

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

Volume 1
TEXT & APPENDICES

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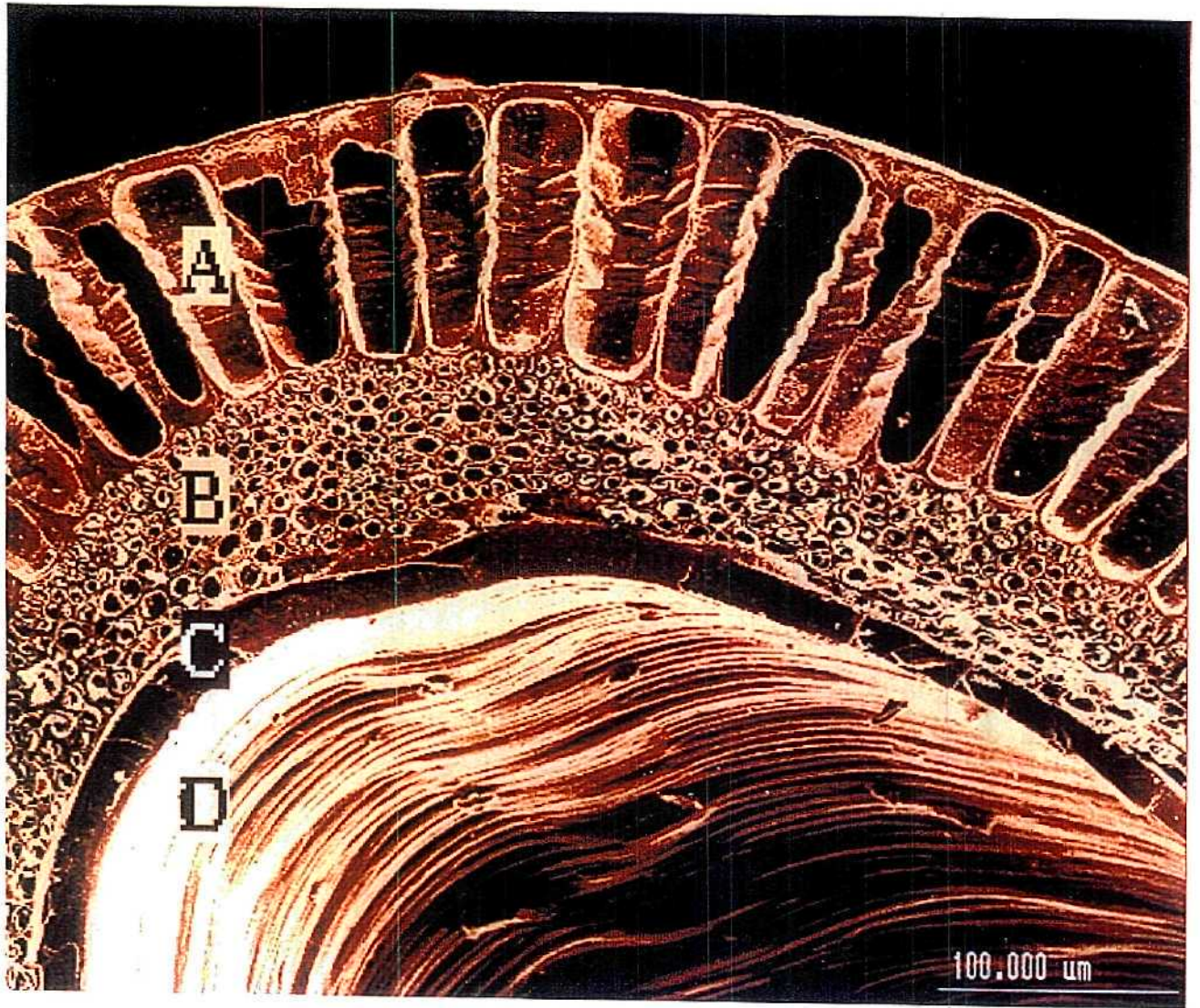
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PREFACE

I hereby declare that this thesis, submitted for the degree of Doctor of Philosophy, University of Natal, Pietermaritzburg, is the result of my own investigations, except where the work of others is acknowledged.

The work was carried out under the supervision of Professors K.D. Gordon-Gray and J. van Staden.

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Frontispiece

Bolboschoenus maritimus (L.) subsp. *paludosus* (A. Nelson) T. Koyama:

Fruit showing pericarp in transverse section.

A. Nelson 3874 (RM): holotype of *Scirpus paludosus* A. Nelson

A, exocarp; B, mesocarp; C, endocarp; D, endocarp surface view (not in transverse section).

ABSTRACT

Using the Scanning Electron Microscope (SEM), fruit surface and pericarp anatomy were investigated in the African species of *Bolboschoenus* (Ascherson) Palla [*B. maritimus* (L.) Palla; *B. glaucus* (Lam.) S.G. Smith; *B. nobilis* (Ridley) Goetghebeur & D.A. Simpson; *B. grandispicus* (Steud.) K. Lewejohann & W. Lobin] and extended worldwide to cover most known species. There was consideration of type specimens wherever possible. Two main patterns of pericarp construction were revealed, with modifications. Using fruit samples from field populations, a surveillance of embryos was carried out to gain some information on percentages of perfect embryo development and variability in embryo outline (as seen in optical, median sagittal section), within and between selected species. Inflorescence structure within African species was studied and illustrated photographically and diagrammatically. The collective information obtained was directed towards better understanding of species limits within the genus and towards gaining evidence of the significance of natural hybridisation as a cause of morphological variability within some taxa. Formal taxonomy including a key to the identification of the African species is provided. Profuse illustrations of pericarp structure of world species are given, as are colour photographs of the African species, excepting *B. grandispicus*. A tentative pattern for subgeneric division of *Bolboschoenus* based primarily on pericarp morphology, is suggested supplemented by a world map illustrating the presently known distribution of the suggested groupings.

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PART 1

INTRODUCTION

AND THE

GENUS IN SOUTHERN AFRICA

CHAPTER 1

THE GENUS *BOLBOSCHOENUS*: ITS HISTORICAL BACKGROUND

Two genera of the family Cyperaceae that are closely allied, both historically and morphologically, are *Bolboschoenus* (L.) Palla and *Schoenoplectus* (Reichb.) Palla. Both incorporate in their generic names the Greek "skoinos", which refers to rush-like plants. "Bolbos" in *Bolboschoenus* is the Greek for bulb, in reference to the base of the culm which frequently becomes swollen into a corm. 'Plecktos' (tissue) in *Schoenoplectus* may refer to the pliable culm tissue of these plants that is useful in basketry. Both genera are segregates from the genus *Scirpus* L. of the tribe Scirpeae.

Accounts of Cyperaceae show that early in the history of the family attempts were made to subdivide it into tribes (Nees 1834; Kunth 1837). The tribe Scirpeae, to which *Bolboschoenus* is ascribed, is distinguished from the tribe Cypereae on the glume arrangement, being spirally arranged in the former and two ranked in the latter, but this, however, is not always clear cut; nor is the distinction that all floral scales are alike and subtending flowers in Scirpeae, as some members of this tribe lack flowers in the lower scales. In spite of inadequate differentiation Scirpeae has remained either as a tribe, or subtribe, or been escalated to subfamilial ranking, throughout periodic revisions. Two recent treatments of Cyperaceae based on a wide range of characters and incorporating cladistic and phenetic analyses, Goetghebeur (1986) and Bruhl (1995), maintain the tribe Scirpeae, but do not fully concur on its constituent genera.

The genus *Scirpus* of Scirpeae has not remained unchanged since its circumscription by Linnaeus in 1753 and 1754. At this time it included numerous species and was even then considered to be heterogeneous. Many of the features used in its generic definition occurred in other genera of the family. Therefore, historically, there has been dissatisfaction with generic limits so that, more recently, attempts have been made to achieve greater homogeneity by segregation as independent genera, groups of species that share common features.

By the late 19th century several such segregate genera had been established including *Schoenoplectus* and *Bolboschoenus*. Reichenbach (1846) described *Schoenoplectus* as a subgenus of *Scirpus*, while Palla (1888) raised it to generic level. *Bolboschoenus* was described by Ascherson (1864) as a section of *Scirpus*, and typified by *Scirpus maritimus* L. Palla (1905) raised the section to generic level. Later attempts to further clarify the constituents of *Scirpus* had been undertaken by Clarke, whose planned classification was published only after his death (Clarke, 1908). Beetle (1942) divided *Scirpus* into two subgenera on the nature of the lowest inflorescence bract, and within these, recognised 13 sections. Koyama (1958) used the shape of the inflorescence and nature of the perianth bristles in addition to the characters used by Beetle. There were no subgenera in Koyama's classification. He recognised *Bolboschoenus* as a section and remarked (Koyama 1958: 278) that on the basis of its nuts and bristles it was close to section *Schoenoplectus*. One of the consequences of his taxonomic arrangement was that *Scirpus*, even at this comparatively late stage in its history, remained heterogeneous and large and still in need of clarification and the possible segregation of further species groups as independent genera.

Work on embryology (Van der Veken 1965) added impetus to the dismantling of *Scirpus* into genera in which uniformity of embryo type occurred. This author's studies indicated that morphologically homogeneous genera were represented by one embryo type, while genera showing morphological variability contained more than one embryo type. He had found six different embryo types to be present in *Scirpus s. l.* Following from Van der Veken's findings, Lye (1971: 290) considered *Bolboschoenus* as a section of *Schoenoplectus* as both possess a *Schoenoplectus*-type embryo. However, it is now known that the *Bolboschoenus*-type embryo is slightly more advanced at time of fruit dispersal than is the embryo of *Schoenoplectus* (Goetghebeur 1986: 342 Table 8.4.1).

An accumulation of anatomical and physiological data applicable to genera of Scirpeae, namely C_3 and C_4 pathways, lead Raynal (1973) to provide a suggested system of classification which assisted later workers. Wilson (1981) expressed the opinion that although there were some problems in achieving effective generic delimitation, it was preferable to separate genera and to point out the problems. Following this policy she took a more

restricted view of the Australian species of *Scirpus s. l.* and transferred them into segregate genera, and then remarked that *Scirpus sensu stricto* is confined to the northern hemisphere. Consensus has not been reached on the full acceptance of segregate genera.

As has been pointed out, the segregate genera *Bolboschoenus* and *Schoenoplectus* are closely allied, and there has been no conclusive agreement on their hierarchical status. Marek (1958: 176), who investigated the anatomy of fruits of European genera in the subfamily *Scirpoideae* Pax, concluded that "Genera *Bolboschoenus* [as *Bulboschoenus*] and *Schoenoplectus* differ from each other in pericarp structures, and Palla is right in classifying them separately." Lye (1971) treated *Bolboschoenus* as a section of *Schoenoplectus*, but Haines and Lye at a later date (1983: 52), considered *Bolboschoenus* as a subgenus of *Schoenoplectus* with one species, *Schoenoplectus maritimus* (L.) K. Lye., stating that it differs from other *Schoenoplectus* species by the possession of a corm, a triangular culm with leaves, 'and an open inflorescence and needle-like setae'.

Wilson (1981: 156) made the point that although *Schoenoplectus* is close to the genus *Bolboschoenus* there are morphological and embryological differences. She noted (Wilson 1981: 157) "in the context of related genera it seems best to treat it [*Bolboschoenus*] as a genus." However, this was not the opinion of DeFilipps (1980: 277) who, a year earlier, maintained *Scirpus* section *Bolboschoenus*. Goetghebeur and Simpson (1991: 170) suggested that species of *Bolboschoenus* [and *Actinoscirpus* (Ohwi) Haines & Lye] are distinct from *Schoenoplectus* on the basis of (1) noded culms with well developed leaves, (2) terminal inflorescence with several leafy involucre bracts, (3) more advanced embryo than the *Schoenoplectus* type (see pg. 87). They support independent generic status for *Bolboschoenus* and *Schoenoplectus*.

Strong (1993: 202, 1994: 29--30) argued for the replacement within *Schoenoplectus* of species already assigned to *Bolboschoenus*. According to his observations there are anatomical, morphological and embryological similarities, and the distinctions as noted above by Goetghebeur and Simpson are not consistent within the two genera. An Asian species, *B. planiculmis* (F. Schmidt) Egorova, was one of the examples used by Strong in his argument

for the non acceptance of *Bolboschoenus* as distinct from *Schoenoplectus*. This species has a sharply three-angled lowest inflorescence bract that continues in line with the culm so that the inflorescence appears pseudolateral. The inflorescence is also frequently a single spikelet (although Koyama 1980: 144, Fig. 1 illustrates an example with several spikelets and a second inflorescence bract). These features of the pseudolateral inflorescence and erect overtopping bract are characteristic of *Schoenoplectus* species, and influenced Strong in his decision not to maintain species in the genus *Bolboschoenus*. He did note, however, that the floral morphology was that of *Bolboschoenus*.

Bruhl (1995: 299, Figure 35), in his cladistic and phenetic analyses of genera of Cyperaceae showed that within the tribe Scirpeae the genus *Bolboschoenus* (and *Actinoscirpus*) are well removed from *Schoenoplectus*. He also stressed that the tribe Scirpeae " seems to be the one in greatest need of taxonomic effort in the Cyperaceae."

For southern Africa, Browning and Gordon-Gray (1992: 380) followed Goetghebeur & Simpson (1991) rather than Haines & Lye (1983) and treated species under *Bolboschoenus*. This policy was maintained when the structure of the pericarp anatomy of southern African taxa of *Bolboschoenus* was elaborated (Browning & Gordon-Gray 1993). Gordon-Gray (1995) likewise maintained *Bolboschoenus*.

There are floras in which species still continue to be treated under *Scirpus s.l.* or under *Schoenoplectus*. However, acceptance of *Bolboschoenus* as a genus in its own right distinct from *Schoenoplectus* (and segregated from *Scirpus*) is becoming increasingly favoured. Recently Smith (1995) made combinations under *Bolboschoenus* for some American species, and in Flora of North America due for publication at a date yet to be determined, the species will be treated under *Bolboschoenus* (Smith, pers. comm.).

From this brief historical outline it can be seen that there have been major problems in attempting to arrange Scirpoid species in relatively uniform naturally related genera. The aim was to reduce heterogeneity and at the same time, to modify, at least partially, the undesirable element of a large genus such as was *Scirpus* L., as for practical purposes and flora

treatments with keys, smaller taxa are more satisfactory; notwithstanding, genera need to be clearly delimited by the use of consistent, reliable characters. Although with the passage of time the corpus of knowledge of many aspects previously not investigated has increased, the inherent problems of lack of suitable reliable distinguishing criteria remain. As a consequence attempts to segregate genera, sometimes on the impetus of new knowledge, have not always received acceptance. A virtual "quagmire" of names exists and synonymy is often complex. The difficulties are compounded by new species still being established within any one of *Scirpus*, *Schoenoplectus* or *Bolboschoenus*.

Until there is better understanding of the extent and causes of the variability encountered, little real progress can be made in attempts to find reliable criteria for satisfactory generic distinction. Extensive regional study followed by continental and global co-operation and consensus is needed to reassess and then to consolidate the situation. This work on African species of *Bolboschoenus*, and the study of pericarp anatomy within the genus worldwide, is an attempt to add to the knowledge, and perhaps to the understanding, of the variability of *Bolboschoenus* species.

Characteristics of *Bolboschoenus* : contrasts with *Schoenoplectus*

Within the African context, *Bolboschoenus* species appear distinct from species of *Schoenoplectus*, although Strong's contention (1993: 202) of the similarity between species of both genera is noted. There are a number of characteristics which set the genera apart. These characteristics may not always all be present or well defined, but if considered collectively can be employed successfully to effect delimitation. The nearest approach in inflorescence similarity to *B. planiculmis* has been seen in some unispicate examples of *B. maritimus* and *B. grandispicus* (Steud.) K. Lewejohann & W. Lobin, but these taxa, with their cauline, eligulate leaves and sharply triangular culms are clearly distinguishable from known *Schoenoplectus* species on the continent. Therefore in this work, and pending further research, *Bolboschoenus* is maintained as a genus distinct from *Schoenoplectus*.

Bolboschoenus plants are perennial, and predominantly present on the rhizomes at the culm

bases are swellings that have been variously termed corms, tubers or bulbs. Their structure shows them to be corms.* Each is initiated at the tip of a lateral rhizome before the erect aerial shoot is above ground level. In some species, within particular habitats and under certain environmental conditions, these corms may be well developed as in *B. glaucus* (Ward 1707), and *B. maritimus* (Browning 927, both NU) (Figure 74). *B. nobilis* (Ridl.) Goetghebeur & D.A. Simpson is the tallest of the southern African *Bolboschoenus* species, and on herbarium sheets plant bases are seldom present. In actively growing plants there is usually basal enlargement of the rhizome/culm junction without the production of a clearly defined corm, while the rhizome is thickened and abbreviated, the culms generally arising in close approximation to one another (Figure 73). In *B. affinis* (Roth) Drobov, one of the smaller species, the corms are relatively large. Corm development, or not, may be related to the extent and duration of an unfavourable season in the growth cycle. Corms are not known for species of *Schoenoplectus* except the American *Sch. subterminalis* (Torrey) Soják (pers. comm. S.Galen Smith).

Cauline leaves, with well developed laminas [up to 8, but according to Kantrud (1996: 8) up to 13 per culm in *B. maritimus*], are a feature of *Bolboschoenus* plants, although some culms may lack them, bearing only basal leaves. In the field these laminate, cauline leaves may lead to confusion with plants of the genus *Fuirena* Rottb.; however, *Fuirena* leaves are ligulate, those of *Bolboschoenus* eligulate. *Bolboschoenus* leaf sheaths, like those of *Fuirena*, are closed, the apices with clearly defined contralaminar tissue; the leaf bases do not break into fibres. Culms in *Schoenoplectus* mostly lack laminate, cauline leaves; the sheaths are also closed, but without clearly defined contralaminar markings; nor do the leaf bases become fibrous. The leaves of *Schoenoplectus* are ligulate, unlike those of *Bolboschoenus*.

The inflorescence of *Bolboschoenus* is terminal, accompanied by several leafy bracts. In young examples, the first (lowest) inflorescence bract may be upright so that the inflorescence appears lateral (pseudolateral), as in certain species of *Schoenoplectus*. In mature inflorescences the lower inflorescence bracts mostly bend away from the vertical. Unispicate inflorescences are not uncommon in some species, for example *B. planiculmis*, *B. affinis*, *B. grandispicus*, and *B. maritimus* s.l. In these, the bract usually continues in the line of the culm.

*Corm. A solid bulblike part of the stem, usually subterranean, as the "bulb" of *Crocus* and *Gladiolus* (Lawrence 1956: 746).

Glumes (floral scales) of all *Bolboschoenus* species have a bifid, often lacerate apex, and the pronounced midrib extends into an erect, outwardly curving or recurved awn. In *Schoenoplectus* glumes are not bifid while the awn is reduced to a mucro. Predominantly glumes in *Bolboschoenus* are abaxially hispid, but in some species the vestiture may be sparse or absent so that the glumes are glabrescent to glabrous. This is comparable with *Schoenoplectus*, although in this genus abaxial glume surfaces are more often glabrous.

It has been stated earlier (pg 3) that Marek (1958: 176) concluded from study of fruit (pericarp) anatomy that the two genera *Bolboschoenus* and *Schoenoplectus* are distinctive. Bruhl (1992) also recorded differences, but there are exceptions within *Schoenoplectus*, for example the African *Sch. scirpoides* (Schr.) J. Browning which has pericarp anatomy closer to that representative of *Bolboschoenus* rather than *Schoenoplectus*. Further study is required. *Schoenoplectus*, *Bolboschoenus* and *Fuirena* have a *Schoenoplectus*-type embryo. However, the embryo in *Bolboschoenus* differs in detail, namely, the cotyledon is more umbonate (raised) and enlarged; the first leaf primordium is sheathing; there is a constriction between the root cap and cotyledon (Browning & Gordon-Gray 1993: 317, Fig. 5).

Distribution, habitat and presently recorded species numbers

Bolboschoenus has a pluricontinental distribution. Ridley (1884: 159) writing of *B. maritimus* states 'The species is probably the most widely distributed of Cyperaceous plants, ranging from Iceland to New Zealand'. Goetghebeur & Simpson (1991: 172) note that 'of the recorded species, *B. maritimus* is perhaps the most well known, and reported to be widespread.' It is probable that other species, less well known, are also widely distributed but that their collection, identification and documentation is inadequate at present.

Some species tend to be restricted to more saline coastal conditions (possibly with underlying fresh water), others are located inland at water bodies of variable salinity (often untested), while there are those that favour the banks of fresh water streams, and flooded lands and river deltas. No information seems available on the mineral constituents that contribute to the salinity of maritime habitats, in contrast to those of the fringes of inland water bodies where

the water source may be subterranean.

The number of *Bolboschoenus* species world wide is unclear. Wilson (1981: 156) and Goetghebeur and Simpson (1991: 172) suggest sixteen species. Smith notes (in a preparatory account of the genus for Flora North America, pers.comm.) *Bolboschoenus* comprises "at least 6 to perhaps 13 known species depending on the treatments of the various members of the *B. maritimus* and *B. fluviatilis* (Torr.) Soják complexes and taxa of probable hybrid origin." Note: if all species, subspecies, varieties and forms listed in Index Kewensis (CDROM 1992) are counted, there are in excess of 40 taxa.

Difficulties of species delimitation

Owing to considerable structural uniformity, vegetative features provide few characters useful in the delimitation of species in *Bolboschoenus*. Characters of the sheath mouth and the contralaminar tissue have been employed (Goetghebeur & Simpson 1991: 173; Smith, in preparation), but only in conjunction with characters of the inflorescence and fruit. It is in features of the inflorescence and fruit that greatest reliance has been placed in undertaking the recognition of taxa. There follows a summary of these:

1. Inflorescence branching (absence or presence of branches, including number and length). This feature has probably given rise to the epithet *compactus* as is used within *Scirpus maritimus* (*Bolboschoenus maritimus*) to differentiate plants with contracted inflorescences (ssp. *compactus* Hoffm.) from the typical expression with longer, more numerous branches. Taxa separation based on this character, which is relatively easy to employ in the field, has been used or mentioned by numerous workers in Europe (Robertus-Koster 1969: 193, 195; Norlindh 1972: 398; Zákavský & Hroudová 1994: 217, 218). Browning & Gordon-Gray (1992: 381) made reference to the form of the inflorescence and its branching in tentatively demarcating Entity 1 and Entity 2 within *B. maritimus* for southern Africa.

2. Inflorescence bracts (number and length). The bracts, if mentioned in accounts at all are usually treated in connection with features of the inflorescence. In *B. planiculmis*, however,

attention has been given to the lowest (first) bract as it continues in line with the culm in mature plants. Such inflorescences with a solitary spikelet and an upright bract occur in most of the smaller species.

3. Spikelet number, length and colour. Characters based on these features have been used in most flora accounts. To adequately qualify and quantify differences in inflorescences from coastal and inland sites at Verlorenvlei (South Africa) these spikelet features were used (see Chapter 4). Goetghebeur and Simpson (1991: 173) mention spikelet number in connection with distinguishing *B. nobilis* from *B. maritimus*, the former having 100--200 spikelets per inflorescence in comparison with up to only 50 in the latter species.

4. Style branch number. This has received considerable attention from Koyama (1958: 333) and Norlindh (1972: 399). A major problem is the occurrence in some species of florets with 2 and 3 styles within the same spikelet.

5. Fruits (outline shape; shape in cross section and colour). As fruit are considered to provide reliable characters for species identification of many cyperaceous genera they have received detailed attention in *Bolboschoenus* species. Evidence of this is seen in the figures accompanying accounts of species (Koyama 1958, fig. 13 pg. 332, fig. 15 pg 335; Robertus-Koster 1969, fig. 2 pg. 196, fig. 3 pg 197; Norlindh 1972, fig. 1 pg 402; Wilson 1993: 365, 366). Some of the illustrations indicate the range in outline shape with the two extremes being obovate and narrowly elliptic. In cross section the variation is from lenticular to subtrigonus to sharply trigonus, while colour has been noted as pale yellow, to various shades of brown through to black.

There are problems with each of the above characteristics as gradation occurs. There are further problems in attempts to use all of the above collectively to distinguish taxa. Koyama (1962: 932--933) expressed the difficulties most clearly as follows:

‘All species .. vary in a similar manner, that is, variations in both vegetative and floral characters are exactly analogous in all related species: (1) the umbelliform, many-spiked inflorescence may be reduced to few- to one-spiked heads; (2) the bracts vary from an

involucre of several dorsiventral blades to a single, erect, culm-like bract that is very similar to the bracts in the section *Actaeogeton*; (3) both tristigmatic and distigmatic achenes may occur in the same species, sometimes even in the same spikelet, although in *S. fluviatilis* achenes are always tristigmatic; (4) culms vary from leafy to almost naked with basal leaves only; (5) the tuber-like enlargements at the base of culms are not always present; and (6) the color of floral scales becomes lighter when the plants grow inland. In most species of this section, the achenes lack taxonomic importance as they are uniformly obovate and differ little in size.'

Raymond (1965: 16) in connection with the inflorescence branching noted

'All species of section *Bolboschoenus* with a normal umbellate inflorescence exhibit a "congested" phase'.

Norlindh some years later (1972: 404--405), after detailed field work in Scandinavia, reported

'The ramification of the inflorescence is non essential character' and finally concludes his account 'The variation in the ramification of inflorescence, the number of style branches and shape of achenes in *Scirpus maritimus* is remarkable and makes any division into clear-cut entities rather difficult'.

Koyama (1979 : 285) in connection with material from Afghanistan wrote:

'Nevertheless, as was pointed out by Raymond (1965a), the morphological boundary between *B. affinis* and *B. maritimus*, which is well established in Indian materials, is obscured by the polymorphism of the former taxon encountered in Afghanistan'.

This tended to confirm the previous findings of Norlindh (1972: 403) in respect of *S. maritimus* and *S. affinis* who wrote:

'all the Indian specimens of *S. affinis* I have hitherto seen are quite characteristic with regard to the shape of the achenes and colour of the spikelets. However, in central and eastern Asia forms transitional between these taxa occur'.

Some years later (1980: 148) Koyama in reference to East Asian representatives of *B. maritimus* continued:

'Because of its digynous pistils and more commonly capitate inflorescences the East Asian representatives of *B. maritimus* have often been referred to *B. compactus* (= *B. maritimus* var./ssp. *compactus*). However, I failed to see the validity of such a digynous taxon within the Eurasian *B. maritimus* complex, for the clinal variations of achenes from trigyny to digyny as well as whether the inflorescences are anthelate or capitate do not show any kind of discontinuity at all nor bear any phyto-geographic significance, hence warranting no value in taxonomic separation as such.'

The above comments by experts working on the genus, in widely separated geographical

areas, show that no characters, either vegetative or reproductive, have been found to operate consistently in the delimitation of all species. This has resulted perhaps, in the establishment of the multiplicity of taxa as previously mentioned.

General uses of *Bolboschoenus*

The production of underground carbohydrate-rich corms gives plants the ability to survive through unfavourable environmental conditions, such as fluctuating water levels and extremes of temperature. Kantrud (1996: 10) notes that dormancy may occur for at least 2 years under conditions of low water levels and high salinity. In addition, the corms provide an efficient method of rapid propagation: buds that grow into aerial leafy culms producing inflorescences and fruit develop on the corms. In *Scirpus maritimus* (*Bolboschoenus maritimus*) corms may exhibit bud dormancy whereby 'some of the 1--5 buds can remain dormant when corms first germinate' (Kantrud, 1996:10). Field work at Verlorenvlei indicated that some of the unispicate culms originated from lateral buds on well established corms.

Stands of *Bolboschoenus* plants may be linked below ground by an interwoven system of roots, rhizomes and corms that stabilise and hold the soil particles. Fragmentation of plants with corms may result in the rapid establishment of new plants, and therefore the spread of clones. At Verlorenvlei, where land previously occupied by *B. maritimus* s.l. had been ploughed for cultivation, the furrows were scattered with pure white discs that were sections of corms sliced by the ploughing. Some species of *Bolboschoenus* (*B. glaucus* and possibly *B. yagara* (Ohwi) A.E. Kozhevnikov ?), because of their ability to survive and reproduce rapidly from corms have become serious weeds particularly within many rice growing countries in Europe, Africa and Asia. Because of these weeds there may be a reduction in rice yields by 60--100% (Kantrud 1996: 36 citing Ampong-Nyarko and De Datta 1991). Once established in rice paddies, the mature nuts of *B. glaucus* may be harvested with the rice, the fruit of which is distributed for further growing and rice breeding programmes. Rice breeding programmes in Senegal and Ivory Coast arrange import and exchange seed with Asian and Latin American programmes. Quarantine is so poor that the importation of weeds is very

possible (D. Johnson, pers. comm., 19 Feb. 1997). Distribution of *B. glaucus* shows some correlation with the cultivation of rice in North America (California), Spain, Italy and Czech Republic (G. Smith, pers. comm.).

The Maori people of New Zealand use the inner parts of corms of *B. fluviatilis* to supplement their diets during food shortages. This is documented on specimens in Auckland Museum (AK) and by Johnson & Brooke (1989: 98).

Inflorescences at time of fruit maturity are highly favoured by a variety of herbivores, both wild and domesticated. At Verlorenvlei in 1996, inflorescences were present only in areas inaccessible to cattle, either because of fences or steep terrain. In one area, close to Redelinghuys on the western bank of the wetland, was an area of approx. one hectare of *Bolboschoenus maritimus* s. l. plants. With searching, three heads were located, but all other culms had been bitten off below the first inflorescence bract. C.J. Ward (pers. comm.) notes the heavy predation of *B. maritimus* plants in the Orange River estuary area of Namibia by feral animals, and Kantrud (1996: 35) reporting for North America, notes that 'bulrushes' (*Bolboschoenus* spp.) are eaten by domestic animals.

Fruit of *B. maritimus* may be produced prolifically, as each spikelet has 30--60 florets. The nuts are high in carbohydrate and crude fat (Kantrud 1996: 15), providing food for seed-eating birds. In southern Africa *B. maritimus* is present in coastal wetlands and lakes. Migrant birds from the northern hemisphere visit these habitats seeking food and shelter, both of which may be provided by *B. maritimus* plants. In North America, Dabbling ducks consume *Bolboschoenus* fruits (Kantrud 1996: 33).

Writing on Plants and People in Ancient Anatolia, Mark Nesbitt (WWW) states that 'In the upper Palaeolithic humans gathered the wild plants and hunted the wild animals of their environment. At a site in oak forest, such as Hallan Emi on a tributary of the Tigris in southeast Turkey, the diet included wild almonds and Pistacia nuts, wild pulses, and the seeds of riverside plants such as club-rushes (*Scirpus maritimus*) and knotweed (*Polygonum*)'.

Bolboschoenus species assist retention and stabilisation of sandy banks of streams and water bodies. Rapid vegetative growth is possible from the corms under favourable conditions, and large stands of leafy culms may be developed, providing food, shelter and nesting sites for birds. For these reasons *Bolboschoenus* plants, mainly *B. fluviatilis*, are being introduced and reintroduced in certain wetland regeneration programmes in Australia. South of Sydney, at Botany Bay, G. Sainty reported (pers. comm. 1994) on his collection of fruit of *B. fluviatilis* that was sent to commercial growers for germination. The resulting seedlings were to be introduced into the wetlands of this area, which at the time of our visit were being mechanically cleared of alien invaders in preparation for *B. fluviatilis* and other selected indigenous plants.

Bolboschoenus robustus (Pursh) Soják and *B. maritimus* are physiologically adapted to prosper in moderate salinities, and to survive when salinities increase beyond that tolerated by many other hydrophytes (Kantrud 1966: 30). This makes them suitable for the regeneration of coastal and inland water bodies. In North America, *Bolboschoenus* species are considered to be important in wild life refugia and may play a part in maintaining and restoring water quality. Stands of *S. maritimus* (*Bolboschoenus maritimus*) successfully filter the faecal pathogen *Escherichia coli* from sewage effluents (Kantrud 1996: 30, quoting Seidel 1971).

The genus in Africa

On the African continent known constituents of the genus include *Bolboschoenus grandispicus*, the type of which is from Senegal. A further type from Algeria, namely *Scirpus tuberosus* Desfontaines, is now known to be *Bolboschoenus maritimus* or a close relative (Smith 1995: 101). *B. maritimus* has been recorded as present in West, East, Central and southern Africa but this name has often been, and still is, applied very loosely. Goetghebeur and Simpson (1991: 172) transferred *Scirpus laeteflorens* C.B. Clarke to *Bolboschoenus* as *B. nobilis* (Ridley) P. Goetghebeur & D.A. Simpson. *B. nobilis* is limited to Angola and Namibia. Goetghebeur & Simpson's account stimulated enquiry into the constituent taxa of *Bolboschoenus* in southern Africa and the African continent as a whole; the number of species, their distribution, habitat preferences and morphological variability. The chapters that

follow document much of the data that has burgeoned from a restricted southern African commencement.

CHAPTER 2

BOLBOSCHOENUS IN SOUTHERN AFRICA: A COMMENCEMENT [Browning & Gordon-Gray (1992) applies: see Appendix 3]

Geographically Namibia falls within the limits of southern Africa, so it was convenient and worthwhile to begin work on *Bolboschoenus* by study of the constituents of the genus in the area south of the Kunene-Zambesi rivers using Goetghebeur and Simpson's (1991) account of *B. nobilis* and *B. maritimus* as a guide.

From the literature, it was apparent that variation in *B. maritimus* in particular was an important consideration. Ridley (1884: 158/159) for Angola, had listed three varieties under *Scirpus maritimus*, namely vars. *macrostachyus*, *amentiferus*, and *terrestris* and had commented 'It is impossible to separate any of these varieties from *S. maritimus* although the two latter ones appear very dissimilar at first sight. A great deal of variation is doubtless caused by their unusual habitats'. Haines and Lye (1983: 53) for East Africa recorded only *B. maritimus* but as *Schoenoplectus maritimus*. Hooper (1972: 301) (under *Scirpus*) for West Africa listed *S. grandispicus* (Steud.) Berhaut and *S. maritimus*. This posed the question as to whether the southern African material under *Bolboschoenus*/ *Schoenoplectus*/ *Scirpus maritimus* equated with plants from East and West Africa south of the Sahara.

Preliminary study was based on examination of specimens in South African herbaria and others kindly loaned from B, BM, M and WIND. Field knowledge was incorporated where such information was available. An advantage was the quite extensive representation of *B. maritimus* available from extra-territorial localities. This made possible comparison of southern African plants with examples from other continents in both northern and southern hemispheres. Details of procedures and the methods followed are given in Appendix 1 of this thesis and in Browning and Gordon-Gray (1992), for which see Appendix 3.

Distinctions between *B. nobilis* and *B. maritimus*

Characters suggested by Goetghebeur and Simpson to assist in distinguishing between *B. nobilis* and *B. maritimus* are given in Table 1 (Vol. 2: 164). Of these, I found anther and anther crest lengths to be most reliable.

In general, the contralaminar part of the sheath apex is as was described for each species by Goetghebeur & Simpson (1991) (see Table 1) but careful observation of several sheath-mouths at about the middle of culm length is recommended. In *B. maritimus*, the larger culms ± 10 mm in width have less deeply cleft sheath mouths that approach the shallowly concave form characteristic of *B. nobilis*, which is a much larger plant with culms that, in general, are wider than those of *B. maritimus*. The wider the culm, the less deeply cleft is the sheath mouth. Other recorded differences are not always clearly defined, but if several sheath apices are observed, the distinctions become apparent. Upper cauline sheaths in *B. maritimus* may produce a pale membranous 'tongue' above the red-dotted tissue of the contralaminar cleft. This tongue may be early deciduous leaving a truncate apex.

Nowhere in the southern African study area did spikelet numbers per inflorescence within *B. maritimus* approach the 100--200 stipulated by Goetghebeur & Simpson (1991) for *B. nobilis*. Always they did not exceed 50. Paradoxically however, less robust Namibian specimens of *B. nobilis* had inflorescences with 50--100 spikelets (very seldom less than 50), and in east tropical Africa there were exceptions with 50--100 spikelets per inflorescence among *B. maritimus* [for example, *Wingfield 1425* (NU) from Tanzania].

Fully mature, plant-ripened fruits of both species are somewhat alike, but there are differences, as expressed by Goetghebeur & Simpson (1991: 173). To their descriptions, other features are added (Table 2, Vol 2: 165).

At the time of our study no underground parts of *B. nobilis*, either from living plants or as part of herbarium specimens, were available for comparison with the cormous shoot bases and lateral rhizomes of *B. maritimus*.

Our study supported the findings of Goetghebeur and Simpson (1991) that *B. nobilis* is

worthy of distinction from *B. maritimus* at specific level.

Distribution and habitats of *B. nobilis* and *B. maritimus* in southern Africa

In Namibia, *B. nobilis*, as its name suggests, is a taller, more robust, coarser, more scabrid plant with far larger, more branching inflorescences of smaller, more obviously hispid spikelets than is *B. maritimus*. It is known from mountainous country, a little inland from the coast, from 17°S to 25°S and from 12°50'E to 17°50'E. Here plants favour the more or less permanent water of the deeper springs that exist along drainage lines among the mountains (J.D. Ward - pers. comm.).

B. maritimus is present, but not frequent, in Namibia being recorded from inland localities at Grootfontein ($\pm 19^{\circ}\text{S}$; 18°E) and in the Gibeon district ($\pm 25^{\circ}\text{S}$; $17^{\circ}50'\text{E}$). Subsequent to our original study it has been located at Orange River estuary $\pm 28^{\circ}\text{S}$; 16°E and in the northern Cape at Port Nolloth $\pm 29^{\circ} 30' \text{S}$; 16°E . This species is also confined to water and drainage lines, but is usually rooted in the black clay soils often underlying sand, or in the chemically-enriched, dark coloured sand itself. Outside Namibia it is well represented in the study area wherever streamlets exist along the southern African coastline south of approximately $31^{\circ}50'\text{S}$; therefore it is present near both western and eastern shores of the subcontinent. It is also represented in Maputaland ($\pm 29^{\circ}\text{S}$; 32°E) and the border area of Swaziland/Mozambique. Further inland are isolated records from the Free State, Transvaal and Botswana. There is an unexpected distributional hiatus between the eastern coastal limits at approximately 32°S latitude and those in Maputaland at approximately 29°S latitude. This remains unexplained. The possibility of extinction resulting from agricultural or industrial disturbance does not seem to apply, for as far as is known, there are no early records of collection from this portion of the land that might antedate such habitat disturbance.

Variability

B. nobilis

There is no literature account that discusses inter- and intra-populational variability within

this species. Herbarium specimens indicated reasonable morphological uniformity, but at this stage of study field confirmation was not available.

B. maritimus

Despite overall general homogeneity each area showed some variation. This was mainly evident in the robustness of plants, with concomitant variability in widths of culms and leaf blades and extent of branching of the inflorescences from an umbellate type (often termed an anthela), to a head of sessile spikelets, to a solitary spikelet.

There were also differences in spikelet shape, size, and coloration, extent of pubescence of the abaxial glume surface and projection of the excurrent, usually reflexed, glume awn. These variations appeared to be associated with particular localities, so that an early impression was gained on inspection of herbarium sheets, that almost each population had its own distinctive appearance. However, more detailed analysis and measurement showed these differences to be largely spurious, because the generalisations deduced were so often modified by exceptions. .

Some tentative generalisations were derived, namely:

1. Plants from coastal situations ranging from approximately 32°S, 18°E to approximately 32°S, 29°E were predominantly characterised by dark brown spikelets, 14--25 mm long by 5--8 mm wide that were ovate in outline. The glumes were closely imbricated, the abaxial pubescence and the excurrent awns being less well marked than in plants from further north and from inland localities. These spikelets, generally 1--20 per inflorescence, were most frequently organised into a head with a few short rays, or were rayless. This aspect of *B. maritimus* was found to relate closely to plants from Europe (Britain, France, Germany, Holland, and Sweden).

2. Plants from north of 30°S, from both coastal and inland localities, were predominantly characterised by light brown spikelets, (14-) 20--44 mm long by (2-) 3--5 mm wide, that were oblong in outline. The glumes were more widely spaced along the rachilla, the abaxial

pubescence and the excurrent awns giving a bristly appearance. These spikelets were generally organised into rayed anthelas [ray numbers (1-) 3--8 (-10)]. Occasionally there was reduction to a head; solitary spikelets were rare or absent. This aspect of *B. maritimus* was found to relate to specimens from tropical Africa and to approach more closely to the facies of *B. nobilis* than did the entity described under 1 above.

Exceptions to the above generalisations existed, for example *Acocks* 17572 (BM, PRE) from Lokenberg (Calvinia Distr.) had oblong spikelets (33 x 4 mm); *Forbes* 739 (J) from Johannesburg had the facies of Cape coastal plants.

On the basis of this variation within *B. maritimus* in southern Africa, the taxon was considered tentatively to comprise two entities, which at this stage in the study were denoted as Entity 1 and Entity 2. The distribution map (Browning & Gordon-Gray 1992: 381, Figure 1) does not reflect this separation, but merely shows the distribution of *B. nobilis* in relation to the combined entities of *B. maritimus* in southern Africa.

From this initial study of herbarium material of *B. maritimus*, it was apparent that additional features should be sought to assist in distinguishing Entity 1 and Entity 2. To see if fruit morphology and embryography might provide useful characteristics, a further investigation was undertaken. This is reported in the chapter which follows.

CHAPTER 3

BOLBOSCHOENUS IN SOUTHERN AFRICA: INVESTIGATION OF FRUIT AND EMBRYO MORPHOLOGY [Browning & Gordon-Gray (1993) applies: see Appendix 3].

Oteng-Yeboah (1974) used the anatomy of the fruit in his infrageneric classification of *Bolboschoenus*, and noted the exocarp structure. He erected Section *Lentischoenus* characterised by 2 (-3) style branches and lenticulate or concave-sided nuts with the cells of the exocarp radially elongated [type species: *B. paludosus* (Nelson) Oteng-Yeboah, from North America]. [Note: this combination was superfluous; it is antedated by *B. paludosus* (Nelson) Soó (1971).] This new section was in contrast to the typical one in which styles were 3-branched, the nuts compressed trigonous to plano-convex with the cells of the exocarp isodiametric [type species: *B. maritimus* (L.) Palla].

Little, if any, attention seemed to have been directed towards pericarp structure following Oteng-Yeboah's (1974) use of it in infrageneric classification. Because of the need for additional characters to supplement those previously used to distinguish Entity 1 and Entity 2 within *B. maritimus*, the question arose as to whether pericarp structure could be used in species delimitation. This necessitated a more detailed investigation of fruit morphology and anatomy, including electron scanning. The material used as a beginning consisted of nuts that had previously been examined in the exploratory work on *B. nobilis* and *B. maritimus* in southern Africa (see Chapter 2).

Concurrent with the investigation of fruit anatomy, and because of the variability encountered in *B. maritimus*, an exploratory study of embryos was undertaken, using in addition for comparative purposes, extraterritorial material. Van der Veken (1965: 290) stated that in his experience variation in embryo length within a species did not exceed 10%. *Bolboschoenus* he considered as a section, *Bolboschoenus* Ascherson, within *Scirpus* (Van der Veken 1965: 316). This embryo type is highly specialised. Goetghebeur (1986: 88, 357) confirmed the specialisation, and related this to the presence of an indentation above and below the root cap that defines this organ from the cotyledon; also the differentiation of a third leaf blade.

Study of embryos involves removal of these soft tissue structures from within the firm pericarp wall of the fruit. Details are given by Van der Veken (1965: 287) for procedures to clear embryos, but no specific instructions or recommendations are included on the best method for the removal of these from the fruit. In *Bolboschoenus* (and *Schoenoplectus*) the pericarp wall is hard and firm, and chipping away sections of this to expose the testa, containing endosperm and embryo within, is a slow and difficult process. A quicker method was found by pressing the nut into a small quantity of malleable compound to hold it, then cutting with a sharp scalpel or razor blade transversely through it at approx. mid-length. With both halves held in the malleable compound, it was then possible to prise out from the basal half the remains of endosperm on top of the embryo. In the process of using this technique to extract the embryo from *B. maritimus* (Entity 1), it was observed that the pericarp wall had a distinctive and interesting conformation particularly of the outermost layer, the exocarp, that was not represented in the pericarp of nuts of *B. maritimus* (Entity2). This difference was followed further. [For details of the method used see Appendix 1 of this dissertation (Materials and Methods) and Appendix 3 in which Browning and Gordon-Gray (1993) is reproduced.]

Figures 1, 2, 3 respectively (Vol. 2: 1--6), show the nut shape in outline, surface topography and pericarp anatomy representative of Entity 1, Entity 2 and *B. nobilis*. Differences are summarised in Table 3 (Vol. 2: 167). The most striking of the features that distinguish the nuts of *B. maritimus* Entity 1 and Entity 2, and *B. nobilis* are found in the structure of the exocarp. In all three entities the mesocarp and endocarp are alike, consisting respectively of longitudinally oriented thick-walled fibres (mesocarp) and transversely oriented thickened fibres (endocarp). These middle and inner zones of the pericarp, because of their uniformity, do not require further mention, except to draw attention to the thickness of the mesocarp in Entity 2 (Figure 2C, D) (Vol. 2: 3, 4). In Entity 1, the radially elongate exocarp cells (seen in section in Figure 1 C, D) contrast with the oblong to square exocarp cells of Entity 2 (Figure 2 C, D) and those of *B. nobilis* (Figure 3 D).

After soaking fruits of *B. nobilis* in water for 24 hours, the outermost walls of the exocarp cells peeled away as a continuous layer (see Figure 3 C). This peeling does not take place in

either Entity 1 or Entity 2 of *B. maritimus*. Figure 4 A, B, shows the pericarp of *B. nobilis* with the outer layer of exocarp in position (A) and removed (B). When removed, the silica bodies within the exocarp cells are defined. Silica bodies of the same type (hat-shaped) are present (but mostly less well developed) in the exocarp cells of Entity 2. It is significant that silica bodies are present in *B. nobilis* and Entity 2, but have not been observed for Entity 1. The reflection of light from the surface of nuts of Entity 1 is also distinctive in comparison with those of both other taxa.

Based on the differences in fruits (shape, size, pericarp structure) three entities may be recognised within *Bolboschoenus* in the area of southern Africa. One of these entities is *B. nobilis*; the other two have, up to now, been included within *B. maritimus*, without infraspecific recognition in hierarchical classification.

Embryo

All embryos examined proved to be of the *Bolboschoenus* type. There were few for *B. maritimus* (Entity 2) and *B. nobilis* because available fruits were sparse; therefore investigations could not be statistically based. The differences in embryo outline as seen in optical, sagittal section are illustrated in Figure 5 (Vol. 2: 9, 10) and summarised in Table 4 (Vol. 2: 167).

In Cyperaceae ovary formation precedes ovule growth, so that the embryo outline is determined in part at least, by the shape of the fruit. The narrow elongate base of the fruit probably accounts for the length and shape of the large coleoptile lip (Figure 5A) in Entity 1, which is more elongate than is this structure in Entity 2 and in *B. nobilis*. The cotyledonary surface that abuts on the endosperm is more markedly umbonate than in the other two entities where this surface is usually shallowly rounded or elliptical. There are differences also in the shape of the cotyledon observed from this upper cotyledonary surface (Figure 5 A1, B1, C1). This accords with the shape of the fruit wall, so that in Entity 2 and in *B. nobilis*, in both of which the nut is trigonous, the cotyledonary outline viewed superficially from above is triangular, whereas in Entity 1 it is more or less elliptical.

The dimensions for Entity 1 differed from those of Entity 2 by more than 10%, suggesting that a more extensive study of embryos should be undertaken when adequate material became available.

Extraterritorial specimens

Specimens from Europe that agree in their morphology with Entity 1 ['Plants from coastal situations ... with dark brown spikelets ... ovate in outline.' (Browning & Gordon-Gray 1992: 381)], possess fruits with the radially elongate exocarp cells described for Entity 1, and have similar embryo form.

Specimens from tropical East Africa that agree with Entity 2 ['Plants from north of 30°S...predominantly characterised by light brown spikelets ... oblong in outline.' (Browning & Gordon-Gray *l.c.*)] agree in all respects of nut and embryo with Entity 2. Unfortunately, no nuts of *Bolboschoenus nobilis* from Angola were available for study.

The information derived from this investigation was indicative that features of fruit and embryo might afford criteria useful in distinguishing species of *Bolboschoenus*, as within *B. maritimus s.l.* in southern Africa the two entities recognised tentatively on gross morphology could be more convincingly separated using these criteria. Further, there was added support for the distinction of *B. nobilis* from Entity 1, but this was less convincing in the separation of *B. nobilis* and Entity 2.

CHAPTER 4

BOLBOSCHOENUS MARITIMUS S.L. IN A SOUTHERN AFRICAN WETLAND : A FIELD STUDY [Browning *et al.* 1998a applies: see Appendix 3]

Early morphological study of *B. maritimus s.l* in southern Africa was based predominantly on the study of herbarium material. Considerable evidence of inflorescence and spikelet variation was noted (Browning & Gordon-Gray 1992). This suggested lack of homogeneity; two entities could be recognised, although differences between them were not sharply defined. Occasional irregular specimens, for example *Acocks 17572* (PRE) from Calvinia district in the Cape and *Forbes 739* (J) from near Johannesburg, were encountered that warranted special study of field populations. Later study that covered aspects of pericarp anatomy and preliminary embryology (Browning & Gordon-Gray 1993) was also conducted on herbarium material, and was hampered by the scarcity of ripe fruit. It was felt that it would be advantageous to investigate a living population in the field in its natural habitat. To this end a suitable wetland was sought.

Detailed information on particular wetlands in southern Africa is only now becoming available. Verlorenvlei, in the Western Cape Province not far from Calvinia, was selected as suitable, as it seemed likely both entities within *Bolboschoenus* reported by Browning & Gordon-Gray (1992; 1993), would be represented.

