

Studies in Cyperaceae in southern Africa 35: a field study of *Bolboschoenus maritimus* s.l. in a western Cape wetland

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An account is given of reproductive features, especially the inflorescence, spikelets and achenes, including pericarp anatomy and embryos, of a population of *Bolboschoenus maritimus* (L.) Palla *sensu lato* at Verlorenvlei, an estuarine lake on the west coast of Cape Province (now Northern Cape), South Africa. The variation encountered is recorded by means of illustrations and tables, and speculative explanation of the range of morphological form reported is offered to promote further study. Some comparisons of achenes, pericarp anatomy and embryos from populations in the general area of the Northern and Eastern Cape are made with those from Verlorenvlei.

Keywords: *Bolboschoenus*; field study; southern Africa; Verlorenvlei.

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Introduction

With the emphasis now being placed upon the provision of water resources for the future, wetlands are at last receiving the attention they merit. Detailed information on the plants of these wetlands is limited; this is especially applicable to members of Cyperaceae, some of which are present, often in considerable number, in most wetland habitats. *Bolboschoenus maritimus* (L.) Palla *sensu lato* is one such sedge. This species complex, which is predominantly European in distribution, has also been reported from Africa, Asia and North America. It requires study for botanical reasons as it is doubtfully homogeneous. In other respects it is worthy of investigation, for it is a food source for both wild and domesticated animals and birds (Kantrud 1996; pers. obs. by J. Browning in South Africa and C.J. Ward in Namibia), while the below-ground system is effective in the stabilisation of soft substrates (Kantrud 1996: 36 quoting Gillham 1957; Kadlec & Wentz 1974) and in the filtration of sewage effluent (Seidel 1971).

For southern Africa, two species of *Bolboschoenus* are recorded (Reid 1993: 110). *B. nobilis* (Ridley) P. Goetghebeur and D.A. Simpson is confined to a limited zone of coastal-hinterland Namibia. (It is also in Angola; it is a sub-Saharan African endemic). *B. maritimus* s.l. is distributed along most of the western, southern and south-eastern coastline. A so far unexplained hiatus separates the most eastern records (Mbashe River estuary) from those slightly inland in the St. Lucia area, northwards into Mozambique and westwards into the interior, where there are scattered records from pans and drainage lines except in the most desertic interior (Browning & Gordon-Gray 1992: 381, Figure 1). This study revealed a lack of uniformity within *B. maritimus* in southern Africa. We detected the possible presence of two entities, referred to by us as Entities 1 and 2. Entity 1 is predominantly coastal (western, southern and south-eastern) having close morphological relationship with extra-territorial examples of *B. maritimus* from northern Europe especially, and tentatively accepted as *B. maritimus sensu stricto*, or close to this. Entity 2 is more tropical, from St Lucia northward and inland and extra-territorially at scattered localities throughout the remainder of sub-Saharan Africa and into India by way of the Middle East. Differences between Entities 1 and 2 are recognisable morphologically in the organs of reproduction (inflorescence form; spikelet shape and size; glume colour, and most reliably, features

of the achene). Van der Veken (1965: 296) had expressed the probability that within a species embryo length was likely to vary only within ten percent of recorded values. We undertook a further study of Entities 1 and 2 in an attempt to reveal more of the achene and embryo structure, but were handicapped by a paucity of fruits of Entity 2. Our results showed well defined differences in achene surface conformation and in pericarp anatomy in transverse section under electron scanning, but embryos were too few for any conclusions to be drawn (Browning & Gordon-Gray 1993). During our earlier investigation we had observed occasional irregular specimens that for one reason or another warranted special study (see Browning & Gordon-Gray 1992: 381), but these lacked fruits. Pursuing these irregularities, it became important to undertake field studies to determine in particular: (i) the range of variability in the reproductive features of Entity 1 from littoral habitats to as far inland as plants could be traced; (ii) to determine whether the pericarp anatomy of Entity 2 could be found within a population with a predominance of the Entity 1 pericarp anatomy. (The most striking difference in this pericarp anatomy is the radial extension, or not, of the exocarp; a single layer of small, more or less square cells in Entity 2, compared with radially extended oblong cells in Entity 1); (iii) to determine whether populations from higher altitudes inland from the western Cape coast of the Clanwilliam, Nieuwoudtville area and the vicinity of the junction of the Fish (Vis) and Orange Rivers had the pericarp anatomy of Entity 1 or Entity 2, or differed from both of these.

Meanwhile, together with colleagues in America (S.G. Smith and A.E. Schuyler) the problem of a possible name for Entity 2, was pursued. As a result of this investigation, it has been equated with a type from Senegal (*Rousillon s.n.*, P) and the necessary combination, *Bolboschoenus glaucus* (Lam.) S.G. Smith, published (Smith 1995: 101). A history of the name, often considered a synonym of *B. maritimus* s.l., together with a formal description of the species, is given in a short paper (Browning *et al.* in press). In the present paper Entity 2 will be referred to as *Bolboschoenus glaucus* (Lam.) S.G. Smith from now on.

Materials and Methods

The field study was carried out during January–February 1996 when plants of *Bolboschoenus* were in peak reproduction. Also given are data on embryos in particular that relate to other Cape and Namibian

populations that were examined in the field and sampled by one of us (CJW). Representative voucher specimens for these populations are preserved in herbaria (see under Citation of specimens).

The study site

Verlorenvlei, an estuarine lake situated at 32°19'–32°23' S, 18°20'–18°28' E, approximately 180 km north of Cape Town, between Elandsbaai on the coast and Redelinghuys about 32 km inland (distance estimated by road along the northern bank), was selected as suitable for a field study. The lake has been well documented in recent accounts (Sinclair *et al.* 1986; Cowan 1995: 17, 18); its features will not be repeated, except to elaborate aspects that are relevant to the study.

The study

1. Sampling sites

A hand drawn map, not to scale (JB), is given to show the relative positions of the seven sampling sites (Figure 1A–G), from which 14 collections were made (*J. Browning* nos 794–802 inclusive, 809, 814, 815, 817). Site G, from which little material could be obtained due to predation (collection 801) will be omitted as it did not provide an adequate number of inflorescences. These sites were not at regularly spaced intervals from the coast to the inland lake limit because of hindrances (the need for a boat; fences; permission required from absentee landowners); nevertheless, effort was made to sample as systematically as possible from differing microhabitats. Sites A, B, C are considered coastal (represented by Figure 2); D–F inland (represented by Figure 3). This is an arbitrary distinction, for change is gradual, not sharp; however, the terms serve usefully as reminders of edaphic differences such as changing salinities (reported as about 11.5 ppt at A; about 0.5 ppt at F. Figure 1, see note), degree of water flow with concomitant levels of oxygenation/stagnation, and effects of grazing animals (predation and excessive nitrogenous input), which could not be assessed or otherwise studied (except visually) in the time of the study.

