verlorenvlei: spikelet lengths and widths (range in mm and mode = m) for each of four collections from three coastal sites and three inland sites (each sample = 45 spikelets; total for each of coastal and inland sites = 180 spikelets). Note: figures given for extremes are of the extremes of the range (in brackets), the figures between the bracketed digits are the most commonly occurring).

Coastal site	Collection no.	Spikelet length (range, mode = m)	Spikelet width (range, mode = m)
A	814	13--26 m 15	5--8 m 7
A	815	10--31 m 15	4--8 m 6
B	817	13--30 m 20	4--7 m 6
C	795	9--25 m 19	3--7 m 5
Extremes		(9-)15--20(-30)	(3-)5--7(-8)
Inland sites			
D	809	15--24 m 20	3--5 m 4
E	796	9--34 m 20	3--5 m 4
E	800	7--25 m 15	3--6 m 4
F	802	16--30 m 25	3--5 m 4
Extremes		(7-)15--25(-34)	(3-)4(-6)

Table 7.

Bolboschoenus maritimus s.l., Verlorenvlei (coastal and inland): nut lengths and widths (range in mm; s = standard deviation). Note: sample for each collection no. from Verlorenvlei = 20 nuts, therefore total for coastal and inland sites respectively = each 80

Verlorenvlei	Site	Coll. no.	Nut length:		Nut width range in mm s = std
			range in mm	s = std	
Coastal	A	<i>Browning</i>	3.1--3.5		2.2--2.8
(80 nuts in total)	A	814			
	A	815	2.8--3.3		1.8--2.3
	B	817	3.0--3.3		1.7--2.2
	C	795	2.6--3.3		1.8--2.3
Extremes			2.6--3.5		1.7--2.8
			S = ± 0.18		S = ± 0.18
Inland	D	<i>Browning</i>	2.8--3.3		1.9--2.5
(80 nuts in total)	E	809			
	E	796	2.7--3.1		2.1--2.4
	E	800	2.8--3.3		1.9--2.3
	F	802	2.6--3.1		1.7--2.3
Extremes			2.6--3.3		1.7--2.5
			S = ± 0.15		S = ± 0.13

Table 8.
Summary of characteristics of nuts of *Bolboschoenus* species in North America.

	<i>Bolboschoenus maritimus</i> s.l.	<i>Bolboschoenus robustus</i>	<i>Bolboschoenus fluviatilis</i>	<i>Bolboschoenus novae-angliae</i>	<i>Bolboschoenus glaucus</i>
Perigonal bristle length and persistence on shed nut	Ca. ½ of nut; not persistent or a few weakly persistent	Ca. ½ of nut length; not persistent or a few weakly persistent	Ca. = nut length; firmly persistent	Ca. ½ to ca. equalling nut length; 0 to all weakly persistent	Ca. ½ of nut length; mostly persistent
Nut shape	Obovate; beak small, abrupt; lenticular or very rarely compressed obtusely trigonous	Obovate; beak small, abrupt; compressed obtusely trigonous or uncommonly lenticular	Obovate to obpyriform; beak large, tapered; nearly equilaterally trigonous	Obovate; beak large, tapered; compressed trigonous or some lenticular	Elliptic-obovate to obovate; beak small, tapered to abrupt; compressed trigonous to lenticular
Nut size	2.3-4.1 x 1.9-2.8 mm	2.7-3.5 x 1.8-2.8 mm	3.8-5.5 x 2-2.9 mm	3-4.3 x 2.3 -3.1 mm	2.5-3.3 x 1.3-2.3 mm
Nut surface when dry	Medium (to dark) brown; glossy; cellular at 20x; anticlinal walls not raised at 600x	Dark (to medium) brown; glossy; cellular at 20x, anticlinal walls not raised at 600x	Grayish to dark brown, often patchy; dull; faintly cellular at 20x or not, anticlinal walls raised	Variable in same nut; dark to medium brown; glossy to dull; cellular at 20x or not; anticlinal walls raised or not	Golden to mostly dark brown; glossy; cellular at 20x or not; anticlinal walls slightly raised
Nut surface soaked in water	No air bubbles at cells; exocarp or its outer layer not detachable	No air bubbles at cells; exocarp or its outer layer not detachable	Air bubbles formed at most cells; exocarp or its outer layer detachable	Air bubbles at some cells in some collections; exocarp or its outer layer detachable	No air bubbles appear at cells; exocarp or its outer layer not detachable
Nut density	Lighter than water	Lighter than water	Heavier than water	Heavier to lighter than water	Heavier than water
Exocarp cell cross section shape	Ca. 3x deeper than wide	Ca. 3x deeper than wide	Ca. isodiametric	Variable between individuals; ca. 1.5-3x deeper than wide	Ca. isodiametric or 2-3x deeper than wide
Exocarp thickness	Ca. 2x mesocarp thickness	Ca. 2x mesocarp thickness	Ca. ⅓-⅔ of mesocarp	Ca. ⅓-⅔ of mesocarp	Ca. ⅓-⅔ of mesocarp