Features of Verlorenvlei

Verlorenvlei, an estuarine lake, is situated at 32° 19'-- 32° 23' S, 18° 20'-- 18° 28' E, approximately 180 km north of Cape Town, between Eland's Bay on the coast and Redelinghuys about 32 km inland (distance estimated by road along the northern bank). Recent accounts [Sinclair *et al.* (1986); Cowan (1995: 17,18)] document its main features, which will be briefly summarised here. The lake "is aligned in a northwest/southwest direction, at 45° to the predominantly north/south coastline" (Sinclair *et al.* 1986: 1). This large water body is presently cut off from the sea at Eland's Bay by a sand barrier, which

under exceptional tide and weather conditions may be breached. This obstruction prevents, for the main, entrance of sea water into the 2.5 km long estuarine section of water body, and it is in this section of this coastal lake that high salinities have been recorded, namely 11.5 parts per thousand (ppt) at the railway bridge [Sinclair *et al.* (1986), quoting Robertson (1980)]. The shallow lake (2.5--5 m in depth) extends inland towards Redelinghuys, where fresh water tributaries of the Verlorenvlei River enter. The salinity therefore decreases from near the coast to inland parts of the lake where a salinity of 0.5 parts per thousand has been recorded (Sinclair *et al.* l.c.).

The area in which the vlei is located experiences a Mediterranean climate with winter rainfall from April to September when the lake reaches its highest levels, fluctuating to the lower levels after evaporation in the summer months. The mean average rainfall (Sinclair *et al.* 1986: 23) is less than 300 mm. The valley and lake surrounds, which are extensively fenced, are privately owned by farmers whose sheep and cattle graze particularly the inland areas bordering Redelinghuys. Disturbances from livestock and farming activities are not recent. Sinclair *et al.* (1986) suggest that these activities have been taking place in this area for some 300 years. As the surrounding areas are sandy and dry, this permanent inland water body is likely to have been attractive to peoples for many centuries. This would have added continuously to the disturbance of the natural vegetation, especially that found either in the water or on the banks of the vlei and its channels.

To the north and east of the lake are extensive sand flats extending to low hills of the Table Mountain Group (Sinclair *et al.* 1986: 14), while the southern side of the lake lies close to hills of this sandstone. The valley occupied by the lake has deposits of Tertiary and recent sands overlain by dark alluvium. Near the coast, in the blocked estuary, are rock deposits overlain by fine orange sands with almost white surface sands. This coastal lake is considered to represent a "drowned valley type" (Hart, In Cowan 1995: 107), exhibiting an earlier history associated with changes in sea level followed later by fluvial sediment infilling.

An account of the vegetation of Verlorenvlei was compiled by S. Dean (in Sinclair *et al.* 1986), who described it as transitional between karroid and fynbos. In a short account of the

marsh vegetation, this author noted that "Verlorenvlei exhibits a transition from salt tolerant species near the mouth to fresh water species further inland." *Scirpus maritimus* (*Bolboschoenus maritimus*) is mentioned as one of the predominant species which is salt tolerant. There is only this reference to the species; no suggestion is made of its possible occurrence in the less saline inland areas of the wetland. Of significance is the statement that "Distribution patterns have remained relatively similar over the periods 1947 to 1980, as shown by an examination of a sequence of aerial photographs."

The vlei is "an important wetland supporting over a thousand waders of more than eleven different species" (Cowan 1995: 18). Pertinent perhaps is the possibility that fruits of exotic plants may have been introduced into this vlei over many thousands of years by migratory birds. The visitors utilise a variety of habitats including streams, reedbeds, pans, lakes and estuaries and coastal habitats [Underhill: 167 in Cowan (1995)]. The migrants, some with known breeding grounds and well documented routes, include birds commonly sighted at Verlorenvlei. The curlew sandpiper is one example. These birds breed in the high arctic tundra of the Taimyr Peninsula and to reach the Western Cape Province take the great circle route over south-eastern Asia, the Caspian Sea, through the Rift Valley of Central Africa to wetlands such as Verlorenvlei. Nuts of *Bolboschoenus* are known to be a food source to some of these birds, or to be ingested with other foods obtained from water. Fruits transported by migrant birds, or peoples, would find suitable growth conditions in either saline, brackish, or fresh water within the total area encompassed by this wetland and the associated Verlorenvlei River.

The field study

1. Sampling sites

A hand drawn map, not to scale (Figure 6), is given to show the relative positions of the seven sampling sites (Figure 6A--G), from which 14 collections were made (*J. Browning* nos 794--802 inclusive, 809, 813-815, 817). Site G, from which little material could be obtained due to predation (*J. Browning* 801) is omitted hereinafter 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 7); D--F inland (represented by Figure 8). 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 6, 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.

The study was carried out in late January and early February, 1995. At this time in the coastal sites (Figure 7) *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* (Schr.) J. Browning, better known as *Schoenoplectus litoralis* (Schr.) Palla s. l. or *Scirpus litoralis* Schr. 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 capensis* (Rohrb.) N.E. Br. (Typhaceae). These tracts of tall vegetation were separated by areas of almost bare ground dotted with occasional low-growing sclerophyllous shrubs (possibly the outcome of overgrazing?). Marginal to the tall vegetation were occasional robust sedges that were ungrazed (for example, *Cyperus glomerata* (Thunb.) Nees, *Cyperus marginatus* Thunb., *C. fastigiatus* Rottb., *C. textilis* Thunb.), with others, low-growing, amongst them, (for example *Isolepis* R. Br. 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 8); where unprotected, denuded of inflorescences and upper leaves; where trampled, short and clearly depauperate.

2. Collection of samples

Note: procedures followed and materials and methods employed are given in detail in Appendix 1 as they are relevant in several chapters of this thesis. Sampling, as carried out in this field study, applies only once and therefore is included in the main text.

From each of the six collecting sites (Figure 6 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 9).

For measurement, nine inflorescences were taken at random from the additional sample of 20 from each sampling site mentioned under 2 above. 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 was measured (length and width). Eight collections from 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.

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. This was to investigate the range of variation rather than to record precise parameters, although the relative frequency of three - to two-branched styles was regarded as important.

3.4. Nuts and perianth bristles

From the inflorescences comprising each of the 13 collections, 20 mature nuts were removed for detailed measurement and examination. Measurement of each nut (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 nut was recorded and the length of the longest bristle measured. Many nuts carried no perianth bristles, these having been lost or left within the subtending glume.

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

From the sample of 20 nuts from each collection site (see under 3. 4 above), three nuts were

taken at random, and examined micromorphologically according to procedures and methods given in Appendix 1. Surface topography was recorded photographically.

Results

The results of this study are presented by means of Tables 5--7 and illustrations (Figures 9--17). 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; DeFilipps 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 '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 5), and most markedly, (iii) from the entire study area (Figure 9 and Table 5 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 subsessile, or with few short rays (Figure 9 A, B and Table 5). In the inland zone more open inflorescences, usually with well

developed rays, were in the majority (Figure 9 D, E, G, H and Table 5). 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 terminated the culm (Figure 9 C). 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 bud on a well-developed corm of a well established plant.

As was 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 5).

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) x (3-)5--7(-8) mm long and wide (Figure 9 A, B, C and Table 6) gradually gave place to yellow-brown, lanceolate-oblong ones (7-)15--25(-34) x (3-) 4 (-6) mm long and wide (Figure 9 G, H, I and Table 6). There was little deviation from this colour and size spikelet gradient.

Fruit

Nuts 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 x 1.7--2.8 mm long and wide (Table 7). There was no appreciable distinction in shape or size between nuts from coastal and inland sites. Some difference in colour existed, namely the golden-brown coastal specimens became darker inland. Most of the significant differences in the nuts 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 nut 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 nuts was of the 'honeycomb' pattern, namely an outline of isodiametric, approximately six-sided cells, the anticlinal walls depressed, the outer periclinal wall slightly raised (Figures 10--13, D--F). Note that one nut from site A, *Browning 814* (Figure 10C, F) and one from site C, *Browning 795* (Figure 13 B, E) deviate slightly in that in the former the anticlinal walls of the exocarp cells are not depressed, while in the latter the cells are slightly longitudinally compressed rather than isodiametric. 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 (Figures 10--13, J--L).

In contrast, the surface of the darker brown inland nuts lacked cellular definition, the pattern, when discernible, was irregular and variable (Figures 14--17, D--F). Occasional nuts showed imperfections in this layer, denoting perhaps failure in development due to malformation or injury of some kind (not illustrated). Exocarp cells were far less deep radially than were those of the coastal examples (Figures 14--17, J--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 nuts in the ratio of approximately 2 : 1 for exocarp depth : mesocarp depth, differed sharply without gradation from the inland examples which were relatively uniform in the ratio of 1 : 2 for the comparable layers (compare Figures 10--13, J--L and 14--17, J--L).

Bristles

Some difference in bristle attachment was noted, namely in coastal examples the bristles had mostly fallen from the nuts by maturity (Figures 10--13, A--C); those (usually only one) that remained attached were easily detached. In inland situations the bristles were usually

persistent and much more difficult to detach (Figures 14--17, A--C). Length of the longest bristle proved an unsatisfactory parameter as many coastal nuts carried only few (sometimes none) of their total complement. Inland nuts are also 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.

Summary and deductions

Historically there has been inclusion principally of two basic types of inflorescence, compacted (branches lacking or short) and expanded (branches elongated), within *Bolboschoenus maritimus* (Raymond 1965; Norlindh 1972; De Filippis 1980; Hooper 1985).

From field studies at Verlorenvlei it was found that there was considerable variation in inflorescence form. This occurred both within groups of plants at a particular site and at different sampled sites from the estuary at the sea coast to approximately 32 km inland at Redelinghuys. These findings are in agreement with those of Norlindh (1972) from work in Sweden. However, at Verlorenvlei, by taking into account with inflorescence type, spikelet shape and colour differences, it was possible to recognise a trend or gradient. Near the coast the more compacted inflorescence form with brown, ovate spikelets predominated, while the extreme inland collecting site at F was represented by an expanded inflorescence form (*Browning 802*) with yellow-brown, narrower, oblong spikelets. Between these extremes was a range that, here and there, was disrupted by occasional plants the inflorescences of which did not conform. These exceptions, as far as could be deduced visually, occupied irregular microhabitats either more favourable or harsher than general for that particular part of the wetland. If consideration is given only to inflorescence variation, it may be deduced that at Verlorenvlei there is one species, *Bolboschoenus maritimus s.l.*, which exhibits a high degree of inflorescence variability as it does in several other countries (Raymond 1965; Robertus-Koster 1969; Hooper 1985: 378).

Features of nut morphology have been used in classifying *Bolboschoenus* (as *Scirpus* or as *Schoenoplectus*) by numerous taxonomists up to the present time. Robertus-Koster (1969)

- Poster -

A field study of *Bolboschoenus maritimus* s.l. in a southern African wetland, Verlorenvlei

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Bolboschoenus maritimus, a sedge with pluricontinental distribution, is frequently present in estuaries and wetlands near the coast. In Europe, the species is regarded as polymorphic. From southern Africa there are numerous herbarium collections but so far there has been no investigation of variation within a single wetland.

In January 1996 a field study was conducted on *Bolboschoenus maritimus* at Verlorenvlei, a large coastal lake in the Western Cape. The vlei supports a range of differing ecological niches from a blocked estuarine section at Elands Bay to where fresh water enters the system from the Verlorenvlei River at Redelinghuys, approximately 30 km inland. Plants were collected from seven sites at irregular intervals through the wetland. Inflorescences were examined, and details recorded of spikelets (colour, shape, number, lengths and widths) and branching (absence/presence and number of branches). Electron microscopy was employed to determine details of surface topography and pericarp anatomy of the fruit.

Results showed that there were differences in plants from the coastal and the inland sites. These results require co-ordination and comparison with studies carried out in other parts of the world. Work has been done in Holland [Robertus-Koster, *Gorteria* 4 (11): 193--200 (1969)], and in Scandinavia [Norlindh, *Bot. Notiser* 125: 397--405 (1972)] and there are other scattered references in the literature that are relevant to extra-European localities. Understanding of the possible causes of this variability should be attempted as a contribution towards improvement of the taxonomy of the genus which, at present, is highly unsatisfactory.

1998a

Browning, J., Gordon-Gray, K.D., van Staden, J. and Ward, C.J.

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

South African Journal of Botany, 64 (1): 70--81.

found variability between populations of *Bolboschoenus maritimus* based on nut characters in The Netherlands. Norlindh (1972: 402, Figure 1) presented six nut illustrations demonstrating nut variation. In my field study less consideration was given to variation in external nut morphology than to pericarp anatomy, particularly since measurements produced little useful evidence to correlate with inflorescence variability. Emphasis was given to nut pericarp structure and the results, if correlated with habitat and inflorescence structure, extend insight into the morphological variability within *B. maritimus* in southern Africa.

Linking categorisations of capitate (contracted) and subumbellate (expanded) inflorescence forms with structural differences of the nut pericarp, it is apparent that plants from coastal habitats of higher salinity may be distinguished from plants of inland sites in brackish to fresh water habitats of lower salinity. This is a simplistic, generalised separation useful as a basis from which to proceed in attempting the formulation of what may be considered reliable morphological discontinuities within the genus. Questions arise concerning both inflorescence and pericarp anatomy that require further investigation.

Inflorescence

From study at Verlorenvlei, it is evident that inflorescence form is excessively variable. A single clone, at any one time, may bear inflorescences that are branched, contracted or may consist of a solitary spikelet only. One or other of these features predominate at any one time, depending presumably on habitat conditions, the age of the plant, the season of the year and its prevailing climate, predation effects etc. Collectively, these effects will be reflected in the population of which the clone forms an individual part. Variability in inflorescence form within a population, and within a species, must therefore be accepted as a natural occurrence and little reliability placed in inflorescence type (as seen on an herbarium sheet) as a means of distinction at the level of species classification. Notwithstanding these conclusions, the question arises whether the range in inflorescence form attributable, for example, to *Bolboschoenus maritimus* is paralleled, for example, in *B. nobilis*, which is a much larger plant with, presumably, a much larger inflorescence. Are the two inflorescences of the same construction; do differences in detail exist?

Pericarp

The observation that nuts of *B. maritimus* from coastal situations at Verlorenvlei differ in pericarp anatomy from those further inland and that no gradient between the two types appears to exist, prompts the question of the reason(s) underlying this. Is the difference ecologically controlled; or is it genetic; or is it the outcome of selective environmental forces acting upon a series of closely allied genotypes? No incontrovertible answer exists at present. How does the pericarp at Verlorenvlei relate to the pericarp anatomy of other populations of *B. maritimus*? Is the variability always of these two types? How do they relate to the pericarp structure of Entity 2 and *B. nobilis* (Browning and Gordon-Gray, 1993)? Can it be that Entity 2 represents another southern African species that in earlier time was sympatric with *B. maritimus* (coastal element) at Verlorenvlei and which has left, by introgression, a genetic contribution that has been selected for in the inland element of *B. maritimus* at Verlorenvlei? This is speculative, but worthy of consideration in attempting understanding of the specific limits applied to *B. maritimus* and the relationships of this species to Entity 2 (is this a good species in its own right?) and *B. nobilis*. From this point onwards the coastal element at Verlorenvlei and populations which are equatable with it will be named *Bolboschoenus maritimus sensu stricto*.

CHAPTER 5

BOLBOSCHOENUS GLAUCUS (LAM.) S.G. SMITH : A NAME FOR ENTITY 2

Results from the study of inflorescences and nuts of *Bolboschoenus maritimus* s.l. at Verlorenvlei showed that there were differences between the two groups defined as coastal and inland. These differences were less obvious in the inflorescence where gradation occurred, than in the pericarp structure in which two types differing in the proportions of tissue layers were represented. The nut affinities of the coastal group were with *B. maritimus* s.s., Entity 1 (Browning & Gordon-Gray 1992, 1993). The nut morphology and pericarp anatomy of the inland nuts, however, presented a problem. While the general structure was the same as for the coastal fruits, detailed features such as surface topography and proportional thickness of exocarp and mesocarp differed. Apart from fruit structure, the plants also exhibited a number of characters that had been found in Entity 2 as given earlier (Chapters 2 and 3). However, there were also differences that indicated that inland Verlorenvlei plants were not equatable with Entity 2, in spite of some shared nut and inflorescence characters. Arising from this situation it became necessary to investigate Entity 2 more fully, particularly to further establish its distinctiveness, its distributional limits and, most importantly, to attempt to determine whether it was an accepted taxon already formally described and named.

From study of loan material, mainly from southern African herbaria, it was apparent that Entity 2 was recorded from Natal, Swaziland, Free State, Northern Cape, Transvaal and Botswana. More records were from Mozambique (including Inhaca island), Zimbabwe, Zambia, and Madagascar. From Angola, some Welwitsch specimens named as varieties under *Scirpus maritimus* (Ridley 1884), were found to closely relate to Entity 2. Further north were records from East African countries, particularly Tanzania and Kenya. Extension of the distribution into West Africa was seen in collections of Berhaut and J & A. Raynal (P). Study of nuts, together with "Xerox" copies of the respective herbaria sheets, increased the recorded range in Africa to Ethiopia, Somalia and Egypt. Examination of material at Kew and the British Museum showed that Entity 2 was not confined to subSaharan Africa, but extended

through Mediterranean Africa to the Middle East and into Pakistan, India and Assam. From this outline of its distribution, it can be seen that Entity 2, which before our work had been included by authors within *B. maritimus* s.l., is widespread and possibly of Gondwanan origin.

Throughout its distributional range, certain of its morphological characteristics are consistent, while others are variable. Of these features, those of the nut are the most reliable. These include size and shape, together with the persistence of 0–6 perianth bristles that are shorter than the nut. Seen in section the nuts are also characteristic, the two abaxial rounded faces meeting at almost 90° on the rounded abaxial centre, while the adaxial face is flat. The nut appears smooth and polished, but magnification of its surface reveals indications of the exocarp cells in the form of minute, closely placed spots. There is no evidence of the hexagonal outlines of the exocarp cells that are so clearly marked in Entity 1 (*B. maritimus* s.s.). Pericarp anatomy in transverse section shows that the exocarp layer, composed of small rectangular cells only just visible at x 40, is far exceeded in depth by the mesocarp (Figure 18).

The second most reliable feature is the trifid style. Reports of 3 and 2 style branches within the same inflorescence exist for Entity 1, *B. maritimus* s.s. [Beetle (1942); Norlindh (1972); Browning and Gordon-Gray (1993)]. From my study of florets from examples of Entity 2 throughout the distributional range, I have found no convincing evidence of 2 style branches. Occasionally it seemed that only 2 styles were present, but more careful microscopic examination usually showed that a style branch had been detached at the point of origin from the style, or that two style branches were adhering so as to appear as a single branch.

Spikelet shape and number (as considered in Chapter 2), when used in conjunction with nut features and style branch number, were found to be useful characters in distinguishing Entity 2. Colour of spikelets was variable throughout the distributional range, but there was a distinctive deep rust brown colouration to the glumes of plants from Egypt, the Middle East countries, Greece and India. Clarke (1893/94 : 659) for British India mentions this colouration of the glumes of *B. maritimus* var. *maritimus*, under which variety Entity 2 has

previously been variously included (see below and Formal Taxonomy), but it is not present in the glumes of plants from West, East, Central and southern Africa.

Based mainly on the criteria as outlined above, it became possible to accept Entity 2 as morphologically relatively consistently defined and recognizable as sufficiently distinct from Entity 1 (*B. maritimus* s.s.) to be accepted as worthy of taxonomic recognition, probably at specific level. Knowing that previously it had been incorporated within the variable species, *B. maritimus* s.l., for which there are a plethora of names, either as synonyms or at infraspecific level, it seemed likely that Entity 2 would have been accounted for nomenclaturally. With this in mind, consideration was given to early type specimens and to labels on collections, particularly those from Africa and India.

Two early names applied to plants from the African continent were *Scirpus glaucus* Lamarck (1791) and *S. tuberosus* Desfontaines (1798). Types are from Senegal (*Roussillon* s.n. holotype, P.) and Algeria (par *M. Desfontaines* s.n., holotype, P.), respectively. Examination of nuts kindly supplied from the latter type supported its identity as *Scirpus maritimus* L. (determined A.E. Schuyler 1966), [that is the Verlorenvlei *Bolboschoenus maritimus* s.s.], or alternatively *Bolboschoenus maritimus* (Desfontaines) Hadac (1961). The former type (*Scirpus glaucus*), which carries no mature fruits, was noted by Smith (1995:101) as equating with specimens in America (probably introduced into California with rice seed) sometimes known as *Scirpus tuberosus* Desf. (the name misapplied by Beetle 1942: 85 and Koyama 1962: 936) and with Entity 2 in Africa (Browning & Gordon-Gray, 1993).

Also from the African continent, are *Welwitsch* 6972, 6974, 6980, 7011 all collected in Angola, and determined by Ridley (1884 : 158--159) as three varieties of *S. maritimus*. This author noted that it was impossible to separate these at specific level. Two of these, (6974, 6980) named var. *macrostachyus*, are definitely *B. glaucus*. Examination of the types of the two other varieties, namely vars. *terrestris* (6972) and *amentiferus* (7011), indicates that both also fall within the limits of *B. glaucus*.

Examination of some of the specimens from Senegal (P), showed that Raynal had determined

as *Scirpus maritimus* L. var. *macrostachys* Vis., some of the collections which resemble *B. glaucus*. The first use of this varietal epithet, but as *macorostachyus*, appears to have been by Willdenow (1809: 78), when he distinguished *Scirpus macorostachyus* from *S. maritimus* and gave as a synonym of the former, Vahl's (1805: 269) reference to Lamarck's *Scirpus glaucus* as a variant from *S. maritimus*. Subsequently the epithet *macrostachys* or *macrostachyus* has been applied, often somewhat uncritically, by many workers as a varietal name on specimens where the spikelets are either unusually wide and/or long. It is an illegal name.

A few Indian collections dated early in the past century have been determined as *Scirpus tridentatus* Roxb. (Roxburgh 1832: 225). Examination of the type at K, and of one immature nut, showed this to have the same pericarp structure as *Bolboschoenus glaucus*, but the glumes of this type appeared pale and concolorous, and lacked the rust colour previously mentioned. On one sheet 'Herb Wight. propr. Peninsula Ind. orientalis' is written ' 1897 *Scirpus maritimus* L. var. *glaucus* NE; *S. tridentatus* Roxb.- Wall L.n. 3504'. It is likely that the author citation 'NE',* if that is what these letters signify, is incorrect. *Scirpus glaucus* Lam. and *Scirpus maritimus* L. var. *glaucus* Wight, are included by Beetle (1942: 84) in his list of thirty three synonyms of *Scirpus maritimus* L.

As the epithet '*glaucus*' has been applied either at varietal or specific level to Indian plants that fit with comparable ones on the African continent, and with those introduced into America, it is here accepted that the combination *Bolboschoenus glaucus* (Smith 1995: 101) be used as the correct name for Entity 2. Its reseggregation from *Bolboschoenus maritimus* s.l. has unmasked aspects that were previously hidden by its incorporation within the heterogeneity of *B. maritimus* s.l. and has therefore enabled clearer understanding of both *B. maritimus* s.s., which equates with Entity 1 (Browning and Gordon-Gray 1992, 1993) and *Verlorenvlei* (coastal aspect), and *B. glaucus* which equates with Entity 2 (Browning and Gordon-Gray 1993).

*Letters NE refer to Nees ab Essenbeck "Contribution to the botany of India, No. 111, Cyperaceae indicae" 1834 (ed) Robert Wight.

SUMMARY OF PART 1

The first section of this dissertation has served to introduce the genus *Bolboschoenus* as a taxon in its own right, segregated from *Scirpus s.l.*, and by many authorities, also from the closely allied *Schoenoplectus*, and to indicate its importance in the natural world. Study of its representatives in southern Africa has revealed three species, *B. nobilis*, *B. maritimus s.s.* and *B. glaucus*. There has also been revealed some indication that some species limits are not clearly defined by assessment of gross morphological characters and that mature fruits when investigated micromorphologically provide additional differences that have not previously been much used in recognising taxonomic units within the genus. Superficially the fruits are relatively uniform, but electron scanning of surfaces and the pericarp in section has shown three types of construction. These types, while useful and apparently reliable for southern African representatives, now need further study in relation to the world-wide distribution of the genus.

Southern Africa (Africa, south of the Kunene/Zambezi rivers) is but a small area of the total world distribution of *Bolboschoenus*. The question immediately arises as to whether comparable fruit morphology is to be found within plants of the same species from other parts of Africa and in these species if present on other continents? What, too, is the extent of variation from these patterns worldwide? Will the evidence of their usefulness as a guide to taxonomy within the genus in southern Africa be supported by the results of further investigation?

PART 2

MORPHOLOGY

OF THE

FRUIT:

ITS PERICARP VARIABILITY

WORLDWIDE

PART 2

Part 2 of this thesis is directed to attempting some answer to the questions posed at the end of the summary of Part 1. It commences with an account of fruit morphology, and proceeds with a survey of world species as far as it has been possible to obtain lists of species for individual continents, specimens, and most importantly, fruits for micromorphological examination.

Type specimens have been traced and studied wherever possible. Where fruits were present in sufficient number on these type sheets, representatives have been examined.

CHAPTER 6

BOLBOSCHOENUS : THE FRUIT AND PERIANTH

The fruit in Cyperaceae is derived from a three or two carpellate ovary, but is unilocular with always a central, basal ovule believed to have been derived from free central placentation in the ancestral stocks (Lawrence 1951: 393, quoting from the morphological studies of Snell 1936 and Blaser 1940). In *Bolboschoenus* the pericarp is thick walled, and in most cases, firm and dry. The fruit, because of these criteria, is termed a nut or nutlet, but there are many references to it in the literature as an achene, which strictly, is derived from a one-carpelled ovary. The term that was selected for use in this dissertation is "nut".

Associated with the nut is a perianth which consists of a short section of the floral axis immediately below the nut that carries two whorls of retrorsely barbed bristles, typically three in each whorl, but occasionally reduced by the reduction or absence of the centrally placed adaxial member. Strictly, this perianth is not part of the fruit, but because in some taxa of the genus all, or some of the bristles, remain attached to the fruit at its abscission, possibly playing a role in its dispersal from the parent spikelet, it is considered in conjunction. Earlier workers have been aware of differences in the perianth, some authorities regarding these differences as helpful in species diagnosis. For example, Koyama (1958: 33) noted "the duration of the hypogynous bristles seems to be a more important character than the number of stigmas and angles of the achene." In the account of the fruit that follows, the perianth will be considered where relevant.

Fruit size and shape

The nuts of *Bolboschoenus* fall within the size range of 2.2--5.5 mm in length measured from base (excluding the perianth) to apex of the beak and from (1.3-) 1.7--2.7 mm in width, measured across the widest extent with abaxial surface uppermost. In planar outline the shape varies from obovate to elliptic. Obovate nuts are characterized by wide "shoulders" and narrow base; elliptic nuts are often relatively quite narrow even at the widest part, but there

are exceptions, as for example the nuts of *B. glaucus* which are elliptic, but quite wide in relation to their length. Outline shape alone cannot be used in isolation as a reliable character in species differentiation.

With planar outline shape is linked configuration, that is whether the fruit is three-angled (trigonus) or two-angled (lenticular). This is best seen in transverse section (that is, the outline shape of the cut surface of a nut sectioned transversely across its greatest width). A trigonus fruit is generally derived from an ovary bearing three style branches, which is indicative of a tricarpeolate construction; likewise a lenticular nut usually carries two style branches and is usually derived from a bicarpeolate ovary. However, there are examples in which trigonus (three-styled) fruits and lenticular (two-styled) fruits occur in an individual inflorescence (for example *Bolboschoenus medianus* (Cook) Soják (Figure 42)). It has been claimed that in *Scirpus* style branch number is not always a true reflection of carpel number (Lawrence 1951: 393, citing Snell 1936 and Blaser 1940). The diminution from three to two carpels has been regarded as a process of evolutionary reduction (Clarke 1896), but this concept needs re-examination in the context of increasing evidence of hybridisation within Cyperaceae.

As seen in transverse section, the trigonus nut may be sharply trigonus (triangular), the abaxial angle approaching 90° (Figure 19 A); or obtusely trigonus with the abaxial angle in particular, being rounded and well exceeding 90° (Figure 19 B); or subtrigonus where there is no obvious abaxial angle (Figure 19 C). The two faces or planes on either side of the abaxial angle are usually flat or slightly convex; occasionally they may be concave (Figure 19 D). In fruits that are lenticular (Figure 19 E--G), both plane surfaces may have equivalent curvature; the faces may be convex, flat or concave. In actuality, there is virtually a continuum between trigonus and lenticular types.

Colour

Accounts in early literature (Torrey 1836: 324; Grenier and Godron 1846: 379), and more recently (Koyama 1958: 335; 1962: 933; Robertus-Koster 1969: 196; Wilson 1993: 365, 366)

give the range of colours for fruits of *Bolboschoenus* as brown, dark brown, greyish or black. Fruit colour may change with the degree of maturity so that it is not reliable as a means of species recognition, except as a guide in conjunction with other features. Figures 38 relates to the colours of fruits observed which are difficult to standardize as no available colour chart covers the required shades.

Pericarp

Surface topography

Viewing of the planar fruit surface under a binocular microscope x 40 shows in outline, the configuration of the outer layer of the pericarp, namely the exocarp cells in outline. The cells at this magnification are small, so that to obtain greater detail, electron scanning at x 600 was carried out. Details of the method used are given in Appendix 1.

Three types of surface topography have been detected within *Bolboschoenus* nuts as the genus has been studied in southern Africa; namely (i) the "honeycomb" pattern; (ii) the *B. glaucus* pattern; (iii) the *B. nobilis* pattern. For each of these patterns there are differences in the degree of development of the perianth bristles and their duration of attachment to the fruit. Details follow.

The "honeycomb" pattern

As observed in outline from the outer periclinal surface, which is **glossy** due to the presence of a thin, waxy coating, the exocarp cells are isodiametric with five to six anticlinal walls that are slightly depressed below the level of the outer periclinal surface. The anticlinal walls are straight (for example *B. maritimus* s.s., Figures 12 F and 45B). Silica bodies have never been observed in the exocarp cells. Associated with nuts with this type of pericarp pattern is a perianth of 5 or 6 slender bristles, all approximately half nut length, that are caducuous, falling before fruit dispersal from the spikelet; any bristles that may remain attached soon break away.

The *B. glaucus* pattern

At a magnification of x 40 the nut surface is **glossy** and **smooth** with no evidence of cellular marking except for closely placed subsurface 'spots'. Under electron scanning x 600, the cellular outline of obscurely 5--6--7 -sided, longitudinally compressed so as to be almost oblong, small exocarp cells with anticlinal walls raised and central zone depressed, becomes evident. With soaking in water for 24 hours the outermost periclinal pericarp walls do not become detachable either in fragments, or as a sheet of tissue. A solitary, hat-shaped silica body is usually deposited on the inner periclinal wall of an exocarp cell.

The *B. nobilis* pattern

This pattern resembles the *B. glaucus* pattern in that, in many cases, the exocarp cells are longitudinally compressed so as to be almost oblong, with raised walls and central zone depressed, except for a central raised area (the apex of the solitary hat-shaped silica body contained within the cell). There is some variation, however, as occasionally the 5--6--7 -sided outline and isodiametric shape of the exocarp cells is more markedly apparent. Always, the exocarp cells are larger than those in the *B. glaucus* type and differ also in that the outer periclinal walls peel away, either as fragments or as a continuous sheet, if nuts are soaked in water for 24 hours.

Associated with nuts of both the *B. glaucus* and the *B. nobilis* patterns, is a perianth of 5--6 bristles, two thirds of or equalling nut length, that are firmly attached to the floral axis and usually shed with it, persisting during dispersal and not easily detached artificially. The bristles themselves are stronger (firmer) than those of nuts of the "honeycomb" pattern with a higher density of retrorse barbs.

Anatomy

In *Bolboschoenus*, the pericarp is composed of three parts, exocarp, mesocarp and endocarp. The endocarp comprises transversely orientated, densely thickened, narrow fibres. The

arrangement of these cells can best be observed when a nut is cut transversely across its greatest width, the seed removed, and the pericarp viewed internally under a binocular microscope x 40. There is little variation, so that the endocarp has no importance in species differentiation.

The mesocarp also consists of densely thickened fibres. These are longitudinally orientated and so are seen in transverse section when the nut is sectioned transversely. From one species to another there may be considerable variation in depth (thickness) of the mesocarp (for example in *B. maritimus* the layer is shallow; in *B. glaucus* it is very much deeper).

The exocarp is always a single layer of cells. From one species to another these cells may vary markedly in depth, and consequently in shape, when viewed in transverse section. In *B. maritimus* s.s. the exocarp cells are radially elongated so that each cell when seen in transverse section is oblong with a depth (length) : width ratio of approximately 4 : 1 (Figure 45 D). In *B. glaucus* and *B. nobilis* there is no radial extension so that individual exocarp cells are rectangular with a depth (length) ; width ratio of approximately 1 : 1 (Figures 18D, E and 21 D). In general, the exocarp cells in *B. nobilis* are slightly larger than those of *B. glaucus*.

Examination of fruits of representative samples of the three southern African species and consideration of the results, led to the conclusion that fruit construction and features of the pericarp seen in surface view and anatomically, provide a useful suite of characters in species differentiation. Of this suite, the micromorphological attributes are new, apart from the introductory findings of Oteng-Yeboah (1974). Three patterns of fruit construction are formulated as representative of the southern African species as given earlier in this chapter. However, at this point attention must be drawn to the results obtained from the study of *Bolboschoenus* fruits at an estuarine site, Verlorenvlei, (see Chapter 4). In coastal habitats at this site the nuts had the conformation and structure of Type 1 exemplified by *B. maritimus* s.s., namely a "honeycomb" surface to the pericarp; oblong (radially elongate) exocarp cells and a narrow depth of mesocarp, the ratio of exocarp depth to mesocarp depth being approximately 2 ; 1. The perianth was caducous. Nuts from inland plants differed in that the surface topography was not clearly of the "honeycomb" pattern, it was far less definite with

the cell outlines far less clearly defined, many of the cells smaller, and irregularly oblong, sometimes with odd patches of isodiametric 5--7 sided cells discernible also. In addition, the exocarp cells were less markedly radially elongate. In these examples the ratio of exocarp depth : mesocarp depth was 1 : 2, that is a reversal of the ratio existing in the fruits from coastal habitats [ratio of depth (length) : width of an individual cell approximately 2 : 1]. No gradient from coast to inland situations was disclosed; examples were of the coastal or the inland form, although other morphological features such as the inflorescence branching showed some evidence of gradual change, with however, occasional exceptions apparently related to differing microhabitat conditions. It must be stressed that no evidence of fruits with the precise pericarp morphology of either the *B. glaucus* type or the *B. nobilis* type were encountered in the Verlorenvlei population. The structural form is of the Type 1 "honeycomb" pattern, but showing a range from precisely this type to a variation of it; the variation variable, but almost unexceptionally with ratio of exocarp depth to mesocarp depth approximately 1 : 2. The perianth bristles were mostly firm in texture and persistent. At present, there is no certain understanding of the reasons governing this variation. But at this stage, underlying causes are secondary to the observation that such variability in fruit construction does exist. It remains to be determined whether populations of *B. maritimus* in other parts of the distributional range exhibit comparable variability.

CHAPTER 7

BOLBOSCHOENUS IN AFRICA, EXTRATERRITORIAL TO SOUTHERN AFRICA

Tropical Africa

Among other species of *Scirpus s.l.*, Clarke (1902: 455, 456) named *S. maritimus* and *S. laeteflorens* for Tropical Africa. *S. laeteflorens* is *Bolboschoenus nobilis* (Goetghebeur & Simpson 1991). The type of this species is from Angola, (*Welwitsch* 6975 BM!). Examination of a fruit from the type sheet (Figure 20) showed it to have the pericarp configuration of the *B. nobilis* type, that is its structural organisation and its perianth is in agreement with characteristics established earlier for this species in Namibia (southern Africa)(Figure 3). The synonymy is further supported by examination of a fruit from a syntype of *Scirpus laeteflorens* (*Baines & Chapman*, K!) (Figure 21). The specimens cited by Clarke (1902: 455, 456) have not all been traced. *Forbes* 12 (Madagascar) and all the *Welwitsch* numbers (except 6975, which is *B. nobilis*) (all BM) are *B. glaucus*. Note that Clarke 1902: 455 gives the locality of *Forbes* (without collector's number) as Mozambique, whereas *Forbes* 12 (BM) carries the locality "Madagascar". Haines and Lye (1983: 53) recorded *Schoenoplectus maritimus* " in saline soil in seasonally wet grassland from sea level to 1700 m... in Kenya and Tanzania, both coastal and inland." Their Figure 64 is *Bolboschoenus glaucus*, as are all the specimens I have seen so far from Tropical East Africa. It is abundantly evident that this species is widespread here, from where its distribution has been traced northwards to Somalia, Egypt and West Africa and to the Middle East (see Chapter 5 of Part 1 and Browning *et al.* 1998b).

Whether *B. maritimus s.s.* is also present in Tropical Africa remains unproven. It may occur along the coastline of Angola, but I have seen no record of its presence northward of the Orange River Estuary. Likewise there is no evidence of it from coastal Mozambique, all specimens from that country known to me are *B. glaucus*.

West Africa

A fourth species from the African continent, *Bolboschoenus grandispicus* (Steud.) Lewejohann & W. Lobin, is recorded from Senegal and the Cape Verde Islands off the west African coast. Its florets carry styles that are two-branched and the nuts are lenticular. Micromorphological examination of a nut from an isotype (P!) of *Isolepis grandispica* Steud. (Herbarium *Perrottet* nr. 838) (Figure 22) and of nuts of other gatherings from Senegal (for example *Berhaut* R.P 1021 (P) Figure 23) showed the pericarp surface topography to be of the "honeycomb" pattern, but with slight modification in that (i) the exocarp cells of both planar surfaces are slightly smaller than those over the angles of the nut and (ii) the anticlinal walls are sometimes sinuous, not always straight. Note: the size difference in the exocarp cells shows clearly in Figure 31 A,C,D, pg 61. Observed in transverse section, the exocarp cells are radially elongated; most prominently so over the angles; gradually less so towards the central zone of each planar surface. The mesocarp is not excessively deep. In general construction therefore, the pericarp is closely allied to, but not identical with, that of *Bolboschoenus maritimus* s.s. It is to be regarded as a modification of the "honeycomb" pattern.

Together with *B. grandispicus* [as *Scirpus grandispicus* (Steud.) Berhaut], Hooper (1972: 309) listed *Scirpus maritimus*. This is in the broad sense of the species, as some of the cited specimens seen (for example *Berhaut* 1101; J.& A. Raynal 5925) are *Bolboschoenus glaucus*. Indeed, the type of *B. glaucus* [*Scirpus glaucus* Lamarck] is from West Africa, [Senegal, *Roussillon* s.n. (P holotype)], which unfortunately does not carry mature fruits suitable for micromorphological study (pers. comm. A. Lourteig). A synonym of *B. glaucus*, namely *Scirpus tridendatus* Roxb. from India (see Formal taxonomy, pg.106 and Browning *et al.* 1998b) does bear fruit, examples of which have been examined micromorphologically (Figure 24). The conformation of the pericarp is of the *B. glaucus* type.

It is uncertain whether *B. maritimus* s.s. (with two and three style branches within an inflorescence and with mainly subtrigonal nuts) does occur in West Africa and/or on the adjacent islands. Further investigation is needed.

Mediterranean Africa (including Egypt)

Herbaria provide numerous records of *Bolboschoenus glaucus* from this northernmost part of the African continent [for example *Schuhwerk* 90/451 (NY); *Davis* 52928, 59498 (BM); *Bornmüller* 11032 (BM)], where populations often grow landward of coastal dunes. *B. maritimus* s.s. is also present, as is exemplified by the type of *Scirpus tuberosus* Desfontaines from Algeria "in locubus prope La Calla" (Smith 1995: 101) (Figure 25). The nuts from the type very kindly provided for sectioning were subtrigonal, the styles already shed. The surface topography and pericarp anatomy were of the 'honeycomb' type and fully representative of this.

Four species, namely *B. maritimus* s.s., *B. glaucus*, *B. nobilis* and *B. grandispicus*, are therefore represented in Africa. These exhibit the three types of pericarp conformation already described. *B. grandispicus* has the "honeycomb" type of *B. maritimus* s.s., with slight modification.

However, when Cook (1947) undertook a revision of the New Zealand taxa, he distinguished three species, two of which he found to 'differ materially' from their American counterparts (Cook 1947, p. 567). This resulted in the establishment of *Scirpus perviridis* and *S. caldwellii*. *Scirpus perviridis* was described as a plant less stout and with a smaller achene than *S. fluviatilis* but resembling it in its consistently three-branched style. The smallest of the three new species was *Scirpus caldwellii* with uniformly two-branched style and broad, compressed achene. *Scirpus medianus* was intermediate in size between *S. caldwellii* and *S. perviridis* with two- and three-branched styles in the same plant. *Scirpus perviridis* has not been maintained as a species. Edgar (1970, p. 173), following Raymond (1959, p. 226) and Koyama (1961, p. 83), placed it in synonymy with *S. fluviatilis*.

Edgar (1970, p. 172) provided a key to the New Zealand species of *Scirpus* in which these three species were identified mainly on the basis of features of the achene and style branches. Wilson (1981, p. 157) who worked on Australian species, recognised these taxa under *Bolboschoenus* and provided a key that again incorporated features of the achene and number of style branches.

The purpose of this paper is to describe and illustrate by micrographs the morphology and pericarp anatomy of achenes of the types of *Scirpus caldwellii*, *S. medianus* and *S. fluviatilis*. Achene sizes from the types are compared with a sample of 50 achenes derived from herbarium or field specimens within the range of distribution of the species in Australia and New Zealand. Reliable descriptions of the three species and their achenes are available in literature already cited.

Materials and Methods

Suitably mature achenes were removed from the isotypes of *Scirpus caldwellii* (V.J. Cook 542), *S. medianus* (V.J. Cook 463) and *S. perviridis* (V.J. Cook 534) deposited in the Auckland Herbarium (AK). Holotypes retained in Cook's private herbarium were not available. These achenes were observed, measured and described using a binocular microscope at $\times 40$ magnification, then prepared for scanning electron microscopy of the surfaces. Finally, achenes were fractured transversely and the exposed surfaces scanned and photographed. Details of the techniques used are given by Browning and Gordon-Gray (1992, p. 380; 1993, p. 312).

In addition, exsiccateae of these three species, *Bolboschoenus caldwellii*, *B. medianus* and *B. fluviatilis*, from New Zealand and Australia deposited in herbaria, were studied. A sample of 50 achenes from at least 15 collections in Australia and New Zealand was obtained for each species. The constituents of each sample were measured (length, including beak, and width) using a binocular microscope at $\times 40$ fitted with an ocular micrometer. The ranges of dimensions were determined from the figures obtained and means and standard deviations from the means were calculated. Several achenes were taken at random from each sample and scanned electronically. Others were hand-sectioned transversely and the cut surface of the pericarp observed under a binocular microscope at $\times 40$. These examples served for comparison with the isotypes.

The abbreviations used to denote herbaria in which specimens are deposited are as listed in Holmgren *et al.* (1990).

Results

Isotypes

Achenes, with perigonal bristles and filaments where these structures remained attached to the achene, are illustrated by the SEM micrographs in Figs 1A–3A. The perigonal bristles were always in two series of three and were retrorsely barbed. There were three filaments that arose within (above) the perigonal bristles. The pericarp was hard and, anatomically, it consisted of three layers, each distinguishable in transverse section (Figs 1C, D, 2C, D, 3C, D), namely: (1) exocarp (epidermis) of one layer of square to rectangular cells; (2) mesocarp multilayered, of thick-walled fibres oriented longitudinally and (3) endocarp of thickened fibres oriented transversely. Cells of the endocarp are not easily distinguished. They may be seen if the achene, sectioned transversely and with the seed removed, is viewed internally using a binocular microscope.

CHAPTER 8

BOLBOSCHOENUS IN THE AMERICAS AND ADJACENT PACIFIC ISLANDS

Recent revision and recircumscription of *Scirpus s. l.* for the account of Cyperaceae to be published in the upcoming Volume of the Flora of North America [Flora of North America, Flora of North America north of Mexico. Volume and date to be determined. (Smith *et al.* 1996: 2--4), Oxford University Press, New York, unpublished], has led to the recognition of five species that will be placed within *Bolboschoenus*. These are named and the salient features of their nuts described in Table 8 (see also Browning *et al.* 1995).

The three types of pericarp construction described for southern African species (Browning & Gordon-Gray 1993) are all represented among the N. American taxa, although, in some instances, with minor modification. The "honeycomb" pattern occurs in *B. maritimus* and *B. robustus* (Pursh) Soják. The *B. glaucus* pattern occurs in plants of that name thought to have been introduced in the form of fruits possibly transported with rice and now established as an important wildfowl food source in bird refuges in California in particular. Nuts from one of these examples is illustrated (Figure 26) and shows features that are not typical of the pericarp of *B. glaucus* but rather a modification of it. The main differences from the typical pattern are the slight radial extension of the exocarp cells as seen in transverse section and a mesocarp not as well developed as is usual for *B. glaucus*.

B. fluviatilis (Torr.) Soják [*Scirpus fluviatilis* (Torrey) A. Gray] is represented by a lectotype [Dr. Baldwin s. n. (NY 7158)] selected by M.T. Strong (1993: 203) under *Schoenoplectus fluviatilis* (Torrey) M.T. Strong. An example of its fruit has been studied micromorphologically (Figure 27) and its pericarp exhibits striking similarity with the *B. nobilis* pattern as exemplified in subSaharan Africa. However there are differing size ranges of fruits for *B. fluviatilis* in America (3.8--5.5 x 2.0--2.9 mm in length and width) and for *B. nobilis* in Africa (2.2--2.8 x 1.3--1.7 mm). These parameters will be referred to later in relation to Australian plants and the Asian species, *B. yagara* (Ohwi) A.E. Kozhevnikov.

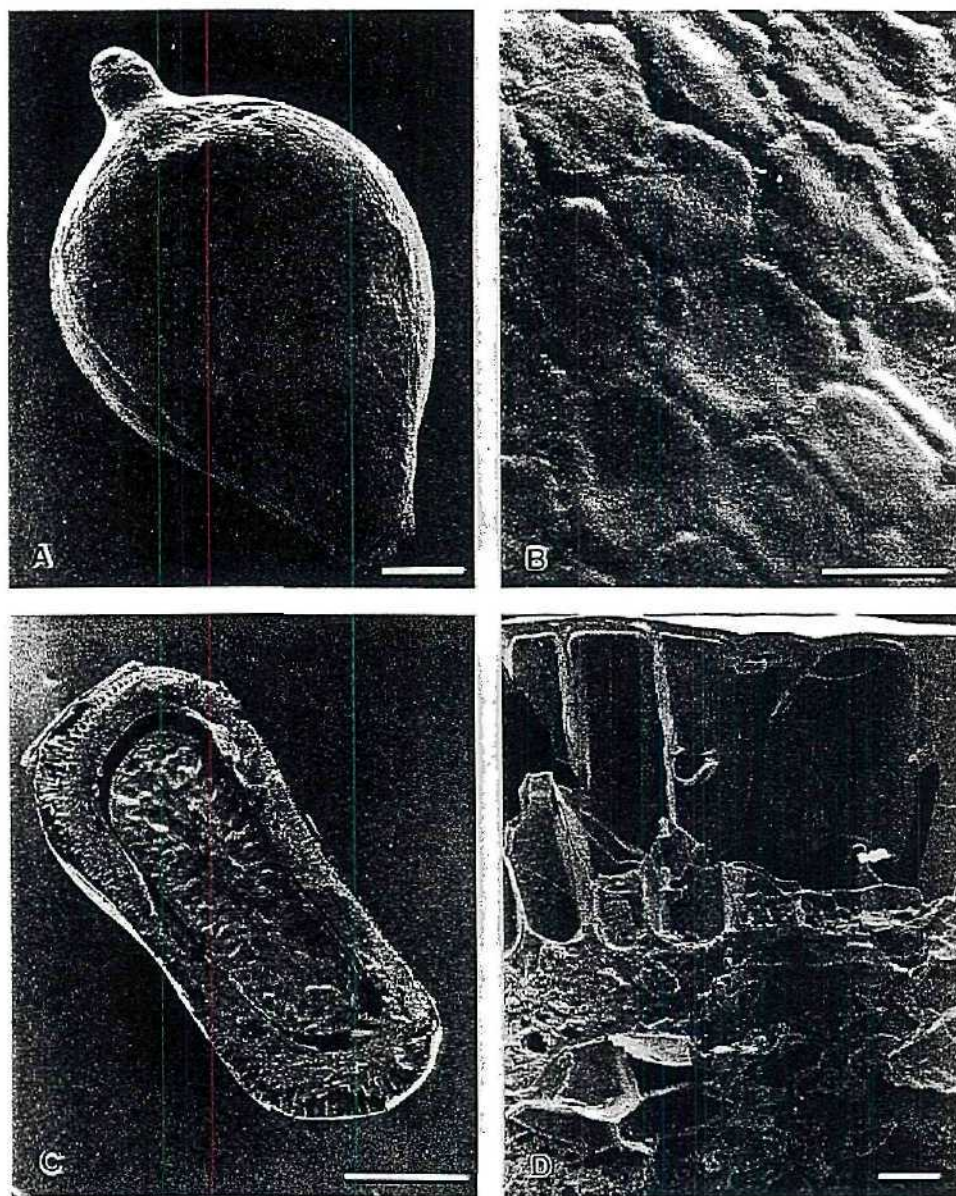


Fig. 1. *Scirpus caldwellii* V.J. Cook 542 (AK 59206). (A) Achene with perigonal bristles fallen; (B) pericarp surface at mid-achene; (C) achene in transverse section, endosperm in situ; (D) detail of pericarp in transverse section showing exocarp fragmented (top) and mesocarp (bottom); endocarp not represented. Scale bars A, C = 500 μ m; B, D = 25 μ m.