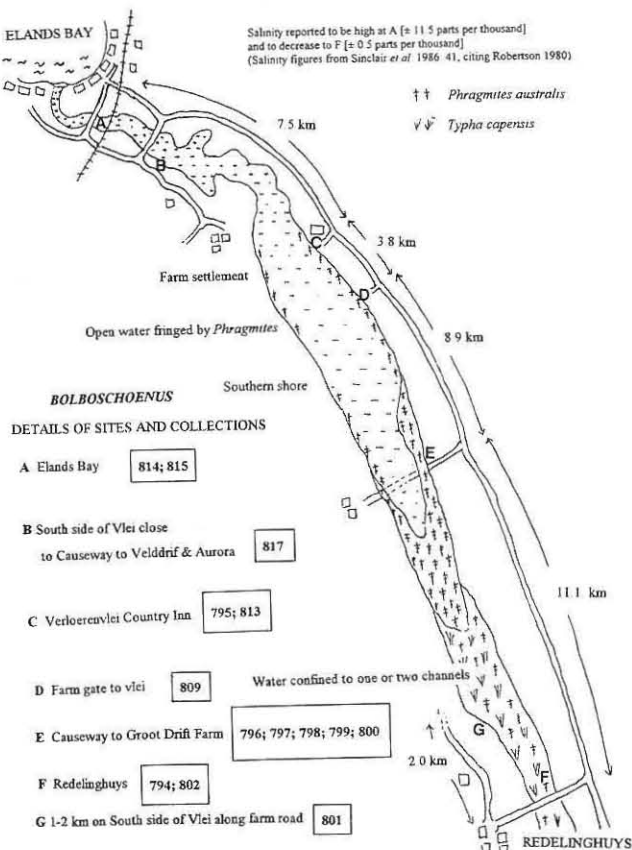


Figure 1 Map of Verlorenvlei showing collection sites.

In the coastal sites (Figure 2) *Bolboschoenus* constituted almost pure stands in water, or in very damp sand from which water had receded as shown by the presence of dried out submerged aquatics (mostly algae) lying on the soil. Its main associate was another sedge *Schoenoplectus scirpoides* (Schrad.) J. Browning, better known as *Schoenoplectus litoralis* (Schrad.) Palla *s.l.* or *Scirpus litoralis* Schrad. *s.l.* (Browning *et al.* 1994) which also grew in almost pure stands in water. There was little evidence of animal predation of these sedges in this coastal area. Inland was open water fringed by stands of *Phragmites australis* (Cav.) Steud. (Poaceae). Near Redelinghuys, the inland limit of the lake comprised a few isolated pools and channels. Here the *Phragmites* stands were intermingled with stands of *Typha latifolia* L. var. *capensis* Rohrb. (Typhaceae). These tracts of tall vegetation were separated by areas of almost bare ground dotted with occasional low-growing sclerophyllous shrubs (possibly resulting from overgrazing?). Marginal to the tall vegetation were occasional robust sedges that were ungrazed (for example, *Carpha glomerata* (Thunb.) Nees, *Cyperus marginatus* Thunb., *C. fastigiatus* Rottb., *C. textilis* Thunb.), with others, low-growing, amongst them, (for example *Isolepis* spp.). Within the area between the open water and the inland limit of the lake was *Bolboschoenus*: where protected, in extensive, dense flowering stands (Figure 3); where unprotected, denuded of inflorescences and upper leaves; where trampled, short and clearly depauperate.

2. Collection of samples

From each of the six collecting sites (Figure 1 A–F) entire plants with rhizomes connecting individual shoots were dug, washed to remove surplus sand and detritus, and prepared for drying in plant presses. The markedly swollen corms basal to the erect leafy shoots were sectioned to facilitate drying, but care was taken to maintain continuity of rhizomes. From each sampling site a further 20 inflorescences were taken randomly to give an adequate number for more detailed assessment of floral parts.

3. Examination of samples

3.1. Inflorescences

From each collection site, one inflorescence that best represented the most usual facies for that site was photocopied. From the image obtained a silhouette was prepared to portray differences visually (Figure 4).

For measurement, nine inflorescences were taken at random from the additional sample of 20 from each sampling site mentioned under 2 above. (This was done by accepting and discarding alternate inflorescences as taken by hand from the full sample until nine had been obtained.) Sites A (coll. nos 814, 815), B (817), and C (795) were coastal. Sites D (809), E (796, 800), and F (802) were inland. For these samples, the following parameters were recorded:

- (i) spikelet number per inflorescence
- (ii) number of rays per inflorescence
- (iii) lengths of rays.

3.2. Spikelets

Spikelet size may vary quite markedly from one inflorescence to another depending, it would seem, upon a number of factors, not all fully understood but including stage of development. In consequence, an extensive sample of spikelets at the stage of fruit maturation of the lower florets, or nearest to this, was drawn from the sampled material in the following way: (i) from the total inflorescence number within a particular collection, each of 45 spikelets nearest the right stage of development were measured (length and width). Eight collections of the total of 13 were treated in this way. This gave a total of 360 spikelets. These collections covered the coastal and inland sites as given under 3.1 for inflorescence. (ii) from the parameters obtained, spikelet size ranges for each site, and for coastal and inland zones, were tabulated as minimum and maximum lengths and widths. Where a mode was clearly defined this was also recorded.

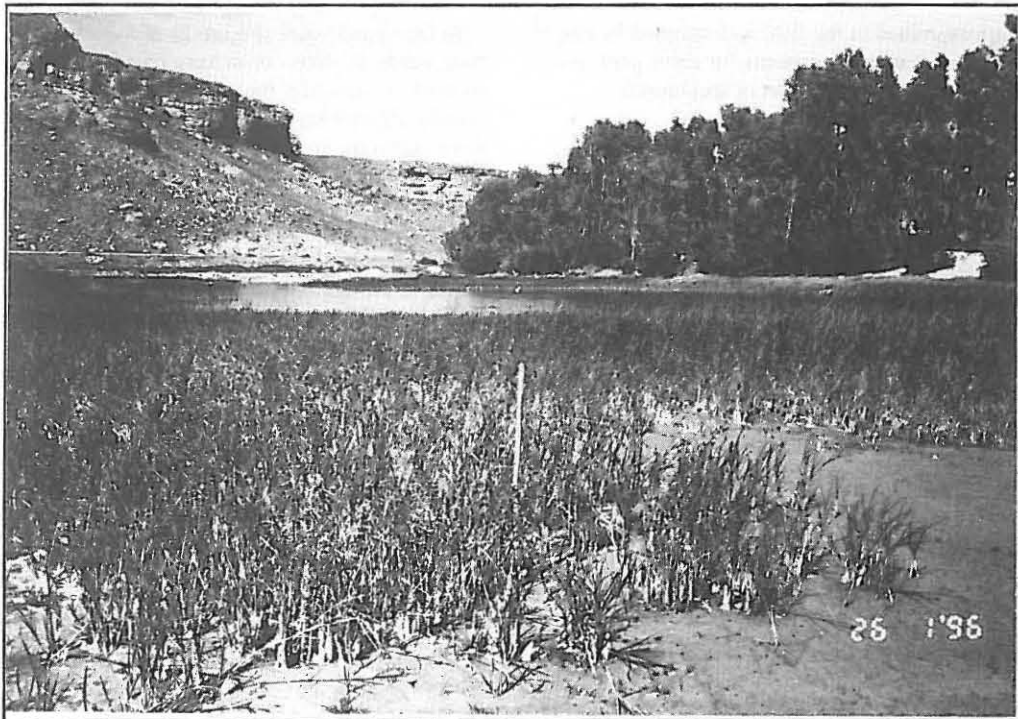


Figure 2 Coastal site with *Bolboschoenus maritimus s.l.* in foreground on wet sand.