Table 9.

Summary of characteristics of nuts of *Bolboschoenus* species in Australia and New Zealand (incorporating types and additional specimens)

Character	<i>Bolboschoenus caldwellii</i>	<i>Bolboschoenus medianus</i>	<i>Bolboschoenus fluviatilis</i>
Perigonal bristle length and persistence on shed nut	Ca. $\frac{1}{2}$ - $\frac{3}{4}$ of nut; not persistent or a few weakly persistent.	Slightly shorter or $\frac{1}{2}$ nut length; 0 to all persistent.	Reaching apex of nut, firmly persistent.
Nut shape	Obovate, summit rounded, slightly sloping; beak well developed; faces biconcave.	Obovate, summit rounded; beak well developed; trigonous, faces slightly concave.	Elliptic, with sloping summit and base; beak well developed, tapered; trigonous, faces convex above to concave towards base.
Nut size	3.0-4.2 x 1.8-2.7 mm	3.2-4.5 x 1.9-2.8 mm	3.3-4.28 x 1.4-2.0 mm
Nut surface when dry	Pale, ochraceus to stramineus; dull or somewhat glossy; cellular at 20 x; slightly waxy.	Pale, ochraceus or dark brown; dull or glossy, variable in same nut; cellular at 20 x or not; slightly waxy.	Pale, ochraceus or dark brown, or black, dull or glossy; cellular at 20 x or not; no wax.
X-section shape	Variable; over rounded angles radially elongate with individual cell ratio depth:width 4:1; over biconcave faces, ratio depth:width 2:1.	Slightly radially elongate, ratio depth : width 1.3-1.7:1.	Rectangular or square, more or less isodiametric.
Exocarp thickness	Variable; deeper or equal to mesocarp thickness at angles; equal or less deep than mesocarp over concave faces, difficult to estimate ratios because of brittleness of exocarp.	Slightly variable, about 1/5- 1/2 mesocarp thickness, except over angles where about 1/3 mesocarp thickness.	Ca. 1/8-1/7 of mesocarp thickness.

Table 10.

Results of study of nuts from The Netherlands donated by Irene Robertus-Koster (E : M expresses ratio of depth of exocarp to depth of mesocarp)