1. *Scirpus caldwellii* (V.J. Cook 542, in AK 59206)

Perigonal bristles caducous, 1 achene with 1 poorly developed 2 mm long bristle attached. *Achenes* (Fig. 1A, C) imperfectly mature, in outline obovate with rounded slightly sloping summit, beak well developed; biconcave, $3.6\text{--}3.9 \times 2.3\text{--}2.5$ mm; ratio of maximum width:basal width = 5:1. *Surface* pale, ochraceous distally to stramineous proximally, dull not glossy except for shoulders and beak; smooth, faintly cellular especially towards base at $\times 25$; exocarp cells at $\times 600$ (Fig. 1B) more or less isodiametric, 5- or 6-sided, walls slightly raised, central zone slightly depressed, sparsely covered with wax-like material. In *transverse*

B. robustus (Pursh) Soják is also represented by a lectotype [Herbarium *Michaux s.n.* (P) that was selected by Schuyler, but published later by J. Ewan (1979)]. Its inflorescence is illustrated (Figure 28). This lectotype lacks mature fruit. A fruit from another collection of *B. robustus* from Louisiana (*Joseph Ewan 17966 NO*) has been studied and is illustrated in Figure 37 E--H. Its pericarp conformation agrees very well with that of the "honeycomb" pattern as exemplified by fruits of *B. maritimus s. s.* from Verlorenvlei, S. Africa, except that the anticlinal walls of the exocarp cells are sinuous.

B. maritimus in N. America is not uniform. It is probable two subspecies will be recognised in the upcoming Flora. One of these, to be regarded as the typical subspecies, has trigonous nuts, two and three style branches within the same inflorescence and a pericarp organisation in agreement with the "honeycomb" pattern. *B. maritimus* subsp. *maritimus* is limited in distribution to the north eastern, more coastal area of N. America, where it is not frequent. It may prove to be adventive. No fruits for micromorphological study were available, so a nut of the holotype of a synonymous taxon, *Scirpus fernaldii* Bicknell is illustrated instead (Figure 29). No valid distinctions in pericarp construction were found in comparison of fruits of *B. maritimus* subsp. *maritimus* and *B. robustus*. These taxa have been frequently confused in the course of their histories (Smith *et al.* 1996b: 3), although there are clearly defined morphological distinctions, especially in spikelet and glume characters. The lectotype of *Scirpus maritimus* selected by Koyama (1962: 932) (U. S. A., Virginia, *John Clayton 570*, LINN 71.43) is a specimen of *S. robustus* Pursh. Much more widespread and more frequent is the second subspecies that will be named *B. maritimus* subsp. *paludosus* (A. Nelson) T. Koyama. This is based on *Scirpus paludosus* A. Nelson [Type: *Aven Nelson 3874*, Granger, July 30, 1897, (RM)]. (Figure 30). The nuts of this subspecies are lenticular in cross section and the florets carry two style branches. The pericarp construction is that of the "honeycomb" type, but with reduction in size of the cells of the planar surfaces and in the degree of radial elongation of these cells when they are seen in transverse section that characterises the pericarp of fruits of *B. grandispicus* in West Africa. This reduction of the exocarp cells of the planar surfaces shows clearly in Figure 31.

The fifth American species *B. novae-angliae* (Britton) S.G. Smith is based on *Scirpus novae-*

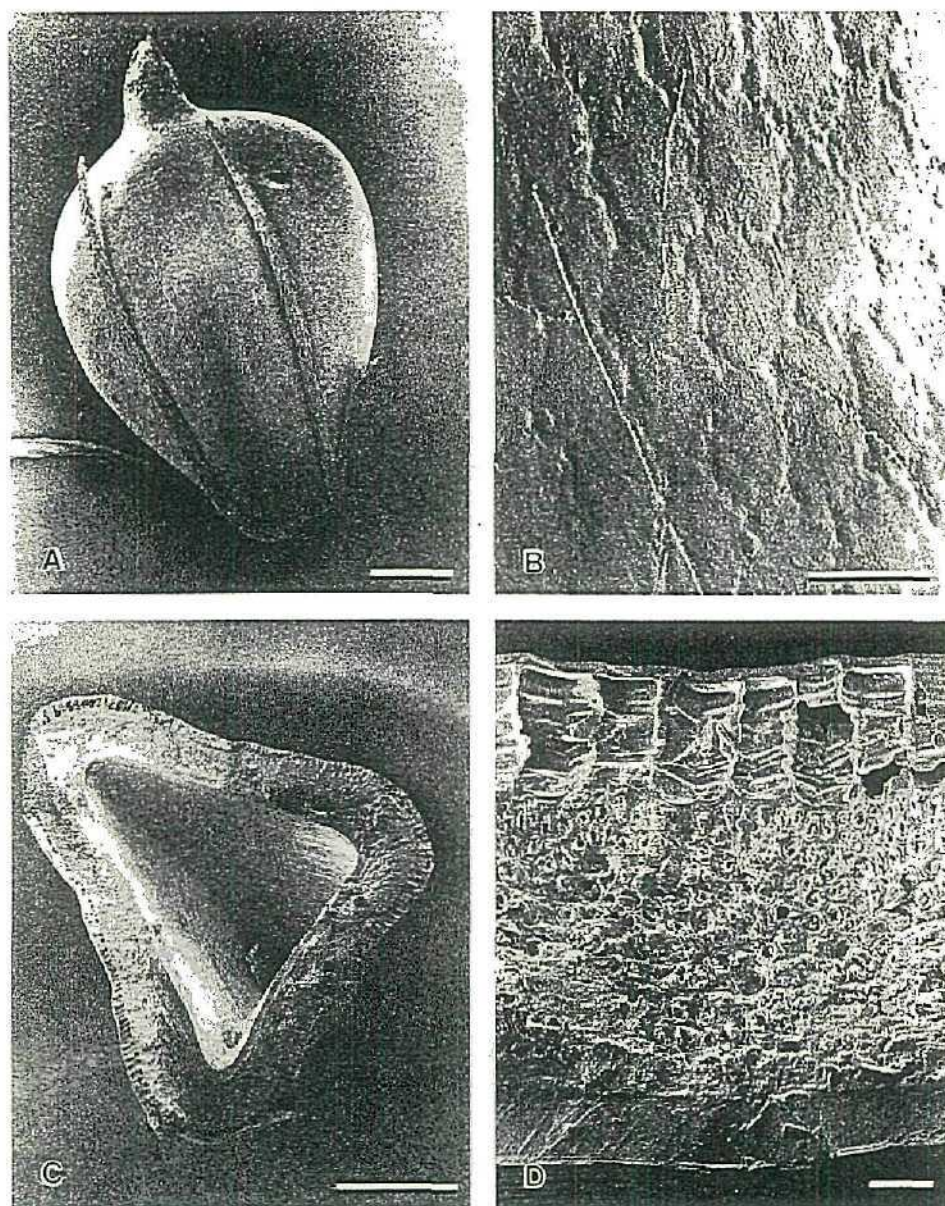


Fig. 2. *Scirpus medianus* V.J. Cook 463 (AK 61798). (A) Achene, with some perigonal bristles persistent; (B) pericarp surface at mid-achene; (C) achene in transverse section, endosperm removed; (D) detail of pericarp in transverse section showing exocarp (top), mesocarp (middle) endocarp (bottom). Scale bars A, C = 500 μm ; B, D = 25 μm .

section (Fig. 1C, D): exocarp cells variable in depth of radial elongation, ratio of depth:width of individual cell more or less 4:1 over rounded shoulders, reduced to more or less 2:1 over biconcave faces (impossible to estimate with great accuracy because of fragility and brittleness of tissue); anticlinal walls straight; silica bodies not observed; exocarp thickness more or less equal to mesocarp thickness over corners, more or less half mesocarp thickness over concave faces.

angliae Britton, the type from Fairfield, Connecticut [Eames s. n. 19 July 1986 holotype NY; isotypes NY (NY 5881), US]. The nomenclature of this species has been discussed under the synonym *Scirpus cylindricus* by Schuyler (1974--75) and later under *Bolboschoenus novae-angliae* by Browning *et al.* (1995: 435). Recent studies have revealed facts that are suggestive of its origin by hybridisation, as the type and other examples "are clearly intermediate between *B. fluviatilis* and *B. robustus* (not *B. maritimus*) in their floral scale texture... and anther colour." (Browning *et al.* 1995: 434, 435). This putative hybrid origin is also supported by the pericarp construction which is novel and unmatched by any African examples, except in some respects, by the nuts from inland situations at Verlorenvlei. The novel features are: (i) the variation in the surface topography, which shows areas of the "honeycomb" pattern adjacent to areas of the *B. nobilis* pattern (in *B. novae-angliae* actually the *B. fluviatilis* pattern, which equates with that of *B. nobilis*). These adjacent patches are evident in Figures 32 B and less clearly in Figure 33 B. They show extremely well in Figure 37 J.. In transverse section, the exocarp cells are approximately intermediate in depth between what is typical for the "honeycomb" pattern (exemplified by *B. robustus*) and what is typical for the *B. nobilis* pattern (exemplified by *B. fluviatilis*), compare Figure 37 D, H and L). These figures also illustrate the differences in the exocarp depth to mesocarp depth ratio in the three taxa, namely approximately 1 : 7 in *B. fluviatilis*, 2.5 : 1 in *B. robustus* and 1 : 2 in *B. novae-angliae*. Another significant feature of the exocarp cells of *B. novae-angliae* is the presence of silica deposited on the inner periclinal wall of each cell (Figure 33 D). Silica deposits are not known for the exocarp cells of the "honeycomb" pattern, but are present in the exocarp cells of the *B. nobilis* / *B. fluviatilis* pattern (Figure 34 A, B). Their presence in the variable pericarp of *B. novae-angliae* may further support the speculated hybrid origin of this species.

Mesoamerica

Adams (1994: 449) for Mesoamerica records only one species, namely, *Bolboschoenus robustus* (Pursh) Soják. The distribution given is Mexico, the Atlantic coast from New Brunswick to Argentina, California, Guyana, Paraguay and Bermudas. Specimens seen do not differ significantly from those of N. America, but nuts are needed for comparison of pericarp construction as none were available during the course of the present study.

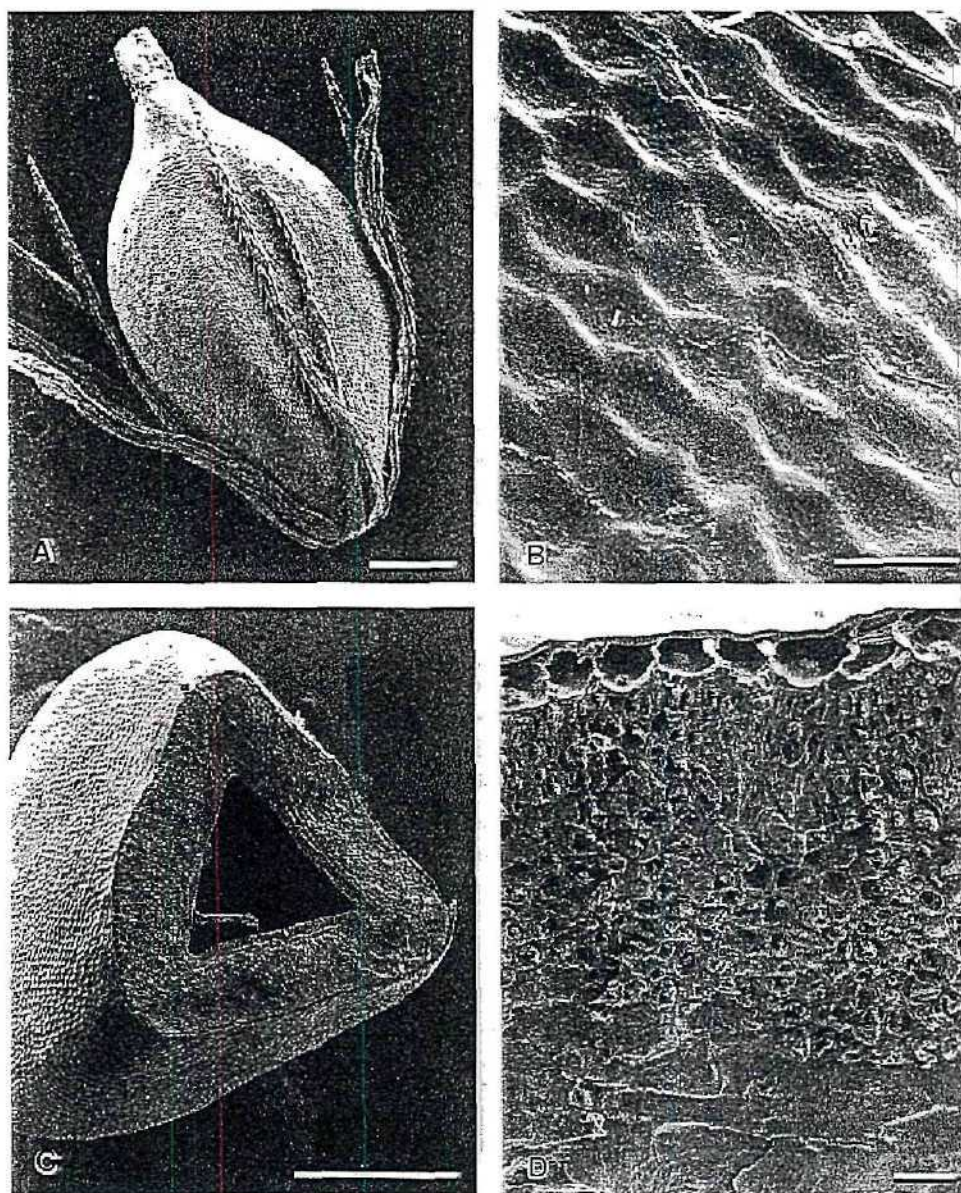


Fig. 3. *Scirpus perviridis* V.J. Cook 534 (AK 59189). (A) Achene with perigonal bristles persistent; (B) pericarp surface at mid-achene; (C) achene in transverse section, endosperm removed; (D) detail of pericarp in transverse section showing exocarp with silica deposits (top), mesocarp (middle), endocarp (bottom). Scale bars A, C = 500 μ m; B, D = 25 μ m.

2. *Scirpus medianus* (V.J. Cook 463, in AK 61798)

Perigonal bristles persistent, 2.5–3.1 mm long, slightly shorter than achene. *Achenes* (Fig. 2A, C) imperfectly mature, in outline obovate with rounded summit, beak well developed; trigonous with abaxial angle rounded, faces slightly concave, adaxial wider than 2 abaxial, 3.5–3.8 \times 2.2–2.4 mm; ratio of maximum width:basal width = 3.3:1.0. *Surface* pale, ochraceous or testaceous, dull not glossy; smooth, cellular at \times 25; exocarp cells at \times 600 (Fig. 2B) longitudinally elliptic, somewhat variable (best described as more or less isodiametric but

Pacific Islands (Northern hemisphere)

The Hawaiian Group

Earlier, this group of islands was known as the Sandwich Islands. Two collections, *Hillebrand 529* (Received July 1865) and *Herb. Forsyth* (purchased 1835, both K) show two style branches. Immature lenticular nuts are present on the former. On the latter is a note by Clarke dated 1887: '*Scirpus maritimus* Linn. This is not exactly = the Indian *affinis*, which has a remarkably small nut = this is exactly = the Australia "digynous" i.e. the 2-fid style form of the Australian *fluviatilis* var. *macrostachys* Mich.' More recent collections from Oahu [*J.F.G. Stokes s.n.*, and *O. Degener 3113* (GENT, K respectively)] are robust, the inflorescences carrying up to 25 and 13 spikelets respectively. The florets carry two style branches and the lenticular nuts examined micromorphologically show the "honeycomb" type of construction, but with the exocarp cells towards the centre of each plane face of the nut becoming gradually smaller in diameter (Figure 35), as in *B. grandispicus* of West Africa (compare Figures 22, 23, and 35).

Revillagigedo Islands

A collection from these islands (*H.L. Mason 1580*, 29 April 1925, K) is of an extremely robust, branched inflorescence with florets with two-branched styles. Notes record the plant height as 4--8 feet, which is far in excess of parameters for all species except *B. nobilis* in Namibia, southern Africa (see Formal Taxonomy, Chapter 14 pg. 102). In my opinion, the affinities of Mason's plant are with the American *B. maritimus* subsp. *paludosus* as the pericarp construction is of the "honeycomb type." (Figure 36)

South America

From South America no nuts were obtained for micromorphological examination, therefore information depends upon the study of herbarium records, which are sparse. I have studied some specimens from Brazil, Argentina and Uruguay and been provided with details of others from Columbia, Guyana and Peru. *Bolboschoenus robustus* is present and fairly widespread,

laterally compressed so that length exceeds width), walls not raised, central zone flat; waxy covering sparse, best developed over distal half. In *transverse section* (Fig. 2C, D): exocarp cells slightly radially elongate, ratio of depth:width of individual cell more or less 1.3–1.7:1.0; anticlinal walls somewhat wavy (walls appear crumpled or folded as in a bellows), silica bodies not observed; exocarp thickness more or less half mesocarp thickness, except over angles where exocarp more or less one third mesocarp thickness.

3. *Scirpus perviridis* (V.J. Cook 534, in AK 59189)

Perigonal bristles persistent, 2.8–3.5 mm long, reaching apex of achene; only 5 per achene observed (protologue states '± 5 subaequalis'). *Achenes* (Fig. 3A, C) imperfectly mature, in outline elliptic with sloping summit and base, beak tapered, well developed; nearly equilaterally strongly trigonous with faces convex above to concave towards base, 3.7–3.8 × 1.7–1.8 mm; ratio of maximum width:basal width more or less 6:1. *Surface* pale ochraceous, dull; faintly cellular at × 25; exocarp cells at × 600 (Fig. 4B) shortly longitudinally elliptic (best described as more or less isodiametric, but laterally compressed so that length slightly exceeds width), longitudinal walls slightly raised, transverse walls faintly marked, central zone depressed; waxy covering lacking. In *transverse section* (Fig. 3C, D): exocarp cells rectangular or square, more or less isodiametric, walls straight, occasionally slightly sinuate; small nodular silica bodies present (Metcalf 1971, figs 4I, 5P); exocarp thickness more or less 1/7 of mesocarp thickness.

The achene of *Scirpus perviridis* is distinguishable from achenes of the other two isotypes on the following characteristics: (1) outline shape; (2) width; (3) the more or less isodiametric shape of the exocarp cells seen in transverse section; (4) the depth of the exocarp in relation to the depth of the mesocarp; and (5) the length of the perigonal bristles. There is variation in the lengths of the bristles of an achene, but one or more equate with achene length.

The significant differences in achene morphology and pericarp anatomy that distinguish the isotypes are summarised in Table 1. Dimensions of achene samples representative of the species in Australia and New Zealand are given in Table 2. Some morphological features by which the achene isotypes are not representative of their achene species sample are discussed below.

Discussion

Isotypes

The achene of *Scirpus caldwellii* is clearly distinct from those of *S. perviridis* and *S. medianus* (see Table 1). The achene of *Scirpus medianus* may be regarded as more or less intermediate between that of *S. caldwellii* and *S. perviridis*, as it exhibits characters of the achenes of both these isotypes. In its trigonous conformation and the depth of mesocarp, there is affinity with *Scirpus perviridis*; but in its outline shape and in the slight radial elongation of the exocarp cells, which is more pronounced over the rounded angles than across the flat faces, there is resemblance to *S. caldwellii*. Its perigonal bristles, while persisting on the shed achene, are shorter than those of *Scirpus perviridis*.

The achene dimensions recorded in Table 2 indicate that parameters for the isotypes fall well within the ranges recorded for representative samples of the species. Of the parameters for the samples, it is only the width of *Bolboschoenus fluviatilis* that is differentiating; however, even this range shows slight overlap with achene width ranges for *B. caldwellii* and *B. medianus*.

The achene parameters of *Bolboschoenus fluviatilis* are worthy of further consideration as they have been used, in part, in the recognition of infraspecific taxa. Koyama (1958, p. 336) reduced *Scirpus yagara* Ohwi (type from Japan; the binomial given to the Asiatic representative of *S. fluviatilis* in a wide sense) to varietal level and included in his key, the following information:

- *achenes obovate, 3.5–4 mm long, 1.8 mm wide, the apex with a small mucro-like beak var. *yagara*
- achenes obovate to broadly so, 4–5 mm long, 2.3–2.5 mm wide, apex with a beak [dimensions for American plants] var. *fluviatilis**

not differing in general facies from N. American examples. *B. maritimus* subsp. *paludosus* (A. Nelson) T. Koyama is also recorded, but from the evidence I have been able to obtain, is localised and may perhaps be adventive. Plants carry florets with two style branches and do not appear to differ significantly from North American examples. Guaglianone (1996: 130) lists three species of *Bolboschoenus* for Argentina, *B. maritimus* [Cabrera 2695 (LP)], *B. paludosus* [Hicken s.n. (SI 3153)] and *B. robustus* [Guaglianone et al. 1291 (SI)]. *B. maritimus* may represent an introduction, but confirmation is needed.

Smith (pers. comm.) noted that a specimen from Turbo, Columbia [R. Callejas et al. 5032 (NY)] was “much like Australian and New Zealand examples of *B. fluviatilis/perviridis*.” This suggests the possible presence of *B. fluviatilis* in north western S. America.

From this limited information it seems unlikely that any novel undocumented pericarp structure exists among South American representatives of *Bolboschoenus*. Further investigation is obviously required.

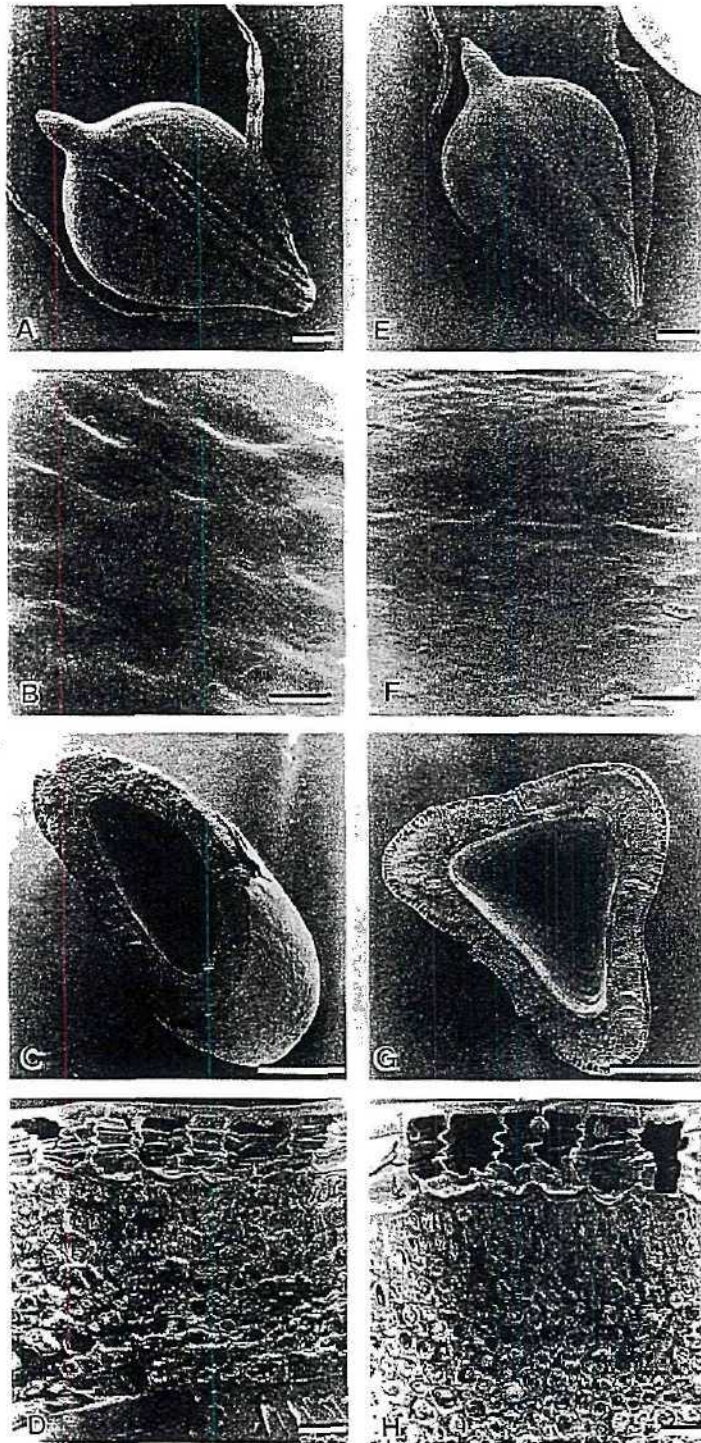


Fig. 4. *Bolboschoenus medianus* (A) Lenticular achene, (E) trigonous achene, both with some filaments and perigonal bristles persistent. Both from *Lepschi 1598* (NU). (B, F) Pericarp surface at mid-achene; (C, G) achene in transverse section with endosperm removed; (D, H) detail of pericarp in transverse section showing exocarp (top) and mesocarp (middle); endocarp just represented in D, absent in H. Scale bars A, E, C, G = 500 μm ; B, F, D, H = 25 μm .

CHAPTER 9

BOLBOSCHOENUS IN AUSTRALIA, NEW ZEALAND AND ASSOCIATED ISLANDS

[Browning *et al.* (1997a) applies: see Appendix 3]

Three species of *Bolboschoenus* are presently described for New Zealand (Edgar 1970: 172) and Australia (Wilson 1981: 157), namely *B. caldwellii* (Cook) Soják, *B. medianus* (Cook) Soják and *B. fluviatilis* (Torr.) Soják. All were first regarded as variants of *Scirpus maritimus* s.l. Cook (1947: 567) cites Cheeseman (1906: 778) quoting Clarke as being of the opinion that “the typical form of the species has not yet been observed in Australia or New Zealand.” The two varieties that were recognised, namely *fluviatilis* Torrey and *macrostachya* Michaux, were subsequently raised to species level as *Scirpus fluviatilis* (Torrey) A. Gray (Gray 1848: 527) and *S. robustus* Pursh (Pursh 1814: 56) respectively. All variants were known under one or other of these names. However, when Cook (1947) undertook revision of the New Zealand taxa, he distinguished three species, two of which he found to “differ materially” from their American counterparts. This resulted in the establishment of *Scirpus perviridis* and *Scirpus caldwellii*. The former was likened to *S. fluviatilis*, but the plants were less stout and the nuts smaller. Styles were uniformly three-branched, unlike the two-branched styles of *S. caldwellii*, which was the smallest in stature of Cook’s trio. The third species *S. medianus* was intermediate in size between *S. perviridis* and *S. caldwellii*, with two and three-branched styles in the same plant. *Scirpus perviridis* has not been maintained as a species. Edgar (1970: 173), following Raymond (1959: 226) and Koyama (1961: 83), placed it in synonymy with *B. fluviatilis*. Nuts from isotypes (AK) of all three of Cook’s species have been studied micromorphologically. Specimen numbers, type localities and a summary of pericarp characters are given in Table 9. Nutlet outline shape and colour are illustrated in Figure 38.

The isotype of *Scirpus perviridis* has the pericarp construction of the *Bolboschoenus nobilis* type, that is, it is in agreement also with the type represented in American examples of *B. fluviatilis* (Figure 39, cf. with Figure 27). The isotype of *Scirpus caldwellii* has the pericarp construction of the “honeycomb” type, but with similar modification to that found in other lenticular nuts, namely *Bolboschoenus grandispicus* of West Africa and *B. maritimus* var.

Table 1. Summary of characters of achenes removed from isotypes of *Scirpus caldwellii*, *S. medianus* and *S. perviridis*

Character	<i>Scirpus caldwellii</i>	<i>Scirpus medianus</i>	<i>Scirpus perviridis</i>
Perigonial bristle length and persistence on shed achene	only 1 achene with 1 bristle observed, 2.0 mm long; caducous	slightly shorter than achene; 2.5–3.1 mm long, persistent	reaching apex of achene, 2.8–3.5 mm long, max. of 5 per achene observed; persistent
Achene 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
Achene size	3.6–3.9 × 2.3–2.5 mm	3.5–3.8 × 2.2–2.4 mm	3.7–3.8 × 1.7–1.8 mm
Achene surface when dry	pale, ochraceous to stramineous; dull not glossy; faintly cellular at × 25; slightly waxy	pale, ochraceous or testaceous; dull not glossy; faintly cellular at × 25; slightly waxy	pale, ochraceous, dull; cellular at × 25; no wax
Transverse-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; wider over angles than on concave faces, difficult to estimate ratios because of brittleness of exocarp	slightly variable, about 1/2 mesocarp thickness, except over angles where about 1/3 mesocarp thickness	c. 1/7 of mesocarp thickness

paludosus of N. America and Hawaii (Figure 40, cf. with Figures 22, 23 and 31). The isotype of *S. medianus* shows some features of both these types (Figure 41). The surface topography resembles that of *S. perviridis* in the outline shape of the exocarp cells, but the anticlinal walls are depressed as in the "honeycomb" type. Seen in transverse section, the depth of the mesocarp is approaching that of *S. perviridis*, but the exocarp cells are slightly radially elongate as in the "honeycomb type." There is also greater elongation of the exocarp cells over the angles of the nut, as in *S. caldwellii*. Notice also the persistence on the nut of some of the bristles (all have been lost from the isotype of *S. caldwellii*). These features of the nuts are not limited merely to the examples of the isotypes examined, but are consistent for other examples of the species from New Zealand and Australian localities that have also been studied micromorphologically. The conclusion is drawn that *Bolboschoenus medianus* may be of hybrid origin, with *B. fluviatilis* and *B. caldwellii* the putative parents. If this conclusion is correct, then *B. medianus* may be found to show the lack of uniformity in pericarp surface topography that is reported for *B. novae-angliae* in America. This has not yet been clearly observed; further studies may reveal it. Further support for the hybrid origin of *B. medianus* lies in the variation in style branch number and in the conformation of the nuts from trigonous to lenticular within a clone (Figure 42).

No novel pericarp pattern has therefore been revealed for *Bolboschoenus* species in New Zealand or Australia.

One aberrant collection that may represent an introduction, is recorded from New Zealand, namely *A.J. Healy & B.J. Hamlin 50/70*, North Island, Hawkes Bay, near Puketapu (CHR, K). This was determined as *B. medianus*, but in my opinion it is *B. glaucus* or a close variant. This is based on the spikelets, glumes and size and micromorphological study of the nuts (Figure 43).

The associated islands

Specimens from New Caledonia [*Wilson 7809* (NSW)], and the Norfolk Islands [*J. MacGillivray 774*; *Milne 161* (both K) and *Metcalf s.n.*; *J. McCornish 179* (NSW)] are all

Table 2. Summary of achene dimensions for *Bolboschoenus* spp. in Australia and New Zealand. Each sample comprised 50 achenes removed at random from available herbarium specimens (measurements in mm)

Species	Length (including beak)	Mean	Standard deviation	Width	Mean	Standard deviation
<i>B. caldwellii</i>	3.0–4.2	3.5	± 0.33	1.8–2.7	2.4	± 0.20
<i>B. medianus</i>	3.2–4.5	3.8	± 0.28	1.9–2.8	2.3	± 0.24
<i>B. fluviatilis</i>	3.3–4.2	3.7	± 0.22	1.4–2.0	1.7	± 0.16

However, he later changed his opinion and commented 'Raymond is correct to treat *S. yagara* from Japan as being quite identical with *S. fluviatilis* and not a separate variety of it.' (Koyama 1961, p. 83).

When treating *Bolboschoenus* for Japan, Koyama (1980, p. 140) again changed his mind and made the new combination *B. fluviatilis* subsp. *yagara* (Ohwi) T. Koyama. He summarised its differences from the typical subspecies, including among them achene parameters, namely, '2.5–3.5 × 1.8–2.2 mm for subsp. *yagara* and 3.8–4.2 × 2–2.5 mm for subsp. *fluviatilis*' [dimensions again presumably for plants from America].

These figures indicate that in Japan, subsp. *yagara* has shorter, narrower achenes than the typical American subspecies. Figures for our samples from Australia and New Zealand are not definitive for one or other subspecies. Achene length suggests the typical entity, but achene width fits best with subsp. *yagara*, but it should be noted that our length measurements include the achene beak while it is not clear whether this was included by Koyama. The question of whether infraspecific taxa occur within *Bolboschoenus fluviatilis* requires study throughout the total range of its distribution.

The sampled achenes of *Bolboschoenus medianus* were not uniform in their conformation, unlike those of *B. fluviatilis* (consistently trigonous) and *B. caldwellii* (consistently biconcave). The achene of the isotype is trigonous as seen in transverse section (Fig. 2C), but in the species sample a few achenes were biconvex among a majority that were trigonous. In the achenes from another population we have studied, *B.J. Lepschi 1598* (NU), similar variability in achene conformation was encountered (Fig. 4A, C, E, G). This variability, considered in conjunction with the presence of two- and three-branched styles within individual spikelets and other morphological criteria such as its intermediate plant height and robustness and the perigonal bristles that are persistent and consistently shorter than the achene, suggest a hybrid origin of *Bolboschoenus medianus*. If the putative parents were not *Bolboschoenus caldwellii* and *B. fluviatilis* themselves, then surely the parental stocks must have been those that gave rise to these, now, clearly distinct taxa.

Bolboschoenus possesses the perennial habit and underground storage organs, that not only make survival possible through a number of seasons, but which permit vegetative multiplication. Therefore, hybrid progeny that might have established where putative parental stocks were sympatric or closely allopatric, might well have continued to survive and to have increased. In addition, growing conditions (marshes and riverine floodplains with varying water levels and perhaps also salinities) are likely to have provided a mosaic of microhabitats in which some, at least, of the dispersed hybrid diaspores might chance to find the inter-mediate conditions needed for their germination and optimal growth.

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Bolboschoenus fluviatilis. This species and the Asian *B. yagara* (Ohwi) A.E. Kozhevnikov are under contention as they are variously regarded as distinct (Hulten & Fries 1986), or as synonymous (Ohwi 1965). Differences are mainly in plant and nut size. I have found no significant difference in pericarp construction.

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1997b.

Browning, J., Gordon-Gray, K.D., Smith, S.G. and van Staden, J.

***Bolboschoenus maritimus* s. l. in The Netherlands: a study of pericarp anatomy based on the work of Irene Robertus-Koster.**

Annales Botanici Fennici, 34: 115–126.

CHAPTER 10

BOLBOSCHOENUS IN EUROPE

Western Europe

Historically, Europe represents the origin and the hub of taxonomic enterprise with the adoption and use of the binomial system of plant nomenclature. For *Bolboschoenus*, the type species, as *Scirpus maritimus* L., is represented in the Linnaean Herbarium by two specimens that are not identical (Clarke 1894: 313). Specimen LINN 71.43, U.S.A., Virginia, J. Clayton 570 ‘...with thick ovate spikelets that are 7 to 11 mm across and aggregated into a head ... the type of var. *macrostachys* Koch by most authors’, was selected as the lectotype by Koyama (1962: 933). As has already been stated (Chapter 8, pg. 52), it has subsequently been shown to be *Bolboschoenus robustus* (Pursh) Soják. Specimen 71.44 ‘... with lanceolate to linear-lanceolate spikelets ... extremely long and narrow...also aggregated into a head’ must also be rejected as its locality is not in agreement with that cited in the protologue, namely Roslagen in Sweden. It carried fruit, which specimen 71.43 does not. A small sample of these was made available for micromorphological study. The pericarp conformation is of the “honeycomb” pattern (Figure 44). A neolectotype is in process of selection (Kukkonen & Smith, pers. comm.) This is likely to be *Orjan Nilsson 9515* (H) from the type locality, or very close to this. Nuts from this proposed neolectotype have been studied micromorphologically and found to have the “honeycomb” type of pericarp construction (Figure 45) that is present also in the coastal plants at Verlorenvlei, southern Africa.

With the concentrated collecting spanning more than two centuries that has taken place in most European countries a wealth of specimens now referable to *Bolboschoenus* exists, while numerous publications provide coverage of the extensive nomenclature that has developed in attempts to bring taxonomic order to the variation encountered. Despite the multiplicity of taxonomic opinions that have been expressed through time, most more recent accounts recognise only one species for Europe, namely, *Scirpus (Bolboschoenus) maritimus* [e.g. Ascherson & Graebner (1904); Suessenguth (1939); Hermann (1956); Schultze-Motel (1967);

Robertus-Koster (1969); Norlindh (1972); Casper & Krausch (1980); DeFilipps (1980)]. Here are included plants with contracted to open inflorescences, bifid or trifid styles (sometimes in an individual spikelet) and lenticular, subtrigonus or trigonus fruits with early caducous or persistent perianth bristles. The habitats occupied are saline, to brackish, to freshwater, and maritime to inland [e.g. Hejny (1960); Schultze-Motel (1967); Robertus-Koster (1969); Casper & Krausch (1980)]. Two of these authors, both of whom undertook detailed studies in attempts to understand more explicitly the underlying causes of the variation, have been given particular attention in pursuit of the present study into pericarp construction. Their work is of special significance in relation to my own findings at Verlorenvlei, southern Africa.

Norlindh (1972) carried out intensive fieldwork in Sweden, where the natural populations he investigated were of plants bearing predominantly three-branched styles and subtrigonus nuts, similar to those at Verlorenvlei. His study incorporated also Eurasia, so that he considered in relation to *Scirpus maritimus*, the eastern European and Asian *Scirpus affinis* Roth [*Bolboschoenus affinis* (Roth) Drobow], with lenticular nuts. His important conclusions expressed doubt of the value of inflorescence form, number of style branches and shape of nuts as reliable features of difference in taxonomic classification. He recognised, for the plants he studied, two geographical races under *Scirpus maritimus*, namely subsp. *maritimus* (with a mainly western European distribution) and subsp. *affinis* (Roth) T. Norl. (mainly Asian), with transitional forms between them in eastern and central Asia.

Robertus-Koster (1969) worked in The Netherlands on natural populations of *Scirpus* (*Bolboschoenus*) *maritimus*. Her investigations covered the study of inflorescences (sometimes with compact, capitate form; sometimes branched and open) and nuts (differences in shape, size and colour). Her conclusion was that in The Netherlands "*S. maritimus* shows a clinal variation, probably in correlation with the habitat." Analysed, this clinal variation seemed to indicate a continuous intergradation, at least in morphological characteristics, between two paramorphs (Huxley, 1940): *maritimus* from inland localities with 4--6 branches to the inflorescence and narrow, dark brown almost black fruits that in cross section were sharply triangular, and *compactus* (*Scirpus compactus* Hoffm.) with 0--2 inflorescence branches and small, broad, brown, semi-spherical to slightly triangular fruits with great

variability within and between the samples.

Neither of these authors had access to electron scanning procedures. It seemed worthwhile to study micromorphologically, nuts from western European plants, particularly examples falling within *Bolboschoenus maritimus* subsp. *maritimus* and subsp. *compactus* (Hoffm.) Hejny, and from more eastern localities, subsp. *affinis* (Roth) T. Norl., which is not recorded for western Europe by Norlindh (1972), DeFilipps (1980) or Hulten & Fries (1986). Robertus-Koster (1969 : 196, 197, Figures 2, 3) had reproduced photographs of nut samples from her collections in The Netherlands. Due to her kindness and co-operation, eleven of her original samples, each except two of approximately 100 fruits that had been safely kept, were made available to me for electron scanning. The study carried out Browning *et. al.* (1997b) is included in Appendices 1 & 3 where materials and methods are detailed and the article reproduced. The results obtained are summarised in this dissertation (Table 10) and supplemented by electron micrographs of nut conformation and pericarp anatomy (Figures 46--51 inclusive). In general, the results parallel and support my independent findings at Verlorenvlei, although there is great variability recorded for The Netherlands that was not present at Verlorenvlei. This variability is speculated as possibly correlated with more extensive species sympatry and much greater natural (?) habitat disturbance in The Netherlands than at Verlorenvlei. From these two studies the following conclusions may be drawn: (i) plants in coastal habitats where higher salinity levels prevail show a "honeycomb" surface to the pericarp and an exocarp depth to mesocarp depth ratio of approximately 2 : 1. The exocarp cells are radially elongated with a depth to width ratio of 4 or 3 : 1 and are covered externally by a waxy deposit. These fruits are borne on inflorescences that are compact with no, or few, short branches. In contrast, plants from more inland habitats where salinity levels are low or where the water is fresh, show a far less well defined, more irregular surface topography in which the cell outlines are not isodiametric but sufficiently laterally compressed to be more or less elliptically oblongate. In section the pericarp has an exocarp to mesocarp depth ratio of approximately 1 : 2. In transverse section the exocarp cells are radially elongated, but with a depth: width ratio of approximately 2 : 1. These fruits are borne on inflorescences that are open with 4--6 or more well developed branches. (ii) nomenclaturally both The Netherlands and the Verlorenvlei plants are *Bolboschoenus maritimus* s.l., but the

Verlorenvlei coastal entity which has been segregated by myself and my collaborators as *B. maritimus* s.s. is not equivalent with Robertus-Koster's paramorph *maritimus*. It agrees better with paramorph *compactus*.

Returning to Norlindh's study (1972), this author distinguished subspecies *affinis* (Roth) T. Norl. from the typical subspecies *maritimus*. The typical subspecies he delimited as characterised by a compact or open inflorescence, two or three-branched style (the latter predominating in most spikelets) and a range from trigonous to planoconvex (lenticular) nuts. Thus Norlindh's opinion incorporates a wide range in morphological form and would encompass all the examples from The Netherlands studied by Robertus-Koster, and equally well, all the examples encountered at Verlorenvlei.

Subspecies *affinis* is based on *Scirpus affinis* Roth from India. Norlindh (1972: 404) remarks that at time of writing he had not been able to trace a suitable specimen to choose as lectotype. He selected as neotype *Stocks, Law etc. s.n.* (C), from India orientalis, Malabar, Concan etc. A fruit from this neotype has been studied micromorphologically (Figure 52). The nut is biconvex, almost round in outline, with clearly defined "honeycomb" surface topography. The exocarp has become brittle and parts of the outer periclinal surface have broken away under sectioning. Nevertheless, it is possible to observe the radial elongation of the exocarp cells, which have greater depth over the angles than towards the central area of each plane face. This is well shown in Figure 53, a specimen of *B. affinis* from Azerbaijan [Kukkonen 12727 (H)]. There is close relationship between this pericarp construction and that found in other lenticular fruits, for example *B. grandispicus* from W. Africa, *B. maritimus* ssp. *paludosus* from N. America and *B. caldwellii* from Australia and New Zealand, which last, however, frequently has biconcave rather than biconvex (lenticular) nuts. According to Norlindh (1972: 403) this morphological construction also falls within the limits of *Bolboschoenus maritimus*, but is recognised at infraspecific status.

Robertus-Koster's sample from Maastricht, which I was privileged to examine micromorphologically [Browning *et al.* (1997b) pg. 123, Figure 5, see also Figure 50 of this dissertation] was of unusual interest because of the narrowness in outline form, the almost

black colouration and the pericarp conformation of the fruits it comprised. All these characters considered collectively, are not those of paramorph *compactus*, nor of subsp. *affinis*. They are more like the Australian *B. fluviatilis* and its associated Asian species *B. yagara*. Could it be that this predominantly Asian species extends into Europe, as might also be the case with subsp. *affinis*? To pursue this question, nuts were obtained from western European specimens deposited in a number of herbaria. These were compared with specimens from Asia, China and Japan. Results of this work showed the presence of a few specimens of *Bolboschoenus yagara* in Germany (Bavaria) and the Czech Republic. Other specimens were regarded as putative *B. maritimus* x *yagara* hybrids [for example, *Schuhwerk* 86/490 (NY) Figure 54]. Further examination of specimens led to the reporting of *B. yagara* for western Europe (Browning *et. al.* 1996) and accumulation of records for this species or its hybrids in Britain, France, Belgium, Germany, Austria (P. Lassen, pers. comm.) Poland, Ukraine, Russia and Romania. *B. yagara* achenes are narrow and tapered to the summit with almost equilateral sides. The putative hybrids of *B. maritimus* x *yagara* have a wider, less tapered outline shape, being more obovate; in transverse section the faces are sometimes concave. Robertus-Koster's Schoonhoven sample is representative of these hybrids [Browning *et al.* (1997b) pg. 124, Figure 6; see also Figure 51 of this dissertation]. Her sample from Punt van Reide R7 contained about 70% of nuts that resemble *B. affinis* in their colour (ochre to khaki, not dark brown) and in their shape in transverse section (the majority not strongly trigonous, some lenticular) (Figure 48 of this thesis). Further reference to *B. affinis* and its putative hybrids will be made when the Asian countries are considered.

Southern Europe : the Mediterranean countries, including Turkey, Greece and associated islands

This zone was not well exemplified by specimens in herbaria. Many specimens that were represented had been collected in the second half of the nineteenth century, were inadequately (sometimes illegibly) documented and frequently were without well developed fruits. In consequence, the account that follows is far from authoritative; a great deal more investigation is required; field work will be particularly advantageous. From this preliminary overview the following species are reported in the countries named. A list of the exsiccatae

examined is given in Appendix 2.

Bolboschoenus maritimus s.s. has been found represented in Spain, Corsica and Romania.

B. glaucus had been found represented in Spain, Malta, Sicily, Italy, Albania, Macedonia, Greece and many of the Greek islands including Kriti.

B. affinis had been found represented in Romania. In my opinion, in addition to the above there are represented in almost all the countries of this southern European zone, examples that must be considered putative hybrids. The putative parental taxa are probably the species named, including in Romania, the possibility also of *B. yagara*.

CHAPTER 11

BOLBOSCHOENUS IN EURASIA AND FAR EASTERN ASIA

The Middle East to northern India

In this zone problems were again encountered as limited specimens were available for study; nor was it possible to consult a comprehensive list of regional floras for each of the countries represented.

Hooper (1985: 374--376) records only *Bolboschoenus maritimus* for Iraq and notes "Inflorescence capitate or subumbellate, of 1--10 solitary or glomerate, sessile or rayed spikelets." She gives the range in spikelet length for this taxon as "... 10--20 (30) x 5--6 mm" and comments on the spikelets "sometimes becoming 'catkin-like' by continued glume production, then cylindrical and up to 50 mm long." The illustration provided (Hooper 1985: 377, plate 87) resembles *B. glaucus* rather than *B. maritimus* and the nut (as achene) measurements (2.25 x 1.3 mm length and width) fit better with my own parameters for *B. glaucus* rather than *B. maritimus* s.s. The habitats given, "by streams; weed in rice fields up to alt. 750 (-950) m" are also the habitats favoured by *B. glaucus*. In the synonymy Hooper includes, *Scirpus tuberosus* Desf. and *Bolboschoenus tuberosus* (Desf.) Hadač. In this dissertation (under Mediterranean Africa pg. 50) it has been stated that the type on which both these names are based is *B. maritimus* (with "honeycomb" pericarp construction, Figure 25), but the name *tuberosus* has been often misapplied, particularly in California, to *Bolboschoenus glaucus* or the variants that possibly represent putative hybrids of that species with *B. robustus* or *B. maritimus*. Specimens on which Hooper's account is based have not been available to me so that nuts were not examined. It is possible three elements may be included in her synopsis of *B. maritimus*, namely *B. glaucus*, *B. maritimus* and *B. affinis*. Further clarification is needed.

Kukkonen (pers. comm.) in his treatment of Cyperaceae in the recently prepared Flora of Iran (in press) lists for this country the same three taxa, *B. glaucus*, *B. maritimus* and *B. affinis*.

Hulten and Fries (1986: 195, Figure 389) cover the entire zone (Middle East, southern Asia and northern India) in their map illustrating the distribution of *Bolboschoenus* species (as *Scirpus* spp.) north of the Tropic of Cancer. For the Middle East, *Scirpus maritimus* var. *tuberosus* (now known to be *Bolboschoenus glaucus*) is shown in scattered localities as far east as Turkey; *B. (S.) maritimus* [var. *maritimus*] is scattered and infrequent throughout, and *B. (S.) affinis* is in southern Asia and northern India. In the text it is noted that "*S. affinis* Roth (or *S. maritimus* subsp. *affinis* [Roth] T. Norl.) and *S. yagara* Ohwi occur mainly in Asia [West Central] and E. Asia respectively." In my opinion, *Bolboschoenus (Scirpus) yagara* is certainly represented in northern India and probably also in southern Asia and the Middle East.

To summarise, it may be stated that the species occurring through the total area of the zone have already been considered from the aspect of pericarp construction, with the possible exception of *Bolboschoenus yagara*, which relates in pericarp conformation to *B. fluviatilis*, and which will be further treated under Eastern Asia. The pericarp conformation of each species is known, so that, even though specimens for study were few and fruits were not available for critical examination, the opinion is confidently expressed that, apart from the effects of possible interspecific introgression which seems to result in minor variations, no completely novel pericarp conformation is anticipated from plants of this zone when a more exhaustive survey is carried out.

North Eastern Asia

(Russian Federation, Mongolia, China, Taiwan, Sakhalin, Korea, Japan, Okinawa)

A brief review of available literature covering the countries of this extensive geographical zone shows the presence of several species of *Bolboschoenus* unreported up to now in this dissertation. For Central Asia, Egorova (1967, 1976) listed three species *B. maritimus*, *B. planiculmis* (Fr. Schmidt) T. Egor. and *B. popovii* T. Egor. Of these, the two latter require some elaboration.

B. planiculmis, as *Scirpus planiculmis* Fr. Schmidt, is based on a type from Sakhalin (the

estuary of the Sussuya river), (*Schmidt 1868*). Rozhevitz (1935) transferred it to *Schoenoplectus*, but listed other related species under *Bolboschoenus*. Koyama (1958: 333) considered the placement as *Schoenoplectus planiculmis* incorrect but understandable, because in his protologue Schmidt described only the single-spikeleted form with the lowest bract remaining erect and continuing the line of the culm, even at the fruiting stage. The type specimen (LE), which I have not seen, is of this form. I am indebted to Dr. Kozhevnikov (pers. comm.) for information that the specimen is young, the solitary spikelet without mature fruit. Koyama (1958: 332, 333) remarked upon the "difficulty" of *Scirpus planiculmis* and discussed its variability, particularly the size and form of its fruits which he illustrated (*l.c.* Figure 13). There is relationship with both *B. maritimus* and *B. affinis*, some authors uniting the three species under *B. maritimus*. Koyama (1958: 333) tabulated the differences he recognised between them and expressed belief in their independent specific status.