3.3. Glumes, stamens and styles

Examination of glumes, stamens and styles (particularly style branch number) of a representative example of about ten spikelets taken at random from material from each collection site, was carried out.



Figure 3 Inland site of *Bolboschoenus maritimus s.l.* protected from predation by a fence.

This was to assess variation rather than to record uniformity.

3.4. Achenes and perianth bristles

From the inflorescences comprising each of the 13 collections, 20 mature achenes were removed for detailed measurement and examination. Measurement of each achene (using a Nikon binocular microscope with ocular graticule) was as follows: (i) length from apex of beak to base (excluding any bristle attachment); (ii) width across abaxial surface. The number of perianth bristles lying on the abaxial face of each achene was recorded and the length of the longest bristle measured. Many achenes carried no perianth bristles, these having been lost or left within the subtending glume.

3.5. Electron scanning of achene surface and pericarp in transverse section

From the sample of 20 achenes from each collection site (see under 3.4 above), three achenes were taken at random, mounted with abaxial surface uppermost, on a brass stub by means of double-sided adhesive tape, coated with gold palladium in a Polaron E 5100 Sputter Coater, examined in an Hitachi S 570 Scanning Electron Microscope and photographed to record surface topography.

A further three achenes from the sample were placed vertically on drops of 'Tissue Tek' on metal discs; discs were then placed in an insulated dish and submerged under liquid nitrogen. With a razor blade tapped sharply at right angles to the length of an achene a transverse fracture was obtained. Both halves were mounted, with cut surfaces exposed, on brass stubs, coated, examined and photographed, as for the whole achenes. Whenever possible, the content of the achene halves (principally endosperm) was removed before coating as this, when present, caused charging during scanning.

3.6. The embryo

From three collections within the coastal area, a further sample of 40 mature achenes was taken from inflorescences. Another sample from three collections from the inland area was similarly obtained. (Note: for numbers of these collections see Table 4.) For each sample, procedure was as follows: (i) each achene was cut transversely to remove the upper third, so that endosperm was exposed; (ii) the cut achenes were boiled for one minute to expand the endosperm, which facilitated its removal together with testa and embryo; (iii) the testa was then split longitudinally and the embryo carefully removed and

Table 1 *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

mounted on a slide in water; (iv) lengths and breadths of embryos were measured using a Nikon binocular microscope with ocular graticule. Note: a preliminary investigation had ensured that boiling did not cause swelling of the embryo and therefore increase in its dimensions. The enclosing lower two thirds of the pericarp and the endosperm are likely to insulate the embryo during boiling.

Results

The results of this study are presented by means of Tables 1–4 and illustrations (Figures 1–8). There follows a discussion in which interpretation of the results is attempted.

Discussion

Inflorescence

Variation in inflorescence form from a compact head comprising relatively few spikelets, to an open, umbellate type with branches and a greater total number of spikelets, has been problematic in the taxonomic history of *Bolboschoenus maritimus* s.l. Opinions have differed in the application of specific limits, so that either the total range has been included, or a narrower view-point has resulted in some exclusion (Raymond 1965; Robertus-Koster 1969; Norlindh 1972; DeFilippis 1980; Hooper 1985). Norlindh's detailed field study showed both compact and open inflorescences could be present on interconnected rhizomes and that extremes and many transitional forms were often represented within a population. His conclusion was that 'ramification of the inflorescence is a non-essential character' (Norlindh 1972: 404).

The field study at Verlorenvlei showed variability in inflorescence form comparable with that described by Norlindh (1972). There was variation: (i) within the sample from an individual collection, different types of inflorescence being borne on the same rhizome system; (ii) within the collection numbers from a collection site (see Table 1), and most markedly, (iii) from the entire study area (Figure 4 and Table 1 represent the total range). Within this total range an overall gradient was detectable. In the coastal zone, inflorescences were predominantly contracted, either lacking rays, the spikelets sessile, or with few short rays (Figure 4 A, B and Table 1). In the inland zone more open inflorescences, usually with well developed rays, were in the majority (Figure 4 D, E, G, H and Table 1). Some irregularity to

this gradient was evident throughout the study area; this was more marked inland than in the coastal zone and sometimes applied to most inflorescences on an individual plant, sometimes to occasional ones. Throughout the area of sampling, occasional inflorescences consisted of a solitary spikelet only that was pseudolateral in origin, but which appeared to terminate the culm. Usually these solitary spikelets were borne on shoots interconnected by rhizomes with shoots carrying either contracted or branched inflorescences comprising more than a solitary spikelet. Often the shoot with a solitary spikelet arose from a lateral

Table 2 *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)

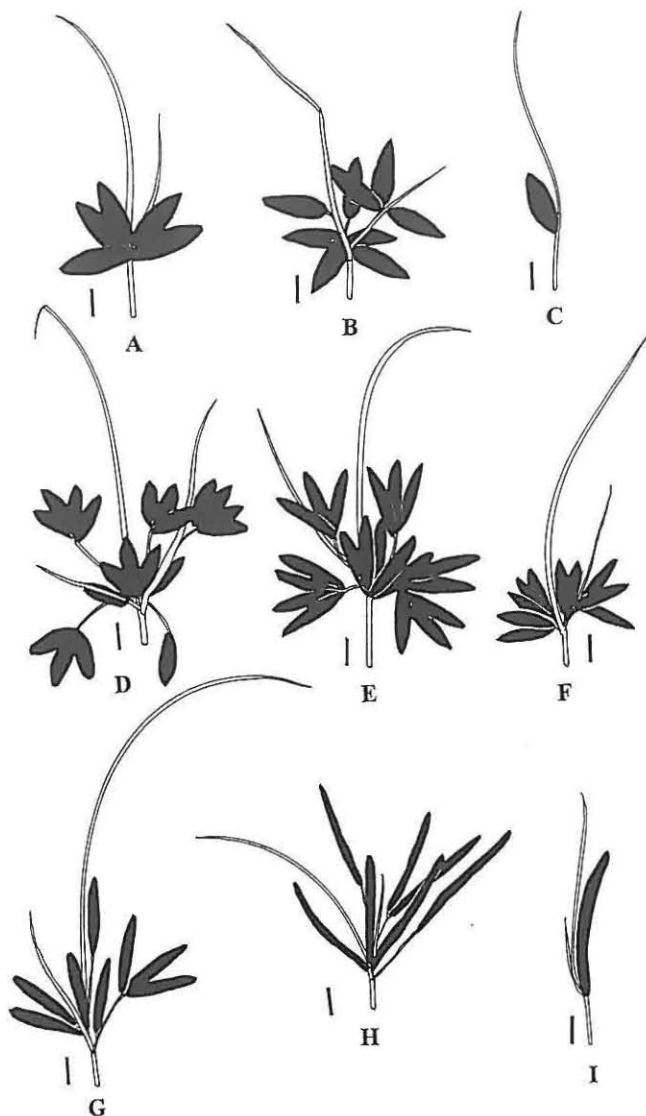


Figure 4 *Bolboschoenus maritimus* s.l., diagrammatic silhouettes of inflorescences and spikelets. A–C representative of coastal sites (A, B, C); D–I representative of inland sites D, E, F. Note: these silhouettes A–I are representative of types of inflorescence; one or more may come from one sampling site as there is frequently variation within the site and even on an individual plant. Scale bar = 10 mm.

bud on a well-developed corm of a well established plant.