	SAMPLE	VARIABILITY, OUTLINE-SHAPE, SIZE, COLOUR, SURFACE TOPOGRAPHY, X-SECTION AND E : M
GROUP 1	Groningen West E2 (Figure 46)	100% obovate; 3.0--3.4 x 2.2--2.8 mm; golden brown; smooth, glossy, cells polygonal, regular; obtusely trigonous. E : M = 2 : 1
	Groningen West Z3	84% obovate; 3.1--3.6 x 2.2--2.7 mm; golden brown; cells polygonal; subtrigonous. 10% narrowly obovate (smaller); dark brown to black; cells faintly marked; subtrigonous. 6% elliptic; golden brown; cells polygonal; lenticular. E : M = 2 : 1
	Haringvliet H4 (Figure 47)	74% obovate; 3.1--3.8 x 2.4--2.8 mm; golden to ochre-brown; cells polygonal; subtrigonous. 14% elliptic; 3.5--4.1 x 2.0--2.5 mm; golden brown; cells polygonal; lenticular. 8% obovate; golden brown; cells polygonal; lenticular. 4% narrowly obovate (smaller); brown (2), black (2); cells faintly marked; subtrigonous. E : M = 2 : 1; but Fig. 47J = 1 : 1
	Haringvliet D1	58% obovate; 3.4--4.3 x 2.3--2.6 mm; golden brown; cells polygonal; subtrigonous. 42% elliptic; 3.7--3.9 x 2.2--2.4 mm; golden brown; cells polygonal; lenticular. E : M = ca. 2 : 1
	Punt van Reide R7 (Figure 48)	70% obovate; 4.0--4.5 x 2.5--2.9 mm; ochre to khaki; cells polygonal, smaller on flat surfaces, larger on nut shoulders; obtusely trigonous. 30% elliptic; 3.9--4.8 x 2.1--2.7 mm; ochre to khaki; cells polygonal but uneven in size; subtrigonous (10), lenticular (5). E : M = ca. 1.5 : 1
	Punt van Reide R4 (not scanned)	65% obovate; 3.1--4.3 x 2.2--2.7 mm; golden brown; cells polygonal; subtrigonous. 25% elliptic; golden brown; cells polygonal; lenticular and a few subtrigonous. 5% obovate; almost black; cells faintly polygonal; lenticular. 5% narrowly obovate; black, cells faintly marked; triangular in x-section. E : M = 2 : 1
	Punt van Reide R6 (not scanned)	60% obovate; 3.1--3.8 x 2.1--2.5 mm; light brown to ochre; cells polygonal but variable in size; subtrigonous. 30% elliptic to obovate; 3.3--3.6 x 1.8--2.0 mm; light brown to ochre; cells polygonal but variable in size; subtrigonous. 10% elliptic; light brown to ochre; cells polygonal but variable in size; lenticular. E : M = ca. 1.5 : 1
	Biesbosch (Figure 49)	74% obovate; 3.0--4.0 x 2.4--2.8 mm; dark brown; cells polygonal, variable, most noticeable on abaxial ridge; subtrigonous. 20% elliptic; 3.6--4.0 x 2.0--2.5 mm; dark brown, cells polygonal, variable, most noticeable on abaxial ridge; trigonous, but not sharply angled. 6% elliptic; golden brown; cells polygonal; lenticular. E : M = 2 : 1
	Slout Flakkee V5	50% obovate to elliptic; 4.0--4.3 x 2.0--2.4 mm; golden brown; cells polygonal appearing small; subtrigonous. 20% obovate; 3.1--3.9 x 2.2--2.6 mm; golden-yellow; cells polygonal; subtrigonous. 18% elliptic; golden, cells polygonal appearing small; lenticular. 10% elliptic; golden-yellow; polygonal; subtrigonous. 2% narrowly obovate; almost black; cells faintly marked; subtrigonous. E : M = 2 : 1
GROUP 2	Maastricht (Figure 50)	90% narrowly obovate; 3--3.5 x 1.5--1.9 mm; black; smooth, glossy, cells faintly marked; triangular in x-section. 6.6% obovate; brown-black; smooth, glossy, cells faintly marked; lenticular (1) and subtrigonous (1). 3.3% obovate; black; smooth, glossy, cells faintly marked; subtrigonous. E : M = 1 : 2
	Schoonhoven L1 (Figure 51)	84% narrowly obovate to obovate; 3.6--3.9 x 2.0--2.3 mm; dark brown, some pale off-white; cells mainly visible on abaxial ridge; triangular in x-section but less so than Maastricht. 8% somewhat obovate; dark brown; cells visible on abaxial ridge; triangular in x-section. 8% obovate, dark brown, cells visible on abaxial ridge; triangular in x-section. E : M = ca. 1 : 1.4--1.7

Table 11. Important qualitative and quantitative inflorescence parameters representative of African species of *Bolboschoenus*
(all measurements in mm).