In Japan, Ohwi (1944: 109) had established *Scirpus biconcavus* for plants close to *B. (Scirpus) maritimus*, but with two style branches and two-angled, biconcave nuts. This species Koyama (1958: 330) placed in synonymy under *Scirpus planiculmis*, and later was followed in acceptance of this conspecificity by Ohwi (1953: 237) himself.

The combination *Bolboschoenus planiculmis* (Fr. Schmidt) Egorova dates from Egorova (1967), but Koyama (1978) apparently unaware of this, erected the superfluous combination *B. planiculmis* (Fr. Schmidt) T. Koyama and continued use of it in subsequent work on Asian Cyperaceae (Koyama 1979; 1980). *B. planiculmis* becomes increasingly complex, for in revising *Bolboschoenus* in Japan, Koyama (1980) differentiated between what he termed "the true *B. planiculmis*" and the "East Asian species, which had been misidentified as *B. planiculmis* by several authors." He explained that the latter "is nothing but a digynous phase of the widespread *B. maritimus*", while the former "has turned out to be a well circumscribed, Far Eastern endemic" that is readily separable by "its characteristically triquetrous leaf and bract blades." The true species is "ecologically confined to the brackish habitats of the inter-tidal zone of estuaries, where it becomes completely submersed under the high tide (Shimizu, 1967)." The type of the "true species" has not been traced. Illustrated (Figure 55) is the pericarp conformation of a specimen of this species identified by Koyama.

It has the characteristics of the "honeycomb" type as exemplified by the majority of species with lenticular achenes.

Kozhevnikov (1988) in treating *Bolboschoenus* in Far Eastern Russia ["the Flora covers a rather narrow area from the Chinese border to the Arctic Ocean including Wrangel Island, Kamchatka, Sakhalin and all other Russian Pacific Islands" (Kukkonen, pers. comm.)], lists four species including *B. planiculmis* and *B. koshevnikovii* (Litv.) A.E. Kozhevnikov *comb. nov.* The latter species, of which I have not seen the type, has inflorescences of more than one spikelet (in contrast to *B. planiculmis* s.s.). In its synonymy is included *S. biconcavus* Ohwi. Kozhevnikov (pers. comm.) is now of the opinion that plants with solitary spikelets (*B. planiculmis* s.s.) and plants with more abundant spikelets in an inflorescence (*B. koshevnikovii*) are the same species. *B. planiculmis* is also included for Siberia [Kozhevnikov (1990:23)]. Restudy of *B. planiculmis* is obviously needed. This is particularly so as Strong (1993: 202) has mentioned this species with "the lower involucral bract appearing as a continuation of the culm", as a link between the genera *Schoenoplectus* and *Bolboschoenus*.

Egorova's (1967; 1976) other new species *Bolboschoenus popovii* is based on a type from China [Kaschgaria, Burgur, 20.08.1929, *M.G. Popov* 795 (LE)]. It is characterised by florets with two style branches that mature lenticular nuts. No nuts, either from the type, or from other specimens have been available to me for examination. Kukkonen in his account of Cyperaceae for the Flora of Iran (in press) includes *B. popovii* within *B. affinis*.

A further species unreported up to now in this dissertation is *B. desoulavii* (Drob.) A.E. Kozhevnikov *comb. et stat. nov.* (Kozhevnikov, 1988: 188). Apart from the florets carrying two style branches, I know little of the taxon. Mature nuts have not been available for study.

Also reported for North Eastern Asia is *Bolboschoenus affinis*, often as *Scirpus maritimus* var. *affinis* on herbarium specimens, for example, Kükenthal's determination of *Harry Smith* 5988 from China (K).

Bolboschoenus fluviatilis (Torrey) T. Koyama subsp. *yagara* (Ohwi) T. Koyama is also

reported for Far Northern Asia. The status of this entity as *B. yagara*, or as a subspecies within the American *B. fluviatilis*, has little consensus of opinion at present.

My own observations on achene morphology and pericarp anatomy of plants from this Far Northern Asian zone, albeit of limited extent, are now summarised.

(i) I found the predominance of nuts from plants in this zone to be lenticular, the faces either convex (*B. affinis*), or concave (*Scirpus biconcavus*), or as variants of these extremes (*Bolboschoenus planiculmis*). Kozhevnikov (pers. comm.) holds the opinion that *Bolboschoenus*, as represented in the Russian Federation, is in need of complete revision as treatments for Central Russia (Egorova 1967, 1976) and those for Far Eastern Russia and Siberia (Kozhevnikov 1988, 1990) are very different. Although fruits of all other described taxa have not been available for critical assessment, what I have seen from this extensive zone suggests that the lenticular nuts have the pericarp construction of the “honeycomb” type, without or with, the modifications already described for two-angled fruits from other zones. It should be noted that during the early part of the present century the tendency among researchers was to include all specimens with two style branches and two angled fruits within a distributional range extending from Middle East countries to those of the Far East in *Scirpus maritimus* var. or subsp. *affinis*.

(ii) The specific epithet “*maritimus*” has been of frequent application to plants from North Eastern Asia, but I encountered no nuts whatever from this zone that equated precisely with those representative of what is regarded as the typical form of *B. maritimus* s.s. from Roslagen, Sweden (Figure 45). Nor did I encounter from this zone, examples in which an individual inflorescence incorporated florets, some with two style branches, others with three, as occurs in spikelets of *B. maritimus* from Europe and America.

(iii) Three angled nuts, either sharply trigonous (*B. yagara*) or subtrigonous were infrequent. What examples there were fell mainly within limits for *B. yagara*, as distinct from the American *B. fluviatilis* with a predominance of larger nuts.

South Eastern Asia

[Peninsular India, Myanmar (Burma), Thailand, Vietnam, Malaysia, Indonesia]

Bolboschoenus glaucus, frequently as *Scirpus maritimus*, is well represented in Peninsular India, which area is generally regarded as more closely related geologically to Gondwanan Africa rather than to Asia. Clarke (1893: 659) cites *Scirpus tridentatus* Roxb. as one of the synonyms of *S. maritimus* in India. A nut of the type of Roxburgh's species (K), albeit a somewhat immature one, has been examined micromorphologically and agrees in pericarp construction with that of *B. glaucus* (Figure 24). Clarke (1893: 659) also cites for India *Scirpus maritimus* var. *affinis*, giving its distribution as "Throughout N. India, in the plains; from the Punjab and Bombay to Assam and Pegu." This is in agreement with my own findings which are that while *Bolboschoenus affinis* is present in Peninsular India, it is less frequent there than in Northern India, which has been included with countries of Eurasia and Eastern Asia in this survey. Pegu is in Myanmar (formerly Burma). I have not seen examples of *B. affinis* from this country. It must be present there and Clarke's reference (1893: 659) to the "extreme state of *affinis* ...the Burmese form, in which the stem is terminated by one very large spikelet one and one third by three fifths of an inch" is in agreement with specimens I have seen from Senegal (Chapter 14 pg. 99) and Eurasia (Caspian area) in which there is only one spikelet to the inflorescence, but this very much smaller in its dimensions.

For Thailand, Koyama (1979: 284) reports *B. maritimus* subsp. *affinis* (Roth) T. Koyama and gives its distribution "from Afghanistan and Turkestan eastwards through northern India to Indo-China." In the same publication he mentions "*Scirpus vulpinicolor* (of which the taxonomic status requires further investigations) [which] approaches *B. maritimus* in its yellowish (not whitish), slightly elongated-acutish spikelets, umbelliform anthelas and rather robust culm ca. 70 cm tall." This would seem to be another element of the *B. maritimus* complex in Asia. I have not seen the type, nor any fruit.

B. affinis is also in Vietnam, for example *Balansa* 4824 (K). Kern 1974: 499 cites only *Scirpus maritimus* for Malesia and records four localities, namely Phillippines (Luzon); New Guinea (Western Highlands and Mount Sarawaket); Papua (Lower Fly River). He remarks

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 (*Roussillon 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

that "The Malesian plants are strictly or predominantly digynous." Those from the Western Highlands in New Guinea are close to *Scirpus medianus* of New Zealand with two or three style branches in flowers of the same spikelet. The Papuan examples (two-styles) he believes are closest to *S. planiculmis*. In Kern's opinion "neither *S. planiculmis* nor *S. affinis* can be separated specifically from *S. maritimus*." A further gathering from Papua/New Guinea [Walker ANU 536 (K)] has three-styled florets and has been placed in *B. fluviatilis*.

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.

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* (Schr.) J. Browning, better known as *Schoenoplectus litoralis* (Schr.) Palla s.l. or *Scirpus litoralis* Schr. 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, *Cyperus glomeratus* (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 culms 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.

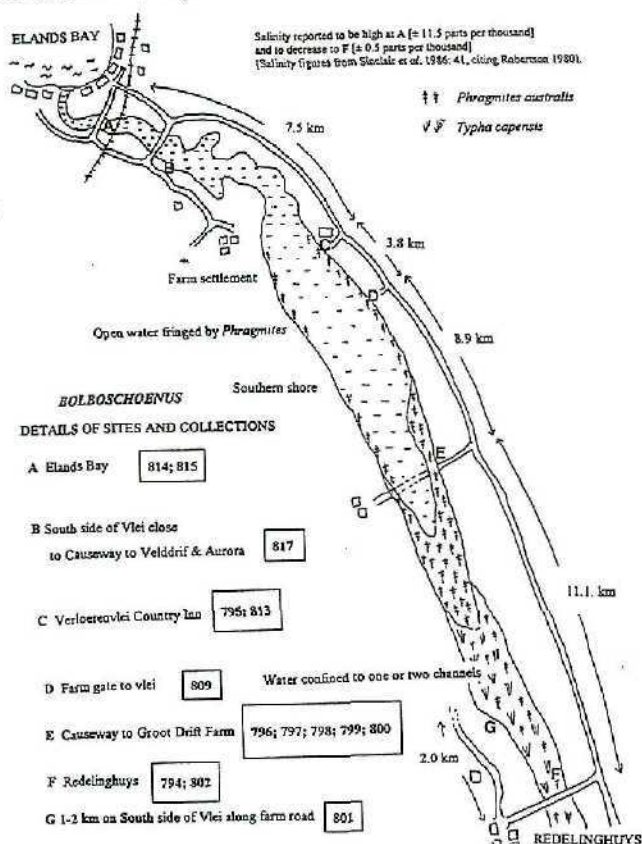


Figure 1 Map of Verlorenvlei showing collection sites.

SUMMARY OF PART 2

From the foregoing world overview of fruit construction within the genus *Bolboschoenus*, especially pericarp anatomy, some useful conclusions may be drawn. It may confidently be stated: (i) that morphological features of the fruit (shape, size, colour) together with anatomical construction of the pericarp (particularly the exocarp and mesocarp), provide a suite of characters, previously not fully explored, that are revealing and therefore helpful in recognition of major (gross) taxonomic grouping within the genus. (ii) This suite of characters in conjunction with other criteria already much used, but not always to be relied upon individually (inflorescence branching, style branch number and features of the perianth bristles) collectively afford clearer understanding of these major morphological patterns within the genus.

To go into greater detail, the overview has shown that the three patterns of pericarp construction described for southern African plants are repeated, with or without modification, throughout world distribution of the genus. The 'honeycomb' pattern is associated predominantly with lenticular fruits which are derived each from a gynoecium with two branches to the style and therefore probably represents a bicarpellate condition. The two other patterns, *B. glaucus* and *B. nobilis*, are closely allied, differing mainly in degree rather than in basic construction. It is not out of place to consider them variants of one another. They are associated with trigonous fruits which are derived each from a gynoecium with three branches to the style and therefore probably represent a tricarpetate condition.

Linking the two main patterns of pericarp construction (if *B. nobilis* and *B. glaucus* types are to be regarded as variants of one type) there exist aberrants (perhaps they should be interpreted as transitional elements ?) which, in one feature or another, express some level of intergradation between the two patterns, or the patterns developed are atypical, generally modified or muted in some respect. As examples, *B. novae-angliae* in America shows an irregular pericarp surface topography under high magnification; in part it is of the 'honeycomb' pattern; in part of the *B. nobilis* pattern. Added to this are two other features that suggest intergradation or interconnection between the two main patterns, namely, the

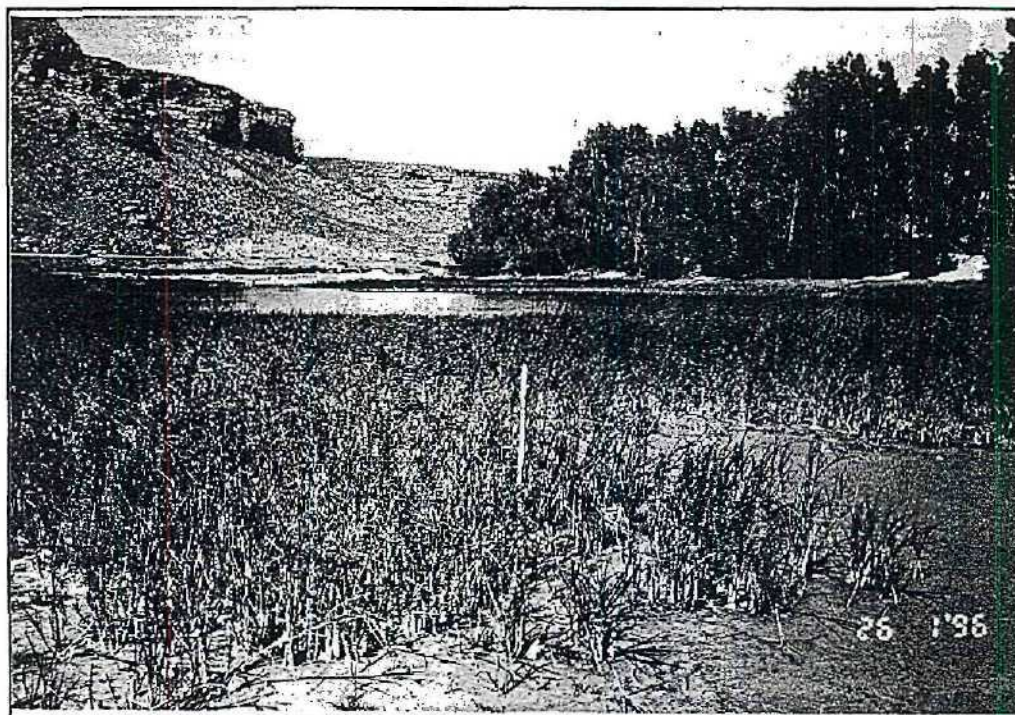


Figure 2 Coastal site with *Bolboschoenus maritimus* s.l. in foreground on wet sand.

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.

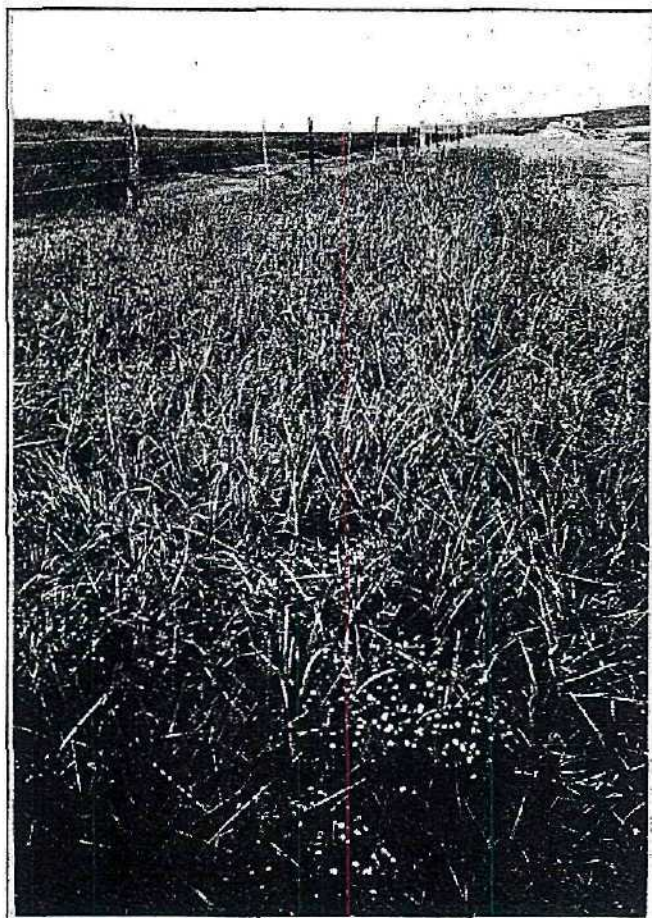


Figure 3 Inland site of *Bolboschoenus maritimus* s.l. protected from predation by a fence.

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

presence in a single spikelet of di- and tri-stylar florets, and silica deposits in the exocarp cells (not known for “honeycomb” pattern, but usual for *B. nobilis* pattern). *B. medianus* in Australia also shows interconnection between the two patterns, but in this case there are occasional lenticular fruits in a spikelet in which trigonous or subtrigonous examples predominate, as well as variation in style branch number and irregularity in pericarp surface topography. *B. maritimus*, perhaps surprisingly, is another example in which this interconnection is expressed.

The inland plants of Verlorenvlei, South Africa, possess fruits that show modification (gradation) of the main patterns rather than direct interconnection or transition between them. So too do some of the Asiatic variants of *B. affinis* (for example *Scirpus biconcavus* and elements that at present are classified as *Bolboschoenus planiculmis*). This “blurring” in some way of one or other of the main patterns of pericarp construction within the genus, is at present without adequate explanation as to its underlying cause or causes. It would seem genetically based but at this stage this is purely speculative.

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; DeFilipps 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)

PART 3

THE INFLORESCENCE

AND THE EMBRYO:

A PRELIMINARY SURVEILLANCE

CHAPTER 12

Inflorescence morphology

Within Cyperaceae inflorescence morphology is diverse and complex. In description in formal taxonomy there have been misunderstandings in the application of terms so that examples incorrect in the organological sense are frequent; uniformity and stability of terminology have been lacking. Some of these shortcomings have arisen through terms devised for dicotyledons having been applied to monocotyledons (Kukkonen 1994: 37); others are the outcome of inadequate study of the inflorescence and its parts, particularly lack of detailed dissection, and sometimes misunderstanding of the organs and their relationship to one another, bracts, prophylls and glumes among others.

Recently effort has been directed towards an improvement of this condition with detailed studies of the inflorescences of genera (Vegetti 1992; 1994) and of selected species (Kukkonen 1984, 1986; Vegetti & Tivano 1991). These studies have elucidated structural patterns, especially branching systems, and have provided a framework for a more accurate terminology (Kukkonen 1994). Much of this advancement has been possible because of the earlier achievement of a growing consensus that the cyperaceous inflorescence, along with that of Juncaceae and all other monocotyledons, is polytelic and open, that is, capable theoretically of indefinite growth (Troll 1964: 178; Weberling 1981: 278, 1992: 224; Kukkonen 1984: 257, 1994: 39).

Bolboschoenus possesses an inflorescence of from one to numerous spikelets carried distally on a leafy shoot or culm. Each inflorescence is bracteated and all, except those that consist of one only, have the spikelets grouped in clusters or solitary at the distal ends of branches developed from the axils of the bracts that arise from closely-placed nodes of the main shoot axis. These lateral branches are often termed "rays" and may, or may not, exceed in length the length of the main axis that bears them. The resultant total inflorescence is therefore often wider than deep, consequently umbel-like, and the terms 'umbel', or more commonly, 'anthela' have been frequently used in description. These terms, however, apply to

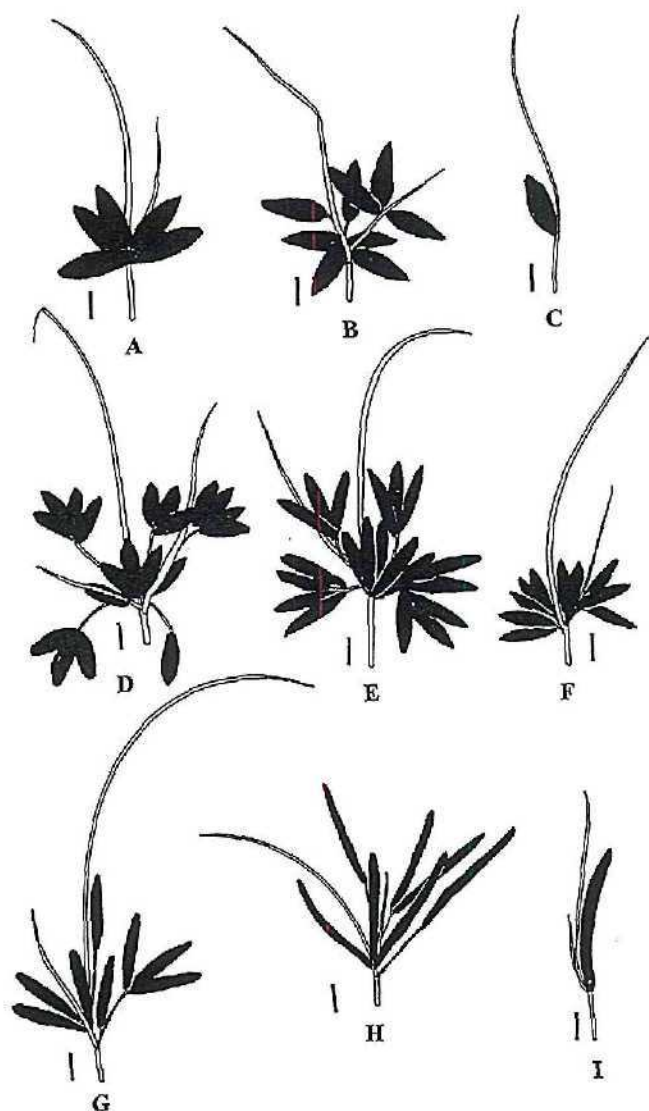


Figure 4 *Bolboschoenus maritimus* s.l., diagrammatic silhouettes of inflorescences and spikelets. A–C representative of coastal sites (A, B, C); D–I representative of inland sites D, E, F. Note: these silhouettes A–I are representative of types of inflorescence; one or more may come from one sampling 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).

determinate, not open, branching systems and must be avoided (Kukkonen 1994: 39, under Inflorescence). Within a species of *Bolboschoenus*, for example *B. maritimus*, the inflorescence may vary from a rayed system, to a compact head, to a solitary spikelet; these variations are often borne upon interconnecting rhizomes and therefore within a single plant (clone or genotype) (Norlindh 1972: 404; Browning & Gordon-Gray 1998a: 73). In other species, for example *B. nobilis*, the inflorescence is much more extensive and less obviously variable, the rays and spikelets forming a mop-like mass distally on a culm, and an inflorescence consisting of a solitary spikelet never occurring. Kukkonen (1984: 257) undertook study of an inflorescence of *B. maritimus* from Finland in which he established a useful illustrative method and a basic terminology. Vegetti & Tivano (1991) and Vegetti (1992, 1994) investigated the inflorescences of *Schoenoplectus* and *Isolepis* R.Br. further broadening terminology. In the study of *Bolboschoenus* inflorescences undertaken during preparation of this thesis, I have benefitted from these earlier accounts. I have adopted, as far as possible, the same terminology used by these authors, whose work is based on that of Troll (1964) and Weberling (1981, 1989), but with modification and adaptation where this was necessary.

The main aims of my study of the inflorescence within *Bolboschoenus* were:

1. to familiarize myself with the structural morphology of the African species, in particular *B. maritimus*, *B. glaucus* and *B. nobilis*. Unfortunately no material of *B. grandispicus* was available for dissection.
2. to attempt to understand the structural basis of the variability so frequent within single plants of species such as *B. maritimus* (including inflorescences from coastal and inland Verlorenvlei) to gain understanding perhaps, of their close relationship and intergradation.
3. to establish a suitable, relatively simple yet accurate terminology for use in description in the formal taxonomy of the species (Chapter 14).

Basic structure and terminology

Figure 56 is a diagrammatic representation of part of a theoretical inflorescence of *Bolboschoenus* that bears rays. For explication, the most complex construction encountered

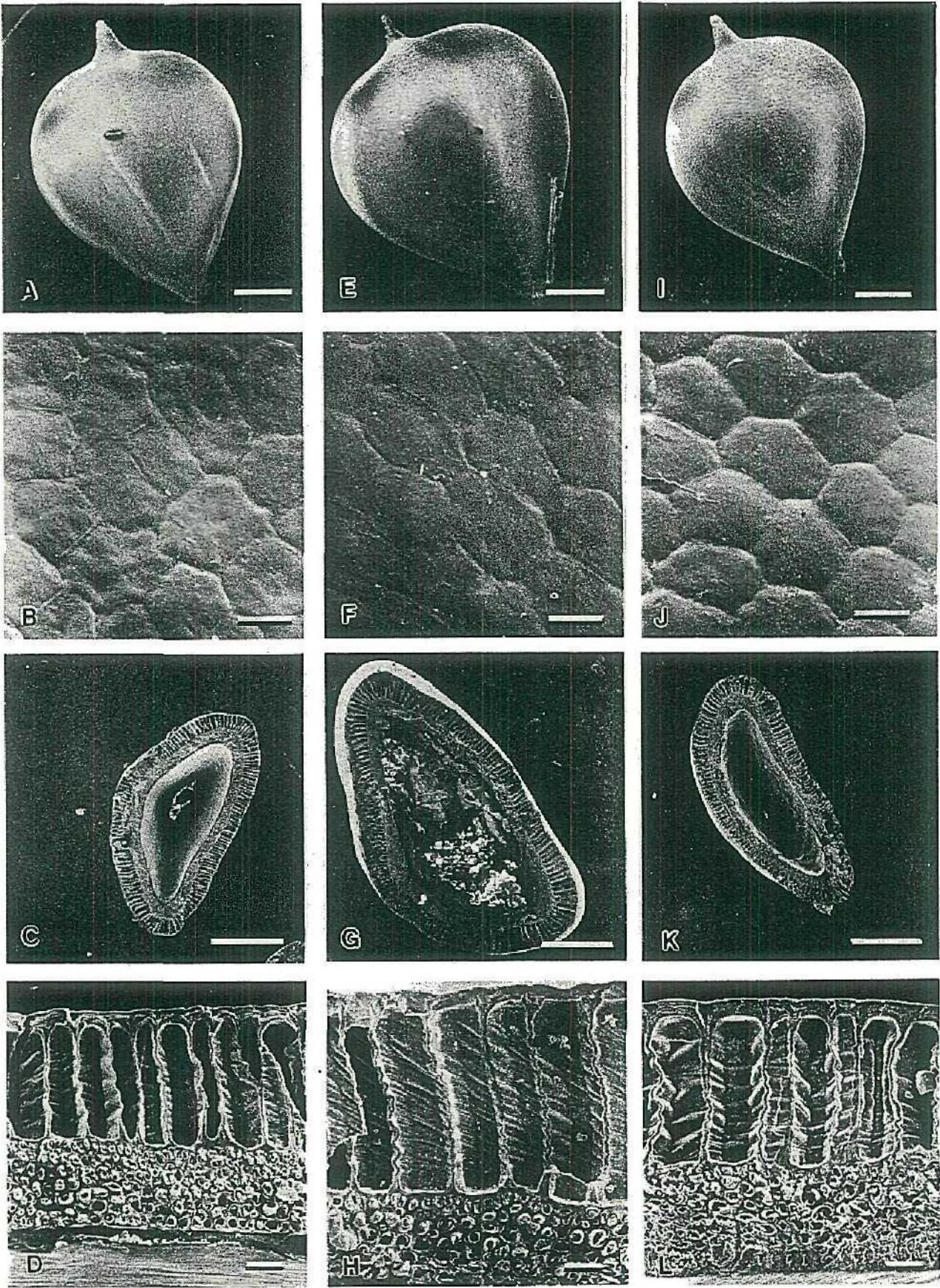


Figure 5 *Bolboschoenus maritimus* s.l., coastal achenes. A, E, I, achene abaxial view (scale bar = 500 µm); B, F, J, exocarp surface (scale bar = 25 µm); C, G, K, achenes in transverse section (with or without endosperm) (scale bar = 500 µm); D, H, L, detail of pericarp structure in transverse section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

during this study has been represented to give a full account of the terminology to be used in the account that follows. This terminology is elaborated by a series of definitions that are based on earlier concepts of Troll (1964); Weberling (1981, 1989); Kukkonen (1984, 1986, 1994); Vegetti & Tivano (1991) and Vegetti (1992, 1994). This comprehensive basic diagram will not be explained in detail. Understanding of it and the terminology applied to its parts should become clear as the account of inflorescence structure that follows is read. The species considered incorporate a range from the simplest inflorescence type known for the genus, to the most complex. In reading, Figure 56 and the glossary of terms should be consulted when necessary.

Glossary definitions (see also Figure 57)

anthelodium (pl. anthelodia) : an indeterminate, polytelic inflorescence that in

Bolboschoenus is crateriform with a compressed main axis that bears lateral partial inflorescences that are peduncled (paracladia; sing. paracladium Pc) and subsessile or sessile (coflorescences CoF). The paracladia often exceed in length the length of the main axis (hence the crateriform shape of the total inflorescence). The main axis is terminated by an indeterminate spikelet (the main central florescence HF) that is closely surrounded by coflorescences that consist each of a sessile spikelet to form a central compact group. The anthelodium in its most developed expression is therefore a synflorescence comprising partial inflorescences.

bract : a reduced leaf that subtends an inflorescence branch. In *Bolboschoenus* inflorescence bracts are of three types, sometimes difficult to categorise as they grade from one to the other:

- foliose (fb): elongate, green, leaf-like [up to 7 per inflorescence in *B. nobilis*; in other species usually 1--2 (-3)].
- laminar (lb) : reduced to a glume-like base with elongate (long acuminate), sometimes greenish apex.
- glumaceous (gb) : reduced to a membranous glume (sometimes slightly larger than the floral glumes); recognizable by position, that is basal to a spikelet and subtending a bud that may develop into an inflorescence branch.

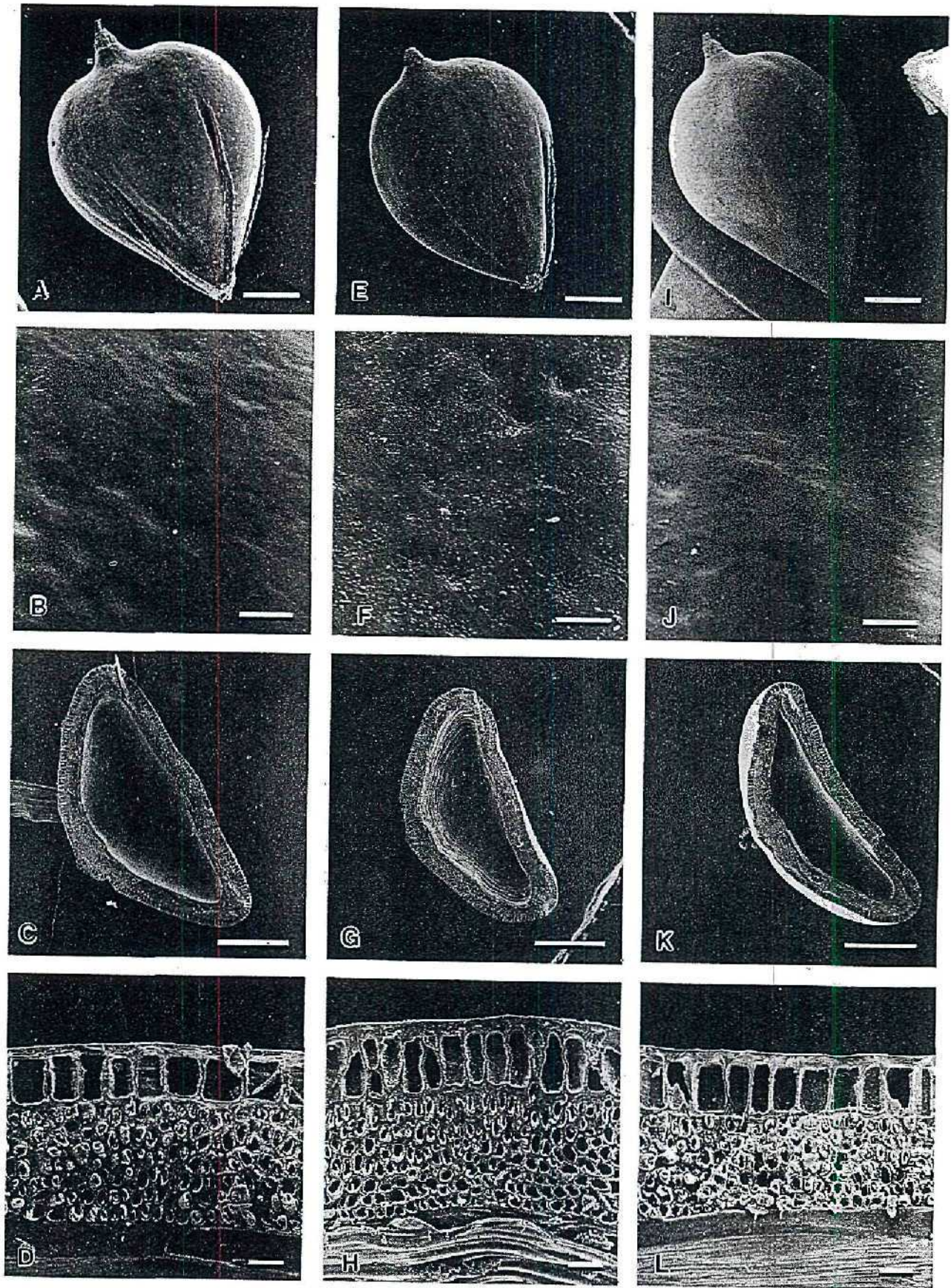


Figure 6 *Bolboschoenus maritimus* s.l., inland achenes. A, E, I, achene abaxial view (scale bar = 500 µm); B, F, J, exocarp surface (scale bar = 25 µm); C, G, K, achenes in transverse section (with or without endosperm) (scale bar = 500 µm); D, H, L, detail of pericarp structure in transverse section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

bud : an incipient shoot; in the inflorescence of *Bolboschoenus* buds may be of two kinds, namely:

- branch bud (○) axillary to a bract and developing into a paracladium or a cوفlorescence. On larger branch buds the lowest leaf (prophyll) is usually distinguishable adjacent to the axis;
- spikelet bud (Δ) which refers to the diminishing series of glumes and flowers that tops every spikelet.

coflorescence: in *Bolboschoenus*, a sessile spikelet developed from a bud in the axil of a bract on the axis of the main florescence or a paracladium. (Note that the symbol $\Leftarrow\Rightarrow$ incorporates the subtending bract which, in reality, is not part of the bud giving rise to the cوفlorescence.)

epipodium : the unbranched internode of a paracladium, that is the peduncular portion between the prophyll and the first (lowest) bract of the partial florescence.

florescence : the reproductive, floral-bearing part of the inflorescence. In *Bolboschoenus*, the florescence in its most developed form is a **synflorescence** made up of the **main florescence** HF and lateral partial inflorescences that are sessile (**coflorescences**) or peduncled (**paracladia**).

Note that the main florescence HF is a spikelet of indefinite growth that lacks subtending bract and prophyll (basal on the main axis) and differs from a cوفlorescence in which a prophyll and subtending bract are detectable. The florescence may also consist of a solitary spikelet only (the main florescence HF).

This is then closely enveloped by a succession of laminar and foliose bracts carried on the very abbreviated proximal portion of the main inflorescence axis.

glume : the membranous reduced leaf that subtends a floret. In *Bolboschoenus* glumes are spiral on the spikelet axis (rachis) and each subtends a bisexual floret, or the bud that will produce such a floret, or such a bud that has aborted. Note: aborted floral buds are difficult to distinguish from very young branch buds.

paracladium : (pl. paracladia) a lateral, peduncled partial inflorescence Pc_1 ; Pc_2 etc: developed from an axillary branch bud. Note that in its most complete form a paracladium consists of a hypopodium; a tubular, sheathing prophyll, that may be pulvinate (glandular) basally (cladoprophyll), and an elongate peduncle (epipodium E)

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	<i>815</i>	2.8–3.3	1.8–2.3
	B	<i>817</i>	3.0–3.3	1.7–2.2
	C	<i>795</i>	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	<i>796</i>	2.7–3.1	2.1–2.4
	E	<i>800</i>	2.8–3.3	1.9–2.3
	F	<i>802</i>	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%		

that carries distally, the reproductive structures (the partial florescence).

prophyll : the first leaf on a branch; within the inflorescence of *Bolboschoenus* of two kinds, namely,

-cladoprophyll : a tubular sheath enveloping a proximal portion of an epipodium.

-glumaceous prophyll : a prophyll resembling a membranous glume, but with two main nerves that face the axis and which are usually extended into acuminate apices.

pulvinus : glandular tissue at the prophyll base that, when turgid, causes depression (outward bending) of the subtending bract and the axis within the bract.

Materials and methods

For an account of the materials used and the methods followed, please see Appendix 1.

Inflorescence structure in the African species of *Bolboschoenus*

This account deals with inflorescence structure in the four species reported for the African continent, namely *Bolboschoenus maritimus* s.s., *B. glaucus*, *B. nobilis* and *B. grandispicus*. Unfortunately, no specimens of the last-named taxon were available for dissection so comments that relate to it are limited to minor observations made from a limited number of herbarium specimens. It is easiest to proceed from the simplest (most reduced) inflorescence type and to elaborate progressively to the most complex. (Note that in the diagrammatic representations A₂, B₂ etc. distances on axes have been exaggerated to accommodate structural features.)

1. The solitary spikelet (Figures 58 A₁ and A₂)

Inflorescences of this type are occasional in *B. maritimus* s.s. and in *B. grandispicus*. The example illustrated is of the former taxon (*Browning 814* NU).

The solitary spikelet terminates a shoot (culm) and appears pseudolateral (Figure 58 A₁.)

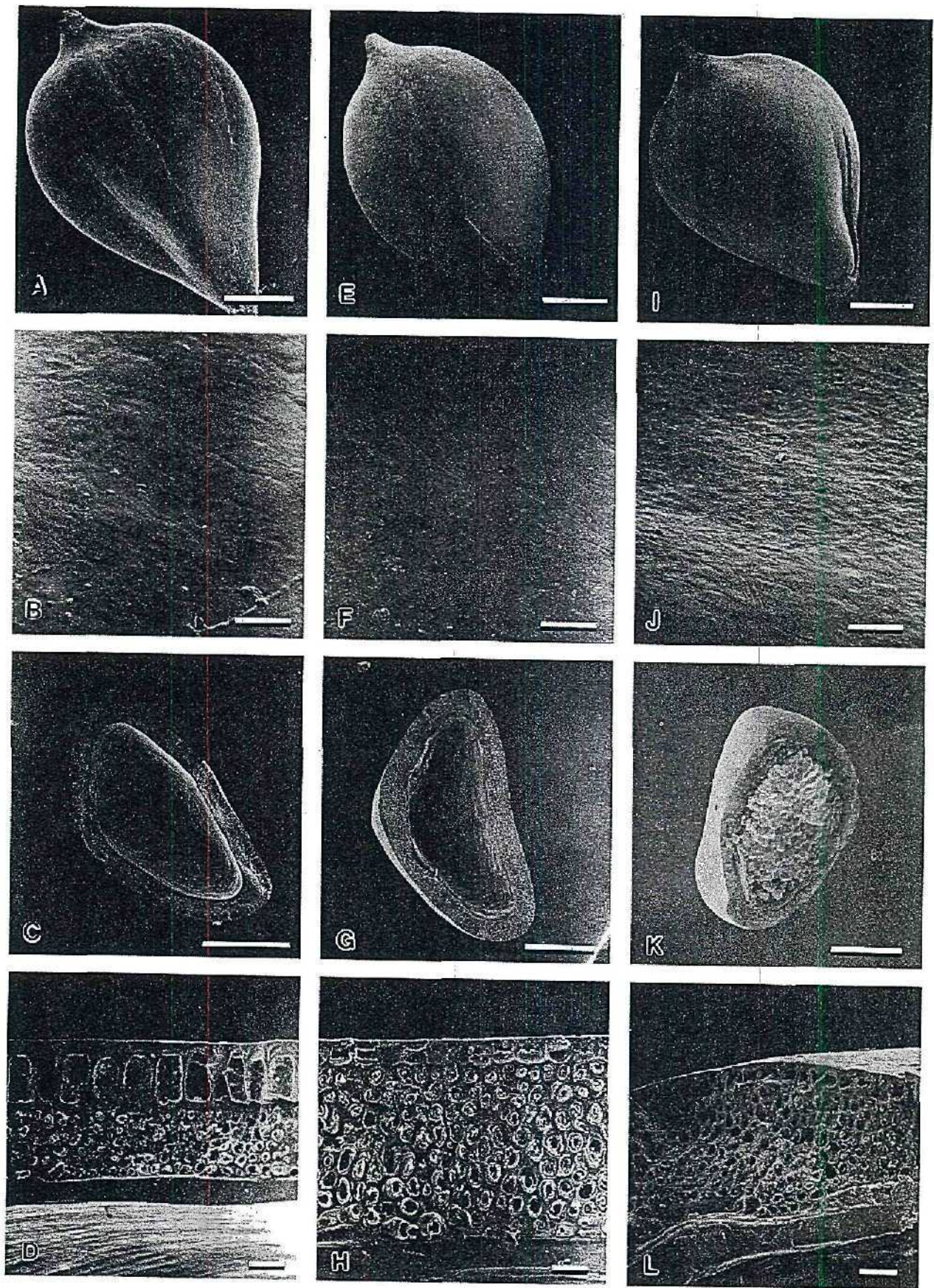


Figure 7 *Bolboschoenus maritimus* s.l. A, E, I, achene abaxial view (scale bar = 500 μ m); B, F, J, exocarp surface (scale bar = 25 μ m); C, G, K, achenes in transverse section (with or without endosperm) (scale bar = 500 μ m); D, H, L, detail of pericarp structure in transverse section (scale bar =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

because the main, lowest, foliose bract (fb1 in Figure 58 A₂) continues in the line of the culm. A second smaller foliose bract (fb2) is present. These are followed sequentially on the axis by two laminar bracts (lb1, lb2). Each bract carries in its axil a branch bud which possesses the capacity for growth. The first leaf (prophyll) of this bud is usually recognizable. Note that it arises from the lateral axillary branch and not from the main axis.) Above the bracts is a series of spirally arranged glumes (usually 30--60) each of which subtends an axillary bud capable of producing a bisexual floret. The glumes diminish slightly in size upwards and some of the upper ones may be sterile. This upper portion of the axis, which carries the meristematic apex that is never terminated by a floret, is marked in Figure 58 A₂ as a bud. This bud therefore differs positionally from the branch buds which are axillary and which, if growth occurs, will give rise to first order branches from the main floral axis. The solitary spikelet is the floral spike of the main axis and is termed the main florescence HF. Note that this main florescence HF terminates at the lowest glume of the spikelet and does not incorporate the laminar and foliose bracts which closely invest it. These are correctly part of the inflorescence.

Two examples of *B. grandispicus* [Adam 17627, 17660 (both P)] differed from solitary spikeletted specimens of *B. maritimus* s.s. in that four foliose bracts, each prolonged and leaflike, were developed instead of the two that are usual in *B. maritimus* s.s.

2. The contracted head (Figure 59 B₁ B₂; C₁ C₂; D₁ D₂).

Inflorescences of this type are common in *B. maritimus* s.s. and *B. grandispicus*. All the examples illustrated are of the former species (Browning 814, 815 NU).

The contracted head (Figure 59 B₁) consists, in the case illustrated, of four closely associated sessile spikelets subtended by two foliose bracts (fb1, fb2). On dissection, it is seen to comprise a main axis carrying sequentially two foliose bracts, two laminar bracts and the main florescence. In the axil of the lowest foliose bract is a branch bud with recognizable prophyll. The branch buds in the axils of fb2, lb1 and lb2 have grown out to form lateral sessile or subsessile spikelets that differ from the main florescence only in that each is

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

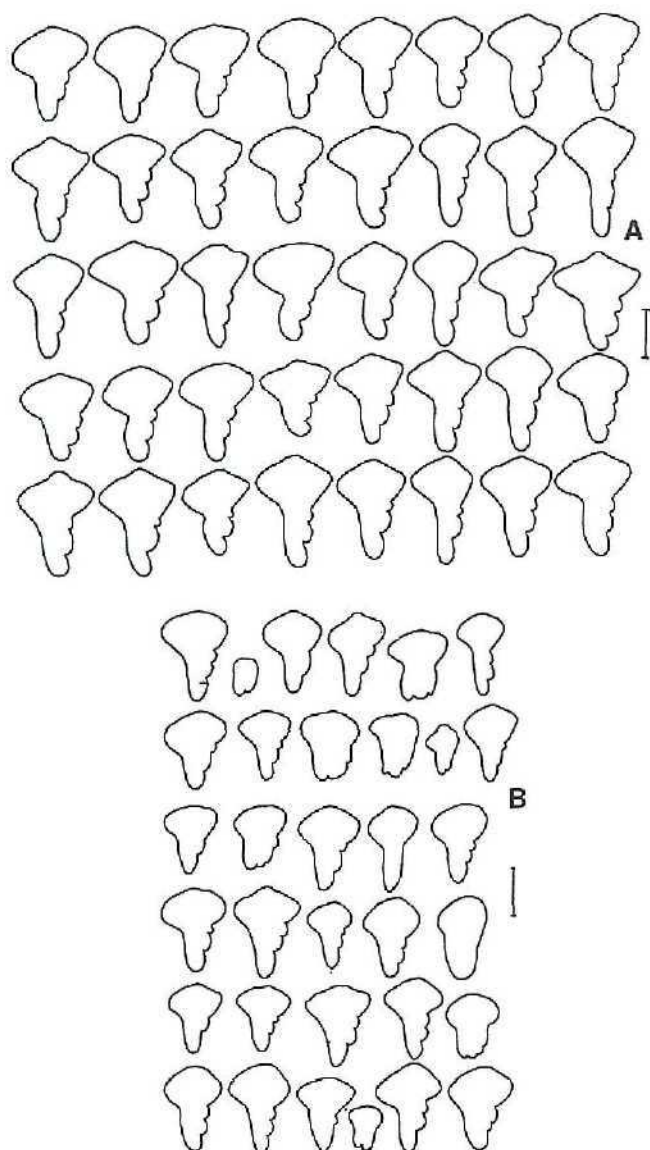


Figure 8 *Bolboschoenus maritimus* s.l. Embryos shown in median longitudinal view, extracted from each of two samples of 40 measured achenes. A. Coastal (Orange River estuary, Ward 12575); B. Inland (Nieuwoudtville, Ward 13973). Scale bar = 0.5 mm. Note: only 33 of Nieuwoudtville achenes contained contents.

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* × *B. 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

bracteated and prophyllate. These lateral spikelets are cوفlorescences (CoF₁, CoF₂, CoF₃). Their axes are first order branches from the main axis. Structurally, the contracted head (Figure 59 B₂) is capable of development from the solitary spikelet shown in Figure 58 A₂. Branch buds axillary to fb2, lb1 and lb2 in Figure 58 A₂ have, in the case of Figure 59 B₂, grown into cوفlorescences.

Some other features of this exemplified inflorescence are worthy of note, namely: 1. the presence of an axillary bud in the lowest glume (glumaceous bract) of the main florescence HF and of cوفlorescence 2 (CoF₂). These axillary buds, if activated into growth, are each capable of development into a cوفlorescence. 2. the presence of a number of aborted floral buds in the cوفlorescences (one only in HF). Aborted floral buds were observed in many inflorescences of *B. maritimus* from Verlorenvlei, South Africa. Note that in Figure B₂ the basal glumes of CoF₁ are denoted as empty; presumably the aborted floral buds had fallen away or were always lacking.

Other examples of contracted heads consisting of two and three spikelets are shown in Figures 59 C₁, C₂ and D₁, D₂ respectively. These have been included to illustrate: 1. the frequency of branch buds in the axils of glumaceous bracts or glumes, and 2. the occasional presence of aborted floral buds.

3. The few-rayed inflorescence (anthelodium) Figures 60 E₁ and E₂)

Inflorescences with 1--3 (-4) rays are also common in *B. maritimus* s.s. and in *B. grandispicus* where the rays are usually 1--3 only. The example illustrated is of a two-rayed anthelodium of *B. maritimus* s.s. (Browning 817 NU). Note that in Figure 60 E₁ the second short ray is obscured. This anthelodium consists of thirteen spikelets in all. Three of these are sessile distally on the elongate ray; the other ten are grouped into a cluster, the arrangement of which conceals a second short ray that bears four spikelets; the remaining six constitute the main central partial florescence. The detailed construction of this anthelodium is illustrated diagrammatically in Figure 60 E₂. Consider first the main central partial florescence. This comprises a central spikelet HF that lacks bract and prophyll, closely accompanied by five

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

Acknowledgements

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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coflorescences (sessile spikelets each bracteate and prophyllate). From foliose bracts fb1 and fb2 arise two lateral partial florescences. Each is termed a paracladium (Pc_1 , Pc_2) and is developed from a branch bud axillary to the foliose bracts of the main axis. A paracladium is a peduncled partial florescence and differs from the main central partial florescence only in that it is a lateral branch from the main axis. It carries a terminal spikelet (HF, without bract and prophyll) accompanied by one to several coflorescences.

This rayed anthelodium is an elaboration of the elements present in the solitary spikelet and the contracted head already described. The basic pattern of construction does not differ. To produce the inflorescence E_1 the main axis must have carried seven branch buds, whereas in A_1 and B_1 there were only four.

4. The many-rayed inflorescence (anthelodium) Figures 61 F_1 , F_2 and Figure 62 G_1 , G_2

Inflorescences with ten and often more rays are usual for *B. glaucus*. The examples illustrated are two ten-rayed anthelodia, one from Senegal (Johnson s.n. 23/Oct. 1997 NU; F_1 , F_2) and one from Mzinene, KwaZulu/Natal, South Africa (C.J. Ward 14201, NU; G_1 , G_2).