As is to be expected, the more contracted coastal inflorescences generally carried fewer spikelets (1–)5–6(–14) than did the more open inland type (1–)6–18(–40) (Table 1).

Spikelet

Correlated with the overall gradient in inflorescence form were changes in spikelet form. In the coastal zone, brown, ovate spikelets (9–)15–20(–30) × (3–)5–7(–8) mm long and wide (Figure 4 A, B, C and Table 2) gradually gave place to yellow-brown, lanceolate-oblong ones (7–)15–25(–34) × (3–) 4 (–6) mm long and wide (Figure 4 G, H, I and Table 2). There was little deviation from this colour and size spikelet gradient.

Achene

Achenes throughout the study area varied little in shape and size, being ovate to obovate in outline and falling within the size range

2.6–3.5 × 1.7–2.8 mm long and wide (Table 3). There was no appreciable distinction in shape or size between achenes from coastal and inland sites. Some difference in colour existed, namely the golden-brown coastal specimens became darker inland. Most significant differences in the achenes became evident only on sectioning transversely and on observation under the scanning electron microscope. These differences incorporate mainly: (i) variation in the topography of the achene surface; (ii) the pericarp anatomy. Of these, the latter is the more striking, particularly the radial extension of the exocarp cells and the ratio of the depth of this layer to the depth of the strongly thickened mesocarp. The innermost pericarp layer, the endocarp, showed little variation.

The surface of the coastal achenes was of the 'honeycomb' pattern, namely an outline of isodiametric, approximately six-sided cells, the anticlinal walls depressed, the outer periclinal wall slightly raised (Figure 5 B, F, J). In transverse section exocarp cells were deeper than wide, that is radially extended, and the depth of these cells was usually approximately twice that of the depth of the adjoining mesocarp (Figure 5 D, H, L).

In contrast, the surface of the darker brown inland achenes lacked cellular definition, the pattern, when discernable, was irregular and variable (Figure 6 B, F, J). Occasional achenes showed imperfections in this layer, denoting perhaps failure in development due to malformation or injury of some kind. Exocarp cells were far less deep radially than were those of the coastal examples (Figure 6 D, H, L). This resulted in the ratio of exocarp depth:mesocarp depth being approximately 1:2, namely a reversal of that recorded for coastal examples.

What is of special note is that for inflorescence form an overall gradient, coastal to inland, was quite clearly evident: for pericarp anatomy, however, the coastal achenes in the ratio of approximately 2:1 for exocarp depth:mesocarp depth, differed sharply from the inland examples which were relatively uniform in the ratio of 1:2 for the comparable layers (compare Figures 5 D, H, L and 6 D, H, L).

Bristles

Some difference in bristle attachment was noted, namely in coastal examples the bristles had mostly fallen from the achenes by maturity (Figure 5 A, E, I); those (usually only one) that remained attached were easily detached. In inland situations the bristles were usually persistent and much more difficult to detach (Figure 6 A, E, I). Length of the longest bristle proved an unsatisfactory parameter as many coastal achenes carried only few (sometimes none) of their total complement. Inland achenes are differentiated from coastal examples in a majority of cases by the greater persistence of filaments. In both groups the large anthers fall immediately following anthesis. Glumes and style branch numbers contributed no features of special significance.

Embryo

Investigation of seeds from a sample of each of coastal and inland fruits, showed that in general structure both sets were typical of the *Bolboschoenus* embryo type (Goetghebeur 1986: Figure 8.4.2, C pg 354). However, some differences were noted, namely: (i) for the coastal sample, 92.5% of fruits contained endosperm and embryo, whereas for the inland sample the figure was 67.5%; (ii) for the coastal sample all fruit with endosperm contained embryos, but in the inland sample 5% of the fruit with fully formed endosperm lacked embryos; (iii) for the coastal sample 7.5% of fruits were empty, in contrast to the inland sample where 27.5% were empty. In addition the embryos from the coastal sample were longer than those from the inland area (Table 4).