Character	<i>B. maritimus</i>	<i>B. grandispicus</i>	<i>B. glaucus</i>	<i>B. nobilis</i>
Number of foliose bracts	2 (-3)	1--2 (-3)	2--3	1--4 (-7)
Inflorescence size (width across widest point : depth from apex of uppermost spikelet to node of 1st foliose bract)	(7-)10--60 15--55	7--60 15--32	55--98 42--65	100--283 55--180
Inflorescence form	a solitary spikelet; a compact head of few sessile or subsessile spikelets or with a few first order rays	a solitary spikelet; a compact head of few spikelets or with a few first order rays	anthelodium of many first order rays only; sometimes first and second order; solitary spikelets unknown.	compound anthelodium of first to third order (rarely fourth order) rays; never a solitary spikelet.
Number of spikelets	1--5 (-20)	1--4 (-5) (few specimens seen)	(16-) 20--35 (-62)	(60-) 100--200 (-450)
Number of first order rays	1--4	1--2	7--10 (-14)	10--15 (-22)
Length of epipodia of first order rays	18--30 (-50)	(10-) 12--15 (-50)	20--35 (-45)	(7-) 40--80 (-100)
Angle of first order rays to main axis	usually less than 90°	usually less than 90°	some 90°	some 90°
Length of main axis (from first foliose bract to base of main florescence)	1--5 mm; not easily observed because inflorescence compact.	1--4 mm; not easily observed because inflorescence compact.	10--14 (-16); generally obvious in mature inflorescences.	18--30 (-37); generally obvious in mature inflorescences.

Table 12.

Bolboschoenus species: contents of nuts (as percentage of sample of 40); lengths and widths of extracted embryos and lengths and widths of nuts from which embryos were removed (range in mm given for the two latter; m = mean; S = standard deviation).