Essentially these more complex anthelodia characteristic of *B. glaucus* differ only in degree from the few-rayed type that is of frequent occurrence within *B. maritimus* s.s. In Figure 61 F_1 the exemplified inflorescence is seen to consist of a central, short contracted group of four spikelets. This constitutes the main central partial florescence (labelled HF in Figure 61 F_2). It consists of a central spikelet, lacking bract and prophyll, that is closely accompanied by three sessile spikelets, each with a subtending bract and a prophyll (coflorescences). Below this group and arising as first order branches from the main axis are four peduncled paracladia Pc_7 -- Pc_{10} that consist of a main florescence only, unaccompanied by coflorescences. They appear in Figure 61 F_1 each as an epipodium carrying a solitary spikelet. Six other more robust paracladia that each carry more than one spikelet make up the total number of lateral partial florescences. Of these, Pc_1 is developed from the axil of the lowest foliose bract (fb1) and is the most robust with an epipodium of 50--54 mm (note that a length range is given because accurate measurement is difficult due to the close arrangement of parts). It also

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carries the greatest number of coflorescences (six). The other five paracladia decrease in length progressively upwards and all carry fewer than six coflorescences. Note that the lowest glumes of the main florescences of paracladia Pc_2 and Pc_3 , also Pc_7 , each axillates a branch bud, so that in this many-rayed inflorescence, the potential for further branching is incipient but unexpressed. In *B. glaucus* branching, except in unusual cases, is limited to the development of first order branches from the main floral axis.

The example from Natal, taken from a population that is at the south-eastern limit of the species in Africa (Figure 62 G_1 , G_2), is built on a similar plan, and differs from the example from Senegal (Figure 61 F_1 , F_2) only in its greater reduction. Notice that the epipodia are shorter, the numbers of coflorescences on the paracladia are fewer, so that, in the example from Natal, epipodia bearing solitary spikelets predominate (6 out of 10), whereas in the example from Senegal epipodia bearing clusters of spikelets are in the majority (6 out of 10).

5. The compound anthelodium (Figures 63--66) H_1 , H_2 , H_3 , H_4 , H_5 , H_6 , H_7 a--i)

This expanded, many spikeletted inflorescence is borne by the tall, leafy shoots of *B. nobilis*. The example illustrated is from Namibia (*C.J. Ward 13245* NU). The illustrations show that it is built on the same basic pattern as the inflorescences already described, but is further elaborated, consisting, in this case, of a main axis about 37 mm long (enlarged in Figure 64 H_3 and diagrammatically in Figure 63 H_2) that bears a spirally arranged sequence of 22 paracladia that surpass a central, contracted group consisting of the main florescence HF, with below it five coflorescences (sessile spikelets). Of the 22 paracladia, the proximal 13 with first to third order branching and the distal 9 with first order branches only, are themselves anthelodia, so the whole, mop-like synflorescence is a compound anthelodium. Analysis of more than one synflorescence in *B. nobilis* has revealed that paracladia are usually in four series rather than gradually decreasing sequentially upwards as in *B. glaucus*. The lowest series (Pc_{1-7}) is the most robust with epipodia of approximately the same length (in this example 88--71 mm) all with well developed cladophylls. The second series has shorter epipodia (all approximately 60 mm) and also with well developed cladophylls. The third series has epipodia of approximately 35--25 mm and these and the fourth series (15--7 mm)

only slightly surpass the coflorescence lengths of the central group of six spikelets that is closely packed distally on the main synflorescence axis. This arrangement is distinguishable in Figure 63 H₂ and less obviously in Figure 63 H₁. It results in a "spread" of spikelets through the extent of the synflorescence which should be advantageous in a wind pollinated plant.

Paracladium (Pc₁), the lowest, was detached and analysed. It is shown in Figure 65 H₅ and diagrammatically in Figure 65 H₆. The paracladia of paracladium Pc₁ were then detached sequentially and each illustrated diagrammatically (Figure 66 H₇, Pc₁¹ -- Pc₁¹²). A detailed account of these second and third order branch rays is not given as the repetitive arrangements of parts should be understandable from the diagrams. Note that the uppermost distal short paracladia (Pc₁¹⁰ -- Pc₁¹²) lack coflorescences and consist each of one peduncled (rayed) spikelet only (the main florescence HF of that paracladium). Figure 64 H₄ shows one first order paracladium after natural abscission of most of the glumes. The spiral arrangement of the anthelodium and the positioning of the laminar bracts and cladophylls is evident. Almost complete abscission of glumes and ripe nuts from synflorescences is a feature of *B. nobilis*. This seems to take place rapidly after fruit maturity, but confirmation of this from further field studies is required. Within the synflorescences of this species, branches of up to the fourth order have been observed [Giess 10502, Meyer 1307 (both WIND)]. First, second and third order branches are always present; fourth order branches are occasional in the largest synflorescences only.

Discussion and conclusions

In the African species of *Bolboschoenus*, the fundamental structure of the inflorescence is that of an anthelodium. Within this basic pattern a considerable range is represented from an inflorescence comprising a solitary spikelet only, to complex, compound structures with three, occasionally four, orders of branches that carry collectively upwards of 400 spikelets. In the account already given it was shown how an inflorescence comprising a solitary spikelet only possessed the incipient capability to produce either a compacted head or a rayed structure with first order branches. Following upon this, the presence of further branching

orders (also developed from incipient axillary buds not mentioned specifically in the account), was exemplified from actual inflorescences (synflorescences) that were dissected and illustrated diagrammatically. In adopting this method of description from simple to complex, it is not in any way implied that this might reflect the route of evolutionary development.

What has become apparent during this study is a possible correlation between the robustness of a plant and the size and complexity of the inflorescence borne by its culms. For example, the stout, tall, leafy culms of *Bolboschoenus nobilis* carry the largest, most complex, most floriferous synflorescences among African (and world) species of the genus. This species, which grows along inland waterbodies where some volume of underground water is likely to be available throughout what must be an almost continuous favourable season has the necessary food reserves to sustain a sizeable inflorescence with the potential to produce a vast number of nuts. Under conditions of predation, the occasional protected inflorescences that do manage to reach maturity are noticeably smaller.

The variability within the inflorescence types produced by clones of *B. maritimus* s.s. has had repeated mention already in this thesis. My experience of southern African specimens has shown that inflorescences consisting of a solitary spikelet are borne upon slender, often shorter shoots, either resulting from poor growing conditions or severe predation, or developed from lateral shoots on established culms. Contracted heads are best represented in coastal microhabitats, while branched anthelodia are commonest where plants have what appear to be the most favourable growing conditions for a population. These are mere observations and are purely speculative, but they do relate to the capacity that exists, as in most plants, for variation in inflorescence size and degree of branching according to food reserve levels within the reproducing organism. It is reasonable, therefore, to consider the inflorescence in *Bolboschoenus* as a variable structure with a range representative of each species. These ranges are not necessarily discontinuous between species; commonly there is overlap, so that inflorescence form in isolation is not reliable in identification. Among the African species *B. nobilis* has the most distinctive inflorescence and is unlikely to be confused with *B. glaucus*, which certainly may overlap with the range that characterises *B.*

maritimus s.s. It must be understood that in this last-named taxon, the range in inflorescence form is wide, and its expression at any one time in any one genotype, the outcome of many interacting factors. This is applicable also to *B. grandispicus*, but the range within African and off-shore African island specimens I have examined, is far more limited than in *B. maritimus*, a range of only one to five spikelets being known. Present evidence suggests that *B. grandispicus* is conspecific with the Asian taxon *B. affinis*. However, to pursue problems of synonymy that incorporate detailed study of non-African taxa is beyond the limits of this dissertation and consequently *B. grandispicus* is presently maintained. If synonymy is established, the inflorescence may be shown to have a wider range of structure with more numerous spikelets in other parts of the distributional range than is indicated here for the African *B. grandispicus*.

In Table 11 are summarised the important features of inflorescence structure and size for inflorescences of the African species of *Bolboschoenus* as derived from the present study. Significant discontinuities are lacking, but when extremes, for example *B. maritimus s.s.* and *B. nobilis*, are considered, the contrasts are striking. At least some of the paracladia of mature inflorescences of *B. glaucus* generally extend laterally at approximately 90° from the main axis, which is unusual in rayed inflorescences of *B. maritimus s.s.* Nevertheless, this is merely a guide in identification and should never be relied upon alone.

In connection with inflorescence construction, it was noted that in all African species occasional axillary floral buds (potential florets) within spikelets had aborted. Few such aborted buds were observed within *B. nobilis*. In *B. glaucus* however, they were prevalent and often numerous in individual spikelets and were encountered also in *B. maritimus s.s.*, but less frequently and in lesser numbers. In inland representatives at Verlorenvlei these aborted buds were very frequent. It is not known whether this might be genetically controlled, or whether it might be the outcome of inundation of the inflorescence during some stage of development. *B. glaucus*, in southern Africa, and as far as I have been able to estimate throughout its range in Africa, is a poor producer of mature nuts. Many spikelets carry no mature nuts at all; others produce a few proximally, then a few distally with many empty glumes between.

Characteristics of the inflorescence of *Bolboschoenus*

The relationship of *Bolboschoenus* to its associated segregate from *Scirpus*, *Schoenoplectus*, has already been considered in the Introduction (pg 3). It was regarded as a possibility that with detailed study of the inflorescence of the African species of *Bolboschoenus*, some distinction of its inflorescence from that of *Schoenoplectus* might be found. This is certainly not so.

In the African species of *Bolboschoenus*, axillary buds in the axils of the prophylls of the basal paracladia which are capable of developing into intraprophyllate paracladia have never been observed. They are present in some species of *Schoenoplectus*, for example *S. californicus* (C.A. Meyer) Soják and *S. validus* (Vahl) A. Love and D. Love, but are lacking in many others, for example *S. pungens* (Vahl) Palla and *S. olneyi* (A. Gr.) Palla (Vegetti 1992: 246). This character, therefore, cannot be used as a distinctive feature at generic level. Vegetti (1992: 246, 247) has pointed out that axillary buds of cladoprophylls are correctly designated “intraprophyllate”, but those of laminar prophylls are “prophyllate” only.

No character of the inflorescence specific only to *Bolboschoenus* was encountered in the present study.

CHAPTER 13

The Embryo

Van der Veken (1965:285) examined the structure of adult embryos of 77 species of *Scirpus sensu lato*. These included four species then included in *Scirpus* L. series *Bolboschoenus* (Aschers.) T. Koyama, all of which are now generally accepted as taxa under the genus *Bolboschoenus*, namely *Scirpus fluviatilis* (Torrey) A. Gray, *S. maritimus* L., *S. paludosus* Nels. and *S. perviridis* Cooke. The embryo conformation of the first two of these species he illustrated as seen in median, sagittal section (Van der Veken 1965: 316, 317, Figure 37 D, E). There are differences in size and in shape, but both are unmistakably of 'the *Bolboschoenus* type', which Goetghebeur (1986: 355) described as 'fungiform, met zeer groot, breed, rhombisch kotel' [fungiform (the outline shape as seen in sagittal section) with large, wide, rhombic cotyledon]. This type is slightly more specialised than that of the allied genus *Schoenoplectus*, because of the sheathing nature of the first leaf primordium (not so in *Schoenoplectus*) and because of a constriction between the root cap and the cotyledon (Goetghebeur 1986: 90, Figure 3.5, compare M and N). Another difference is that in the *Bolboschoenus* embryo a third leaf primordium is usually developed, which is not the case in the embryo of *Schoenoplectus* (Goetghebeur 1986: 92, in key).

From his studies, Van der Veken (1965: 290), made certain statements on quantitative variation of the embryos. He found: 1. that variation in length of the embryos extracted from a single herbarium specimen did not exceed 5%; 2. between different specimens of the same species this variation remained below 10%. In an early study of the fruit and its embryo in *Bolboschoenus* (Browning & Gordon-Gray 1993: 311--318), some slight evidence had been obtained that: 1. embryo shape is governed, at least in part, by inner conformation of the pericarp; 2. embryo size is related to fruit size; 3. variation in embryo size for different species may exceed 10%.

The study carried out as part of this dissertation was aimed primarily at the investigation of embryos extracted from mature fruits from populations in the field in order to determine: 1.

the percentage of perfect embryo development within the sample; 2. the variation in form and dimensions of length and breadth within and between populations sampled; 3. whether any character of the embryo might be considered sufficiently reliable to be useful in species differentiation; 4. any other features of special interest.

In more general terms, it was hoped that from the studies attempted, an overview of the results might yield some evidence in support of interspecific hybridisation within the genus. Before embryographic studies were commenced, it had been observed that *Bolboschoenus glaucus* was a poor producer of mature nuts, which could be indicative of genetic instability arising from hybridisation.

Materials and methods

The materials used and the methods followed are given in Appendix 1, Volume 1 pgs 143--147. There were problems and consequent shortcomings in obtaining suitable, comparable samples of fruits for embryo extraction. The embryo extraction itself proved time consuming and difficult, particularly with current season fruits of *Bolboschoenus glaucus*. Once extracted, the embryos were not easily measured. Image analysis had limitations in that samples of 40 embryos could not be collectively assessed. These and other problems encountered during the embryography study are considered in some detail in the appendix.

Results

The information obtained is limited, and from several aspects unsatisfactory; nevertheless, results will be considered, as some deductions are possible.

The sample for each population consisted of the embryos extracted from 40 nuts. As has been explained in Appendix 1 these nuts, as far as possible, were taken from a particular collection number, for example *C.J. Ward 12575* (NU) and often from a single inflorescence of that number. However, this was not always possible because of paucity of fruits and other reasons and the samples studied are not satisfactorily uniform; one at least (*B. medianus*) is derived from two populations in the same general locality but some distance apart. The results are

presented as a series of outline diagrams that have been considerably reduced for convenient comparison. These diagrams relate to: (i) southern African species, namely three allopatric populations of *Bolboschoenus maritimus*, one from Namibia and two from the western Cape, one of which, Verlorenvlei, was further subdivided into two samples, namely coastal (*B. maritimus* s.s.) and inland (*B. maritimus* s.l.) Figure 67 A, B, C, D; (ii) two populations of *B. maritimus* s.l. from the Netherlands Figure 68 E, F; (iii) one West African (Senegal) population of *B. glaucus* Figure 69 G; (iv) one American (Wisconsin) population of *B. fluviatilis* Figure 69 H; (v) one Australian (Perth) population of *B. caldwellii*, Figure 70 I, and another Australian (New South Wales) population of *B. medianus* Figure 70 J. Further details are given in Table 12, in which see also quantitative parameters of nuts and of the embryos extracted from them. Note that only approximate percentages of perfectly formed embryos are given in column 8 as occasionally some doubt of perfection existed. The figures in column 8 express, as a percentage, the number of fully formed embryos in relation to the total number possible for the sample, that is 40.

1. The southern African species (Figure 67 A--D)

Of the four samples studied, one exhibited great uniformity with 100% of the nuts containing well formed embryos and endosperm. These embryos varied little in length and width and in profile (sagittal section) (Figure 67 A; Table 12). Another sample (Figure 67 B) also showed good uniformity of size dimensions (Table 12) but with greater profile variation than that exhibited in Figure 67 A. In addition, only 92.5% of the sampled nuts contained embryo and endosperm and only approximately 83% of the total sample contained perfectly formed embryos.

The other two samples (Figure 67 C, D and Table 12 C, D) differed markedly in that only 67.5% and 82.5% respectively contained embryo and endosperm, and of the total nut samples only approximately 48% and 53% respectively contained perfect embryos. The imperfect examples resulted in the more extensive length and width ranges recorded in Table 12.

2. The European samples of *B. maritimus* (Figure 68 E, F; Table 12 E, F).

Compared with the South African examples of this taxon, the European samples differed little from the Orange River sample in good development of embryo and endosperm (97.5%). However, the outline profiles and the size dimensions of the embryos, of which about 90% and 88% respectively were fully formed, were far more variable. These samples are noteworthy from another aspect that will be considered in the conclusions that are given later in this chapter.

3. The West African sample of *B. glaucus* (Figure 69 G).

Only 80% of the sampled nuts contained embryo and endosperm; 20% were empty. The embryos present, all of which were perfectly formed, were uniform in profile and size dimensions. They were shorter and narrower than the embryos of the most perfect southern African sample of *B. maritimus* (Figure 67 A and Table 12 A).

4. The American sample of *B. fluviatilis* (Figure 69 H)

This sample gave 97.5% formation of embryo and endosperm with about 95% of embryos perfectly formed. Profile outline was somewhat variable, but nevertheless characteristic of the species, as were the size parameters (Figure 69 H and Table 12 H). It is significant that 1. the profile outline related closely to the illustration given by Van der Veken (1965: Figure 37D) for *Scirpus fluviatilis* from Europe (Belgium). In 1965 this taxon was not much reported for Europe. Recent findings have recorded *Bolboschoenus yagara* (possibly syn. *Scirpus fluviatilis*) for this continent (Browning *et al.* 1996a: 129). Characteristic is the peak of the cotyledon and the narrowness of the breadth relation to the length, a ratio of 0.6--0.8: 1.0--1.4, whereas for *B. glaucus* (Senegal) the ratio is 0.6--0.8:0.8--0.9). In profile outline therefore, embryos of *B. glaucus* are noticeably different from those of *B. fluviatilis*.

5. The Australian sample of *B. caldwellii* (Figure 70 I)

This species has lenticular nuts and therefore differs from the other species sampled, all of which have nuts that are triangular, with well defined (*B. fluviatilis*; *B. glaucus*), or less well

defined angles (*B. maritimus*). Because of the inner contour of the pericarp, the *B. caldwellii* embryos are flat, not rounded to 3-angled, and consequently are more easily measured. The most notable feature of these embryos is their asymmetry. As seen in profile in sagittal section, left and right hand outlines of the umbonate cotyledon differ in angle; the left hand side is usually more strongly sloping (occasionally there is better symmetry, Figure 70 I). This sample showed 92.5% of the nuts with endosperm and embryo present. About 85% of the total possible embryos were perfectly formed.

6. The Australian sample of *B. medianus* (Figure 70 J)

[*B. medianus*] "differs from the other [Australian] species in its unequally trigonous nut and style varying from 2-fid to 3-fid in the one inflorescence. Vegetatively [it is] very similar to *B. fluviatilis*." (Wilson, 1993: 366). In the field it is not easily distinguished from *B. fluviatilis*, plant size being the most significant criterion; in the herbarium, differences depend upon style branch number (always three in *B. fluviatilis*; two or three in a spikelet in *B. medianus*) and on perianth bristle length (as long as nut in *B. fluviatilis*; shorter than nut in *B. medianus*) (personal studies by J. Browning and pers. comm. with Australian botanists.) In New South Wales both species may be sympatric with *B. caldwellii*, within which plants are small with uniformly two branched styles (see also above).

The sample of 40 nuts of *B. medianus* from which embryos were extracted was derived from field samples taken by B.J. Lepschi in April 1994 from two populations (coll's nos 1598, 1604) "about 50 km apart at 35° 21' S; 149° 18' E and 35° 04' S; 149° 39' E respectively." Nuts were removed from the dried inflorescences gathered from each population and kept apart. Twenty nuts were taken without selection from each of the total samples to give the composite number of 40. 75% contained endosperm and embryo, and of total possible embryos only approximately 36% were perfectly formed. Figure 71 illustrates examples of malformed and arrested (A, C) and fully developed embryos (B, D) extracted from nuts of the samples of each of the Lepschi numbers. Another example of an arrested embryo from a nut on an herbarium sheet (E) shows that faulty embryo development within *B. medianus* is not limited to the populations samples by Lepschi. Also included, for comparison with (B, D), is

a fully developed embryo of *B. maritimus* s.s. from Namibia, southern Africa (F).

The following features of the nuts and embryos of *B. medianus* are worthy of note: 1. perfectly formed embryos, as seen in profile in sagittal section are similar in form to embryos of *B. fluviatilis* and differ from those of *B. maritimus* s.s. (compare Figure 71 B, D, with F and these photographs with outline diagrams Figure 67 A and Figure 70 J). Note that the slender form and cotyledonary peak suggestive of *B. fluviatilis* is also reflected in nut lengths: 2. Table 12 shows that in *B. medianus* nut length may surpass 4 mm. The only other samples studied in which this length was attained are the American *B. fluviatilis* and the two samples from the Netherlands, both of which are suspected of possessing some genetic contribution by way of hybridisation from *B. yagara* (considered synonymous or included within *B. fluviatilis* in the opinions of most authorities).

The embryo conformation, the nut size and the occurrence of 2-fid and 3-fid styles within individual spikelets of *B. medianus* appear to support the speculation that the taxon is of hybrid origin from the putative parents *B. fluviatilis* and *B. caldwellii*.

Discussion and Conclusions

From the above results it is evident that samples of mature fruits taken from field populations vary in seed set. Not every mature fruit contains a seed with endosperm and perfectly formed embryo. Some fruits are entirely empty; others contain endosperm and lack an embryo; in others the embryo is imperfect, either malformed or arrested in development. The majority, however, have endosperm and well developed embryo and therefore are assumed to be viable. The percentages of fruits each with a perfectly developed seed varied in the samples studied from 100% to approximately 48% and 36%. Low seed set of a approximately 48% was obtained for the Verlorenvlei inland population (*B. maritimus* s.l.) and approximately 36% for the New South Wales population of *B. medianus*. Close to these examples was the Nieuwoudtville population (approximately 53%).

Based on other criteria of morphological form, *B. medianus* has been regarded as probably of hybrid origin; such an interpretation has also been tentatively suggested for inland plants of *B. maritimus* s.l. at Verlorenvlei and the population at Nieuwoudtville. The poor seed set may be indicative of genetic imbalance and therefore supportive of this possible hybrid origin.

High percentages of seed set were obtained for the Orange river Estuary population of *B. maritimus* s.s. (approximately 100%) and for the American population of *B. fluviatilis* (approximately 95%). The embryos extracted from these fruit samples were remarkably uniform in profile outline and in size within a sample. This may be attributable, perhaps, to extraction of the fruits from inflorescences of a clone, rather than from inflorescences of a number of plants within a population. Evidence derived during this study, limited though it is, is in support of statements made by Van der Veken (1965: 290) (see Chap. 13: 87).

Presumably this author considered only perfectly formed embryos and therefore recorded little variability. In other samples of this present study, recorded ranges in embryo lengths and widths included malformed or arrested embryos and others that had shrunk prior to disintegration. Inclusion of parameters recorded for imperfect embryos may be misleading in the assessment of embryo sizes for different taxa. There certainly are differences in lengths and widths of embryos from species to species. Compare, for example, parameters obtained for *B. fluviatilis* and *B. glaucus* (see Table 12). These differences may be anticipated from fruit dimensions, as fruits of *B. fluviatilis* (America) are larger than fruits of *B. glaucus* (West Africa). Despite this relationship with fruit size, embryo parameters must be dismissed as of aid in species delimitation because of impracticality. Firstly, they are difficult to assess and secondly, they are insufficiently differing when a totality of species is considered. What may perhaps become useful, especially in exceptional cases, is embryo profile outline. Compare, for example, the embryo profiles of *B. fluviatilis* and *B. maritimus* s.s. in Figure 71, and of *B. fluviatilis* and *B. glaucus* in Figures 69 H and G respectively. The embryo of *B. fluviatilis*, as seen in sagittal section, is long and narrow with a definite cotyledonary peak and so differs from the smaller, proportionately wider embryo of *B. glaucus* and the more robust embryo of *B. maritimus* s.s. Both the latter have more rounded cotyledonary surfaces than that of the peaked *B. fluviatilis*. However, it may be that when embryo profile outlines of world species are considered, these small differences may no longer be adequately indicative of individual

types (taxa). Meanwhile embryo profiles have proved informative in investigating samples from The Netherlands. Two of the nut samples studied by Robertus-Koster (1969), namely Punt van Reide R7 and Schoonhoven L1, were made available to me for electron scanning after having been in storage for more than 20 years. In August 1996, this author recollected fruits from these localities and provided me with two further samples from which embryos were extracted (not done for the 20 year old samples). The variability in the nuts of the early samples [see J. Browning *et al.* (1997b Table 1: 117., 118 and Table 10 of this dissertation)] is reflected again both by the nuts and the embryo outlines of the recent samples. A few of the embryos in the recent Reide sample (Figure 68 E) and more in the Schoonhoven sample (Figure 68 F) have the outline suggestive of *B. fluviatilis*, which relationship was earlier detected from morphological consideration of nut conformation and pericarp anatomy. If this example does nothing more, it serves to illustrate that the variability in these Netherlands populations is consistent and of long standing.

Embryos also differ in conformation according to whether they developed in trigonous or in lenticular nuts. Therefore the flattened embryos of *B. caldwellii* are distinctive in comparison with the cylindric (three angled) embryos of the other species studied. However, once it is proved that the embryos of other *Bolboschoenus* species with lenticular nuts are flattened, as will surely be the case, this difference may be accepted from nut conformation, without extraction and assessment of their embryos.

In final consideration of this exploratory surveillance of embryography, it may be summarised as having produced scant information that is noteworthy and none that is entirely novel.

PART 4

FORMAL TAXONOMY OF THE AFRICAN SPECIES

CHAPTER 14

FORMAL TAXONOMY OF AFRICAN SPECIES

BOLBOSCHOENUS (Ascherson) Palla in E. Hallier et A. Brand, Koch's Syn. Deutsch. Schw. Fl. ed 3. 2: 2531 (1905).

Scirpus section *Bolboschoenus* Ascherson, in Fl. Prov. Brandenburg 1: 753. Jan-apr. (1864).

Schoenoplectus section *Bolboschoenus* (Ascherson) Lye, Bot. Not. 124: 290 (1971).

Schoenoplectus subgenus *Bolboschoenus* (Ascherson) Lye, in The sedges and rushes of east Africa : 53 (1983).

Type: *Bolboschoenus maritimus* (L.) Palla [*Scirpus maritimus* L.- Neoelectotype selected by Smith & Kukkonen (in press)].

NOTE: The generic description that follows applies to the African species only.

Perennials, herbaceous up to 1.5 m, except *B. nobilis* to 4.5 m. *Rhizomes* horizontal, elongate, tough, wiry, 1--10 mm in diameter, swollen into rounded corms at culm bases and/or at intervals on rhizome, adventitious roots from corms only; in *B. nobilis* clearly sympodial, thickened up to 50 mm in diameter, especially at culm bases, root bearing; scale leaves in both rhizome types soon disintegrating, in *B. nobilis* into dark fibres. *Culms* leafy, noded, internodes trigonous becoming rounded in age (*B. nobilis*), uppermost often elongated. *Leaves* 5--10 (-35) green to bluish; *sheaths* tubular, ventral tissue not differentiated except at mouth where truncate to V-shaped, membranous, discolourous; eligulate; *blades* V-shaped in transverse section, tapering, margins and midrib scabridulous (smooth in *B. grandispicus*), apices acute. *Inflorescence* variable, bracteate, a solitary spikelet appearing pseudolateral, a compact head or a simple or compound anthelodium bearing up to 450 spikelets. *Bracts* 1--3 (-7), lowest longest, leaflike, erect or spreading, reduced in length progressively upwards.

Spikelets ca. (5-) 8--40 (-85) x 3--11 mm long and wide, cylindric, many flowered, solitary or clustered, sessile or pedunculate, ovoid or elliptic in outline, pallid or light brown. *Glumes* (*floral scales*) spiral, imbricate, ovate to elliptic, membranous to hyaline, midrib prominent, prolonged into pronounced, irregularly curved or recurved awn, flanks nerveless, puberulous to glabrous abaxially, margins minutely ciliate; apex bifid often lacerate. *Perianth bristles* generally 6, shorter than or equalling mature nut length, needle-like, densely retrorsely spinulose, brown at maturity, caducous or persistent. *Florets* bisexual. *Stamens* 3, anthers linear, 1--4 mm in length, extending into spinulose crest. *Style branches* 2 or 3 (sometimes within same spikelet), half to twice style length. *Nut* 2.2--3.5 x 1.3--2.8 mm long and wide, trigonous or lenticular, ovoid to obovoid to obpyriform in outline, slightly beaked, style base not enlarged, persistent on beak; surface smooth to irregular, faintly cellular or not x 20. Embryo of *Schoenoplectus*-type but more advanced.

Key to the species of *Bolboschoenus* in Africa

The key that follows is designed for use primarily in subSaharan Africa, and may not encompass the variation that is found when the total range of a widely distributed species is considered. This applies particularly to *Bolboschoenus glaucus* where no measurements for plants from Mediterranean Africa have been included, as too little is known of them at present.

1a. Styles uniformly two-branched; nuts lenticular; perianth bristles caducous; Cape Verde Islands and West coast of Senegal 1. *B. grandispicus*

1b. Styles uniformly three-branched, or with few to approximately half two-branched among the three-branched styles of the same spikelet; nuts subtrigonous and /or lenticular; perianth bristles caducous or persistent; widespread in subSaharan Africa 2

2a. Mature plants exceeding 1.5 m in height; leaves grey-green (glaucous), not bright shiny green; contralaminar tissue pronounced as a dark brown narrow band; spikelets many (in excess of 50); glumes 4--5 mm in length, brown with pronounced pale, almost white, midrib

extending into 1--2 mm awn; anthers 2--2.8 mm long with a spiny crest 0.5--1.0 mm long.

Angola and Namibia (inland) 2. *B. nobilis*

2b. Not precisely as for the contrast 3

3a. Spikelets elliptic when young, 3--4 mm wide; occasionally becoming oblong and sometimes catkin-like; glumes (excluding awn) 5--6 mm long; styles uniformly three-branched; nuts subtrigonal 2.6--2.8 (-3.2) mm long x 1.7--2.0 (-2.2) mm wide; bristles mostly persistent; nut surface x 20 lacking "honey-comb" pattern of cells 3. *B. glaucus*

3b. Spikelets ovate 5--7 (-8) mm wide; catkin-like spikelets not observed in African examples; glumes (excluding awn) (5-) 6--7 (-8.5) mm long; styles three-branched only or two- and three-branched within a spikelet; nuts 2.6--3.4 mm long x (1.9) 2.1--2.7 mm wide; bristles mostly caducous; nut surface x 20 with "honey-comb" pattern of cells 4. *B. maritimus* s.s.

Aberrant examples that display characters of both 3a and 3b may be encountered.

Distinction is then most securely based on micromorphological features of the nut pericarp structure (for details and figures see Chapter 4, p. 32.) and on inflorescence branching and spikelet parameters. Citation of such examples, which are considered putative hybrids, follows after citation of specimens of *B. maritimus* (pg. 121).

Enumeration of species

1. *Bolboschoenus grandispicus*

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

Forschungsinstitut Senckenberg, 52: 267 (1982). Vanden Berghen in Flore Illustrée du Sénégal: 149--150 (1988). Type: Senegal; Herbarium Perrottet nr. 838 (iso P!).

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

Scirpus grandispicus (Steudel) Berhaut, in Bull. Soc. Bot. Fr. 100: 176 (1953); Fl. Sén. ed. 2: 361, 369 (1967); Hooper in Fl. W. Trop. Afr. 3: 309 (1972)..

Note: Clarke 1902: 456 placed *Isolepis grandispica* in synonymy under *Scirpus maritimus* (this noted by Vanden Berghen 1988: 150). Clarke cites for Upper Guinea, *Perrottet 318*! It is likely he is referring to the page of publication in Steudel Syn. Pl. Glum ii : 318 as the *Perrottet* isotype (P) carries the number 838. Also under *Scirpus maritimus* Clarke (1894: 626) cites *Perrottet 818* for Senegal; this number requires checking; it may be a typographical error for 318.

Perennial, 0.05--0.63 m high. *Rhizomes* 1--2 mm in diameter, corms about 4 x 8 mm long and wide, developed close to culm base (infrequent) or on rhizome extensions. *Culms* erect, single, occasionally sparsely tufted, proximal two-thirds to half of total culm length leaf-bearing, nodes inconspicuous, or 1--3 visible; internodes trigonous, 1--2 (-3) mm wide, glabrous, distal remainder (uppermost internode before inflorescence), sharply three-angled, glabrous. *Leaves* 5--7(-8), lowest 1--2 reduced to membranous, bladeless sheaths, remainder laminate with blades increasing in length upwards; *sheaths* of laminate leaves closed, usually pale green, ventral tissue not differentiated except at 1--2 mm deep mouth that in living state, especially in upper leaves, is membranous, margin truncate to rounded, veins adjacent to sides of mouth prominent, converging below; *blades* up to 190 x 1--3 (-4) mm long and wide, shallowly V-shaped to flat in cross-section at middle, tapering distally into long fine apex, glabrous, midrib grooved adaxially, projecting abaxially especially towards apex which may be triangular, midrib and margins glabrous. *Inflorescence* a solitary spikelet, or a reduced anthelodium (a compact head with 0--2 paracladia), 15--32 x 7--60 mm long (deep) and wide, carrying 2--4 (-5) spikelets; *epipodia* 10--20(-50) mm long, terete to three-angled in cross section, smooth. *Bracts* leaf-like, 1--2 (-3), lowest best developed, (30-)50--80 (-120) mm long, far surpassing inflorescence and continuing line of culm especially in young stages of development and where inflorescence size reduced. *Spikelets* (12-)15--17 (-25) x (6-) 8--10 (-

11) mm long and wide, ovate in outline. *Glumes* (floral scales) 6--7(-8.3) mm long (excluding awn) x 3.0--3.5 mm wide, oblong to narrowly oblong-elliptic, glabrous, pale brown (concolorous) or bicoloured with light green flanks and brown midnerve prominent abaxially and excurrent into recurved awn 1.0--1.5 mm long, flanks nerveless, not streaked or spotted, margins hyaline, silvery, apex emarginate, lobes 2, acute; sometimes lacerate. *Perianth bristles* 1--6, unequal, not exceeding half to three quarters nut length, spinulose, brown at maturity, caducous. *Anthers* (1.3-) 1.5--1.6 (-1.8) mm excluding 0.2--0.4(-0.5) mm crest that is linear-triangular, scarcely spinulose; connective and crest red. *Style branches* 2, about twice style length, flattened when dry. *Nut* (2.8-) 3.0--3.1 (-3.5) x (1.5-) 2.1--2.5 mm long and wide, lenticular, obovate in outline, beak short with extreme base of style persistent; light to dark brown, somewhat light reflective; pericarp surface smooth x 20, with "honeycomb pattern" x 600, cells larger on angles becoming smaller towards centre of plane surfaces. [Figure 22, details of nut; Figure 72 (holotype)].

Morphological variability

Some collections, including the type and isotypes, each with a single or two spikelets, are short plants (0.1--0.15 m); however there are examples of larger plants up to 0.6 m [*Berhaut 1021*, *Adam 16857* (P)] with 1--4 spikelets and 1--2 rays up to 50 mm in length. Mature nuts are present on both the smaller and larger examples. It is noted that the types are dated 1824 and 1829, while the larger plants were collected in the 1960's.

In some examples with solitary spikelets [*Adam 17627*, *17660*, (P)] the lowest two to three glume-like structures have prolonged awn-like extensions and are, in fact, laminar bracts. In the axil of each bract is a branch bud from which a ray (paracladium) may develop.

Bristles are readily shed, remaining within the glume [*Adam 12262* (P)]. In *Adam 17660* five bristles were found within the glume, reaching the shoulders of the slightly immature nut. As most nuts are dispersed without the bristles it is likely that the impression is gained that bristles are usually absent. Clarke on an isotype sheet of *Isolepis grandispica*, *Perrottet 838*(P), wrote in Oct. 1888. "*Scirpus maritimus* Linn. var. *ε affinis* (sp. Roth) (forma setulis

subnullis)". Bristle size and number require investigation in both *Bolboschoenus grandispicus* and *B. affinis* (Roth) Drobow.

As has been stated, few sheets were available for examination and therefore an adequate assessment of variation, apart from the features noted above, has not been possible.

Habitat preferences

Collectors' notes indicate that in Senegal plants favour humid, hot conditions from sandy coastal situations to fringing mangrove swamps. On the desertic island of Boa Vista (Cape Verde Islands), *B. grandispicus* grows abundantly, together with other wetland sedges, in wet places near a small river in one of the valleys 1--2 km from the sea (W. Lobin pers. comm.).

Morphological relationships

Bolboschoenus grandispicus has uniformly two-branched styles and two angled (lenticular) nuts. These features serve reliably in its differentiation from other African species, but not from other world species of the genus. More comprehensive revision of *Bolboschoenus* than has been possible in this study, may sufficiently prove the conspecificity of *B. grandispicus* with *B. affinis*. My comparison of type specimens revealed no noteworthy differences, as did my study of nut structure (compare Figures 22 and 52 respectively). There is also possible relationship between both these taxa and other taxa with uniformly two-branched styles.

Other noteworthy features of *B. grandispicus*, which in Africa is most similar morphologically to *B. maritimus* s.s. are :

1. leaf margins smooth apically (usually scabridulous in other African taxa);
2. glumes glabrous; flanks frequently green on either side of the keel; margins silvery (of comparable size with glumes of *B. maritimus* s.s. which are mid to dark brown; margins hyaline, not silvery);
3. anthers (1.3-) 1.5--1.6 (-1.8) mm long excluding 0.3--0.4 (-0.5) mm crest as compared with the longer anthers of *B. maritimus* s.s. (2.3-) 2.5--3.7 (-4.0) mm excluding the (0.1-) 0.2--0.4

mm crest.

Distribution (Figures 75 and 82)

From known collections *B. grandispicus* has been recorded from only a few localities in western Senegal and Cape Verde Islands. This may indicate that the species is a possible introduction that is now naturalised.

Citations

Cape Verde Islands:

-16.25 N, 23.64 W: Boa vista; *W. Lobin, 2021 (K)*

Senegal

-12.24 N, 16.35 W: Basse-Casamance. Mossor; *C. Vanden Berghen 9571 (BR)*.

-12.52 N, 16.42 W: Basse-Casamance. Abéné; *C. Vanden Berghen 7771a, 9529, 9850 (BR)*.

-13. 99 N, 15. 74 W: Déni Biram Ndao , extrémité NE du L. Retba (rive N); *J. & A. Raynal 6087 (P)*; L. Retba. *J.G. Adam 17627 (P)*.

- 14.73 N, 17.32 W: Mboro. *J. G. Adam 17660, 17664 (P)*.

-14.74 N, 17. 42 W: Dakar; Hann. *J. & A. Raynal 5965 (P)*, *J.G. Adam 16857 (P)*; Lagune de Hann *J.G. Adam 12.262 (P)*;

-14.91 N, 16.93 W: Niayes; Hann Mbao Sangalkam, Nayar; Presqu île du Cap Vert Dakar. *R.P. Berhaut 1021, 2697 (P)*.

2. *Bolboschoenus nobilis*

Bolboschoenus nobilis (Ridley) Goetghebeur & D.A. Simpson, Kew Bulletin 46: 173 (1991); Browning & Gordon-Gray, S. Afr. J. Bot. 58: 383 (1992), S. Afr. J. Bot. 59: 316–317 (1993); Reid, Mem. bot. Surv. S. Afr. 62: 110 (1993). Type: Angola, Mossamedes, Maiombo river,

Welwitsch 6975 (BM, lectotype designated by Goetghebeur & D.A. Simpson, 1991!).

Basionym: *Scirpus nobilis* Ridley, Trans. Linn. Soc. ser. 2 II: 159 (1884).

S. maritimus L. var. *nobilis* (Ridley) C.B. Clarke in Consp. fl. Afr.: 627 (1894).

S. laeteflorens C.B. Clarke in Fl. Trop. Afr. 8: 456 (1902); Podlech in Prod. Fl. S.W. Afr. 165: 49 (1967); Reid in Mem. bot. Surv. S. Afr. 51: 75 (1985). *S. maritimus* L. var. *laeteflorens* (C.B. Clarke) Kükenthal, Fed. Repert. 40: 392, 398 (1937), *quoad comb.* Syntypes: South West Africa [Namibia] *Chapman & Baines s.n.* (K!); Hereroland, *Fleck 112A* (not located).

S. maritimus auct., non L.: C.B. Clarke in Fl. Trop. Afr.: 456 (1902) *quoad Welwitsch 6975*.

Perennial, (0.3-)1.5--4.5 m high. *Rhizomes* (8-) 10--20 (-50) mm in diameter, woody except for narrow outer zone; nodes 5--10 mm apart, each bearing one more or less triangular, membranous, brown, scale leaf. On young parts scale leaves overlap, but are early caducous, leaving scars on mature portions; no corms on rhizomes noted but thickening present at culm bases (Figure 73 A, B). *Culms* erect, single, with many inconspicuous nodes, densely leafy throughout except immediately below inflorescence, mid-culm internodes 7--10 (-18) mm in diameter, terete to faintly three-angled, smooth; uppermost leafless internode 3--5 mm in diameter, sharply three-angled, scabrid. *Leaves* up to 35 per culm (usually about 12), lowest 1--4 reduced to membranous, bladeless sheaths, remainder laminate, blades increasing in length upwards; *sheaths* of laminate leaves closed, mouth truncate to shallowly V-shaped, demarcated by narrow, finely pleated, dark brown, membranous tissue; *blades* up to 790 x 9--17(-26) mm long and wide, shallowly V-shaped to flat in cross-section, tapering distally into a long fine apex, glabrous; midrib grooved adaxially, projecting abaxially, midrib and margins scabridulous, especially apically. *Inflorescence* a compound anthelodium, 55--180 x 100--283 mm long (deep) and wide, carrying in total (60-) 100--200 (-450) spikelets, comprising main axis up to 37 mm long, of closely placed, bracteate nodes bearing proximal paracladia that far surpass the distal compacted cluster of sessile or subsessile spikelets; epipodia oval to triangular in cross section, smooth to scabridulous. *Bracts* 1--4 (-7), leaf-like,

lowest best developed, up to 370 (usually 100--200) mm long, surpassing inflorescence and continuing line of culm especially in young stages of development and where inflorescence size reduced. *Spikelets* (5-) 8--10(-17) x 3--5 mm long and wide, ovate-oblong in outline when young, oblong and somewhat lengthened before glume abscission. *Glumes* (*floral scales*) 4.0--5.0 x 2.5--3.0 mm long and wide (excluding awn), oblong to narrowly oblong-elliptic; adaxially scabridulous or glabrous, uniformly light brown, midnerve prominent abaxially, pale yellow or white, excurrent into outward curving awn 1.5--2.0 (-2.5) mm long, smooth or minutely scabrid; flanks nerveless, not striated or spotted, margins hyaline, ciliolate, apex emarginate, lobes 2--3, acute, sometimes lacerate; glumes abscising naturally at maturity of nuts. *Perianth bristles* 1--6, unequal, not exceeding half to three quarters nut length, densely retrorsely spinulose, brown, persistent or caducous. *Anthers* linear-oblong, (2.0-) 2.2--2.8 (-3.0) mm long, excluding (0.5-) 0.8--1.0 mm long, linear-triangular, bristly crest. *Style branches* 3, about half style length, terete, lacking hairs or papillae. *Nut* 2.2--2.8 x 1.3--1.7 mm long and wide, obtusely trigonous, obovate to elliptic in outline, base narrowed, beak poorly defined; grey to black, spotted or blotched, poorly light reflective, surface rough, faintly cellular x 20, raised anticlinal walls x 600 with central zone depressed except over underlying silica bodies.

[Figures 20 & 21 nuts of lectotype (*B. nobilis*) and isotype (*Scirpus laeteflorens*) and Figures 73 (rhizome) and 77 (plants in colour)] .

Morphological variation

Field knowledge of this species is limited to populations in Namibia (Hoanib River; Brandburg Mountains). I am indebted to Mr. C.J. Ward for his excellent collections, notes and photographs and his careful assessment of these natural stands. Nothing, except sparse collectors' notes, is known of field populations in Angola. From all information available it seems that the species is uniform morphologically. There is predation by Herero goats (P. Craven, collector's notes) and by elephants (C.J. Ward pers. comm.). Where such damage becomes intense, only isolated, well protected plants survive to reproduce; others are reduced to approximately ground level and shoots that do develop are slender (C.J. Ward). In herbaria, occasional inflorescences are smaller than usual for the species, presumably because of earlier

predation or unfavourable microhabitat conditions.

Rhizomes are illustrated in Figure 73 . These underground organs are unrepresented in most herbarium collections and require further study. From the Namibian specimens available, the rhizome is robust, hard and solid with an outer thin dark “bark” that becomes friable. There is swelling at each culm base; food deposition begins before a culm is fully expanded (Figure 73, lower photograph A) and continues until the culm base is rounded and cormlike. This rhizome therefore differs in appearance from those of the other African species of the genus in which rounded corms are irregularly placed along a much thinner, wiry rhizome, usually, but not always, at culm nodes (Figure 74).

Habitat preferences (Namibia only)

Bolboschoenus nobilis is recorded from damp sandy river beds and banks, or seepage areas and springs, in mountainous coastal hinterland to inland localities where small to extensive stands may be present (Figure 77). There are no records from coastal situations or from water courses immediately prior to their descent to coastal sands.

Morphological relationships

On gross plant size and rhizome and inflorescence development *B. nobilis* does not closely resemble either *B. maritimus* or *B. grandispicus*. It is closest to *B. glaucus*, particularly when the latter has inflorescences with relatively short spikelets which is the case in early stages of reproduction. Both taxa are present in Namibia and Angola and if doubt exists in their distinction nuts should be studied. There are, however, common features here too, for in both taxa the exocarp cells in transverse section are more or less square, not radially elongated (Figures 20 and 18). The most significantly divisive features of the nuts are their surfaces; the smooth, almost non cellular, brown to dark brown of *B. glaucus*, contrasting with the slightly roughened, faintly cellular, dull grey to greyish black of *B. nobilis*.

Distribution [Figures 75; 76; Figure 82 (world)]

B. nobilis is an African endemic from Angola and Namibia.

Citations

ANGOLA

Mossamedes, Maiombo river, *Welwitsch* 6975 (lecto. BM)

Caiombe - Cambeno, *Mendes* 154 (LISC).

NAMIBIA

-1712 (Posto Velho): Otjomborombonga, near main kloof to the south (-BB), *Leistner et al.* 144 (PRE); Baines Mts. at Otjipemba (-BB), *Meyer* 1307 (PRE, WIND); Kapupa Valley (-BC), *Story* 5873 (PRE).

-1713 (Swartbooisdrif): Tributary of Kunene River NW of Ombepera (-BA), *Leistner et al.* 284 (PRE); Koakoveld. 19 km W of Epembe, Otjitangariviers bei Oma (-CB), *Giess* 10502 (WIND).

-1812 (Sanitatas): Purros (-DD), *Craven* 3244 (WIND).

-1913 (Sesfontein): Hoanib River (-AC), *Craven* 1069 (WIND); Opuro Distr: Ongongo Waterfall (-BB), *Ward, C.J.* 13708 (NU); Hoanib River: Khowaib Schlucht (lowermost road crossing) (-BD), *Ward, C.J.* 13707 (NU); Palmwag Guest farm (-DD), *Ward, C.J.* 12055 (NU).

-1914 (Kamanjab) Farm Palm, OU 708, Quelle (-CC), *Giess* 3965, 8110 (WIND).

-2114 (Uis): Brandburg, Tsisab Valley (-AB/BA), *Hilliard* 4700 (NU); Ugab River, Brandberg Mountains (-BA), *Dixon* 979 (WIND); Tsisab Valley (-BA), *Ward, C.J.* 13244, 13245, 13249 (NU); White Lady's Fountain, lower Tsisab (-BA), *Craven* 2318 (WIND); Tsisab Ravine, (-BC), *Wiss* 1486 (PRE); Omaruru Rivier, W. of Kleinsiedlung von Gruttemeyer (-DC), *Giess* 9564 (WIND).

-2215 (Trekkoepje): Farm Tsabichab Teil von Farm Nawachab; KAR 58 (-BA), *Giess* 14698 (PRE, WIND).

-2216 (Otjimbingwe): Farm Otjozondi (-AA), *Giess* 3443 (NBG, PRE, WIND),

-2315 (Rostock): Above Ababes, Tsondab River bed (-DD), *Pearson* 9194 (BOL).

-2317 (Rehoboth) Farm Buellspoor (-AC), *Strey* 2172 (PRE, BOL), 2281 (NBG, PRU, PRE).
 -2416 (Maltahohe) Bergzebra Park Naukluft; MAL 9. (-AA), *Giess* 10422 (WIND),
Merxmüller & Giess 28156 (LISC, PRE, WIND); Naukluftpark (-AA), *Zietsman* 1759
 (WIND); Naukloof Mts. at Bullsport (-AB), *Rodin* 2891 (BOL, LISC); Maltahohe Fun., von
 Friedland nahe der ..(-CB) *Herb. Wind* 1532 (WIND).

3. *Bolboschoenus glaucus*

Bolboschoenus glaucus (Lamarck) S.G. Smith, *Novon* 5: 101 (1995). Type: *Roussillon s.n.*,
 West Africa, Senegal (P holotype, Herb. Lamarck, sheet 673/14, det. as *Scirpus maritimus*
 L. by J. Raynal, 1966; NU photo. !).

Basionym: *Scirpus glaucus* Lamarck, *Tabl. Encycl.* 1: 142 (1791).

S. maritimus L. var. *theta* (Lamarck) Vahl, *Enum. pl.*: 269 (1805).

S. maritimus L. var. *glaucus* (Lamarck) Nees in Wight, *Contr. bot. India*: 111 (1834).

S. macrostachyus Willdenow, *Enum. Hort. Berol.*, 1.: 78 (1809). *S. macrostachyus* Nees in
Linnaea 10: 184 (1835). *S. maritimus* L. var. *macrostachyus* (Willdenow) Bertoloni in *Flora*
italica 1: 298 (1834). *S. maritimus* L. var. *macrostachyus* (Lamarck) Visiani, *Fl. Dalm.*, 1 :
 109 (1842).

Bolboschoenus maritimus (L.) Palla subsp. *macrostachys* (Willdenow) J. Soják, *Cas. Nár.*
Muz.: 19 (1983) comb. only: no citation of specimens..