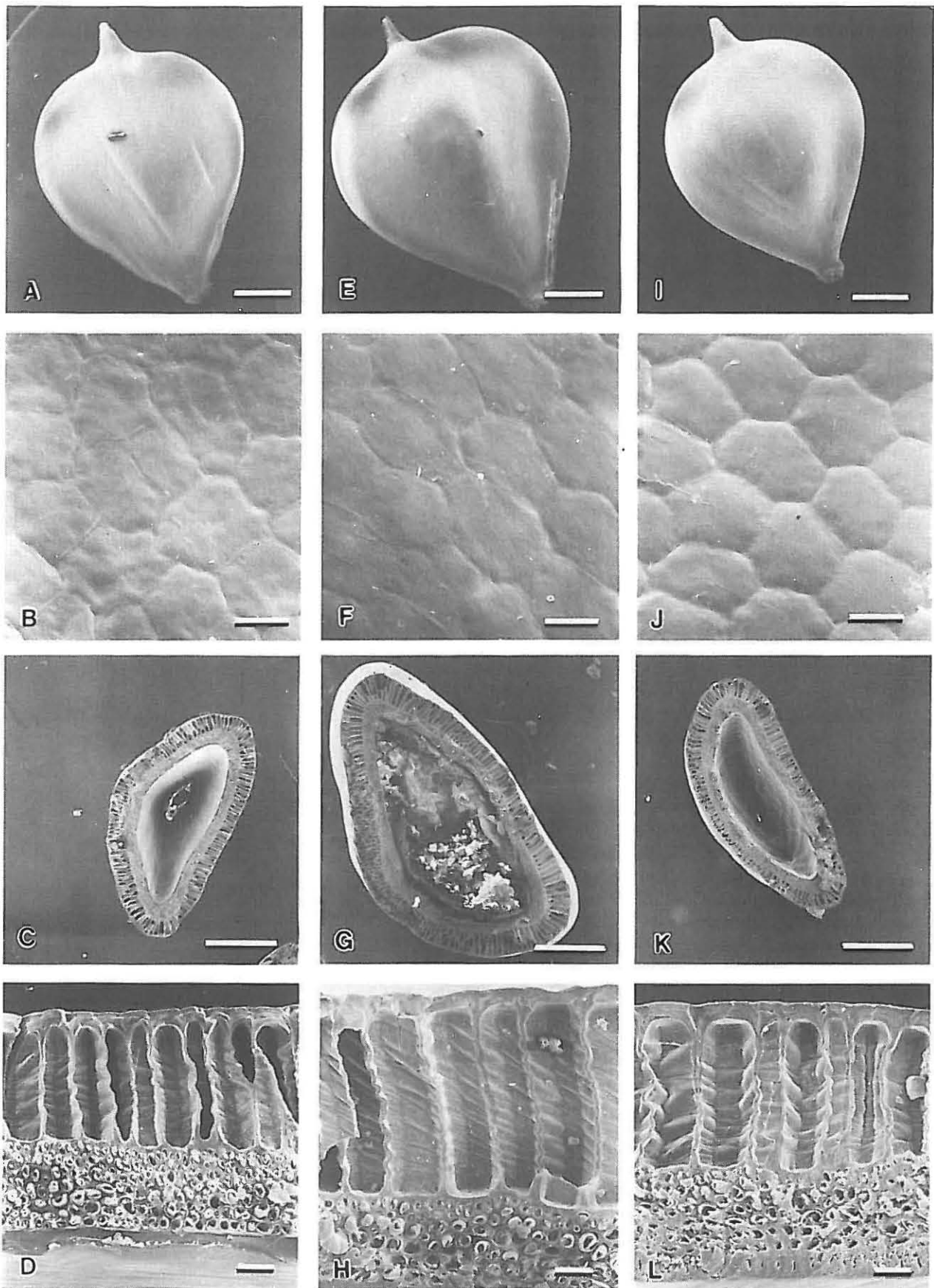


Figure 5 *Bolboschoenus maritimus* s.l., coastal achenes. **A, E, I**, achene abaxial view (scale bar = 500 μ m); **B, F, J**, exocarp surface (scale bar = 25 μ m); **C, G, K**, achenes in transverse section (with or without endosperm) (scale bar = 500 μ m); **D, H, L**, detail of pericarp structure in transverse section (scale bar = 25 μ m). **A–D** = *J. Browning* 795; **E–H** = *J. Browning* 814; **I–L** = *J. Browning* 817.

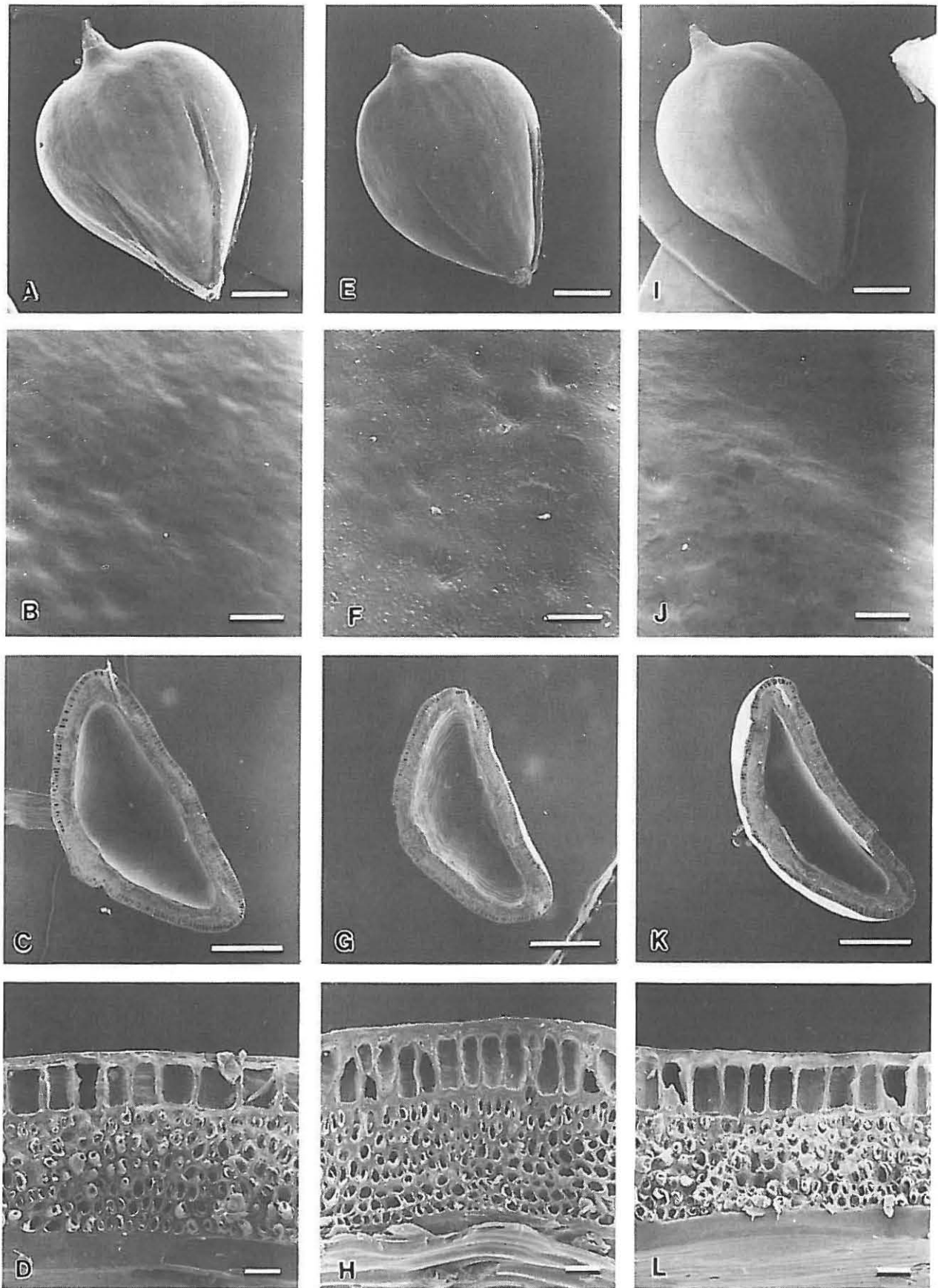


Figure 6 *Bolboschoemus maritimus s.l.*, inland achenes. A, E, I, achene abaxial view (scale bar = 500 μ m); B, F, J, exocarp surface (scale bar = 25 μ m); C, G, K, achenes in transverse section (with or without endosperm) (scale bar = 500 μ m); D, H, L, detail of pericarp structure in transverse section (scale bar = 25 μ m). A–D = J. Browning 796; E–H = J. Browning 802; I–L = J. Browning 809.