Species	Figures	Locality	Coll.+No.	Endosperm	Endosperm,	Empty	Embryo	Embryo	Embryo	Nut length:	Nut width:
				+ embryo	no embryo	%	fully formed	length:	width:	range	range
<i>B. maritimus</i>	67A	Namibia, Orange R. Estuary	C.J. Ward 12575	100	0	0	± 100	0.8--1.2 m = 1.0 S = ± 0.07	0.7--0.9 m = 0.8 S = ± 0.05	2.9--3.4 m = 3.2 S = ± 0.13	2.0--2.7 m = 2.3 S = ± 0.13
"	67B	S.Africa, Verlorenvlei coastal	Browning 795, 814-- 817	92.5	0	7.5	± 83	0.9--1.2 m = 1.0 S = ± 0.07	0.5--0.9 m = 0.7 S = ± 0.08	2.6--3.5 m = 3.0 S = ± 0.18	1.7--2.8 m = 2.1 S = ± 0.18
"	67C	S.Africa, Verlorenvlei inland	Browning 796, 800, 802, 809	67.5	5.0	27.5	± 48	0.5--1.0 m = 0.8 S = ± 0.11	0.3--0.8 m = 0.6 S = ± 0.13	2.6--3.3 m = 3.0 S = ± 0.15	1.7--2.5 m = 2.1 S = ± 0.13
"	67D	S. Africa Nieuwoudtvill e	C.J. Ward 13973	82.5	0	17.5	± 53	0.3--0.9 m = 0.7 S = ± 0.14	0.2--0.7 m = 0.6 S = ± 0.12	2.6--3.1 m = 2.9 S = ± 0.12	1.5--2.1 m = 1.8 S = ± 0.14
"	68E	Netherlands Reide	Robertus- Koster s.n. Aug. 1996	97.5	2.5	0	± 90	0.8--1.3 m = 1.1 S = ± 0.09	0.6--1.0 m = 0.8 S = ± 0.08	3.0--4.3 m = 3.9 S = ± 0.23	1.7--2.7 m = 2.3 S = ± 0.22
"	68F	Netherlands Schoonhoven	Robertus- Koster s.n. Aug. 1996	97.5	2.5	0	± 88	0.8--1.2 m = 1.0 S = ± 0.09	0.5--0.8 m = 0.6 S = ± 0.06	3.3--4.1 m = 3.7 S = ± 0.18	1.8--2.4 m = 2.1 S = ± 0.13
<i>B. glaucus</i>	69G	W.Africa Senegal	Johnson s.n.	80	2.5	17.5	± 80	0.8--0.9 m = 0.8 S = ± 0.03	0.6--0.8 m = 0.7 S = ± 0.04	2.9--3.5 m = 3.1 S = ± 0.13	1.4--1.8 m = 1.6 S = ± 0.08
<i>B. fluvialis</i>	69H	U.S.A Wisconsin	S.G. Smith 8620	97.5	0	2.5	± 95	1.0--1.4 m = 1.3 S = ± 0.08	0.6--0.8 m = 0.7 S = ± 0.04	4.1--4.9 m = 4.5 S = ± 0.23	2.1--3.3 m = 2.5 S = ± 0.20
<i>B. caldwellii</i>	70I	Australia Perth	Lepisci & Lally 1758	92.5	0	7.5	± 85	0.7--1.1 m = 0.9 S = ± 0.06	0.7--0.9 m = 0.8 S = ± 0.04	3.0--3.5 m = 3.3 S = ± 0.15	2.2--2.9 m = 2.5 S = ± 0.14
<i>B. medianus</i>	70J	Australia N.S.W.	Lepisci 1598, 1604	75	2.5	22.5	± 36	0.6--1.1 m = 0.9 S = ± 0.15	0.4--0.7 m = 0.6 S = ± 0.10	3.7--4.4 m = 4.0 S = ± 0.16	2.0--2.3 m = 2.2 S = ± 0.09

Table 13.

Bolboschoenus: summary of quantitative parameters for the African species (all except style branch numbers in mm): * indicates criteria most reliable in species differentiation. Note: inflorescence length (depth) is from origin of lowest bract to top of inflorescence.)

	<i>B. grandispicus</i>	<i>B. nobilis</i>	<i>B. glaucus</i>	<i>B. maritimus</i>
Plant height	(50-)200-400(-630)	280-4500	300--800(-1500)	260--830(-1500)
Spikelet length	(12-)15-17(-25)	(5-)8--10(-17)	(12-)15--20(-85)	15--22(-25)
Spikelet width *	(6-)8--10(-11)	(3-)4--5	3-4(-5)	5-7 (-8)
Glume length *	6-7 (8.3)	4-5	5-6	(5-)6--7(-8.5)
Anther length	(1.3-)1.5--1.6(-1.8)	(2.0-)2.2--2.8 (-3.0)	(1.9-)2.5--3.1(-3.5)	(2.3-)2.5--3.7(-4.0)
Anther crest length	0.2--0.4 (-0.5)	(0.5-)0.8--1.0	(0.1-)0.2--0.3(-0.4)	(0.1-)0.2--0.4
Inflorescence length (depth)	15-32	55-180	42-65	15-55
Inflorescence width (breadth)	7-60	100-283	55-98	10-60
Nut length	(2.8-)3.0--3.1 (-3.5)	2.2-2.8	2.4-3.3	(2.6-)2.7--3.4
Nut width	(1.5-)2.1--2.5	1.3-1.7	1.6-2.2	(1.9-)2.1--2.8
Number of style branches*	2	3	3	2 and 3 within a spikelet