Scirpus tridentatus Roxburgh, *Hort. Beng.* 81 (1814), *nomen*; *Fl. Ind.* ed. Carey & Wall., i.
 228 (1820); *Fl. Ind.*, ed. Carey, i. 225 (1832). Type: Herb. Roxb. no. unclear, possibly 419
 (K!), or *Wall. Cat.* nos 3504, 3505 (K) ?

S. maritimus L. var. *macrostachyus* Ridley, *Trans. Linn. Soc. ser 2*, II: 158 (1884) *non* Willd.
 1797: 306. Syntypes: *Welwitsch* 6974, Angola, Mossamedes, prope Giraül. Julio 1859;

Welwitsch 6980, Angola, Icolo e Bengo, frequens ad Lagoa da Funda (BM lectotype, selected J. Browning 1998, NU photos !; there are probably isosyntypes at LISU, COI and perhaps other herbaria.)

S. maritimus L. var. *amentiferus* Ridley, Trans. Linn. Soc. ser 2, II: 158 (1884). Type: *Welwitsch 7011*, Angola, fluminis Bengo, prope Funda, Sept. 1854 (BM holotype, NU photo. !; probably isotypes elsewhere).

S. maritimus L. var. *terrestris* Ridley, Trans. Linn. Soc. ser 2, II: 158, 159 (1884). Type: *Welwitsch 6972*, Angola, Mossamedes, cotton field weed, July 1859 (BM holotype, NU photo. !; probably isotypes elsewhere).

Scirpus maritimus L. *pro parte, sensu auctorum non* L.: C.B. Clarke in Consp. fl. Afr. V : 626 (1894) at least the *Welwitsch* numbers excluding 6992 and 7003 which have not been seen; C.B. Clarke in Fl. Trop. Afr.: 456 (1902) at least the *Welwitsch* numbers, excluding 6975 which is *Bolboschoenus nobilis*; other cited specimens not seen; Napper, Journ. E. Afr. Nat. Hist. Soc.: 13 (1965) specimens not cited; Podlech in Prod. Fl. S.W. Afr. 165: 50 (1967) (*Volk 1096, 12140*); Hooper, Fl. W. Trop Afr.: 309 (1972) at least *J. & A. Raynal 5925*, other cited specimens not seen.

Schoenoplectus maritimus (L.) Lye *sensu auctorum*: Lye, Blyttia 29: 145 (1971); Haines & Lye, Sedges & Rushes E. Afr.: 53 (1983), including Figure 6; Lye, Cyperaceae in Fl. Ethiopia & Eritrea, VI: 397 (1997), including Figure 212.9.

Bolboschoenus maritimus (L.) Palla *sensu auctorum*, Browning & Gordon-Gray, S. Afr. J. Bot. 58: 381 (1992) element (b) only; Browning & Gordon-Gray, S. Afr. J. Bot. 59: 312 (1993) Entity 2 only, which equates with element (b) of 1992; Reid (Cyperaceae) in Mem. bot. Surv. 62: 110 (1993) *pro parte*; Gordon-Gray, Strelitzia 2: 25 (1995) including Figures 8, 9, see note page 209.

Perennial, 0.3--0.8 (-1.5) m high. *Rhizomes* exceeding 150 mm in length, 5--8 mm in

diameter, spongy when young due to narrow, soft outer cortex that rapidly decays leaving tough, almost woody, persistent stele; young parts with nodes 90--100 mm apart, each bearing a membranous, brown scale leaf that soon disintegrates; corms at culm base and/or on rhizome, 16--20 (-33) x 15--20 mm long and wide, central storage zone white or ochre yellow; roots arising from corms not rhizomes. *Culms* erect, proximal two thirds to one half of total culm length leaf bearing, nodes inconspicuous, usually 1--3 visible, mid-culm internode (2-) 4--5(-8) mm in diameter, trigonous, smooth to scabridulous on angles; uppermost leafless internode below inflorescence sharply three-angled, smooth or scabridulous; occasionally so well developed that leaves all appear basal. *Leaves* up to 10 per culm (usually ca. 7), lowest 1--3 reduced to membranous, bladeless or short-bladed sheaths, remainder laminate with blades increasing in length upwards. *Sheaths* of laminate leaves closed, usually pale green, ventral tissue not differentiated except at 4--5 mm deep V-shaped mouth that in living state, especially in upper leaves, is membranous, brown, the margin truncate to rounded, in lower leaves disintegrated except for narrow, brown remnant line, veins adjacent to sides of V, prominent, converging below base of V; *blades* up to 570 x 4--10 mm long and wide, shallowly V-shaped to flat in cross-section at middle; tapering distally into a long, fine apex; midrib grooved adaxially, projecting abaxially especially towards apex, midrib and margins scabridulous especially apically. *Inflorescence* a simple or compound anthelodium 42--65 x 55--98 mm long (deep) and wide, carrying in total (6-) 22--35 (-62) sessile or peduncled spikelets; main axis 10--14 (-16) mm long, with closely placed, bracteate nodes, bearing paracladia proximally and distally a cluster of sessile spikelets; paracladia progressively shorter upwards, elliptic to three angled in cross section, glabrous, sometimes with second order branches. *Bracts* leaf-like, 1--2 (-3), lowest up to 185 (usually 90--100) mm long, surpassing inflorescence, considerably longer and better developed than next upper and continuing line of culm especially in young stages of development and where inflorescence size reduced. *Spikelets* solitary or clustered, (12-) 15--20 (-85) x 3--4 (-5) mm long and wide, ovate-oblong in outline when young, in age oblong and markedly lengthened becoming "catkin-like". *Glumes* (*floral scales*) oblong to narrowly oblong-elliptic, 5--6 x 2.5--4.0 mm long and wide (excluding recurved, smooth or scabrid awn of 1--2 mm length); adaxially glabrous to scarcely scabridulous, uniformly mid brown to light brown, midnerve prominent abaxially, flanks nerveless, not streaked or spotted, margins hyaline, ciliolate, apex

emarginate, lobes 2--3 or more, acute, sometimes lacerate. *Perianth bristles*, 4--6, unequal, shorter than to equalling nut length, densely retrorsely spinulose, brown at maturity, persistent. *Anthers* linear oblong, (1.9-) 2.5--3.1 (-3.5) mm long, with or lacking red colouration in connective and crest, crest (0.1-) 0.2--0.3 (-0.4) mm long, acute. *Style branches* 3, about half style length. *Nut* 2.4--3.3 x 1.6--2.2 mm long and wide, obtusely trigonous,, obovate to elliptic in outline, summit sloping, beak poorly defined, extreme base of style persistent on beak; light to dark brown, light reflective, surface smooth, non cellular x 20, faintly marked with longer than wide, 5--6-sided cells x 600. [Figure 18, nut; Figures 74 (rhizome) and 79 (plants in colour)].

Note: the measurements given in the above description are based mainly upon southern African specimens with some from East Africa. West and North African, Mediterranean, and Asian collections were not included.

Morphological variability

Plants in tropical Africa are, in general, more robust and taller (up to 1.5 m), with leaves longer and wider (600 x 10 mm), than those in southern Africa, but there are many exceptions, dependent it would seem, upon local microhabitat, climatic and predation effects. The inflorescences of tropical examples also attain greater overall size and may carry 50--62 spikelets, for example *Wingfield 1425* (NU), whereas spikelet numbers for those from more southerly latitudes seldom exceed 30--35. Of course, there is a size range for every population, often much reduced when plants are short and slender (the effect perhaps of adverse microhabitat conditions including drought and predation?), but inflorescences of a single spikelet only are not known for *B. glaucus*. First order inflorescence branches (paracladia) are usually quite numerous (6--14), and may branch again to form second order rays. Under *Schoenoplectus maritimus*, Haines and Lye (1983: 53) report for East Africa 'Most spikelets sessile on primary branches, secondary inflorescence branches therefore rare.' An assessment of branching on 94 sheets of African plants (exsiccatæ from South African herbaria and LISC) showed 60 % to lack second order branching, which is supportive of the statement by Haines and Lye.

Spikelet shape and length vary markedly. Much of this is associated with age of development, young spikelets at time of main anthesis being more compact, shorter and more ovate-elliptical than those carrying maturing nuts which tend to have elongated to become linear-oblong. There are extremes worthy of consideration. These are catkin-like spikelets that form tassel-like clusters [examples *J. & A. Raynal* 7069, Senegal (P); *Welwitsch* 7011, Angola (BM); *C.J. Ward* 13862, Namibia (NU); *P.A. Smith* 2557, Botswana; *Culverwell* 0220, Swaziland (both PRE)]. Ridley (1884: 158) recognised such an extreme among *Welwitsch*'s *exsiccatae* as var. *amentiferus*, but this author's var. *macrostachyus* also distinguishes large (long) spikelets. Examination of one long spikelet of *J. & A. Raynal* 7069 (P) showed no nuts, nor any evidence of projecting filaments nor style branches; lifting of the glumes revealed bristles, but no enlarging ovaries were observed. Catkin-like spikelets are not confined to plants of *B. glaucus* in Africa. Hooper (1985: 376), in her treatment of *B. maritimus* for Iraq, comments on spikelets 'sometimes catkin-like by continued glume production, then cylindrical and up to 50 mm long.' In my experience the glumes are set further apart in these elongated examples, which suggests exaggerated growth of the spikelet axis to form internodes that are longer than usual; however, there may also be increased glume numbers (Figure 79).

Habitat preferences (southern Africa only)

B. glaucus favours inland situations on the banks of rivers, streams and pans often not far from the coast, for example Kwa Zulu/Natal, Mzinene. Saline conditions (salinity records 1.5--4.0 parts per thousand) and black mud are noted as habitat preferences in collectors' notes. The altitudinal range in southern Africa is from ca. 10 m at inland swamps close to the coast in KwaZulu/Natal, to 1500 m inland in the Free State. From Namibia there are records from the Fish (Vis) river immediately above the confluence with the Orange River that are also inland but relatively close to the coast at an altitude of 74 m. *B. glaucus* is not known from coastal winter rainfall areas, the favoured habitat of *B. maritimus* s.s.

Morphological relationships

For a considerable period of time *Bolboschoenus glaucus* has been included within the morphologically variable and widely distributed *B. maritimus s.l.* My earlier and present studies have served to clarify and elaborate upon some of the differences between these taxa as they are known in southern Africa (*B. maritimus s.s.* rather than *B. maritimus s.l.*).

Distinction in other parts of their common distributional range is not straightforward as *B. maritimus s.l.* comprises variants that differ morphologically from the southern African (and northwestern European) *B. maritimus s.s.* The main features that distinguish *B. glaucus* and *B. maritimus s.s.* in southern Africa are listed in Table 13.

B. glaucus also shows morphological similarity with *B. nobilis*, which however, under suitable conditions of growth for both species, is very much larger and more robust. Inflorescences of large, robust plants of *B. glaucus* superficially resemble those borne by less robust, probably predated specimens of *B. nobilis*, especially when the spikelets are relatively young. The lengthened, catkin-like spikelets frequently reported for *B. glaucus* are unknown for *B. nobilis*, which differs again in that natural abscission of the glumes takes place almost as soon as fruits reach maturity. The fruits have several features in common, but pericarp surfaces show some differences that are useful in cases of doubtful identification. Details are given under *B. nobilis* (morphological relationships).

Anther crest length in the two taxa differs; this becomes more striking when the ratios of anther length to anther crest length are compared, namely:

<i>B. glaucus</i>	anther length	:	anther crest length
	(1.9-) 2.5--3.1 (-3.5)	:	(0.1-) 0.2--0.3 (-0.4)
	ratio approximately 2.8 : 0.25, that is about 11 : 1		
<i>B. nobilis</i>	(2.0-) 2.2--2.8 (-3.1)	:	(0.5-) 0.8--1.0
	ratio approximately 2.5 : 0.9, that is about 3 : 1		

These parameters indicate that in *B. glaucus* anther length is about 11 times anther crest length, whereas in *B. nobilis* anther length is approximately 3 times anther crest length.

Distribution [Figures 75; 76; Figure 82 (world)]

For Africa and Madagascar gross distribution is shown in Figure 75 and more detailed distribution for southern Africa (including Namibia and Botswana) in Figure 76. Collections are predominantly from inland localities. *Bolboschoenus glaucus* is not known from coastal winter rainfall areas, the favoured habitat of *B. maritimus* s.s.

Selected citations for southern Africa are given below. The taxon is not confined to subSaharan and Mediterranean Africa. It extends into Mediterranean Europe, the Middle East and India and is reported as an introduction in North America. (For citations see Appendix 2.)

Selected citations

- 1824 (Kachikau): Savuti, Chobe Nat. Park. Botswana (-CA), *Jacobsen, N.H.G.*, 3025 (PRE); Savuti R, just above the Savuti Marsh (-CB), *Gibbs-Russell, G.E.*, 2318, 2326 (PRE).
- 1918 (Grootfontein): Abenab (-AC), *Schoenfelder, E.* 1096 (PRE).
- 1923 (Maun): Nqamaqa Island (-BC), *Smith, P.A.*, 1737 (PRE).
- 1924 (Joverega): 19,08S; 24,02E. 2 km n. of Segxebe Pan (-AA), *Smith, P.A.*, 2452 (PRE).
- 2025 (Mompwe): 3 mls, NE Makarikari Pan (-DA), *Drummond & Seagrief* 5145 (LISC, PRE).
- 2026 (Nata): Nata River near Nata Village (-AA), *Ngoni, J.F.*, 521 (PRE).
- 2124 (Rakops): Botletle River, Toromoja (-BA), *Ngoni, J.F.*, 420 (PRE); Botletle River (-BB), *Smith, P.A.*, 2557 (PRE); Channel of Botletle R., N. of Lake Dow (-BC), *Wild & Drummond* 7227 (LISC, PRE).
- 2126 (Thada Mabeli): Flats N of Mopipi dam near Orapa. (-AD), *Allen, A.*, X 402 (J).
- 2229 (Waterpoort): Farm Weipe 617, adjoining Limpopo R. Dongola Reserve (-BC), *Codd & Dyer*, 3867 (NU, PRE, PRU).
- 2330 (Tzaneen): Hans Merensky Nature Reserve (-DD), *Zambatis, N.*, 685 (PRE).
- 2417 (Mariental): Haribes, am Dammufer (-DA), *Volk* 12140 (M).
- 2517 (Gideon): ohne Fundortsangabe, *Volk* 1096 (M).
- 2524 (Vergelee): Northern Cape. Nimrod's Vlei Farm. On Molopo River bed (-CD), *Gubb, A.A.*, 249 (KMG, PRE).
- 2632 (Bela Vista): Western entrance of Umbuluzi Poort (-AA), *Culverwell, J.*, 0220 (PRE);

Tembe Elephant Park. Tembu Crossing. Mosi Swamp (-CD), *Ward & Farquharson 10037* (NU, PRE), *Ward, M.C., 1067* (NH), *Browning 831* (NU).

-2726 (Odendaalsrus): Bothaville Distr., Schoonspruit (-DA), *Fuls, E.R., 268* (PRU).

-2732 (Ubombo): 16 miles east of Pongola River to Maputa (-AB), *Moll, E.J., 4633* (NU, PRE); Lower Mkuze floodplain (-CB), *Ward, C.J., 8788* (NU, PRE), Mpempe Pan (-CB), *Taylor, R.H., 386* (NH), *Musil, C.F., 386* (NH, PRE); Nibela (-CD), *Ward, C.J., 1707* (NU, PRE); Lower Mzinene River (-CD), *Ward, C.J., 7750* (NH, NU, PRE), *Browning, 829, 830* (NU).

-2817 (Vioolsdrif): Karas Region. Fish River, above confluence with Orange Riv. (-AA), *Ward, C.J., 12482, 13862* (NU).

-2824 (Kimberley): Barkly West, Newlands. Inundated banks of the Harts R (-AD), *Paton, H., 1323* (PRE, KMG).

-2832 (Mtubatuba): Lower Nyalazi River towards entrance to False Bay (-AB), *Ward C.J., 3485* (NU, PRE), Nibela Flood Plains (-AB), *Faure, J., H 638* (PRE).

-3020 (Brandvlei): Farm Lemoenkop 337, c.2 km S. of Lemoenkop house on Grootvloer flood area (-BA), *le Roux, A. & Lloyd, J.W., 93* (PRE).

-3022 (Carnarvon): Boesakleegte. Leegte (-AC), *Erasmus, H., 427* (PRE).

Indecisive (may be *B. glaucus*, but lacking confirmation from mature nuts)

-2628 (Johannesburg): Rolfe's Pan Isando. Pan no. 9 (-AA), *Allan, D., pp 199* (PRE).

-2630 (Carolina): Chrissiesmeer (-AD), *Coetzee, J.P. 2094a* (NU, PRU).

-2826 (Brandfort): Langs pad na Brandfort Alt. 4500 ft. (-AC), *Muller, DB 1173* (PRE).

4. *Bolboschoenus maritimus*

Bolboschoenus maritimus (Linné) Palla in E. Hallier et A. Brand, W.D.J. Koch's Synopsis der deutschen und schweizer Flora 3: 2531 (1905); Reid in Mem. bot. Surv. S. Afr. 62: 110 (1993) *pro parte*, Cape localities only. Type: a neoelectotype is under selection by I. Kukkonen and Galen Smith (pers. comm.).

Scirpus maritimus Linnaeus Sp. Plant. ed 2: 74 (1753); Thunberg Prod.pl. Cap: 17 (1794); Thunberg. Fl. Cap. ed 2: 369 (1811); Nees in Linnaea 7: 509 (1832); Nees in Linnaea 10: 184 (1835); Kunth Enum. pl. 2: 167 (1837); Boeckeler in Linnaea 36: 722 (1869); C.B. Clarke in Consp. fl. Afr. V: 626 (1894) *pro parte* at least *Burchell 514*, *Drège 2452*, *7402*; C.B. Clarke in Fl. Cap. 7: 232 (1898) *pro parte*, at least *Drège 2452*, *7402*, *Burchell 514*, *Bolus 4814*, *Flanagan 983*, other cited specimens not all located. Levyns in Fl. Cap. Peninsula: 107 (1950); Bond & Goldblatt in Jl. S.Afr. Bot. suppl Vol.13: 45 (1984).

Scirpus maritimus L. var. *digynus* non Godron (1844), *sensu* C.B. Clarke in Consp. fl. Afr. V: 627, at least *Bolus 4814*, *Flanagan 983*.

Scirpus tuberosus Desfontaines Fl. Atlant. 1: 50 1798. *S. maritimus* var. *tuberosus* (Desfontaines) Roemer & Schultes, Syst. Veg. 2: 139 (1817); *Reigera maritimus* [var.] *tuberosus* (Desfontaines) Opiz, Seznam: 83 (1852).

Bolboschoenus tuberosus (Desfontaines) Hadač, Bull. Coll. Sci. Baghdad 6 :13 (1961); *B. maritimus* (L.) Palla subsp. *tuberosus* (Desfontaines) T. Koyama, Acta Phytotax. Geobot. 31: 148 (1980); *B. maritimus* (L.) Palla subsp. *tuberosus* (Desfontaines) J. Soják, Cas. Nár. Muz. (Prague) 152: 19 (1983). Type: in locubus propre La Calla, 'Herbier de la Flore Atlantique, donne au Museum, par m. Desfontaines'(P).

Perennial, 0.26–0.8 (–1.5) m high. *Rhizomes* 3–5 (–7) mm in diameter, wiry, nodes bearing inconspicuous scale leaves and erect aerial culms either widely spaced, or grouped into sparse tufts; culm bases eventually hard, thickened forming oval to circular corms (7–) 10–12 (–14) mm in diameter. *Culms*, erect, leaf bearing, nodes inconspicuous, mid culm internode 3–7 mm in diameter, trigonous, glabrous; upper leafless internode about 2 mm in diameter, sharply three angled, glabrous to minutely scabridulous immediately below inflorescence. *Leaves*, (5–)6–8(–9) per culm, lowest 1–3 reduced to membranous short-bladed or bladeless sheaths, remainder laminate with blade increasing in length upwards; *sheaths* of laminate leaves closed, mouth deeply V-shaped, (shallower for culms \pm 6 mm wide), prominent veins adjacent to sides converging below base of V, narrow tongue of tissue within V,

membranous, dark with convex margin and central zone pale, becoming red spotted in older lower sheaths; *blades*, (190-) 200-400 (-450) x 3-5 (-7) mm long and wide, shallowly V shaped to flat in cross section at middle, tapering distally to a long fine triangular apex; midrib grooved adaxially, projecting abaxially, midrib and margins glabrous to slightly scabridulous at apex. *Inflorescence* variable, a solitary spikelet, a compact head or an anthelodium often on the same rhizome; 15-55 x 10-60 mm long (deep) and wide, carrying collectively (1-) 4-30 spikelets; paracladia (when present) 1-4 (1st order branches only) elliptic to three angled in cross section, glabrous. *Bracts* leaflike, 1-2 (-3), lowest (70-) 80-135 (-235) mm long, surpassing inflorescence, better developed than next upper and continuing line of culm particularly in young stages of inflorescence development. *Spikelets* solitary or clustered, 15-22 (-25) x 5-7 (-8) mm long and wide, ovate to oblong in outline, golden to dark brown. *Glumes* (*floral scales*) ovate to elliptic (5-) 6-7 (-8.5) x 3-4 (5) mm long and wide (excluding glabrous to scabrid awn 1.5-2.5 mm long), flanks nerveless, papery, faintly streaked, mid to dark brown, glabrous to scabridulous abaxially, midnerve prominent, margins somewhat hyaline, ciliolate, apex emarginate, 2-lobed, acute, sometimes lacerate. *Perianth bristles* (1-) 3-6, about half nut length, retrorsely scabrous, markedly caducous. *Anthers* linear-oblong, (2.3-) 2.5-3.7 (-4.0) mm long, with or lacking red colouration in connective and crest; crest (0.1-) 0.2-0.4 mm long, minutely spinulose. *Style branches* generally 3, sometimes 2 on some lower florets, or up to half in the same spikelet, about half style length, terete to flattened, lacking hairs or papillae. *Nut* (2.6-) 2.7-3.4 x (1.9-) 2.1-2.8 mm long and wide, obtusely trigonous, rarely somewhat lenticular, obovate in outline, crowned by persistent triangular style-base 0.1-0.3 mm long, golden to dark brown, light reflective, surface smooth, clearly marked by honey-comb pattern of exocarp cells x 20, becoming more clearly defined x 600 [Figure 74B (rhizome); 45 (neoelectotype) and 80 (plants in colour)].

Morphological variability

Considerable variation was noted in inflorescence form, both in living populations and in the herbarium specimens examined. The latter tend to emphasize the differences, because culms are quite frequently detached from other plant parts. Study of field populations is essential if

Bolboschoenus maritimus s. l. in The Netherlands: a study of pericarp anatomy based on the work of Irene Robertus-Koster

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Electron microscope scanning results of *Bolboschoenus maritimus* (L.) Palla *sensu lato* (= *Scirpus maritimus* L.) achenes, collected from natural populations in The Netherlands and investigated earlier by Irene Robertus-Koster, are given. Speculative conclusions suggest the variability observed may be the outcome of introgression through earlier generations influenced by ecological effects not adequately understood.

Key words: achene study, *Bolboschoenus maritimus*, (Cyperaceae), The Netherlands

INTRODUCTION

Robertus-Koster (1969) reported upon the different taxonomic interpretations applied to *Scirpus maritimus* L. s. l., in which taxon the inflorescence is sometimes a compact head, sometimes branched and open. These interpretations ranged from separate species to habitat forms. The problem invited further study, which this author undertook in The Netherlands, where natural populations were available for investigation. Results showed a low number of branches per inflorescence (0–2) in coastal samples where salinity was

higher, compared with inland freshwater samples where inflorescences were open with clearly defined branches (4–6). The extremes were linked by transitional forms that showed gradual increase in inflorescence branch number from coastal to inland habitats. Culture experiments over two years suggested the observed differences were genotypical. External achene features of shape, size and colour were also considered. Results showed correlation in that plants from coastal, saline localities carried achenes that were predominantly light brown to brown, variable in width (but mostly broad) and in their shape in

it is to be understood that as Norlindh (1972: 398) also found for Scandinavian populations, a range of variants may be connected by a common rhizome. Importance, even in the segregation of genera (*Bolboschoenus*, *Schoenoplectus* see Introduction pg. 6) has been attached to the occurrence in some species of inflorescences consisting of a solitary spikelet. In my experience of southern African populations of *B. maritimus* s.s. such inflorescences often with the spikelet appearing pseudo-lateral, arise most commonly on weaker shoots from lateral buds on well established corms, and are of quite frequent occurrence and are merely part of a natural range of structural form.

B. maritimus s.s. is generally described as having both two-branched and three-branched styles within the same spikelet. Norlindh (1972: 399) noted for Scandinavian plants that the two-branched styles (few) were generally at the spikelet base while the remainder carried three-branched styles. In my experience of *B. maritimus* s.s., the three style branches do not always arise from the style at the same point. Where this does happen, the three branches are of equal thickness and are easily observed. More frequently two branches develop, from one of which, at varying distances from the main style branch junction, a third thinner, shorter branch may arise. This is frequently twisted about the style branch from which it originates, so that only two styles are at first apparent. Determination of the number of style branches is therefore not easy. This is exacerbated by the difficulty of assessing style branch number in florets of herbarium specimens not recently collected. Here the style branches are brittle and break away, hence their number is often inaccurately recorded.

My examination of specimens has shown that in southern African specimens of *B. maritimus* s.s. two-branched and three-branched styles may be present within a single spikelet. Spikelets of some inflorescences included only few two-branched styles (1--2) whereas in others, the number was greater and approximated to the number that were three-branched [*Pillans* 3886, *Levy* 8637 (both BOL)]. However, because of the difficulty of counting, this statement must be accepted with caution; it is made to document the fact that the proportions of two-branched and three-branched styles within an inflorescence is variable. A thorough study of young, living inflorescences from a range of localities should really be carried out to produce dependable results.

transverse section (subtrigonus to lenticular), whereas those from inland situations were dark brown to almost black, narrower in width and triangular in transverse section.

Independently, a field study of *Bolboschoenus maritimus* (L.) Palla s. l. (= *Scirpus maritimus* s. l.) carried out in a southern African wetland (Verlorenvlei, Atlantic coast, W. Cape Province, S. Africa) (Browning *et al.* unpublished) produced comparable results. In this later study, achenes were subjected to electron scanning, an examination technique not used by Robertus-Koster (1969). The results revealed differences in achene surface and in pericarp anatomy in coastal and inland extremes. Robertus-Koster (1969: 196 and 197, figs. 2 and 3) had reproduced photographs of achene samples. It seemed opportune to enquire whether these samples had been preserved and if they might be made available for micro morphological investigation. Due to the kindness of Irene Robertus-Koster, eleven of her original samples of about 100 achenes were provided for a study comparable with the electron scanning carried out on achenes from Verlorenvlei.

This paper reports the findings on the achenes from The Netherlands. These support and supplement the results given by Robertus-Koster (1969). The results obtained for the southern African samples will be published in detail later as part of the complete Verlorenvlei study, in which a summary of differences observed between the achene samples from The Netherlands and South Africa will be included.

MATERIALS AND METHODS

The eleven achene samples were examined individually using a binocular microscope $\times 40$. This revealed a degree of variability within each sample. To quantify this, 50 achenes were removed at random from each sample, except for those from Maastricht and Punt van Reide 4, where the reduced size of the sample originally received permitted removal of 20 only.

Within each sub-group of 50 or 20 achenes, those showing marked differences in outline shape and colour were separated, counted, and the percentages for each main aspect calculated: sizes were measured for each aspect.

From the eleven original samples, nine were taken as representative of coastal to inland habitats: these were used for electron microscopy. Six achenes were taken from each of the nine samples; of these six, three were mounted with abaxial surface uppermost on stubs, three were fractured

according to the methods described by Browning and Gordon-Gray (1993). Whole and fractured achenes were viewed under an Hitachi S570 Scanning Electron Microscope and photographed. Ratios of exocarp to mesocarp were determined by measurement of micrographs. These were supported by binocular microscope ($\times 40$) measurements of transverse sections (x-sections) of further achenes from each sample.

RESULTS

Results are summarised in Table 1, which is supplemented by six figures of electron micrographs (Figs. 1–6). These are representative of the nine coastal to inland habitats mentioned in Materials and Methods and named in the table. Table 1 and Figs. 1–6 should be considered in conjunction.

Two groups were found to be present, namely:

Group 1 (Table 1, except last two samples; Figs. 1–4).

Localities: Groningen West E2; Haringvliet H4; Punt van Reide R7; Biesbosch. Of these, Haringvliet and Biesbosch were tidally influenced (Robertus-Koster, 1969: 198, table 1).

Achenes: variable (see Table 1), but predominantly obovate in outline, with pericarp light brown to brown, the surface glossy and marked by regular polygonal cell outlines forming a honey-comb pattern; the polygonal cells with depressed anticlinal walls and raised outer periclinal walls. In x-section predominantly compressed subtrigonus, with exocarp cells radially elongate; ratio of exocarp depth to mesocarp depth ca. 2:1.

Group 2 (Table 1, last two samples only; Figs. 5 and 6)

Localities: Maastricht, Schoonhoven L1. Of these, Schoonhoven was tidally influenced; Maastricht, further inland and not collected by Robertus-Koster (personal communication), is not included in table 1 by Robertus-Koster (1969: 198).

Achenes: somewhat variable (see Table 1), but predominantly narrowly obovate in outline, with pericarp dark brown to black, the surface glossy (Maastricht) or dull (Schoonhoven), marked only faintly by cell outlines, the honey-comb pattern modified, sometimes imperfect; cells with anticlinal walls raised, outer periclinal walls frequently depressed. In x-section trigonous, with exocarp cells radially elongate, but less deep than in Group 1; ratio of exocarp depth:mesocarp depth ca. 1:2 (Maastricht) 1:1.4–1.7 (Schoonhoven).

Anthers in *B. maritimus* s.s may or may not have red colouration in the connective and crest. No significant difference between the anthers of *B. maritimus* s.s. and *B. glaucus* was found, but *B. grandispicus* has shorter anthers with a longer crest (further details are given under Morphological relationships, *B. grandispicus* pg. 99).

Habitat preferences

In southern Africa *Bolboschoenus maritimus* s.s. is located in coastal situations at the mouths of estuaries and on sandy banks bordering lagoons. In the vicinity of Cape Town, it has been collected at inland vleis on the Cape Flats. This is a sandy region extending across the peninsula with an altitude that in parts approximates that of sea level.

Morphological relationships

The morphological similarities of *B. maritimus* have been dealt with under the species already considered in this chapter; it is not necessary to recapitulate here, except to recall that the entity from coastal habitats in the western and eastern Cape (*B. maritimus* s.s.) is closely allied to plants from Sweden studied by Norlindh (1972). In the broader sense (*B. maritimus* s.l.) from more inland microhabitats along the Cape coastal zone already mentioned, and from other parts of its presently defined world distributional area, shows wide morphological variability not yet adequately understood. Studies from aspects other than morphology are required.

Distribution [Figures 75, 76; Figure 82 (world)]

Bolboschoenus maritimus s.s. in southern Africa has a predominantly coastal distribution. It is well represented and collected in the western Cape Province, particularly in the environs of Cape Town which experiences a Mediterranean climate with winter rains. It extends up the west coast as far as the Orange River Mouth; collections are mainly confined to vleis and pans in Nature Reserves. No collections were recorded between Eland's Bay and Orange River Mouth, but this does not necessarily indicate that the species is absent from this section

Table 1. Results of achene study of material from The Netherlands donated by Irene Robertus-Koster (E:M expresses ratio of exocarp depth to mesocarp depth).

Sample	Variability, outline-shape, size, colour, surface topography, x-section and E:M
Group 1	
Groningen West E2 (Fig. 1)	100% obovate; 3.0–3.4 × 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 × 2.2–2.7 mm; golden brown; cells polygonal; subtrigonus. 10% narrowly obovate (smaller); dark brown to black; cells faintly marked; subtrigonus. 6% elliptic; golden brown; cells polygonal; lenticular. E:M = 2:1
Haringvliet H4 (Fig. 2)	74% obovate; 3.1–3.8 × 2.4–2.8 mm; golden to ochre-brown; cells polygonal; subtrigonus. 14% elliptic; 3.5–4.1 × 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; subtrigonus. E:M = 2:1; but Fig. 2J = 1:1
Haringvliet D1	58% obovate; 3.4–4.3 × 2.3–2.6 mm; golden brown; cells polygonal; subtrigonus. 42% elliptic; 3.7–3.9 × 2.2–2.4 mm; golden brown; cells polygonal; lenticular. E:M = ca. 2:1
Punt van Reide R7 (Fig. 3)	70% obovate; 4.0–4.5 × 2.5–2.9 mm; ochre to kharki colour; cells polygonal, smaller on flat surfaces, larger on achene shoulders; obtusely trigonous. 30% elliptic; 3.9–4.8 × 2.1–2.7 mm; ochre to kharki colour; cells polygonal but uneven in size; subtrigonus (10), lenticular (5). E:M = ca. 1.5:1
Punt van Reide R4 (not scanned)	65% obovate; 3.1–4.3 × 2.2–2.7 mm; golden brown; cells polygonal; subtrigonus. 25% elliptic; golden brown; cells polygonal; lenticular and a few subtrigonus. 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 × 2.1–2.5 mm; light brown to ochre; cells polygonal but variable in size; subtrigonus. 30% elliptic to obovate; 3.3–3.6 × 1.8–2.0 mm; light brown to ochre; cells polygonal but variable in size; subtrigonus. 10% elliptic; light brown to ochre; cells polygonal but variable in size; lenticular. E:M = ca. 1.5:1
Biesbosch (Fig. 4)	74% obovate; 3.0–4.0 × 2.4–2.8 mm; dark brown; cells polygonal, variable, most noticeable on abaxial ridge; subtrigonus. 20% elliptic; 3.6–4.0 × 2.0–2.5 mm; dark brown, cells polygonal, variable, most noticeable on abaxial ridge; trigonus, 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 × 2.0–2.4 mm; golden brown; cells polygonal appearing small; subtrigonus.

(Continues ...)

of the coast. No loan material of *B. maritimus* s.s. was obtained from Angola. Specimens for that country from LISC were either *B. nobilis* or *B. glaucus*. Field studies there should be carried out, but political unrest has not favoured such work.

Eastwards from the Cape Peninsula, *B. maritimus* s.s. extends to Morgans Bay (-3228 Butterworth), and possibly to the Transkei as noted by Browning and Gordon-Gray (1992: 384). At that date, however, *B. maritimus* included *B. glaucus*. Gordon-Gray, *JL.*, 1050 (NU) from Transkei, The Haven, Bashee River, compares with the general facies of plants from slightly inland habitats at Verlorenvlei (see Chapter 4. pg. 33), while Gordon-Gray, *JL.*, 841 (NU) from approximately the same locality bears only very young reproductive organs. Further collecting and field work along the Transkei coast near Port St. Johns is needed to determine if indeed *B. maritimus* s.s. is present. No further more northerly collections are known for the east coast of Africa, except one isolated collection ["Entomologie" *H.* 642 (PRU)] from Richard's Bay. It is probable that the locality given for this specimen is questionable as enquiry at PRU elicited only that the collector was one of an unspecified group of entomology students visiting the approximate environs of Richards Bay. Mr. C.J. Ward working and collecting extensively over many years in this and neighbouring east coast areas has not found *B. maritimus* s.s. to be present at Richard's Bay.

Anomalies and collections of uncertain identification

One anomaly in the distribution of *B. maritimus* in southern Africa is an inland collection, Forbes, *PL.*, 739 (J, NU), from a marshy area in the vicinity of Johannesburg. Although no fully mature nuts were available on the compact heads of spikelets, the developing fruit on one sheet indicated radial elongation of the exocarp cells, a characteristic of the pericarp *B. maritimus* s.s. It is possible that originally this was an introduction into the area by migrant birds (particularly members of the family Scolopacidae), which have 'stop-over' points at inland pans and marshes during their migration from the northern hemisphere to the Cape and back.

Two collections from Isoetes Vlei on the Cape Peninsula were unmatched. Their very dark

Table 1. Continued.

Sample	Variability, outline-shape, size, colour, surface topography, x-section and E:M
	20% obovate; 3.1–3.9 × 2.2–2.6 mm; golden-yellow; cells polygonal; subtriangular. 18% elliptic; golden, cells polygonal appearing small; lenticular. 10% elliptic; golden-yellow; polygonal; subtriangular. 2% narrowly obovate; almost black; cells faintly marked; subtriangular. E:M = 2:1
Group 2	
Maastricht (Fig. 5)	90% narrowly obovate; 3–3.5 × 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 subtriangular (1). 3.3% obovate; black; smooth, glossy, cells faintly marked; subtriangular. E:M = 1:2
Schoonhoven L1 (Fig. 6)	84% narrowly obovate to obovate; 3.6–3.9 × 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

DISCUSSION

The most striking feature of this study of achenes from The Netherlands is their variability, which is evident in outline shape (obovate to narrowly obovate), colour (golden brown, light brown to ochre or dark brown to nearly black) and size (3–3.5 × 1.5–1.9 mm, Maastricht, to 4.0–4.5 × 2.5–2.9 mm, Punt van Reide R7). However, despite this variability, the achenes fall into two main groups, the features of which are given in Results. The most significant of the differences in the two groups are outline shape, pericarp colour and surface patterning, shape in transverse section and ratio of exocarp depth to mesocarp depth.

Robertus-Koster (1969) likewise distinguished two groups from her study of more comprehensive samples. She recognised 'fruits ... small, broad, brown, semi-spherical to slightly triangular [in outline], with great variability within and between the samples', (compare our Results, Group 1) and 'fruits; narrow [in outline], dark brown to almost black, in cross-section sharply triangular. The variability of the fruits within a sample and between samples of different places

is small.' (Robertus-Koster 1969: 200, English summary; compare our Results, Group 2).

Robertus-Koster related her group with small, brown, semi-spherical achenes to plants that carried compact inflorescences with a small number of inflorescence branches (0–2) which grew in coastal or tidal (usually more saline) habitats. Her group with dark, almost black, narrowly-triangular achenes was representative of plants with open branched (4–6) inflorescences from inland (usually less saline to fresh water) habitats. She was careful to stress that the groups, representing extremes, were linked by transitional forms so that, at least in morphological characteristics, there was intergradation between what she termed *paramorphs compactus* (Group 1) and *maritimus* (Group 2).

From our study of the samples, we are able to add for each of these extremes, further details of achene structure revealed by electron scanning, namely achene surface features and ratio of exocarp to mesocarp depths (see Results, Table 1 and Figs. 1–6). We are also able to support the major distinctions between Groups 1 and 2 from the results of the independent study carried out at

brown, enlarged spikelets (25--30 mm x 6 mm), with florets with a predominance of two style branches differed from other Cape specimens of *Bolboschoenus maritimus* s.s. Unfortunately both collections are immature, without nuts or developing ovaries. Another gathering from Robben Island [Lloyd, *JW.*, 505 (PRE, STE)], has yet larger spikelets, with anthers up to 4.75 mm in length; and this too is immature. These aberrant entities (if there are two ?) require further detailed investigation in the field. Attempts to relocate the plants at Isoetes Vlei were unsuccessful because of the search taking place at the end of the dry season: also both localities are not easily explored because of present social unrest.

B. maritimus s.s is present in coastal situations in Algeria, for the type of *Scirpus tuberosus* Desfontaines is from La Calla. *Scirpus tuberosus* was a name previously often misapplied to *B. glaucus* which is certainly well represented in most West and North African countries including Algeria. From Morocco three collections at BM were noted to be *B. maritimus* s.s., namely *J. Lewalle* 9008, *E. Jahandiez* 796 and *Dr. Font Quer* s.n. (listed with localities in Appendix 2). A collection by *Michel Gandoger* s.n. (MO) (photostat NU) was considered by Galen Smith perhaps to represent *B. maritimus* x *B. glaucus*. In this connection some sheets collected by M. Gandoger (LD) carried notes indicating that the collections from Morocco 1908--1911, were in fact collected in France.

Citations

- 2628 (Johannesburg): S. of Alberton on Wadeville/Alrode Roads (-AC), *Forbes, PL.*, 739 (J, NU).
- 2816 (Oranjemund): Orange River Estuary (-CB), *Ward, CJ.*, 12575, 13979 (-NU); Ex island in lower Orange R. estuary (-CB), *Ward, CJ.*, 14005 (NU); Karas Region, Oranjemund, Pink Pan. (-CA), *Ward, CJ.*, 12289, 13760 (NU).
- 3218 (Clanwilliam): Velddrif area; Rocher Pan Nature Reserve (-CB), *Coetzer, A I* (STE); *van Rooyen & Ramsey* 5, 543 (PRE, STE), *Heyl, C* 12 (PRE, STE), *Le Roux & Ramsey* 6 (STE).
- 3219 (Wupperthal): Houdenbekrivier dam cistern, on Excelsior farm (-CD), *Hugo, L* 2288 (PRE, STE).

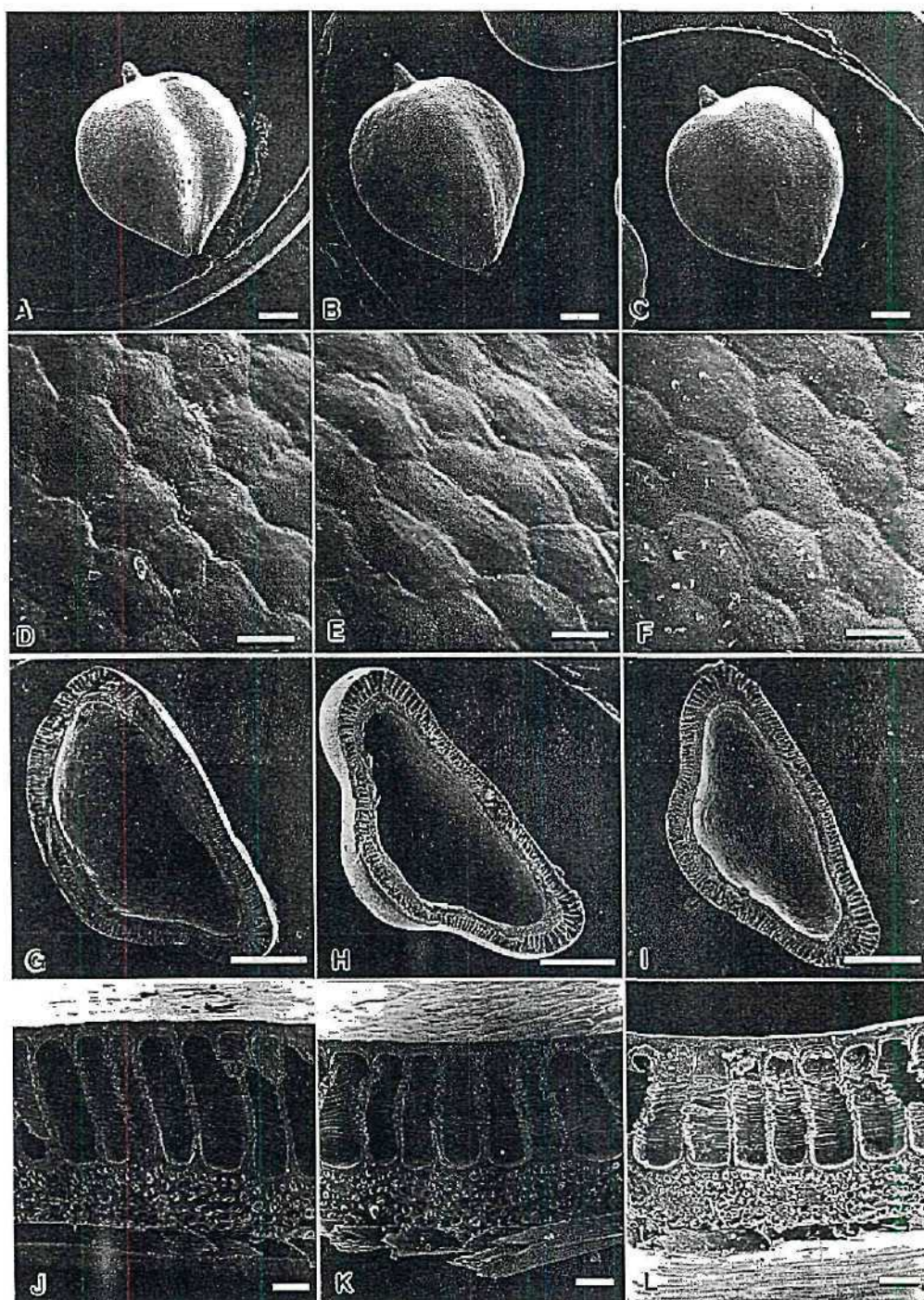


Fig. 1. *Bolboschoenus maritimus* (L.) Palla, Groningen West E2. — A–C: Achene abaxial view ($\times 20$, scale bar = 500 μm). — D–F: Exocarp surface ($\times 600$, scale bar = 25 μm). — G–I: Achenes in transverse section ($\times 40$, scale bar = 500 μm). — J–L: Detail of pericarp structure in transverse section ($\times 400$, scale bar = 25 μm).

-3228 (Butterworth): Morgans Bay; banks of the estuary (-CB), *Sonnenberg, B.* 427 (GRA, NU), *Ward, C.J.* 13922 (NU); Marshy spots nr. Kei Mouth (-CB), *Flanagan* 983 (BOL, GRA, PRE, SAM).

-3318 (Cape Town): Mud River Kloof; Malmesbury Distr. 4.7 ml from main rd. along rd to Bokbaai (BC), *Taylor, H.C.*, 5494 (PRE); 'In humidis prope CapeTown (-CD), *Bolus, H.* 4814 (BOL); Mowbray, *Marloth, R.H.* 7266 (PRE); 10 mls from Malmesbury on road to Cape Town, *Clarkson, D.J.* 380 (BOL, NU), Malmesbury, *Henderson, M.R.*, 1856 (NBG); Paarden Eiland, Klein Zoar vlei (-CD), *Linder, H.P.L.*, 2183 (BOL); Riet Vlei near Tygerberg (-DC), *Moss, C.E.*, 9067 (J); Banks of the Black River at Rapenburg, *Pillans, N.S.*, 3886 (BOL, PRE); capensis prope Durban Road (-DC), *Macowan* (BOL, PRE); Cape Flats Nature Reserve, University of Western Cape (-DC), *Low, A.B.* 747 (STE); Tygerberg Nature Reserve (-DC), *Loubser* 3252 (STE); Reepenbergh (Rapenburg ?) Vley (-DC), *Wolley-Dod, A.H.* 2103 (PRE); Opposite Parow Municipality Nursery Beacon Street, Tiger Valley (-DC), *Low, A.B.*, 419 (STE); Vaarsche (Vars ?) Vlei [confluence of Black & Liesbeeck Rivers on Peninsula- P. Lorber, pers. comm.] *Levyyns, M.R.*, 8637 (BOL).

-3322 (Oudtshoorn): George Dist. Wilderness. (-DC), *Mogg, A.O.D.*, 11864 (PRE).

-3325 (Port Elizabeth): Uitenhage distr. (-CD), *Zeyher, C.L.* 4422 (PRE), *Zeyher, C.L.*, 23 (PRE, SAM); Zwartkops River (-DB), *Archibald, E.E.A.*, 5180 (GRA); Zwartkops River Estuary (-DC), *Archibald* 5014 (GRA, PRE); Near mouth of Zwartkops River, *Drege s.n.* (SAM 24115); Redhouse (-DC), *Paterson, T.V.*, 445 (BOL, GRA, PRE); Dist. Port Elizabeth, Creek (DC), *Drege* 647 (GRA).

-3326 (Grahamstown): Reit River Mouth, Bathurst Div. (-AA), *Lubke, R.A.*, 93 (NU); Riet River. At margin of lagoon near beach. (-AA), *Archibald* 4138, (GRA); Dist. Alexandria; Springmount (-CA), *Archibald* 5865 (GRA, PRE); Kowie West, Salt Vlei. (-DB), *Britten, L.*, 2841, (GRA); Dist. Bathurst, Kowie. Salt Vlei (-DB), *Britten* 2997 (GRA, PRE); Salt vlei, Port Alfred (-DB), *Mauve & Wells* 9 (GRA, PRE); Port Alfred next to lagoon (-DB), *Arnold, T.H.*, 608 (PRE); Waters Meeting, Kowie R. Kowie Nature Res. Bathurst (-DB), *Burrows, H.H.* 2787 (GRA); Port Alfred; Along Kowie River (-DB), *Vorster, P.*, 2286 (PRE); Ghio Wetland Nature Reserve- Alexandria Distr., Bushmans river (-DA), *Schmidt, S. et al.* 6 (GRA).