Table 3 *Bolboschoenus maritimus s.l.*, Verlorenvlei (coastal and inland), Orange River estuary (coastal) and Nieuwoudtville (inland). Achene lengths and widths (range in mm; S = standard deviation). Note: sample for each collection no. from Verlorenvlei = 20 achenes, therefore total for coastal and inland sites respectively = each 80 achenes : for Orange River estuary and Nieuwoudtville each sample = 40 achenes

Verlorenvlei	Site	Coll. no.	Achene length: range in mm S = standard deviation	Achene width: range in mm S = standard deviation
Coastal	A	<i>Browning 814</i>	3.1–3.5	2.2–2.8
	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 S = ± 0.18	1.7–2.8 S = ± 0.18
Inland	D	<i>Browning 809</i>	2.8–3.3	1.9–2.5
	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 S = ± 0.15	1.7–2.5 S = ± 0.13
Orange River estuary	N/A	<i>Ward 12575</i>	2.9–3.4 S = ± 0.13	2.0–2.7 S = ± 0.13
Nieuwoudtville	N/A	<i>Ward 13973</i>	2.6–3.1 S = ± 0.12	1.5–2.1 S = ± 0.14

Conclusions and summary

The factors that underlie and control the morphological differences in reproductive organs between the coastal and inland plants of *Bolboschoenus maritimus s.l.* at Verlorenvlei that are reported here, are unknown. Attempts at explanation must be regarded as purely speculative.

Firstly, plants in more exposed coastal situations are likely to be subject to more extreme microhabitat conditions of, for example, soil salinity and wind effect, (especially winds carrying high levels of salt spray), than those further inland. The inland plants may be subject to periodic inundation, and possibly temporary stagnation with concomitant fall in levels of available oxygen,

and perhaps an imbalance in available nutrients. It can only be assumed that these effects may result in poorer growth conditions nearer the sea than further inland, resulting in turn, in smaller plants bearing contracted inflorescences with fewer, wider, shorter, darker spikelets. It will explain, too, the more numerous irregularities to the overall gradient inland where microhabitats are more varied than close to the sea. Reasons underlying the difference in spikelet colouration, and more particularly, the considerable radial extension of the exocarp cells of coastal achenes, are more difficult to speculate upon. Koyama (1962: 933) noted the paler glumes of inland plants in comparison with coastal examples, but offered no explanation. Oteng-

Table 4 *Bolboschoenus maritimus s.l.*, Verlorenvlei (coastal and inland), Orange River estuary (coastal) and Nieuwoudtville (inland). Contents of achenes and ranges in lengths and widths (in mm) of extracted embryos (when present). (Note: Each sample consisted of 40 achenes taken randomly from inflorescences from collection nos as follows: Verlorenvlei, coastal, nos *J. Browning 814, 815, 817*; inland nos *809, 796, 800*; Orange River estuary *C.J. Ward 12575*; Nieuwoudtville *C.J. Ward 13973*)

Verlorenvlei	No. with endosperm & embryo	No. with endosperm, no embryo	No. without contents	Embryo length (range) S = standard deviation	Embryo width (range) S = standard deviation
Coastal	37	0	3	0.9–1.2 S = ± 0.07	0.5–0.9 S = ± 0.08
Percentage	92.5%	0%	7.5%		
Inland	27	2	11	0.5–0.9 S = ± 0.11	0.4–0.8 S = ± 0.13
Percentage	67.5%	5%	27.5%		
Orange River estuary	40	0	0	0.8–1.2 S = ± 0.07	0.7–0.9 S = ± 0.05
Percentage	100%	0%	0%		
Nieuwoudtville	33	0	7	0.3–0.9 S = ± 0.14	0.2–0.7 S = ± 0.12
Percentage	82.5%	0%	17.5%		

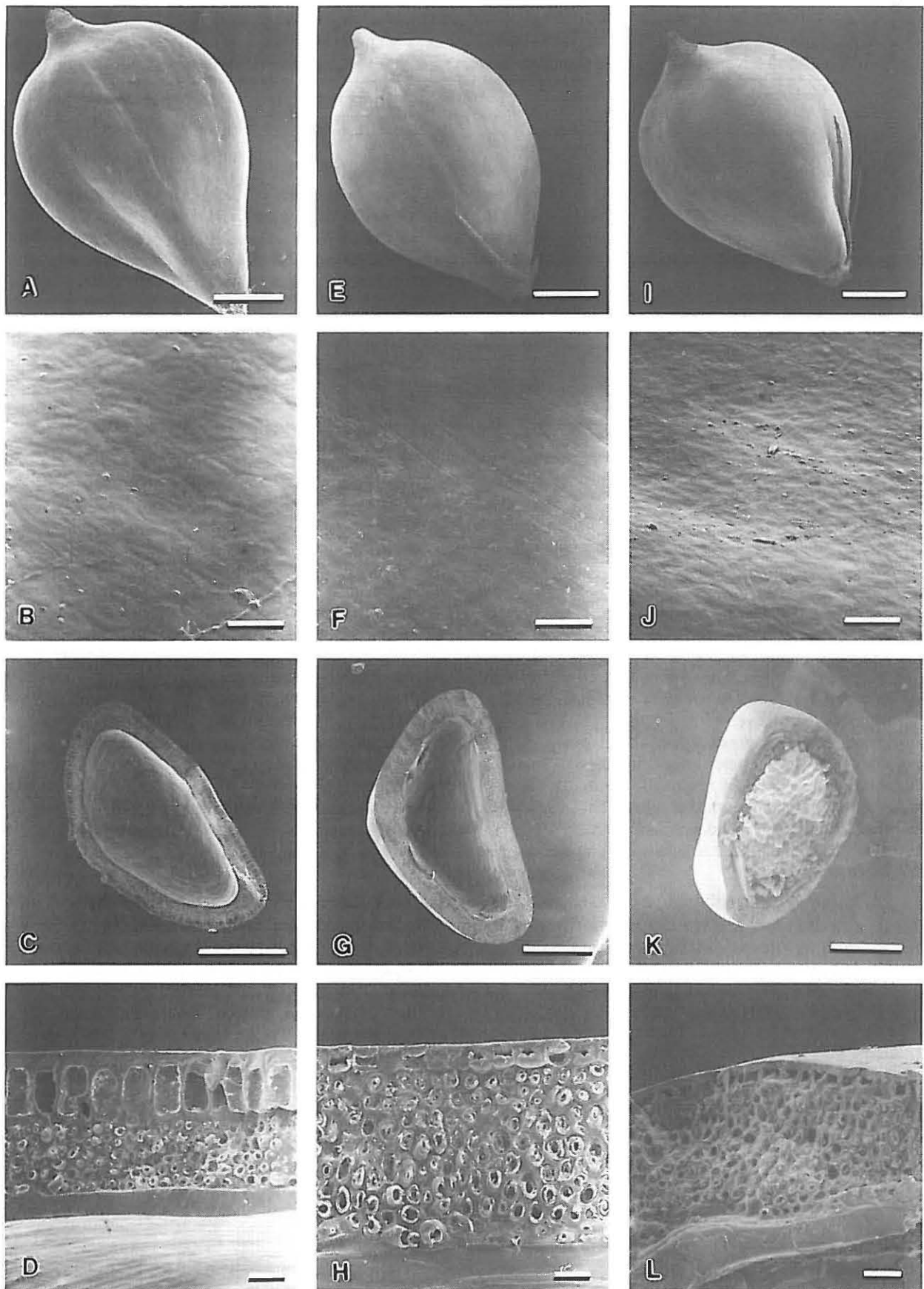


Figure 7 *Bolboschoenus maritimus* s.l. A, E, I, achene abaxial view (scale bar = 500 µm); B, F, J, exocarp surface (scale bar = 25 µm); C, G, K, achenes in transverse section (with or without endosperm) (scale bar = 500 µm); D, H, L, detail of pericarp structure in transverse section (scale bar = 25 µm). A–D = C.J. Ward 13973; E–H = C.J. Ward 13862; I–L = Faure 638 (PRE).