-3327 (Peddie): 2.2km before Hamburg (-AD), *Arnold, T.H.* 575 (PRE); Hamburg; vlei east of main coastal road. (-AD), *Vorster, P.*, 2259 (PRE); Tyolomnqa (Chalumna) River (-BA),

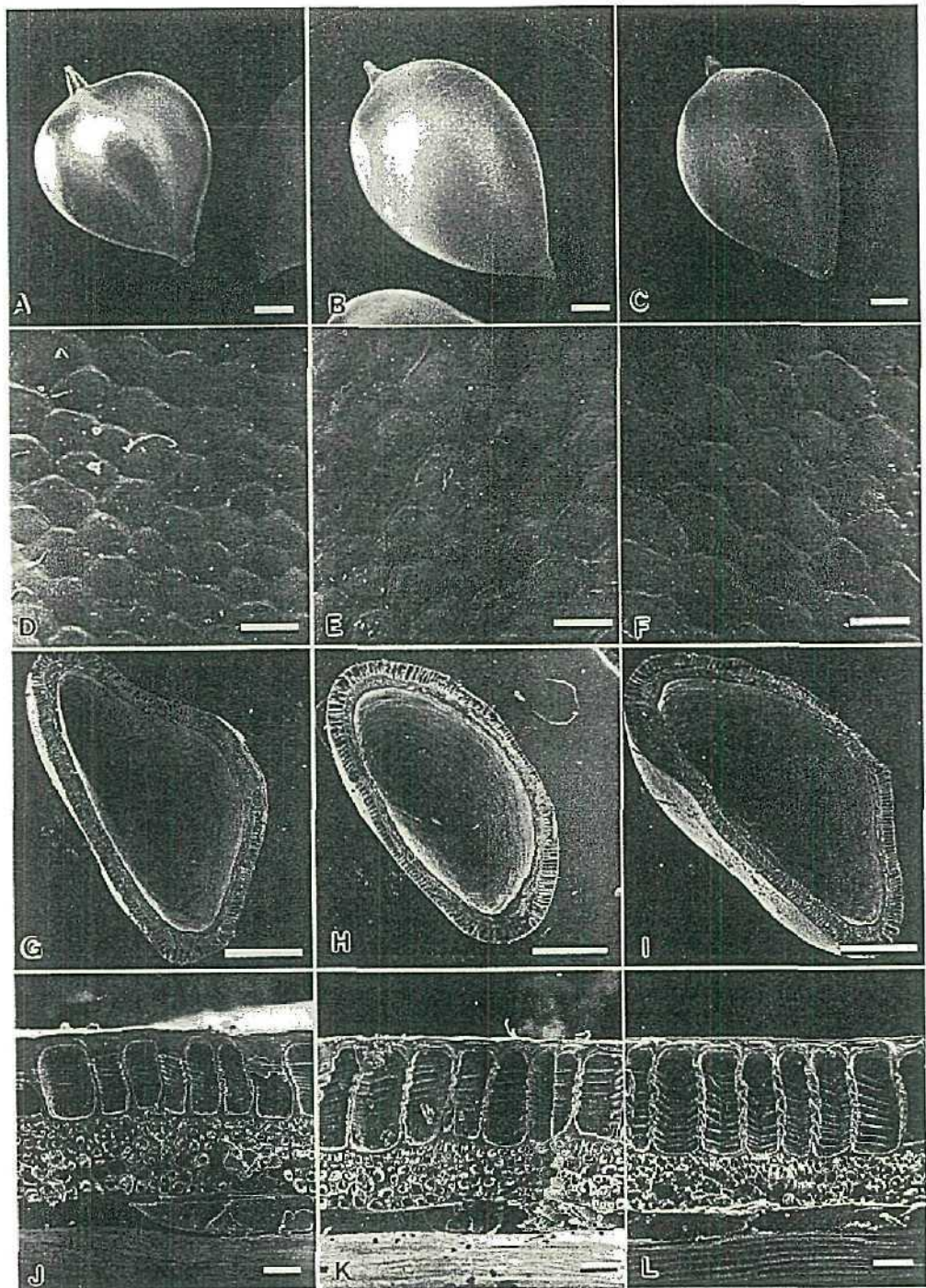


Fig. 2. *Bolboschoenus maritimus* (L.) Palla, Haringvliet H4. — A–C: Achene abaxial view ($\times 20$, scale bar = 500 μm). — D–F: Exocarp surface ($\times 600$, scale bar = 25 μm). — G–I: Achenes in transverse section ($\times 40$, scale bar = 500 μm). — J–L: Detail of pericarp structure in transverse section ($\times 400$, scale bar = 25 μm).

- Ward, C.J.*, 13929 (NU); Near Fish river mouth (AC), *Phillipson, P.B.*, 304 (PRE).
- 3418 (Simonstown): Fish Hoek (-AB), *Moss, C.E.*, 2316 (J); Muizenberg - near vlei - muddy ground. (-AB), *Mitchell, M.R.*, 6030 (BOL); Noordhoek salt pan (-AB), *Walker, I.* 5 (BOL); Muizenberg- Strandfontein Rd. (-AB), *Forbes, P.L.*, 609 (J, LISC, NU); Lakeside Fire Station (-AB), *Getliffe, F.*, 1021 (J, NU); Faure to Macassar Roadside at Zandvliet (-BA), *Boucher, C.*, 3499 (PRE, STE); Hottentots Holland (-BB), *Zeyher, C.L.*, s.n. (PRE); Pond between Strand and Gordon's Bay (-BB); *Parker, R.N.* 4368 (BOL); Mouth of the Klaasjagers River (-AD), *Rourke, J.P.*, 1363 (PRE).
- 3420 (Bredasdorp): Bredasdorp Div. Roadside ditch near Stormsvlei (-AA), *Esterhuysen, E.*, 13563 (BOL, PRE).
- 3421 (Riversdale): Coast nr. Still Bay (-AD), *Muir, J.*, [Pre 4180] (PRE).
- 3422 (Mossel Bay): Wilderness lagoon (-BA), *Jacot-Guillarmod, A.*, 8329 (PRE).

Putative hybrids of *B. maritimus* x *B. glaucus*

Note: those marked by an asterisk are immature and lack nuts. They are tentatively assumed to be putative hybrids on the basis of inflorescence form and spikelet lengths and widths.

- 3118 (Vanrhynsdorp): Lutzville, Olifantsriver bridge (-CB), *Arnold, T.H.*, 914 (NU, PRE).*
- 3119 (Calvinia): Nieuwoudtville (-AC), *C.J. Ward* 13973 (NU, UDW); Lokenberg. Along river. Alt.c. 640 m. (-CA), *Acocks* 17572 (BM, PRE); 54 km from Clanwilliam on road to Calvinia, next to bridge over river (-CC), *Arnold, T.H.*, 737 (PRE).*
- 3218 (Clanwilliam): Verlorenvlei, between Elandsbaai and Redelinghuys (-AD), *Browning* 794--802, 809, near Redelinghuys (-AD), *Taylor, P.B.*, s.n.; *Kotze, D.C.*, 310 (all NU).
- 3326 (Grahamstown): Ghio marsh, farm Spadona (-DA), *Skead, C.J.*, Sn 2 (PRE)

Indecisive

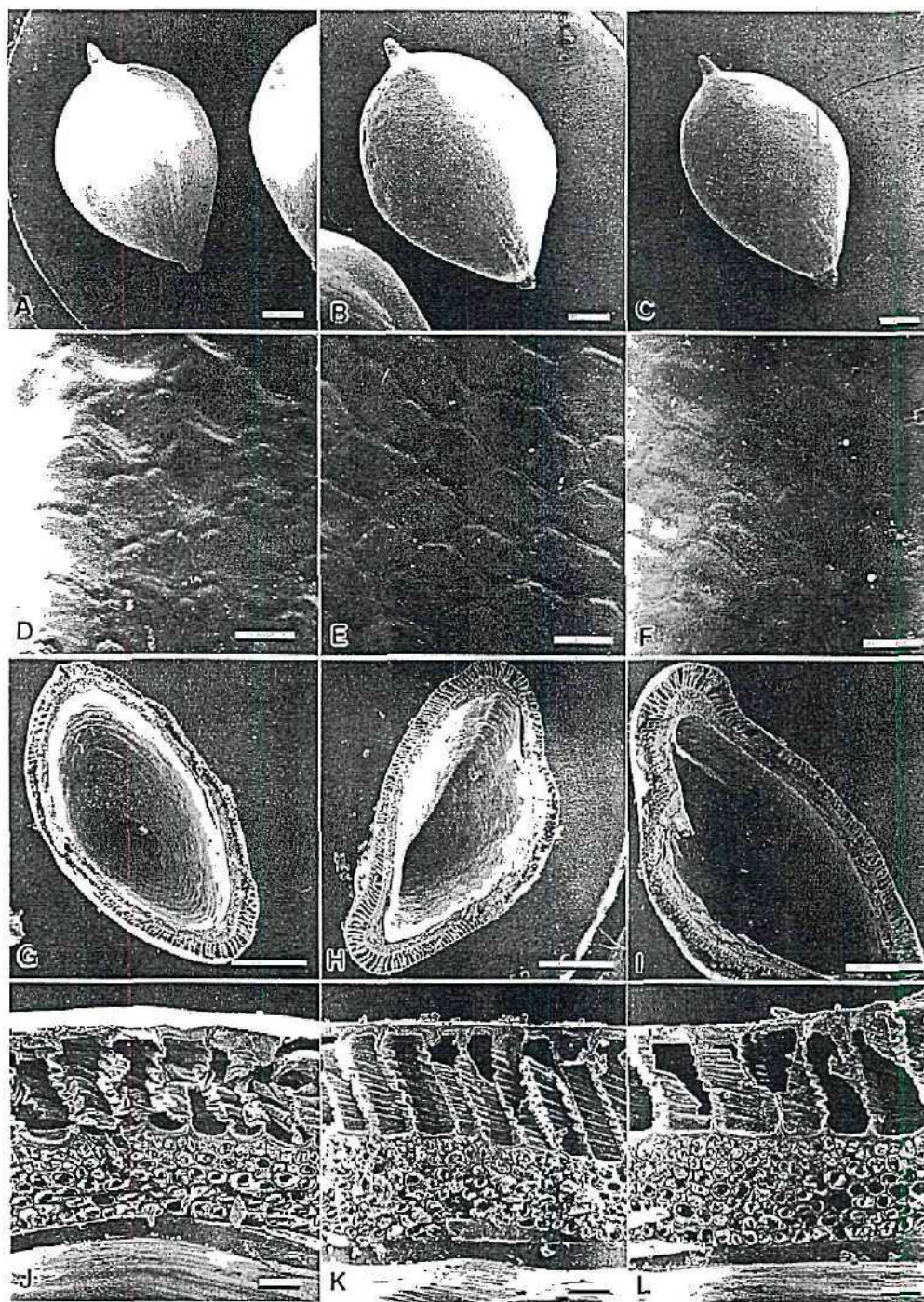


Fig. 3. *Bolboschoenus maritimus* (L.) Palla, Punt van Reide R7. — A–C: Achene abaxial view ($\times 20$, scale bar = 500 μm). — D–F: Exocarp surface ($\times 600$, scale bar = 25 μm). — G–I: Achenes in transverse section ($\times 40$, scale bar = 500 μm). — J–L: Detail of pericarp structure in transverse section ($\times 400$, scale bar = 25 μm).

- 3318 (Cape Town):Robben Island. At the lepers bathing site, *Lloyd, J.W.*, 505 (PRE, STE).
- 3325 (Port Elizabeth): The Drift near Addo (-DA), *Heard, HW.*, s.n. (STE).
- 3418 (Simonstown): Isoetes Vlei; Cape Flats (-BA), *Mathews, MR.*, 42 (NBG); *Gubb, AA* 128 (NBG).

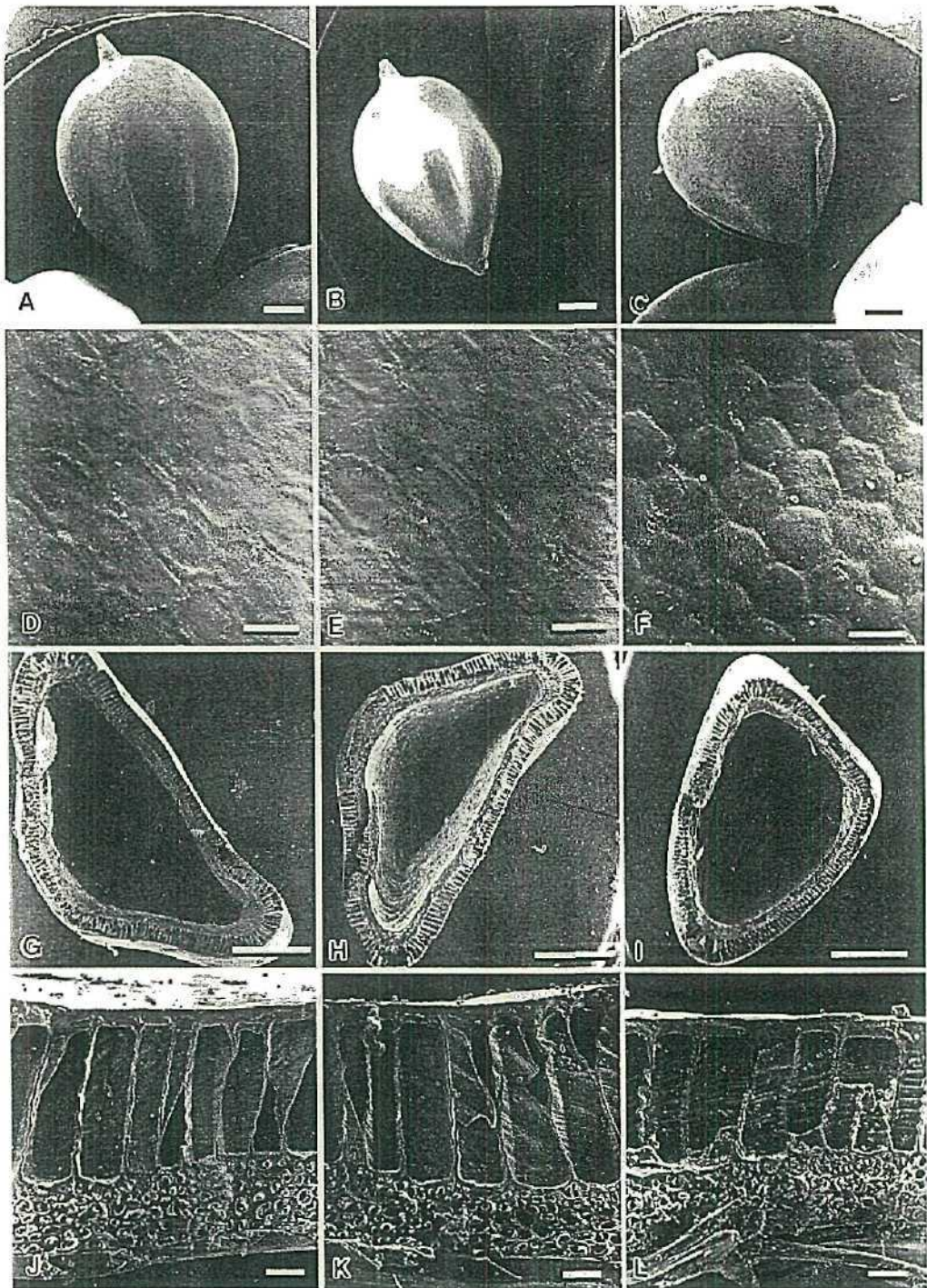


Fig. 4. *Bolboschoenus maritimus* (L.) Palla, Biesbosch. — A–C: Achene abaxial view ($\times 20$, scale bar = 500 μm). — D–F: Exocarp surface ($\times 600$, scale bar = 25 μm). — G–I: Achenes in transverse section ($\times 40$, scale bar = 500 μm). — J–L: Detail of pericarp structure in transverse section ($\times 400$, scale bar = 25 μm).

PART 5

SUMMARY

AND

OUTSTANDING PROBLEMS

CHAPTER 15

Summary and outstanding problems

Based on past and present morphological studies worldwide, there is still some uncertainty as to whether, or not, accepted generic characteristics adequately differentiate *Bolboschoenus* from its close ally *Schoenoplectus*. Nor, within *Bolboschoenus*, is species differentiation clear cut; discontinuities are poorly defined and may appear “blurred” by variability, the causes of which are insufficiently understood. The criteria presently used to delimit taxa are few, and critically considered, are predominantly quantitative. Definitive qualitative discontinuities are mostly absent and a suite of features, including plant dimensions, extent of inflorescence branching, and spikelet numbers, all of which may be environmentally influenced by factors as diverse as soil water salinity, parent plant maturity and extent of predation, are relied upon together with some characters of the reproductive organs, for example, style branch number and fruit conformation. In *Bolboschoenus*, as in other Cyperaceae, these reproductive organs, that in other plant groups are mostly constant and therefore acceptable as reliable in taxonomic classification, are less convincing. In *Bolboschoenus* are taxa that are uniform in the development of a two-branched style surmounting a two-angled (lenticular) fruit; others uniformly produce three-branched styles surmounting sharply three angled nuts; yet others produce a proportion of two-branched styles and two angled fruits among a preponderance of three styled, three angled fruit type, all within a single spikelet. Nut colour, shape, size and superficial surface markings and texture viewed under low magnification offer possibilities in species differentiation, but again the extent of variability, in some localities at least, is disquieting.

In southern African representatives as an exploratory commencement, fruits examined micromorphologically at high magnification, both externally and anatomically, gave promise of structural pericarp characters perhaps reliable enough to enable some refinement of current taxonomic delimitation. The main purpose of this dissertation has been, therefore, to substantiate these preliminary southern African findings, then to extend them to the plants of subSaharan Africa, and given satisfactory results, to survey the genus from this limited aspect

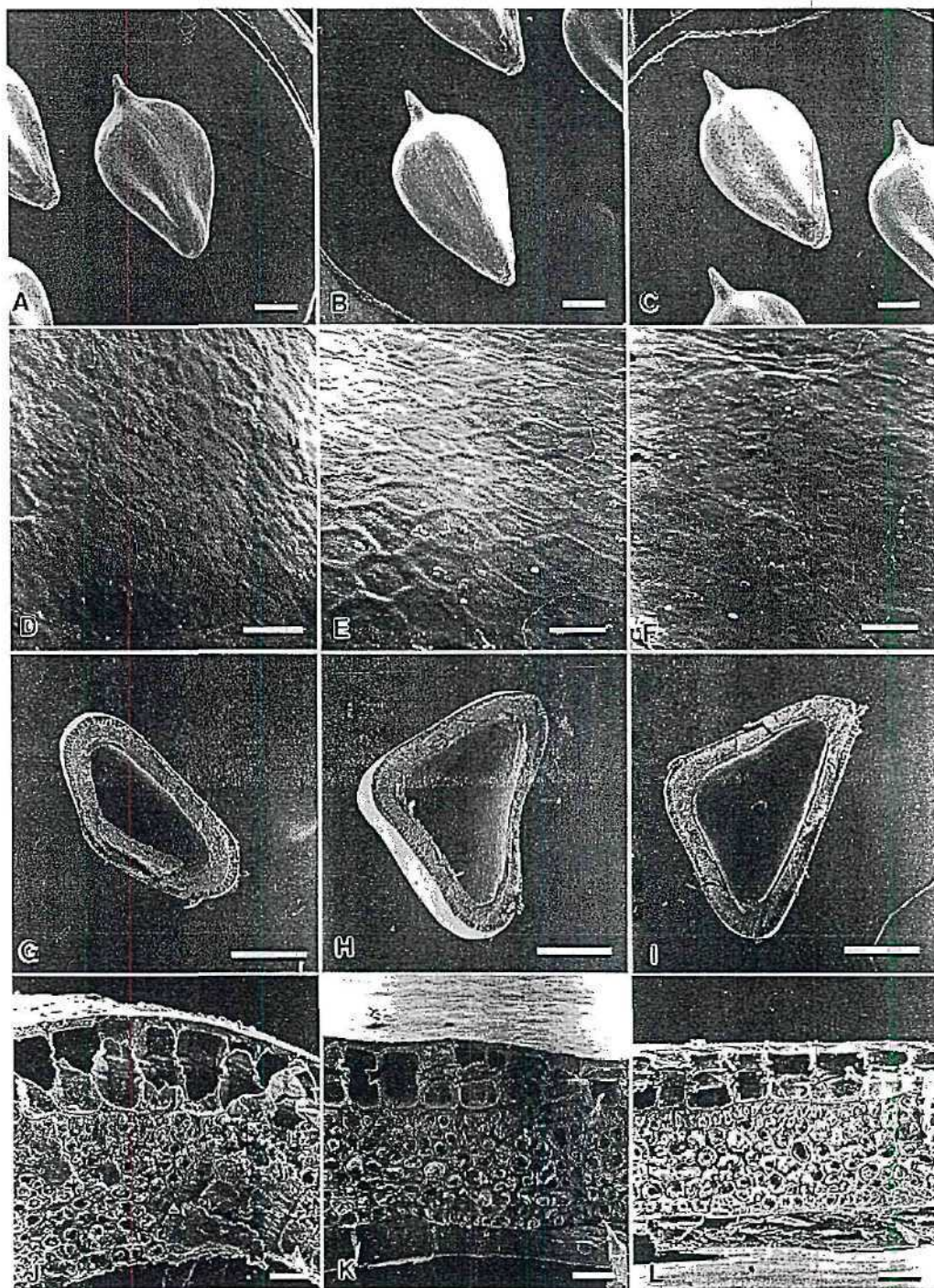


Fig. 5. *Bolboschoenus maritimus* (L.) Palla, Maastricht. — A–C: Achene abaxial view ($\times 20$, scale bar = 500 μm). — D–F: Exocarp surface ($\times 600$, scale bar = 25 μm). — G–I: Achenes in transverse section ($\times 40$, scale bar = 500 μm). — J–L: Detail of pericarp structure in transverse section ($\times 400$, scale bar = 25 μm).

across its known world distribution. In this context, it was considered advisable as a lateral aim, to investigate type specimens as a guide to the application of correct names and in so doing to establish a useful reference collection.

A second purpose was investigation of the inflorescence. Foundations of structure already well laid by earlier workers (Chapter 12) gave a sound basic knowledge and a revised terminology from which to consider the range of inflorescence structure known for representatives of *Bolboschoenus* on the African continent (variation from a solitary spikelet to an elaborate mop-like branched "head" carrying some 450 spikelets; incidentally the latter the most complex inflorescence known for the genus worldwide). Are the inflorescences of the same basic pattern throughout? Is the pattern, if only one, identical with either of the patterns already determined for *Schoenoplectus*? From structure, is straightforward explanation of inflorescence variability within single clones of *B. maritimus* s. l. possible? How useful in species delimitation among the African representatives is inflorescence form; are discontinuities recognizable or is there a sequence in which each taxon is represented by a wide range and these ranges overlapping? Attempts were made to answer these questions.

With Van der Veken's (1965: 317, Figure 37D, E) diagrams of embryo outline showing slight but recognizable interspecific differences and limited personal experience of differences in size and outline among the species of southern Africa as background, it seemed logical and worthwhile to pursue embryography. Despite its cryptic location and the time required for its extraction and preparation for observation, might the embryo provide critical interspecific differences useful in problems when identity is doubtful? Could embryography in any way reveal evidence of possible hybrid origin for any taxon within *Bolboschoenus*?

Embryographic investigation became a third aim, least cogent, and regarded only as a superficial surveillance because of underlying uncontrollable problems in obtaining suitable, comparable fruit samples.

In this concluding chapter an attempt is now made to consider objectively the general and more specific advances achieved from the study carried out in relation to set aims and purposes. Lastly are briefly outlined problems that require the attention of subsequent workers

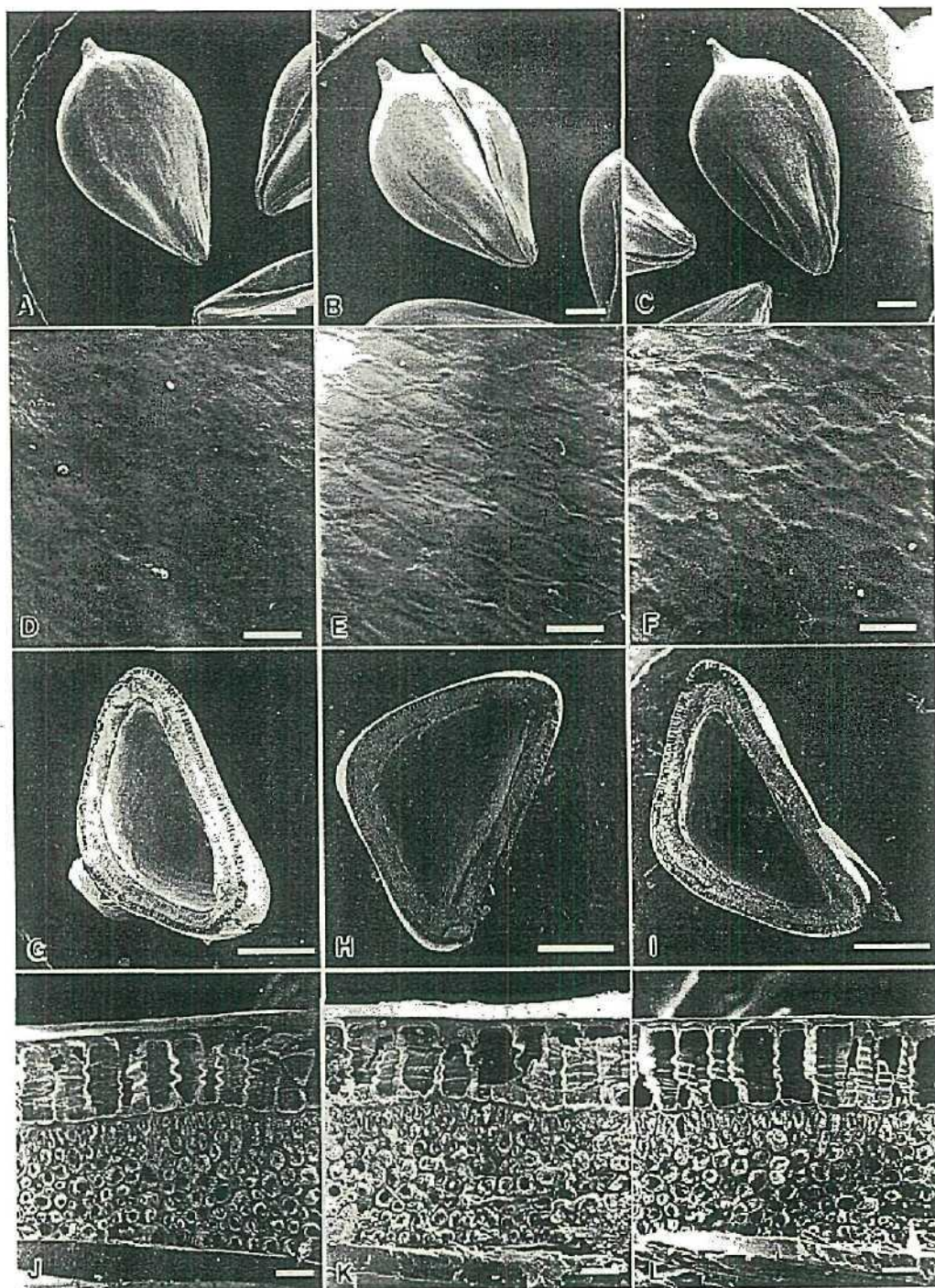


Fig. 6. *Bolboschoenus maritimus* (L.) Palla, Schoonhoven L1. — A–C: Achene abaxial view ($\times 20$, scale bar = 500 μm). — D–F: Exocarp surface ($\times 600$, scale bar = 25 μm). — G–I: Achenes in transverse section ($\times 40$, scale bar = 500 μm). — J–L: Detail of pericarp structure in transverse section ($\times 400$, scale bar = 25 μm).

if knowledge of the genus is to proceed.

Advances arising from study of the fruit

Micromorphological study of the surface of the nut and the anatomy of its pericarp is definitely advantageous as a guide to species delimitation. Amongst southern African plants, this study has served usefully in the differentiation of two entities within the previously widely defined *Bolboschoenus maritimus* s. l., namely *B. maritimus* s. s. and *B. glaucus*. Applied over the area of world distribution of the genus, it has aided the elucidation of *B. glaucus* as a taxon of subSaharan Africa and beyond to Mediterranean Africa, southern Europe, the Middle East and southern India. In consideration of North American representatives, micromorphological study of the fruit has usefully supplemented other grosser morphological criteria and permitted confirmation of some doubtful issues; in particular it has elucidated and emphasized similarities between *B. fluviatilis* and the Asian *B. yagara*. It has aided materially towards understanding that the northwest European and Scandinavian *B. maritimus* with radially expanded cylindric exocarp cells (*B. maritimus* s. s.) differs from some other European entities previously included within *B. maritimus* s. s., [for example *B. maritimus* subsp. *maritimus* sensu Casper & Krausch (1980) (Hroudová *et al.* 1997: 387)]. With the elucidation of species limits that its application has achieved, it has indirectly implemented distributional information, so that with recognition of the congruency of the Scandinavian *B. maritimus* s. s. with plants of the southwestern Cape, it has permitted speculation that these outliers owe their presence in this southern subcontinent to introduction. A comparable explanation is also speculated for the occasional presence of localised stands of *B. maritimus* s. s. on the northeastern coast of N. America (Figure 82).

Micromorphological examination of the fruit wall of lenticular nuts has shown the uniformity in construction of fruits of plants from Asia (*B. affinis*), North America (*B. paludosus*; syn. *B. maritimus* ssp. *paludosus*), Australia (*B. caldwellii*) and West Africa (*B. grandispicus*) [this last perhaps another introduction?]. Added to this list must be *B. planiculmis* (F. Schmidt) T.V. Egorova another Asian taxon presently urgently in need of taxonomic recircumscription and nomenclatural revision.

Verlorenvlei in southern Africa, namely, differences in achene outline shape, surface texture and markings and exocarp/mesocarp depth ratios. There was also a difference in achene colour, the achenes from inland freshwater habitats being noticeably darker than those from the coast, but no southern African examples were nearly black, so that the contrast between coastal and inland extremes was not as well marked as in the two groups from The Netherlands. Some differences between the set of samples from The Netherlands and the set from southern Africa warrant more detailed discussion, namely:

1. The variability within the The Netherlands samples.
2. The longer lengths of the The Netherlands achenes. The ranges recorded as length (including projecting apex) \times width, in mm, were: The Netherlands 3.0–4.8 \times 1.8–2.9
Verlorenvlei 2.6–3.5 \times 1.7–2.8
The lengths of achenes from Punt van Reide R7 (4.0–4.5) were not matched at Verlorenvlei where maximum recorded lengths were 3.1–3.5 for one coastal sample (no. 814).

In connection with these differences, we believe species sympatry for the two areas must be taken into account. Widely separated geographically and with different geological, climatic and biotic histories, we consider it unlikely that the western Cape Province has undergone the extent of habitat disturbance experienced in the area of collection in The Netherlands. We speculate that through past generations, introgression may have been more active in The Netherlands than in the Cape Province, resulting in increased variability within the taxon known as *Bolboschoenus maritimus* s. l. in the former country, as compared with the same taxon in the latter. Our deductions have been based on the information that follows.

For the Cape Province *Bolboschoenus maritimus* s. l. is known and *B. glaucus* (Lam.) S. G. Smith (Smith 1995: 101) only tentatively. *Bolboschoenus glaucus* is a species of eastern (and western?) tropical Africa, Madagascar, India and southwest Asia (not authoritatively known for Europe, except perhaps the eastern Mediterranean zone?). Achenes of African plants of *B. glaucus*

(studied as *B. maritimus*, Entity 2, see Browning & Gordon-Gray 1993: 314, fig. 2A, B and D and also in subsequent unpublished work) were found to have a very narrow exocarp, the cells not radially elongated, and the exocarp:mesocarp depth ratio about 1:4 to 1:6. The pericarp surface showed only faint traces of cell outlines, the cells not arranged in a defined 'honey-comb' pattern. Achenes were also of small size (2.4–3.3 \times 1.8–2.2 mm) (Browning & Gordon-Gray 1993: 316, table 1). These features are perhaps reflected in the achenes from Verlorenvlei as compared with the achenes from The Netherlands which are larger (see also Browning *et al.* 1995: 442, fig. 4, where a putative *B. maritimus* \times *glaucus* achene is illustrated).

In Europe, in addition to the variable *Bolboschoenus maritimus*, there has now been reported *B. yagara* (Ohwi) A. E. Kozhevnikov and putative hybrids between these species (Browning *et al.* 1996: 129). In eastern Asia (Eurasia?) there is *B. affinis* (Roth) Drobov, which Norlin (1972) regarded as differing from *B. maritimus* at sub-specific level only. Achenes from Maastricht (Fig. 5) are narrowly obovate in outline and triangular in transverse section; the exocarp in surface view shows raised anticlinal walls. These are characters of *B. yagara* and this relationship is borne out also in the exocarp:mesocarp depth ratio of the Maastricht achenes (compare Browning *et al.* 1996 fig. 11–L with Fig. 5 of the present paper). The Schoonhoven achenes (Figs. 6) are wider than those from Maastricht and have a pericarp anatomy resembling that of putative *B. maritimus* \times *yagara* hybrids (Browning *et al.* 1996, fig. 2A–L). The very large achenes from Punt van Reide R7 (The Netherlands) resemble *B. affinis* in their shape in transverse section (majority not markedly nor strongly trigonous, some lenticular) and in their colour (ochre to khaki, not dark brown).

CONCLUSIONS

Introgression through past generations may have contributed to the extensive variability in achene morphology in *Bolboschoenus maritimus* s. l. observed in The Netherlands, as compared with

Along with these advances has been amplification of features of fruit wall surface and pericarp anatomy of type specimens whenever these carried approximately mature fruits, samples of which were made available for study by the kindly cooperation of directors of curating herbaria.

As an outcome of this fruit wall study worldwide that has supplemented previously accumulated morphological information, the genus *Bolboschoenus* appears to fall into two main groups, one of which is further divisible into two subgroups. At the present stage of knowledge these units are of course speculative and are given no formal taxonomic status.

Figure 82 illustrates their main characteristics, namely:

1. nuts lenticular (plane surfaces convex or concave), elliptic in outline, bearing 2-branched styles and caducous perianth bristles; nut surface marked by "honeycomb" cell patterning; in transverse section the exocarp cells radially elongate, larger and deeper over the angles than across the plane surfaces, lacking silica deposits.
2. nuts trigonous (angles usually sharply defined) narrowly elliptic to elliptic-obovate in outline, bearing uniformly 3-branched styles and persistent perianth bristles; nut surface smooth to faintly cell patterned (never "honeycomb"); in transverse section the exocarp cells not radially elongate, more or less uniformly isodiametric (square to slightly laterally oblong, with silica deposits).

There is a third, apparently "intermediate" linking group, in which is expressed greater morphological variability than is present in either 1 or 2 above. Its main characteristics are:

3. nuts predominantly trigonous, variable with abaxial angle clearly defined to broadly rounded, often one to several lenticular present within a spikelet or clone, variable in outline form from narrowly elliptic-obovate to broadly obovate, bearing predominantly 3-branched styles with some to about half two-branched within a spikelet; perianth bristles variable in persistence on the nut; surface variable (in some cases within a single nut) silica sometimes present.

The composition of this third group includes two species that studies in America and Australia respectively have given a basis for interpretation as of possible hybrid origin, namely *B. novae-angliae* (Browning *et al.* 1995: 434--435) and *B. medianus* (Browning *et al.* 1997a: 57). Also included, however, are two species that, apart from the occurrence of two-branched and three-branched styles within individual spikelets, do not express sufficient evidence in their morphological form to permit speculation as being of possible hybrid origin. These are *B. robustus*, a species known only from the Americas, and the problematical *B.*

the relative uniformity observed for achenes of the same taxon in a southern African wetland. In this speculated genetic interchange, species sympatry must have been influential, as also extent of habitat disturbance, perhaps as major factors. However, this is by no means an adequate explanation and does not effectively account for the differences observed in pericarp anatomy for coastal and inland achenes in both The Netherlands and southern Africa. That these structural differences in achenes are correlated with differences in inflorescence form, which in turn are related to salinity levels in the microhabitat, suggests there are in operation ecological effects, as yet it would seem, poorly understood, that act upon, either directly, or more covertly by gradual selection, changes brought about by generic recombination.

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Browning, J., Gordon-Gray, K.D. and van Staden, J.

***Bolboschoenus maritimus* s.l. in a southern African Wetland, Verlorenvlei.**

Scripta Bot. Belg. 15,: 33. eds E. Smets, L.P. Ronse Ducrene and E. Robbrecht.
(Proceedings of 13th Symposium Morphology, Anatomy and Systematics.)

maritimus s. l. The latter is widely variable, which may in part be attributable to the inclusion within its presently defined limits of elements better excluded: as a complex it is certainly in need of detailed study throughout its range.

Considered from the standpoint of distribution (Figure 82), the first group with two-branched styles and lenticular nuts is circumPacific with but few outliers, namely extension into Pakistan and the Caspian area of Eurasia and perhaps into eastern Europe, and West Africa and offshore islands (thought to be introduced in West Africa, but this not proven). The second group with three-branched styles and trigonous nuts falls into two sub-divisions; the one predominantly African and Indian with extension into Mediterranean Europe, the Middle East, Turkey, Turkmenistan, Uzbekistan, Afghanistan, Pakistan and Kazakhstan (*B. glaucus*, and with distribution only in western, southern Africa, *B. nobilis*); the other subdivision is also circumPacific, but poorly represented in S. America (*B. robustus* only) which continent is however, still poorly investigated floristically. *B. fluviatilis* / *B. yagara* in their morphological similarity with *B. glaucus* / *B. nobilis* are suggestive of being the northern (?) counterpart of the African/Indian (Gondwanan ?) southern (?) *B. glaucus* / *B. nobilis* subgroup. The third intermediate group appears, in a sense, superimposed upon the "primary" distribution pattern already outlined. *B. novae-angliae* is "definitely known only from Atlantic coastal estuaries where it is sympatric with *B. fluviatilis*, *B. maritimus* and *B. robustus* over much of its range" (Browning *et al.* 1995: 434). *B. robustus* has been confused with *B. maritimus* "by many western N. American authors" (Browning *et al.* 1995: 443). *B. medianus* is eastern Australian and New Zealand where it is sympatric with *B. caldwellii* and *B. fluviatilis*. In distribution, as in its taxonomic limits and nomenclature, *B. maritimus s. l.* is problematic. It has been reported by many authors for Russia and north eastern Asia, where it may, or may not, be present when more precisely circumscribed taxonomically. Up to now *B. maritimus* has been almost synonymous with the presence of *Bolboschoenus* (*Scirpus*, section *Bolboschoenus*) as a genus, the name *maritimus* serving as a repository for a complex of variable entities. Its main distributional area (Figure 82) is western Europe and Scandinavia, from where it appears to have been distributed to western north Africa, western South Africa and the Atlantic coast of N. America. It is predominantly in the northern hemisphere.

This interpretation of world distribution of *Bolboschoenus* is incomplete because large areas, in particular northern Eurasia, Canada and South America remain inadequately known to the present author. What has been written (including Figure 82) may eventually prove to be oversimplification with omissions and errors. It is given here as a beginning upon which to build and to refine. So also the preliminary plan of groups within the genus. Both these have "grown" as it were, from study of the fruit examined micromorphologically in conjunction with attention being given to all other morphological features of the plants.

Advances arising from study of the inflorescence

Investigation of inflorescence structure of African representatives of *Bolboschoenus* has shown there to be one basic plan of construction in which intraprophyllate paracladia are not developed. This plan of construction is well represented in *Schoenoplectus*. As far as it has been possible to determine, and there are limitations as inflorescences of the American and Asian *B. fluviatilis* / *B. yagara* have not been considered, there is therefore no feature of the *Bolboschoenus* inflorescence that serves in its generic distinction from *Schoenoplectus*.

The pattern of construction is a "flexible" one, which by the development, or not, of branch buds, permits a range of inflorescence form and size within a single genotype. The range actually expressed during any one reproductive phase is dependent, it would seem, upon many factors, some of these internal, for example, the extent of food reserve within the reproducing parental organism; others more directly external, for example season conditions, including among many others the possibility of inundation during floral initiation. Therefore inflorescence form is influenced by overall conditions, edaphic, climatic and the state of the reproducing organism itself, particularly its degree of maturity and its history of conditions of survival; so, at any one time there is likely to be a particular inflorescence form predominant within a range for an individual clone and for the population of which the clone is a representative. The range in inflorescence form reported for clones, populations and infraspecific taxa within *B. maritimus* s. l. is therefore quite acceptable as natural variability. However, the "flexibility" does impose a warning on reliance being placed by the taxonomist on inflorescence form as a guide in species delimitation. The survey carried out for this

dissertation has served to show that amongst African species at least, there are no clear-cut discontinuities in inflorescence form: rather there is a series from large plants located in habitats with a more or less continuous growing season that, because of the extent of food reserves, produce large, compound inflorescences carrying many spikelets (*B. nobilis*) to much smaller plants, limited in some way(s) by adverse growing seasons that reach their simplest inflorescence expression in the development of solitary spikelets (*B. grandispicus*, *B. maritimus* s. l.). Within this overall range taxa occupy "zones" that are themselves not fixed and which usually incorporate overlap from one taxon to another. It stands to reason that extremes of the overall range are likely to be discontinuous and distinctive.

Advances arising from embryography study

Evidence from the limited investigations carried out has reinforced previous conclusions that embryo profile outline as seen in sagittal, optical section may differ among species. These variations are slight and considering problems of extraction from fruits and, in some taxa, of obtaining fruits at all, embryo shape and dimensions must be considered impractical as a means of species delimitation. Nevertheless, embryos extracted from fruits of putative hybrid populations offer some possibility of: 1. evidence in support of hybrid origin; 2. the detection of putative parental affinities. Such evidence at this stage is tentative indeed, but in study of embryos extracted from populations from the Netherlands it was possible to detect in their outline profiles resemblance to the Asian *B. yagara*. The population samples also gave evidence that the putative hybrid species *B. medianus* had a low percentage ($\pm 36\%$) of fully formed embryos, as did the inland Verlorenvlei ($\pm 48\%$) and the Nieuwoudtville samples ($\pm 53\%$) of *B. maritimus* s. l. These results must, however, be contrasted with the Orange River Estuary population of *B. maritimus* s. s. which gave 100% perfect embryos, and the coastal Verlorenvlei population (*B. maritimus* s. s.) also with a high percentage ($\pm 83\%$). There are many factors that may govern these differences; not every interspecific cross necessarily results in genetic imbalance and resultant poor embryo development; time also plays a factor, for in plants capable of vegetative propagation, as with *Bolboschoenus*, genetic balance after hybridisation may gradually be regained. It is possible that if *B. maritimus* is of hybrid origin (an allopolyploid) it has regained a good level of genetic balance, unlike *B. medianus*. This

Bolboschoenus yagara (Cyperaceae) newly reported for Europe

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We report the Asian species *Bolboschoenus yagara* (Ohwi) A. E. Kozhevnikov (Cyperaceae) from Europe, where only *B. maritimus* (L.) Palla has previously been recorded. Critical differences between these species lie mainly in achene structure, particularly anatomy of the pericarp, and in the persistence of the perianth bristles on the achenes, which we illustrate with SEM micrographs. We also report putative hybrids (*B. maritimus* × *yagara*) on grounds of the intermediate structure of the achenes. The presence of *B. yagara* and hybrids in Europe bears on the typification of *Scirpus maritimus* L., which is problematic. We recognize *B. affinis* (Roth) Drobov pending further research.

Key words: *Bolboschoenus affinis*, *B. maritimus*, *B. yagara*, Cyperaceae, Europe, *Scirpus*, taxonomy

INTRODUCTION

Bolboschoenus (Ascherson) Palla is herein accepted as a distinct genus following Goetghebeur and Simpson (1991). *Bolboschoenus* is taxonomically difficult (Wilson 1981, Goetghebeur & Simpson

1991), in part because of the paucity of reliable macromorphological features available for infrageneric classification. In particular, *B. maritimus* (L.) Palla is differently constituted by different workers in different parts of its range on several continents (e.g., Koyama 1958, 1980, Browning *et al.* 1995). Norlindh's (1972) valuable account for Eurasia drew

does not, however, account for the low percentage of perfect embryos from the inland Verlorenvlei population. At present there are far too many unknowns for the embryography carried out to be more than suggestive. If it is to be proceeded with, it must be accompanied by karyological studies of individual clones that will give information on chromosomal complements and details of meiotic pairings. Karyological studies within the genus, essentially with careful preservation of voucher specimens, will add considerably to knowledge available to the taxonomist.

Problems outstanding

It is obvious that the work that has been done is in many ways incomplete or preliminary so that there are problems revealed that require extensive and intensive further study.

1. Taxonomy and Nomenclature

Paramount among these is the need for the taxonomic revision of *Bolboschoenus* worldwide with due attention being given to nomenclature. As the main aims and purposes of the present study were not revisionary some policy had to be adopted for the application of names to taxa. Locally applied names have been used; problems of synonymy have not been pursued. This has led to what perhaps may be considered inconsistencies and shortcomings. Examples follow.

(i). *B. fluviatilis* and *B. yagara*

In this dissertation the name *B. fluviatilis* has been used for American and Australian plants, whereas for Asia the taxon has been termed *B. yagara*. From my preliminary surveillance, I conclude the Australian entity agrees better with its Asian rather than with its American counterpart. Figure 81 shows nuts of these taxa in colour. There are differences in size and in pericarp colouration, but the overall similarity is undeniable.

(ii). *B. grandispicus* and *B. affinis*

attention to the variability of the inflorescence, the number of style branches, and the shape of the achenes, all of which have been used frequently in the delimitation of *B. maritimus* or its infraspecific taxa. Because of the variability he found, Norlindh doubted the value of these characters in the definition of species. Robertus-Koster (1969) illustrated the variability in achene shape for populations in Holland. Browning and Gordon-Gray (1993), following initial work by Oteng-Yeboah (1974), showed that S African plants, previously collectively identified as *Bolboschoenus maritimus* (Browning & Gordon-Gray 1992), were divisible into two entities on the basis of gross morphology of the achenes, pericarp anatomy, and the persistence of the perianth bristles on the shed achenes. Subsequently Browning *et al.* (1995) used these criteria to help clarify the species limits within *Bolboschoenus*, including *B. maritimus*, in the area of the Flora of North America (FNA). They showed that *B. maritimus* and *B. robustus* (Pursh) Soják may be clearly distinguished from other North American species on the basis of achene structure and the non-persistence of perianth bristles on the achenes.

In W Europe, most taxonomists in recent years have recognized only one species in *Bolboschoenus*, namely, *Scirpus (Bolboschoenus) maritimus* (e.g. Ascherson & Graebner 1904, Suessenguth 1939, Hermann 1956, Schultze-Motel 1967, Robertus-Koster 1969, Casper & Krausch 1980). They included within the limits of *S. maritimus* plants with capitate to open inflorescences, bifid or trifid styles, and lenticular to trigonous achenes with caducous to attached perianth bristles. Several authors have also pointed out that *B. maritimus* occurs both in saline to brackish (maritime and inland) habitats and in fresh-water inland habitats in Europe as described by Hejny (1960), Schultze-Motel (1967), Robertus-Koster (1969) and Casper and Krausch (1980). In Flora Europaea, DeFilipps (1980) recognized only *Scirpus maritimus* but with two subspecies, namely subsp. *maritimus* with "reddish or dark brown glumes [and] nut plano-convex or trigonous", and subsp. *affinis* (Roth) T. Norlindh, with "glumes whitish-yellow, stramineous or silvery membranous [and] nut lenticular". This interpretation clearly follows that of Norlindh (1972), who stated that he considered *Scirpus affinis* Roth to be only a geographical race of *S. maritimus*. We herein recognize *Bolboschoenus affinis* (Roth) Drobov pending further research. For

E Europe and Asia a greater number of species are generally recognised, but there are differences of opinion (e.g. Koyama 1958, 1980, Ohwi 1965, Egorova 1976a, 1976b, Hultén & Fries 1986, Kozhevnikov 1988); nor is the taxonomy of the genus stabilized in Africa (Browning & Gordon-Gray 1992, 1993); in North America (e.g. Browning *et al.* 1995); and in the S Pacific (e.g. Wilson 1981).

Bolboschoenus yagara (Ohwi) A. E. Kozhevnikov (basionym *Scirpus yagara* Ohwi: type from Japan, Kyoto, Ohwi 9238; holotype KYO, isotype TNS) has previously been reported only from Asia (Koyama 1958, 1980, Hultén & Fries 1986, Kozhevnikov 1988). Koyama (1958, 1980) reduced *B. yagara* to *Scirpus (Bolboschoenus) fluviatilis* var. / subsp. *yagara* and Ohwi (1965) placed it in synonymy under *Scirpus fluviatilis*. Other authors (e.g. Hultén & Fries 1986), however, treat *B. yagara* as a distinct species restricted to Asia and *B. fluviatilis* restricted to North America. In this paper we treat *B. yagara* as a species distinct from *B. fluviatilis* pending further research.

Bolboschoenus yagara, as characterised by Koyama (1958, 1980) and Ohwi (1965), differs from *B. maritimus* and *B. affinis*. Distinguishing features are outlined in the summary that follows. The differences distinguishing *B. yagara* and *B. fluviatilis* from *B. maritimus* and *B. affinis* appear to be more strongly marked in our opinion than are the differences that distinguish *B. fluviatilis* from *B. yagara* and *B. maritimus* from *B. affinis*. All these taxa require more extensive study.

Bolboschoenus yagara: Inflorescence compound or rarely head-like, usually with 3–8 branches each carrying 2 or 3 spikelets; glumes reddish to darker brown; perianth bristles rather strong, remaining attached to mature achenes, mostly ca. equalling achene; styles trifid; achenes nearly equilaterally strongly trigonous, apex tapered to a stout beak 0.2–0.6 mm long.

Bolboschoenus fluviatilis differs from *B. yagara* mainly in its larger overall plant size and in its larger achenes. Achene sizes as given by Koyama (1980) are 2.5–3.5 × 1.8–2.2 mm for *B. fluviatilis* subsp. *yagara* and 3.8–4.2 × 2.0–2.5 mm for subsp. *fluviatilis*; Browning *et al.* (1995) give 3.8–5.5 × 2.0–2.9 mm for North American *B. fluviatilis*.

Bolboschoenus maritimus: Inflorescence head-like or with 1 or 2 short branches; glumes reddish or dark brown; perianth bristles weak, caducous. to

Consideration of types and of a limited range of herbarium specimens revealed no reliable morphological characters on which to distinguish these species. Nevertheless, West African plants are named *B. grandispicus*, those from Asia *B. affinis*.

(iii). *B. maritimus*

Plants from coastal habitats in western southern Africa have been segregated as *B. maritimus* s. s. as they conform with plants from Sweden (Roslagen), the type locality designated by Linnaeus (1753: 75). Plants from inland habitats in southern Africa and other parts of the distributional range of the species, which differ somewhat in pericarp construction, have been named in the wider sense (*B. maritimus* s. l.), but the species as a whole requires further careful study before these designations can be accepted with confidence; particularly does *B. maritimus* s. l. remain problematical in eastern Europe and Asia.