Yeboah (1974) observed radially extended exocarp cells in the American species *Bolboschoenus paludosus* (A. Nelson) Soo (as *Scirpus paludosus* A. Nelson), but merely used this character in supraspecific classification. We surmise these inflated exocarp cells may maintain flotation of the achene in water for longer periods at the coast, than is likely (and perhaps advantageous) further inland. In support of this we have noted the presence of a waxy coating on the surface of the coastal examples, that is less well developed to more or less undeveloped, on the inland ones.

To summarise, it seems probable that ecological factors that are not adequately understood, and therefore not able to be clearly formulated, may have some effect upon the morphological form, particularly of the reproductive organs, in populations of *Bolboschoenus maritimus* s.l. that occupy coastal to more inland situations. In addition, and quite apart from the above, it is necessary to consider what information, if any, the results of this study provide in the delimitation of the species within the genus. From previous work carried out on the achenes of *Bolboschoenus nobilis* (Browning & Gordon-Gray 1992), we are satisfied

that the population at Verlorenvlei is distinct at specific level from this Angolan and Namibian species, which is much larger and differs in underground organs and in other characteristics. The Verlorenvlei populations and representatives of *Bolboschoenus glaucus* (= Entity 2) from St Lucia in Natal and northwards into sub-Saharan Africa, differ most importantly from one another in achene features, notably the size in transverse section of the exocarp cells and the ratio of exocarp depth:mesocarp depth (Browning & Gordon-Gray 1993). However, the morphological correlation between the inland plants at Verlorenvlei and *B. glaucus* is much more marked than between coastal Verlorenvlei examples and *B. glaucus*. This greater correlation is expressed in spikelet shape, size and colour; in achene size, colour, surface topography and pericarp anatomy. Overall, there is also greater similarity in the general facies of whole plants, emphasized particularly by the open inflorescences and the long, more slender, more numerous spikelets. The coastal plants at Verlorenvlei are not clearly distinguishable morphologically from representatives from northern coastal Europe, Sweden in particular, that are tentatively accepted as *Bolboschoenus maritimus* s.s. or close to this. Plants from the St. Lucia area of Kwa-Zulu-Natal and northwards and westwards through Africa and from Egypt through the Middle East to India are *B. glaucus*, a taxon that for a good part of its history has been included within *B. maritimus* s.l. The inland plants at Verlorenvlei show characteristics of both these species, in fact they are best considered as falling within the range between *B. maritimus* s.s. at one extreme and *B. glaucus* at the other. However, they are not strictly intermediate, for they themselves form the semblance of a series showing morphological affinity with *B. glaucus*, but all expressing some degree of relationship with *B. maritimus* in the nature of the pericarp. No evidence whatever has been found at Verlorenvlei for plants with the precise pericarp structure of *B. glaucus*, as known for tropical sub-Saharan Africa.

These findings have led to further speculation on the possible origins of the Verlorenvlei population. Can it be that *B. maritimus* s.s. in southern Africa is a long-standing emigrant from northern Europe, now naturalised and presently occupying coastal locations wherever habitat has proved suitable, from the Orange River estuary in the west to the Mbashe River estuary in the south east? Ample apocryphal evidence exists for the introduction of its fruit to have been possible by birds, particularly migrant waders from northern Europe, and/or later by man in his cereal foodstuffs (wheat and rice). Widespread as it now is over sub-Saharan Africa, in the Middle East and in southern India to the Punjab, *B. glaucus* may be interpreted as having had a southern origin from the Gondwanan flora. Geological records suggest that climates in Miocene time (ca. 15 million years before present) in southern Africa were warmer than now and that a more tropical lush vegetation existed in Namibia and the northern Cape (Ward & Corbett 1990: 19; Bamford in press). Might *B. glaucus*, or its ancestral stock, have been represented in this vegetation? Evidence from Poland has shown that fossilised achenes of *Schoenoplectus* [*Sch. lacustris* (L.) Palla and *Sch. tabernaemontani* (Gmel.) Palla] not unlike those of *Bolboschoenus* (both segregates from *Scirpus*) existed in Europe in Miocene time (Klimko 1992, English summary). It is therefore not unreasonable to speculate that populations of *B. glaucus* and *B. maritimus* might have undergone introgression, subsequent selective processes having resulted in the gradient from coastal to inland that now exists. Putative *Bolboschoenus* hybrids have been reported from N. America (Browning *et al.* 1995: 434). These include putative *B. maritimus* × *glaucus* hybrids in California. In support of the hypothesis that the Verlorenvlei population, or part of it, might be of hybrid origin, other populations from higher altitudes at more inland localities and at other points along

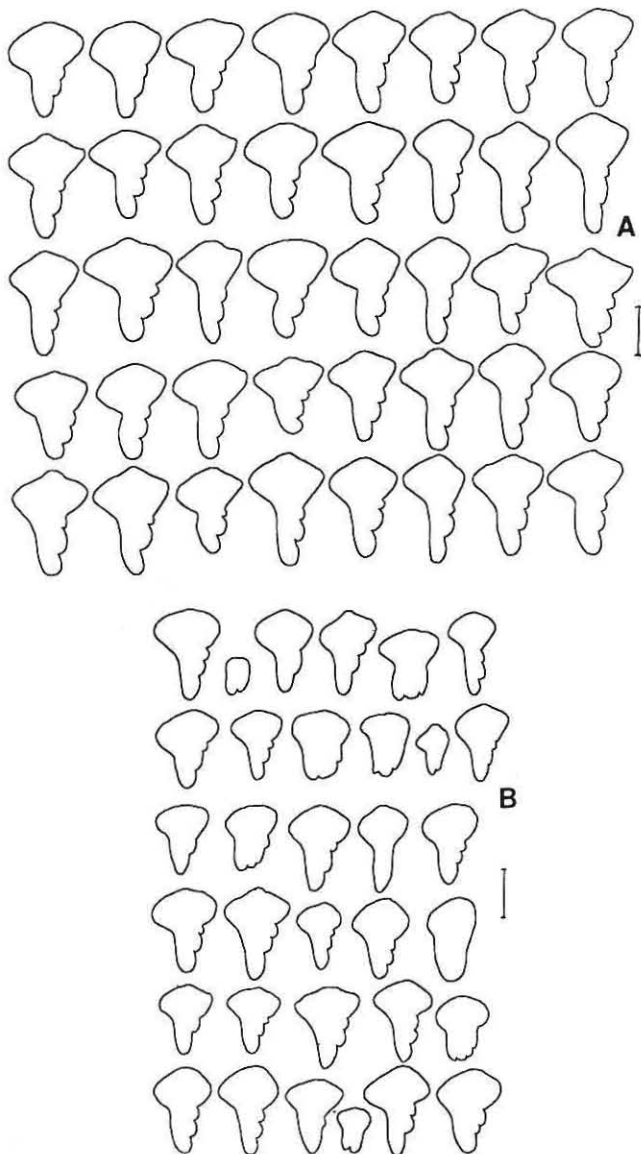


Figure 8 *Bolboschoenus maritimus* s.l. Embryos shown in median longitudinal view, extracted from each of two samples of 40 measured achenes. **A.** Coastal (Orange River estuary, Ward 12575); **B.** Inland (Nieuwoudtville, Ward 13973). Scale bar = 0.5 mm. Note: only 33 of Nieuwoudtville achenes contained contents.

the western and southern coastline were sampled by one of us (CJW) and have been compared with Verlorenvlei specimens in the laboratory and the achenes by micromorphological methods. Studies were not as exhaustive as for Verlorenvlei, but they have yielded useful supportive information, particularly in relation to embryography. This will now be summarised.

Additional information

The additional populations investigated fall under the collector's numbers *C.J. Ward 12575, 13862, 13922, 13929, 13973*, for details of which see under Citation of specimens. Vouchers of these numbers are deposited in the herbaria indicated. The population of which *Ward 13862* forms a part, was subjected to severe flooding and inundation soon after the date of collection. The *Ward 13973* population at Nieuwoudtville is not far from Lokenberg, the locality for *Acocks 17572*, one of the specimens earlier regarded as irregular (Browning & Gordon-Gray 1992: 381).

Plants under the numbers *C.J. Ward 12575, 13922* and *13929* fall within already established limits for *Bolboschoenus maritimus* s.s. in southern Africa and agree well in general facies with plants from Verlorenvlei (coastal). They are not further considered, except that a sample of 40 achenes was removed from *Ward 12575* for achene and embryographic study, following the methods given for achenes from Verlorenvlei. Populations *13862* and *13873* both relate to inland Verlorenvlei specimens (and therefore to *B. glaucus* rather than to *B. maritimus* s.s.), but differ in minor details, one from the other, and from inland Verlorenvlei plants. Particularly does this apply to *13862* in which long, narrow spikelets predominate. Such elongated, narrowed spikelets are not uncommon, however, and have been noted in specimens named by us as *B. glaucus* from Angola and from Senegal (Browning *et al.* in press). Population *13973* yielded 40 mature achenes that have been studied micromorphologically (Figure 7 A–D) and embryographically (Figure 8 B). Population *13862* did not provide an adequate number of mature achenes for embryographic comparison, but some were studied micromorphologically (Figure 7E–H) and compare closely with achenes of *Bolboschoenus glaucus* from more tropical localities in Africa, for example *Faure H638* (PRE) from Nibela, St. Lucia (Figure 7 I–L).

The results of study of the achenes and embryos of these additional populations have been included in Tables 3 and 4 to make comparison with the Verlorenvlei examples convenient.

The following conclusions may be drawn: (i) achene lengths and widths for these additional populations hardly differ from coastal and inland Verlorenvlei samples, except that the Nieuwoudtville achenes show slight reduction in width compared with those from Verlorenvlei (inland); (ii) embryo lengths for coastal Verlorenvlei agree closely with those from Orange River estuary; the widths are also in agreement except that the minimal length of coastal Verlorenvlei is slightly less; (iii) the Nieuwoudtville embryo lengths and widths show lower minima than those recorded for inland Verlorenvlei.

These differences probably relate to what we consider the most important finding of this embryographical study, namely the percentages of achenes containing fully formed embryos, as compared with the percentages of achenes lacking contents (Table 4 and Figure 8 A, B). Coastal Verlorenvlei gave a figure of 92.5% for fully formed contents, and this was supported by the 100% from Orange River estuary. In contrast, inland Verlorenvlei achenes showed only 67.5% with fully formed contents, which, in turn, was supported by Nieuwoudtville which gave a higher percentage (82.5%), but this was 10% less than coastal Verlorenvlei, and 17.5% less than Orange River estuary. Figure 8 illustrates the two sets of embryos that showed greatest

(Orange River estuary) and least (Nieuwoudtville) uniformity. The reduced percentage of achenes with fully formed contents from inland localities may perhaps be indicative of hybridisation in their populational history. As Figure 8 A shows, all embryos from Orange River estuary were well formed and probably viable, in comparison with those from Nieuwoudtville in which of the 33 present, three were small (presumably imperfect and perhaps sterile), while some others were poorly developed (irregular and not showing the uniformity of the embryos of the Orange River estuary sample). A populational history involving natural hybridisation must be regarded as an extremely tentative explanation, as other factors may be causative of the results obtained, for example, differing habitat conditions such as possible inundation, may have had an influence on fertilization and embryo development, as may time of collection in relation to achene maturation. The literature records that '*Scirpus maritimus* [*Bolboschoenus maritimus*] achenes germinate poorly at maturity, but 97% germination can be obtained 2 months later'. (Kantrud 1996: 9). There is an after-ripening period (Isley 1944) during which change in embryo form is possible. Far too little is known at present for any decisive conclusion to be arrived at. The present study is offered as a stimulus to further investigation.

Citation of specimens

—**2816** (Oranjemund): Orange River Estuary 28°34' S; 16°28' E, alt. c. 2.5 m (–CB), *C.J. Ward 12575* (NU, UDW).

—**2817** (Violsdrif): Orange/Fish River confluence, 28°5' S; 17°10' E, alt. c. 74 m (–AA), *C.J. Ward 13862* (NU, UDW).

—**3119** (Calvinia): Nieuwoudtville (–AC), *C.J. Ward 13973* (NU, UDW); Lokenberg. Along river. Alt.c. 640 m. (–CA), *Acocks 17572* (BM, PRE).

—**3218** (Clanwilliam): Verlorenvlei, between Elandsbaai and Redelinghuys (–AD), *Browning 795–802, 809, 813, 814–817*; near Redelinghuys (–AD), *P.B. Taylor s.n.; D.C. Kotze 309, 310* (all NU).

—**3228** (Butterworth): Morgans Bay . 32°42' S, 28°20' E. alt. 1–1.5 m.s.l (–CB), *C.J. Ward 13922* (NU, UDW).

—**3327** (Peddie): Tyolomnqa (Chalumna) River, 33°12' S, 27°34' E, alt. c. 1.5 m.s.l. (–BA), *C.J. Ward 13929* (NU, UDW).

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A poster summarizing the main results of the field study at Verlorenvlei was presented by J. Browning at the 13th Symposium Morphology, Anatomy and Systematics, held at Leuven, Belgium in April 1997. Thanks are expressed to the Organizers and Committee for this privilege. A brief account was published in the Proceedings covering the conference. Dr. P.D. Morant of CSIR, Stellenbosch, kindly provided an aerial photograph of the vlei and its surroundings. We also thank the University of Natal Research Fund for financial aid, and staff members of the Centre for Electron Microscopy, University of Natal, Pietermaritzburg, who assisted with scanning electronmicrographs.

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