2. Natural hybridisation

Another major question requiring investigation is that of the role of hybridisation in the history of the genus, particularly as a means of speciation. Considered morphologically there is evidence that *B. novae-angliae* in America (*B. robustus* x *B. fluviatilis*) and *B. medianus* in Australia (*B. caldwellii* x *B. fluviatilis*) are both of putative hybrid origin. Evidence, gradually accumulating, is suggestive that natural hybridisation may take place without restriction within the genus wherever sympatry permits. From this it may be implied that reproductive isolating mechanisms are not effective, or operate only at low levels of efficiency (Browning *et al.* 1995: 443). Within this context *B. maritimus* s. l. is of special concern. Its variability in differing parts of its range is notable and well reported by numerous authors who, from time to time, have established many infraspecific (and specific) names to accommodate the differences observed. These names, or some of them, and the structural variations they reflect, are beginning to have significance in the possibility that *B. maritimus* s. l. is perhaps a plexus, a product of introgression. Evidence for this relies to some extent upon characters of the nut (outline shape and volumetric configuration, colour), the pericarp (surface and anatomy) and the persistence or not of the perianth bristles. In Europe species that seem to have contributed

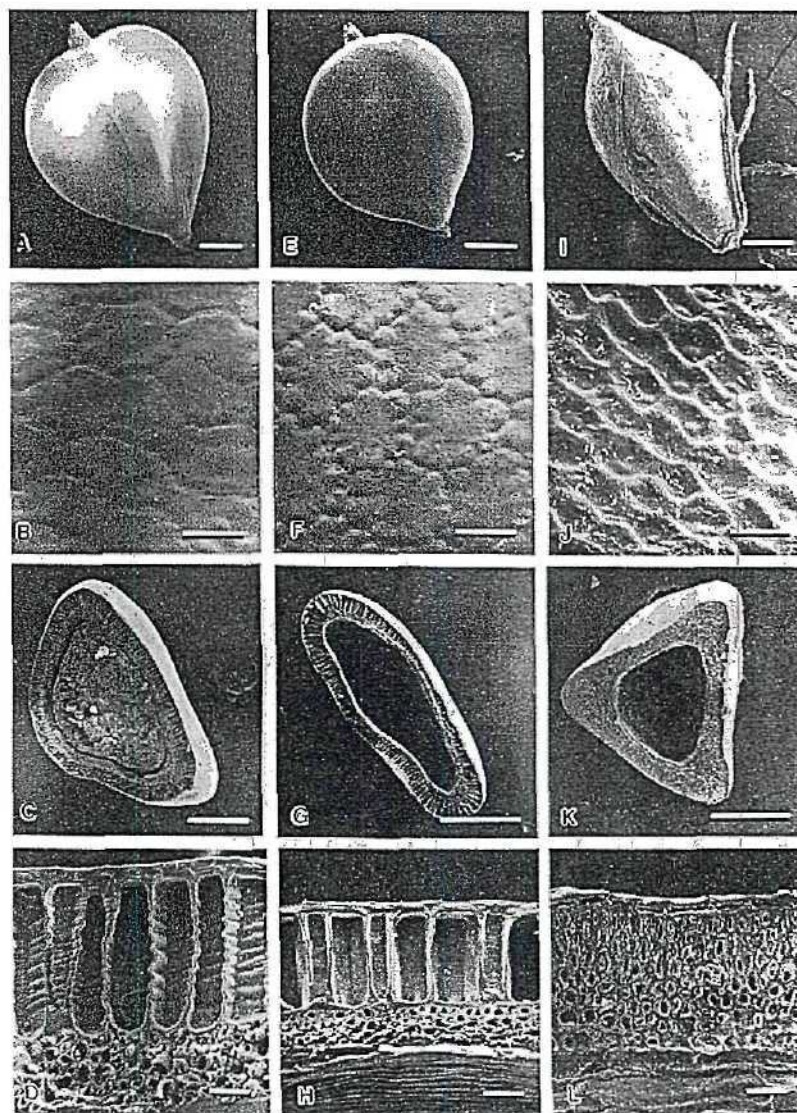


Fig. 1. Scanning electron micrographs of achenes. — A–D: *Bolboschoenus maritimus* (L.) Palla (from Nilsson 9515, H). — E–H: *B. affinis* (Roth) Drobov (from Kukkonen 12727, H). — I–L: *B. yagara* (Ohwi) A. E. Kozhevnikov (from Baenitz II Lf. 109, MO). — A, E, I: Abaxial views. B, F, J: Surfaces of exocarp. C, G, K: Transverse sections. D, H, L: Transverse sections of pericarp, exocarp at top. Scale bars: A, C, E, G, I, K = 500 µm. B, D, F, H, J, L = 25 µm.

about 2/3 of achene length; styles bifid, or trifid, or variable in a spikelet; achenes flattened, plano-convex to biconvex to obscurely trigonous to trigonous, apex abruptly contracted to a mucro 0.2–0.4 mm long. Almost all plants of *B. maritimus* in North America have bifid styles and plano-convex to lenticular achenes (Browning *et al.* 1995), and all of the rather few specimens we have seen from Asia and South America on which style number or achenes can be observed are digynous. In contrast, trifid styles and trigonous achenes are more common in Europe and in Africa (Browning *et al.* 1995).

According to Norlindh (1972), and our unpublished observations of a limited number of speci-

mens, *Bolboschoenus affinis* differs from *B. maritimus* mainly in its smaller overall plant size; its pale whitish-yellow, stramineous or silvery membranous glumes (generally bright brown in *B. maritimus*); and its consistently bifid styles and lenticular achenes.

The purposes of this paper are to show 1) that *Bolboschoenus yagara* occurs in Europe; 2) that it has previously been incorporated within *B. maritimus* there; 3) that *B. maritimus* and *B. yagara* may readily be distinguished by characters of the achene surface and pericarp anatomy in addition to the gross morphological characters given above; 4) and that the problem of species differentiation in W Europe is exacerbated by the presence of putative *B. mari-*

genetically are *B. yagara*, and *B. affinis* as an example of one of the taxa of the two-branched stylar group; *B. planiculmis* is another possibility; in southern Africa, *B. glaucus* may have been another contributor.

With DNA analysis now an established technique, it may become possible to investigate these speculations and eventually to obtain more precise knowledge of *B. maritimus*, its associated species and their histories and in time to establish with certainty the generic independence of *Bolboschoenus*.

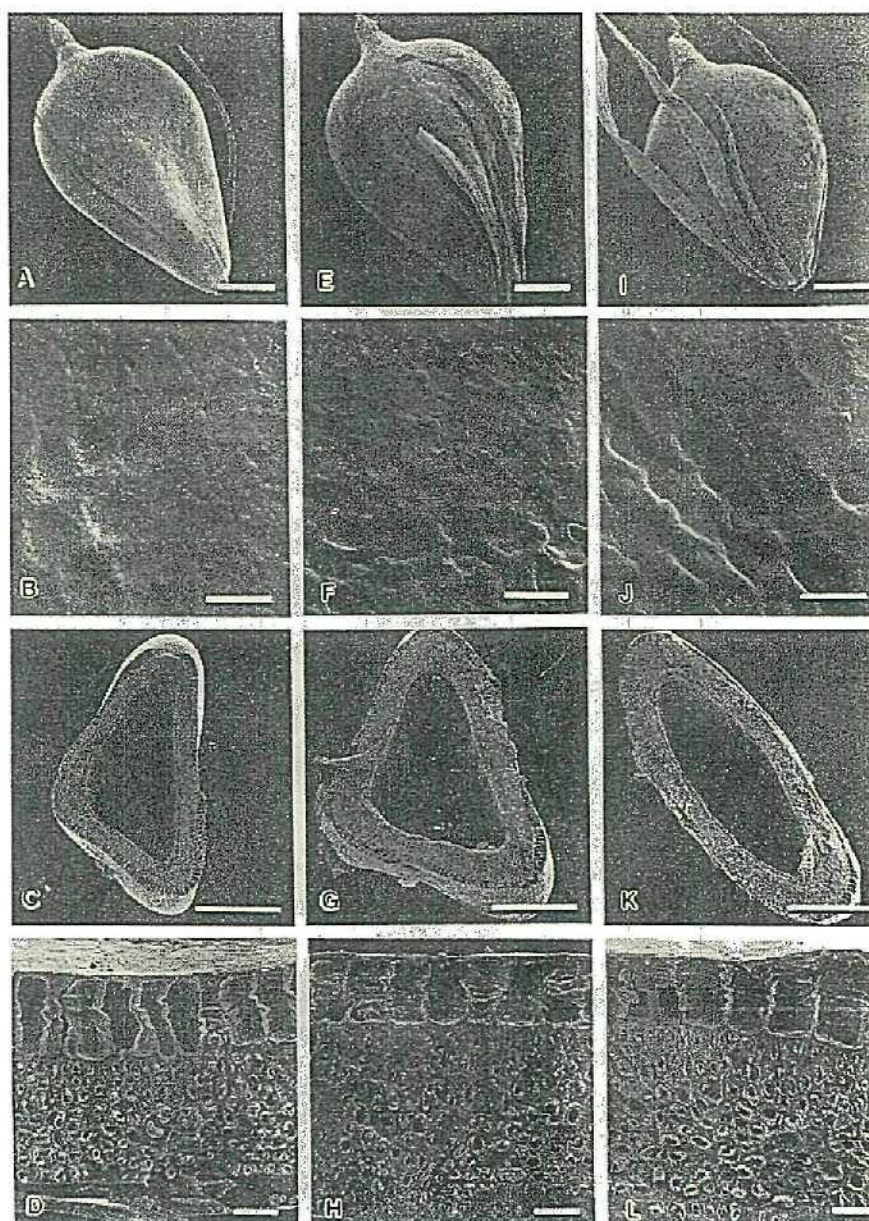


Fig. 2. Scanning electron micrographs of achenes of putative *Bolboschoenus maritimus* (L.) Palla x *yagara* (Ohwi) A. E. Kozhevnikov hybrids. — A–D: (from *Firket s.n.*, WIS) — E–L: Trigonous and lenticular achenes (from *Schuhwerk 7039/2*, NY). — A, E, I: Abaxial views. B, F, J: Surfaces of exocarp. C, G, K: Transverse sections. D, H, L: Transverse sections of pericarp, exocarp at top; endocarp not visible in H and L. Scale bars: A, C, E, G, I, K = 500 µm. B, D, F, H, J, L = 25 µm.

timus x *yagara* hybrids which are recognizable as such on the basis of their achene morphology.

MATERIALS AND METHODS

We selected fruiting specimens labelled as *Bolboschoenus/Scirpus maritimus* from the Eurasian material at the following herbaria: MO, NU, NY, WIS, and in addition some fruits were provided by GENT, H and NU. We compared the European specimens with specimens from China, Japan and far E Russia, two of which Koyama identified as *B. fluvialis* subsp. *yagara*. We studied some achenes from these specimens with

dissecting microscopes and others using SEM at the University of Natal, Pietermaritzburg, according to the methods described by Browning and Gordon-Gray (1993). We identified the specimens using the diagnostic characteristics of the achenes as described by taxonomists. Data on these collections are given at the end of this paper.

RESULTS

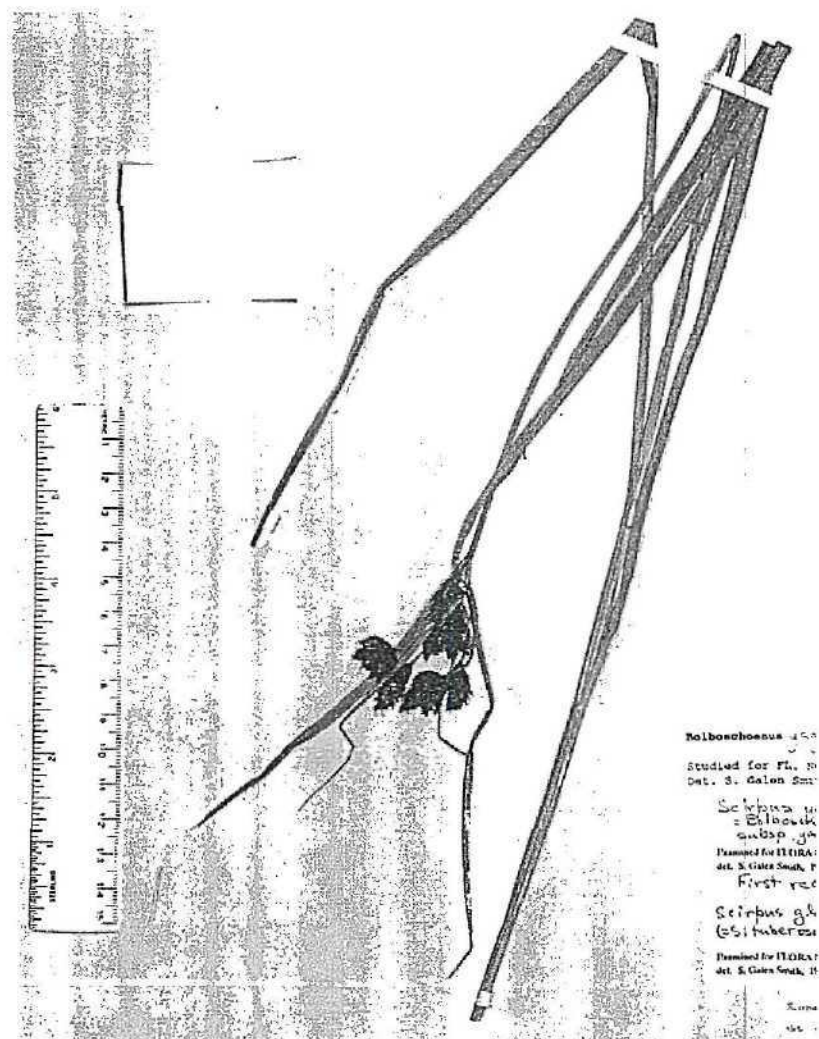
Figs. 1 and 2 illustrate features of fruit gross morphology and pericarp anatomy of *Bolboschoenus*

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Fig. 3. Photograph of the herbarium specimen of *Baenitz II Lf. 109* (MO), from which the achene illustrated in Fig. 1 was extracted.



maritimus, *B. affinis*, *B. yagara*, and putative *B. maritimus* x *yagara* hybrids. Figs. 3 and 4 show photographs of herbarium specimens of European *B. yagara* and a putative *B. maritimus* x *yagara* hybrid. We identified the European specimens as follows:

- 1) Two sheets of one collection (*Baenitz Lf. II. 109*, Germany) as *Bolboschoenus yagara*. A photograph of the specimen from which we studied the achenes with SEM is shown in Fig. 3 and its achene structure is shown in the SEM micrographs in Fig. 1I–L.
- 2) Five specimens as putative *Bolboschoenus maritimus* x *yagara* hybrids. A photograph of one of these (*Schuhwerk 7039/2*, Germany) is shown in Fig. 4 and the achene structures of three of them are shown in Fig. 2E–L.
- 3) Many specimens as *Bolboschoenus maritimus*. The achene structure of one specimen (*Nilsson 9515*, Sweden) is shown in Fig. 1A–D.
- 4) Some specimens from Caucasia as *Bolboschoenus affinis*. The achene structure of one of these (*Kukkonen 12727*, Azerbaijan) is shown in Fig. 1E–H.

The main achene and perianth bristle characteristics of the three taxa as shown in Fig. 1 are:

- 1) The bristles are not persistent on the mature achenes in *Bolboschoenus maritimus* and *B. affinis* but are persistent in *B. yagara*.
- 2) The outline of the achenes is usually broadly

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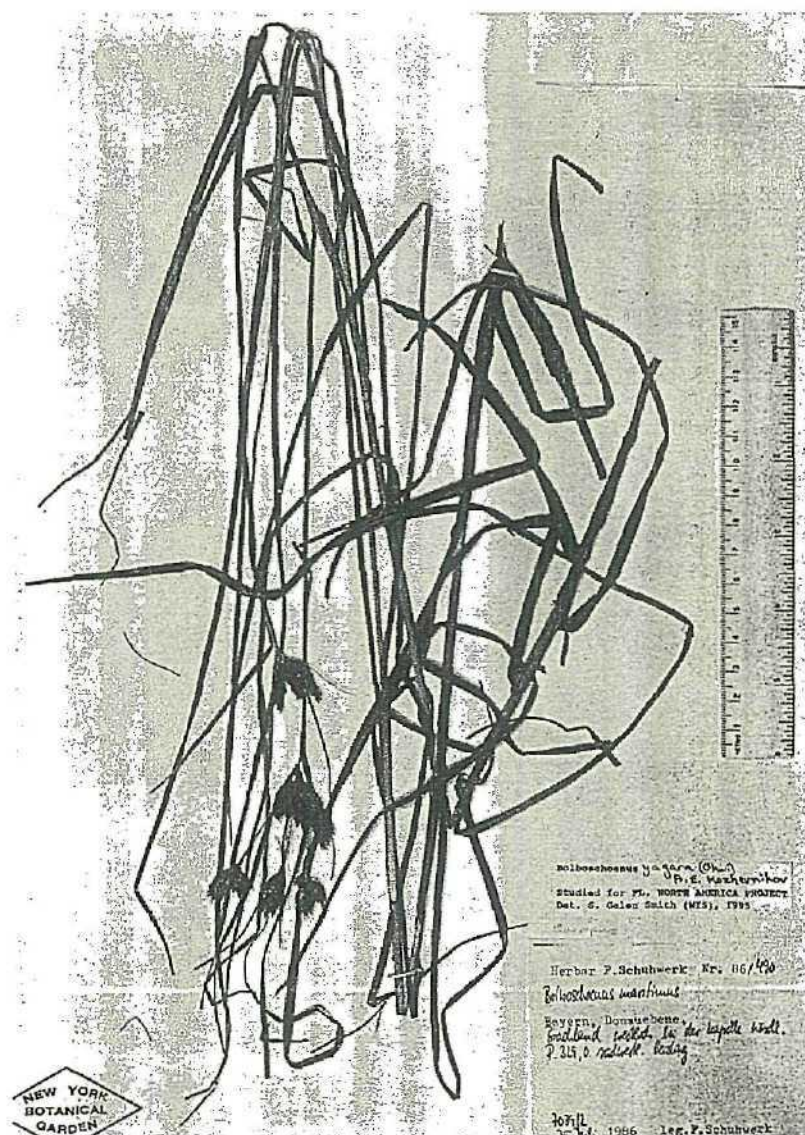


Fig. 4. Photograph of the herbarium specimen of *Schuhwerk 7039/2* (NY), from which the achenes illustrated in Fig. 2 were extracted.

obovate with summit rounded or truncate narrowing to a slender mucro in *Bolboschoenus maritimus* and *B. affinis* but is narrowly obovate with summit tapered in *B. yagara*.

- 3) The achenes are lenticular in *Bolboschoenus affinis*, vary from compressed-trigonus (as in the specimen illustrated herein) to lenticular in *B. maritimus*, and are nearly equilaterally trigonus in *B. yagara*.
- 4) Several details of the sculpturing of the achene surface differ in the three taxa.
- 5) In the pericarp anatomy, the exocarp (epidermis)

is very deep and the mesocarp very shallow in *Bolboschoenus maritimus* and *B. affinis*, while the exocarp is very shallow and the mesocarp very deep in *B. yagara*.

The fruit gross morphology, surface features, and pericarp anatomy of putative *Bolboschoenus maritimus* x *yagara* hybrids as seen in electron micrographs (Fig. 2) are intermediate between those of *B. yagara* and *B. maritimus* as shown in Fig. 1. Note that in *Schuhwerk 7039/2* (Fig. 2E–L) both trigonus and lenticular achenes occurred; in the other four specimens the achenes examined were all trigonus.

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The main characteristics of the putative hybrids as shown in Fig. 2 are:

- 1) The perianth bristles (Fig. 2A, E, I) are present but not always firmly attached.
- 2) The achene outline (Fig. 2A, E, I) is intermediate between that of *Bolboschoenus maritimus* and *B. yagara*.
- 3) The achene shape in transverse section (Fig. 2C, G, K) is compressed-trigonous with low rounded abaxial angle or sometimes lenticular.
- 4) The sculpturing of the achene surface is variable (Fig. 2B, F, J).
- 5) As seen in transverse section, the relative thickness of the exocarp (epidermis) and the mesocarp differ in the putative hybrids as compared with those of *Bolboschoenus maritimus* and *B. yagara* (contrast Fig. 2D, H, L with Figs. 1D, H, L.).

The main features of the inflorescences of *Bolboschoenus yagara* and putative *B. maritimus* x *yagara* hybrids are illustrated in Figs. 3 and 4.

DISCUSSION AND CONCLUSIONS

Critical differences between *Bolboschoenus maritimus* and *B. yagara* lie in their achene structure and the persistence of perianth bristles on the achene at time of its shedding from the spikelet. The following additional differences are less reliable because of infraspecific variation but are useful in making provisional identifications when specimens lack mature achenes: 1) The inflorescence in *B. maritimus* varies from capitate (branches lacking) to open with branches ca. 4 and generally with less than half of the spikelets on branches, while in *B. yagara* it is open with branches ca. 3–9 and with more than half of the spikelets on branches. 2) The summits of the leaf sheath orifices of *B. maritimus* usually have the veins diverging below the summit leaving a V-shaped membranous or hyaline area, while those of *B. yagara* have veins reaching nearly to the summit and anastomosing there.

The specimens that show intermediate achene structure (Fig. 2) we hypothesize as being *Bolboschoenus maritimus* x *yagara* hybrids. This concept is supported by the variability of the achene cross-section shape (*Schuhwerk* 7039/2), and in the achene surface. There are also differences in

the relative thicknesses of exocarp and mesocarp as shown in transverse sections of the pericarp. This intermediacy is very similar to that of the achenes of the North American *B. novae-angliae* (Britton) S. G. Smith, which we hypothesized is derived from *B. fluviatilis* x *robustus* hybrids (Browning *et al.* 1995).

The presence of *Bolboschoenus yagara* and putative hybrids in Europe is especially important because all of the existing original elements (specimens and illustrations) of *Scirpus maritimus* may belong to *B. yagara* or *B. maritimus* x *yagara* hybrids or to other species. Typification will be dealt with in another paper by I. Kukkonen, S. G. Smith and others.

Fruiting specimens studied (those illustrated in scanning electron micrographs herein are indicated by SEM). — *Bolboschoenus yagara*. Germany. Görlitz, leg. Baenitz, in Nord- und Mitteldeutschlands Juncaceen und Cyperaceen Lief. 2: 109 (MO) [SEM]. Russia. "Fl. Amur.", Pavlenko 2791 (MO) and Pavlenko 5003 (MO, WIS). China. Kiangsu Prov., Nanking, 1922, Merrill 11426 (NSW, NY). Japan. 1914, Makino s.n. (MO). Putative *Bolboschoenus maritimus* x *yagara* hybrids. Belgium. Bords de la Meuse à la Visé, 1872, Firket s.n. ex Herb. Thielens (WIS) [SEM]. Germany. West-Prussia, Tiegenhof, 1900, Gross s.n. (NY); Bayern, Donauebene, 1986, Schuhwerk 7039/2 (NY) [SEM]; Gras-Herbarium No. 12, Wagner s.n. (NY); Frankfurt, 1820, Engelmann s.n. (MO). *Bolboschoenus maritimus*. Finland. Regio aböensis (Ab), Askainen, 1972, Hinneri & Laine s.n. (NU). Sweden. Gotland, Östergarn parish, Herrvik, Natviksudden, 1994, L.A. Nilsson s.n. (NU); E Uppland (Roslagen), par. Börstill, 2 km W Kallö. 1995, Ö. Nilsson 9515 (H) [SEM]. France. Pays-Bas, Flandre zélandaise, N Hedwige Polder, 1970, Duvalneaud 12024 (GENT). *Bolboschoenus affinis*. India. W coast. "Malabar" [Kerala], "Conkan" [Konkan, Maharashtra] etc., Stocks, Law etc., s.n. (C, neotype). Azerbaijan. Hanlar, Caspian coast 10 km S Baku, Kukkonen 12720 (H); Bejuk Sor 8–10 km N Baku, Kukkonen 12727 (H) [SEM].

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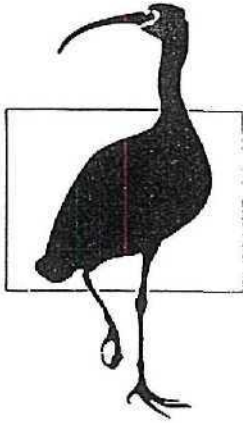
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Taxonomy and distribution. In H.A. Kantrud, The alkali (*Scirpus maritimus* L.) and saltmarsh (*S. robustus* Pursh) bulrushes: a literature review.

National Biological Service Information and Technology Report 6.



U.S. DEPARTMENT OF THE INTERIOR
NATIONAL BIOLOGICAL SERVICE

INFORMATION AND TECHNOLOGY REPORT 6

SEPTEMBER 1996

**THE ALKALI (*SCIRPUS MARITIMUS* L.)
AND SALTMARSH (*S. ROBUSTUS* PURSH)
BULRUSHES:**

A LITERATURE REVIEW

by

Harold A. Kantrud

1991). Other researchers have documented the reproduction, habitat requirements, and management of *S. robustus* (Neely 1960, 1962; Palmisano and Newsom 1968; Mall 1969; Palmisano 1972; George 1980; Prevost and Gresham 1981).

I present here a synthesis of life histories and management assessment of alkali and saltmarsh bulrushes. The information is mostly from reports written in English, from reports with English summaries, and from some foreign material. I did not reference the simple occurrence of either bulrush in various wetlands worldwide or early taxonomic and genetic studies.

Taxonomy and Distribution

by

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Scirpus maritimus L. and *S. robustus* Pursh belong to a small, worldwide group of the family Cyperaceae, in North America often called the "tuberous bulrushes," that needs a taxonomic revision (Wilson 1981; Hulten and Fries 1986; Goetghebeur and Simpson 1991). Taxonomic confusion as reviewed here is due to disagreement about species boundaries, infraspecific variation, misapplication of names, probable hybridization, and introduction of species. The same name (especially *S. maritimus*) may refer to more than one species and to hybrids, and several names are correctly or incorrectly used for the same species. For the references reviewed herein, the names and the species to which they apply therefore must be carefully evaluated.

The group of bulrushes is recognized by perennial rhizomatous habit; large, hard, carbohydrate-rich corms or "tubers" on the rhizomes; leafy, sharply triangular stems; leaflike bracts accompanying the inflorescence; large spikelets; and floral scales that are minutely hairy and apically trifid with prominent midrib extensions ("awns"). Fernald (1950) placed these bulrushes in *Scirpus* section *Phyllantheli* Beurl. and Koyama (1962) called the group the "*Scirpus maritimus* complex." Lye (1971), Haines and Lye (1983), and Strong (1993, 1994) placed the group in the genus *Schoenoplectus*. Other authors (e.g., DeFilipps 1980) treated the group as either *Scirpus* section *Bolboschoenus* Ascherson, or, with the division of *Scirpus* into more natural genera in recent years, segregated the group into the genus *Bolboschoenus*

(Aschers.) Palla (e.g., Hejny 1960; Caspar and Krausch 1980; Koyama 1980; Wilson 1981; Browning and Gordon-Gray 1993; Browning et al. 1995). The group will probably be placed in *Bolboschoenus* in an upcoming volume of *Flora of North America* (Flora of North America Editorial Committee. Cyperaceae. Flora of North America north of Mexico. Volume and date to be determined. Oxford University Press, New York, unpublished) in which case the correct names of *S. maritimus* and *S. robustus* will be *Bolboschoenus maritimus* (L.) Palla and *Bolboschoenus robustus* (Pursh) Sojak (S. Galen Smith, Department of Biology, University of Wisconsin-Whitewater, Whitewater, Wisconsin, personal communication).

For North America, recent taxonomists (Beetle 1942; Fernald 1943, 1950; Koyama 1962; Schuyler 1975; Browning et al. 1995) have interpreted species boundaries variously. Browning et al. (1995) provided several new diagnostic characters using scanning electron microscopy of achenes and argued that hybridization where the species grow together is responsible for much of the taxonomic confusion in this group (see especially *Scirpus novae-angliae* and *S. glaucus* below). We herein recognize the following five species for North America: *S. maritimus* L., *S. robustus* Pursh, *S. fluvialis* (Torr.) Gray, *S. novae-angliae* Britt., and *S. glaucus* Lamarck (introduced from the Old World). For North American synonymy we mostly follow Kartesz (1994).

We treat *S. maritimus* as "s. lat." ("*sensu lato*", or "in a broad sense") pending further studies because the species is very difficult to delimit and is treated as s. lat. in much of the ecological literature. For North America and Hawaii, some authors (e.g., Beetle 1942; Fernald 1950; Schuyler 1975) segregated most plants of *S. maritimus* into *S. paludosus* A. Nelson, while others, especially recently (e.g., Gleason 1952; Koyama 1962, 1990; Gleason and Cronquist 1963, 1991; Hitchcock et al. 1969; Cronquist et al. 1977; Scoggan 1978; Boivin 1992; Smith et al. 1993; Kartesz 1994; Browning et al. 1995) treated *S. paludosus* as a synonym, variety, or subspecies of *S. maritimus*. Synonyms of *S. maritimus* L. for North America as herein treated are: *Scirpus brittonianus* Piper; *S. campestris* Britt.; *S. fernaldii* Bickn.; *S. interior* Britt.; *S. maritimus* var. *feraldii* (Bickn.) Beetle; *S. maritimus* var. *paludosus* (A. Nelson) Kuek.; *S. pacificus* Britt.; *S. paludosus* A. Nelson; *S. paludosus* A. Nelson var. *atlanticus* Fern.; *S. robustus* var. *compactus* Davy ex Jepson; *S. robustus* Pursh var. *paludosus* (A. Nelson) Fern.; *Bolboschoenus maritimus* (L.) Palla; *B. maritimus* (L.) Palla subsp. *paludosus* (A. Nelson) T.

Koyama; *B. paludosus* (A. Nels.) Soo; *Schoenoplectus maritimus* (L.) K. Lye.

For Europe, most recent taxonomists have recognized only *Scirpus maritimus* but with various subspecies, varieties, and forms (e.g., Suessenguth 1939; Schultze-Motel 1980; Hulten 1964; Hulten and Fries 1986). Some taxa reportedly occur variously in alkaline or acid fresh waters or in waters of greater or lesser salinity (Hejny 1960; Robertus-Koster 1969; Caspar and Krausch 1980). Nordlindh (1972) and Dykyjova (1986) reviewed the taxonomy and biogeography of *S. maritimus* s. lat. in Eurasia. For *Flora Europaea*, DeFilipps (1980) followed Nordlindh (1972) in recognizing only *S. maritimus*, placing *S. compactus* Hoffm. in synonymy, and treating the mostly Asian *S. affinis* Roth as *S. maritimus* subsp. *affinis* (Roth) Nordlindh. In addition, recent work has shown that *S. yagara* Ohwi (*S. fluviatilis* subsp. *yagara* [Ohwi] Koyama) and probable *S. maritimus* × *yagara* hybrids occur in Europe and are probably included within the concept of *S. maritimus* there (Browning et al. 1996).

For eastern Asia, Koyama (1958, 1980) recognized three taxa: *S. maritimus*, *S. fluviatilis* subsp. *yagara*, and *S. planiculmis*; he also showed that most plants previously called *S. planiculmis* F. Schmidt belong in *S. maritimus* and that the true *S. planiculmis* is a very different Pacific coastal endemic. For Australia, New Zealand, and various southern Pacific islands, taxonomists (e.g., Cook 1947; Wilson 1981) recognize the three species: *S. caldwellii* V. J. Cook, *S. medianus* V. J. Cook, and *S. fluviatilis*. The latter species is also North American. For southern Africa and elsewhere, Browning and Gordon-Gray (1993), Smith (1995), and Browning et al. (1995) showed that *S. maritimus* s. lat. as previously treated includes *S. glaucus* Lamarck and probable hybrids (see following sections).

Taxonomists have generally treated trigynous plants (with trifid styles and trigynous achenes) as "typical" *S. maritimus* (e.g., Ascherson and Graebner 1902-1904; Fernald 1943, 1950; Koyama 1958; Gleason 1952, 1963; Robertus-Koster 1969; Nordlindh 1972; Caspar and Krausch 1980; Boivin 1992) and have placed digynous plants (with bifid styles and lenticular achenes) in various infraspecific taxa such as *S. maritimus* var. *digynus* Gordon or in separate species such as *S. paludosus* A. Nels., *S. affinis* Roth, *S. compactus* Hoffmann, and *S. planiculmis* F. Schmidt (misapplied). Trigynous plants are common in Europe and southern Africa but rare in North America (Browning et al. 1995).

Scirpus maritimus and *S. robustus* differ by very few achene and other characters (e.g., Schuyler 1975; Browning et al. 1995). These species have been confused by several authors, especially on the Pacific coast; for exam-

ple, Mason (1957), Munz and Keck (1959), and George (1963) erroneously placed *S. maritimus* in synonymy under *S. robustus*. Correll and Correll (1975) treated *S. robustus* under its synonym *S. maritimus* var. *macrostachyus* Michx. These two bulrushes are especially variable in their zones of sympatry on the northern Atlantic coast as described by Fernald (1943) and Schuyler (1975) and in California (S. G. Smith, unpublished). Some of this variation is the basis for infraspecific taxa recognized by, for example, Fernald (1943, 1950) and Hulten and Fries (1986). Browning et al. (1995) ascribe much of this variation to hybridization. Synonyms of *S. robustus* are *Bolboschoenus robustus* (Pursh) Sojak and *Scirpus maritimus* L. var. *macrostachyus* Michx.

Scirpus novae-angliae, known only from northern Atlantic coastal estuaries, is controversial. Beetle (1942), Gleason (1952), and Gleason and Cronquist (1963) placed this bulrush in *S. robustus*, while Fernald (1950) and Koyama (1962) placed it in *S. maritimus*. Koyama (1962) reduced *S. novae-angliae* to var. *cylindricus* (Torr.) T. Koyama of the unrelated *S. subterminalis* Torrey. Schuyler (1975), under *S. cylindricus*, clarified the nomenclature of *S. novae-angliae* and described its morphology and habitat, and Ferren and Schuyler (1980) further described its habitat. Browning et al. (1995) argued that *S. novae-angliae* originated as *S. fluviatilis* × *robustus* hybrids because it: (1) is morphologically intermediate; (2) grows in habitats intermediate between the saline habitats of *S. maritimus* and *S. robustus* and the freshwater habitats of *S. fluviatilis*; and (3) is known almost only from the zone of sympatry of its putative parents. Synonyms of *S. novae-angliae* are: *S. campestris* var. *novae-angliae* (Britt.) Fern.; *S. maritimus* var. *cylindricus* Torr.; *S. robustus* Pursh var. *novae-angliae* Beetle; *S. cylindricus* (Torr.) Britt.; *S. subterminalis* Torr. var. *cylindricus* (Torr.) T. Koyama; *Bolboschoenus novae-angliae* (Britt.) S. G. Smith; and *Schoenoplectus novae-angliae* (Britt.) M. T. Strong.

Beetle (1942), Mason (1957), George (1963), Munz and Keck (1959, 1973), and Smith et al. (1993) also included a species that they called *Scirpus tuberosus* Desf. Koyama (1962) reduced this species to *S. maritimus* var. *tuberosus* (Desf.) T. Koyama. Smith (1995), however, showed that the name *S. tuberosus* Desf. is a synonym of *S. maritimus*, and that *S. glaucus* Lamarck (*Bolboschoenus glaucus* [Lam.] S. G. Smith) is a correct name for this species. Browning et al. (1995) showed that *S. glaucus* and *S. maritimus* differ greatly in their achene structure, and that many specimens from wildlife refuges, rice fields, and waste sites

in California are probably *S. glaucus* × *maritimus* hybrids. *Scirpus glaucus* is widespread in Asia and Africa, where it is often included in the concept of *S. maritimus* (Browning et al. 1995 and personal communication). *Scirpus glaucus* was introduced into North America, where it is definitely known from California, Oregon, Idaho, and New York (S. G. Smith, unpublished).

Below we list the common or colloquial names that have been applied to *S. maritimus* and *S. robustus*, but possibly erroneously to other closely related species as reviewed above. Besides alkali bulrush (Scott and Wasser 1980), *S. maritimus* is locally known as bayonet grass, perennial nutsedge, prairie bulrush, purua grass, salt-marsh bulrush, sea club-rush, seacoast bulrush, and tule (Wetmore 1921; Christensen et al. 1947; Fernald 1950; Hyer 1963; Batten 1967; Nakagawa et al. 1973; Kim and De Datta 1974; Yamanaka 1975). Scott and Wasser (1980) prefer the common name saltmarsh bulrush for *S. robustus*. Others call the plant buttergrass, coco, goose grass, leafy three-cornered grass, leafy three-cornered rush, leafy sedge, leafy three square, leafy three-cornered sedge, nut grass, robust bulrush, saltmeadow bulrush, sea club rush, stout bulrush, triangle sedge, and wild chufa (McAtee 1939; Lay and O'Neil 1942; Lynch et al. 1947; O'Neil 1949; Brown 1959; Beter 1957; Kimble 1958; Linthurst and Seneca 1980; Hackney and Cruz 1982; Payne 1992; Anonymous 1994).

Chromosome numbers reported for *S. maritimus* worldwide vary from approximately $n=40-57$ ($2n = 80-114$) as summarized by Chapman (1974) and Cronquist et al. (1977), and for *S. robustus* in Massachusetts, n = approximately 53-55 (Hicks 1928). Although these reports demonstrate that aneuploid series occur in this complex, chromosome numbers cannot be definitely assigned to species because the taxonomy is so confused as reviewed above and identifications must be confirmed by study of voucher specimens.

Scirpus maritimus s. lat. is one of the most widely distributed plants of the Northern Hemisphere. The species is more or less circumpolar in boreal and temperate regions on coasts and in the interior (Hulten 1964; Ranwell 1972; Koyama 1980; Hulten and Fries 1986) and ascends to at least 3,000 m in Tibet and 2,900 m in Colorado (Hulten 1964). In Europe, *S. maritimus* ranges from just above the Arctic Circle on Russia's Kola Peninsula south to the Mediterranean region. This bulrush occurs in much of North America from about 62° N in Alaska's Cook Inlet area and Northwest Territories, to approximately 55° N on James Bay (where disjunct; Riley and McKay 1980), to about 51° N on the Atlantic coast in Quebec and south to Mexico. *Scirpus maritimus* is absent from the Atlantic coast south of New Jersey and

from the gulf coast, except possibly for a small area in Texas. This species is an important member of the Pacific coastal marshes between 35° N and 55° N (Macdonald 1977; Hutchinson 1986). In the interior, *S. maritimus* occurs in saline places rarely in the East and commonly in the West, south to Missouri and Mexico.

Elsewhere, *S. maritimus* occurs in Mexico (Saunders and Saunders 1981) and the Hawaiian Islands (Koyama 1990) and is local in South America (West 1977; S. G. Smith and J. Browning, unpublished) and Africa (Browning et al. 1995 and unpublished). Reports of *S. maritimus* from the southern Pacific (Australia, New Zealand, Tasmania, New Caledonia, etc.; e.g., Congdon 1981) and from the Philippines and New Guinea (e.g., Kern 1974; Kim and De Datta 1974) may refer to *S. caldwellii* V. J. Cook and other species. Many reports of *S. maritimus* and *S. tuberosus* from various warm parts of the Old World, especially in the Middle East, Asia and Africa, may refer to *S. glaucus* Lam. (Browning et al. 1995 and unpublished).

Scirpus robustus Pursh is definitely known only from saline places at low elevations on or near the coasts of North and South America and the Caribbean (S. G. Smith, unpublished). In North America, this species occurs in the East along most of the Atlantic and gulf coasts from New Brunswick and Prince Edward Island to northern Mexico. According to Shisler (1990), *S. robustus* is especially common south of Delaware. On the Pacific coast this bulrush is common in the San Francisco Bay region and very local north to Washington and south to Baja California (Smith et al. 1993; S. G. Smith, unpublished). The distributions of *S. robustus* and *S. maritimus* overlap along the northeast Atlantic coast, on the Pacific coast, and in a small region near the gulf coast of Texas (S. G. Smith, unpublished).

Autecological Classification

Scirpus maritimus and *S. robustus* are perennial emergent macrophytes that reproduce sexually and vegetatively. Lacking salt glands, succulence, and other adaptations of true halophytes, *S. maritimus* and probably *S. robustus* are facultative halophytes that show decreased growth and reproduction in increasingly saline environments yet may persist for centuries in nonsaline habitats (Arnold 1955; Ranwell 1972; Ustin 1984; Kruger and Kirst 1991). These bulrushes are best considered brackish water species that are adapted to flourish at salinities that cause high

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Achene morphology and pericarp anatomy of the type specimens of the Australian and New Zealand *Bolboschoenus* species (Cyperaceae).

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Achene Morphology and Pericarp Anatomy of the Type Specimens of the Australian and New Zealand Species of *Bolboschoenus* (Cyperaceae)

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Abstract

Three species of *Bolboschoenus* (Ascherson) Palla are reported for Australia and New Zealand. *Bolboschoenus caldwellii* (V.J.Cook) Soják and *B. medianus* (V.J.Cook) Soják are based on types from New Zealand (under *Scirpus* L.). *Bolboschoenus fluviatilis* (Torrey) Soják has been lectotypified by a specimen from North America. *Scirpus perviridis* V.J.Cook, the type of which is also from New Zealand has been considered conspecific with *Bolboschoenus fluviatilis*. Achene morphology and pericarp anatomy of achenes removed from isotypes of Cook's three species, *Scirpus perviridis*, *S. caldwellii* and *S. medianus*, are described and illustrated by electron micrographs. These achenes are compared with a representative sample of achenes of each of the *Bolboschoenus* species named above, taken from herbarium specimens collected in Australia and New Zealand. Intraspecific taxa within *Bolboschoenus fluviatilis* are briefly outlined. Features of *Bolboschoenus medianus* suggest a possible hybrid origin.

Introduction

The genus *Bolboschoenus* (Ascherson) Palla, a segregate from *Scirpus* L., is in need of world-wide taxonomic revision (Goetghebeur and Simpson 1991), as species limits are not clearly defined. Oteng-Yeboah (1974) drew attention to the importance of the shape and anatomy of the fruit in infrageneric classification within *Bolboschoenus* and his observations have been extended to the species of southern Africa (Browning and Gordon-Gray 1993) and North America (Browning *et al.* 1995). In the latter paper, it is stated (p. 434) that 'Achene surface features and anatomy provide a hitherto largely unused but very useful suite of characters that supplement the rather few morphological characters readily available to taxonomists in this group.' If this suite of characters is to be useful, then the salient features of achenes in the type specimens (at least those that carry mature fruits in sufficient number to permit examination) should be studied.

Three species of *Bolboschoenus* have been recorded for Australia and New Zealand. These species, *Bolboschoenus caldwellii* (V.J.Cook) Soják, *B. medianus* (V.J.Cook) Soják and *B. fluviatilis* (Torrey) Soják, were first described as variants of *Scirpus maritimus* L. Cook (1947, p. 567) gave a summary of their early history pointing out that two varieties, *fluviatilis* Torrey and *macrostachya* Michaux, were recognised (Cheeseman 1906, p. 778). On revision of *Scirpus*, these varieties were subsequently raised to species level as *S. fluviatilis* (Torrey) A.Gray (Gray 1848, p. 527) and *S. robustus* Pursh (Pursh 1814, p. 56) respectively. *Scirpus fluviatilis* is typified by a lectotype from North America (designated by Strong 1993, p. 203 and under *Schoenoplectus* (Ascherson) Palla).

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APPENDIX 1

MATERIALS AND METHODS

APPENDIX 1

MATERIALS AND METHODS

Nut Studies (Part 2)

A. Light microscopy

Fully matured, plant-ripened fruits were selected from herbarium sheets or from field samples of inflorescences. Study of external features, for example surface topography, was carried out by means of an Olympus Stereo Dissecting microscope (x 4--40 magnification).

Measurements, using an ocular micrometer, were made of a minimum of 3 mature nuts from each spikelet examined; where a sample permitted, up to 40 nuts from a collection number were measured at x 40 magnification.

The presence of bristles attached to nuts was recorded. Bristle length was estimated against nut length and the length of the longest bristle measured.

B. Electron Microscopy

1. Sectioning for anatomical study

Nuts were fixed to a metal plate by means of "Tissue-tek". The plate was then submerged in liquid nitrogen (-150°C). While submerged, each nut was fractured transversely at approx. mid-length using a razor blade held at right angles to the length of nut and tapped sharply with a small hammer. With cut surfaces exposed both halves were mounted on brass stubs by means of double-sided adhesive tape, to which was applied a layer of double sided aluminium tape. Whenever possible the contents of the nut halves (principally endosperm) was removed as this, when present, causes charging during scanning. The stubs were then coated with gold palladium in a Polaron E5100 Sputter Coater, and examined in an Hitachi S570 Scanning Electron Microscope under accelerating voltages of 10kv and 15kv respectively.

2. Photography

Black and white photographs were obtained using a Mamiya RB 67 camera attached to the Scanning Electron Microscope using 120 film.

The frontispiece image was captured using the Digital Imaging facility of a Link exL II Energy dispersive X-ray microanalysis system, attached to the Hitachi S-570 SEM and printed using a Mitsubishi CP200E colour video copy processor.

Inflorescence study (Part 3)

Fresh inflorescences of plants of *B. maritimus* from specific collection sites at coastal and inland situations were observed and collected during field work at Verlorenvlei in January-February 1996 (for further detail of sites see Browning *et al.* 1998: 71). Some of these inflorescences were dried and others were preserved in 80% alcohol for further study. Voucher specimens of corresponding entire plants were deposited in NU. Populations of *B. glaucus* in Maputaland were visited and sampled in May 1996; voucher specimens are deposited in NU.

Recently collected herbarium material, mostly provided by C.J. Ward, was used in the study of inflorescences of *B. nobilis* and *B. glaucus*. In addition, inflorescence material of *B. glaucus* from Senegal and of *B. maritimus* from Denmark was used for dissection and detailed examination leading to the construction of diagrams to illustrate inflorescence morphology. This served for comparison with southern African specimens.

Dissection of the above material was performed using a Nikon dissecting microscope with magnification being varied as required, up to x 40. Drawings were made and diagrams of inflorescences constructed. Close proximity of parts necessitated changing and exaggerating dimensions in these diagrams for purposes of clarification and to accommodate the form of a naturally spiralled structure on the two dimensions of a flat sheet of paper.

Embryo Study (Part 3)

The samples

As far as possible, recently gathered inflorescences taken from populations in the field were used as source material. Where fruit set permitted this, 40 mature nuts were extracted from one inflorescence, or from more than one inflorescence of the same plant (clonal sample). In *B. glaucus* in particular, fruit set was poor and the sample had to be obtained from more than one inflorescence of a collection, or from several collections from a population (population sample: the number of clones providing nuts unrecorded). Samples from beyond southern Africa were not personally monitored; details kindly provided by the collectors had to be relied upon; uniformity of the samples could not be relied upon. The time between collection and extraction of embryos was also uncontrolled and differed from one sample to another, as did conditions under which inflorescences had been stored after gathering. Nothing is known of the morphological changes that may take place during this after ripening period.

Embryo extraction

Each nut of a sample was treated individually as follows: pressed into a small amount of plastic rubber on a slide; cut transversely approximately one third from base (under binocular enlargement); presence/absence of endosperm recorded. Basal portions were boiled in water (1 minute) to facilitate endosperm and embryo removal from testa and pericarp. Using fine forceps, and under binocular enlargement, endosperm was discarded and the embryo carefully removed, mounted in water in a cavity slide, measured by means of an ocular graticule, and drawn to scale on squared paper. Scale drawings of the 40 individual embryos were cut out, pasted to a sheet of paper and the sheet photocopied. The photocopy was traced and scanned to produce a computer file of embryo profiles for a sample. During measurement and for illustration it is important that the embryo be seen in sagittal section. Orientation is often difficult, especially with three-angled embryos, such as those of *B. fluviatilis*.

Embryo measurements

Measurement of length : taken from uppermost point or position on the curve of the cotyledonary surface to the extreme tip of coleoptile.

Measurement of width : taken across the greatest width of the cotyledon.

Length was measured with less difficulty than width; therefore length parameters are regarded as the more reliable.

Limitations and shortcomings

Embryos were very difficult to remove from recently collected nuts of *B. glaucus*; testa adhered to endocarp and great care had to be taken in removal to avoid damage, with consequent expenditure of time.

In early stages of the embryographical study practice runs were carried out to determine: 1. if boiling the lower portion of the nut affected dimensions of the embryo. This was found not to be the case. 2. if water was absorbed by the extracted embryos on standing. Embryos should be measured immediately following removal; after 24--48 hours in water increase in length was recorded. Embryos placed in Gurr's water soluble mountant decreased dimensions within 24 hours. 3. Orientation and measurement of embryos was difficult because of movement within the liquid in the cavity slide; using a flat slide was no advantage because of difficulty in maintaining a set position. The depth of the embryo within the water and its angle affected final measurement. The lenticular (flattened) embryos of *B. caldwellii* were markedly easier to handle and to measure than were the cylindrical to 3-angled examples:

Image analysis

For reasons of difficulty given above, image analysis (length and width measures only) was tried out in comparison with parameters obtained from measurement using an ocular graticule, on a sample of *B. caldwellii* embryos. Refinement in results was found to be negligible; a great disadvantage was that only 3 embryos could be mounted for measurement at one time and a sample of 40 could not be dealt with collectively. This technique was therefore not pursued.

General morphology (Part 4)

A range of herbarium material deposited in South African and foreign herbaria (covering a collection period of almost two centuries) was examined. For listing of these herbaria see Appendices 2 and 5 (Volume 1). In addition to this, field populations of southern African species were monitored and sampled.

APPENDIX 2

EXSICCATAE

EXAMINED

APPENDIX 2

EXSICCATAE

In this appendix the extra southern African exsiccatae studied in the course of preparation of this thesis are listed for reference purposes.

The arrangement is as follows:

1. Specimens are listed under species according to my determination of them, irrespective of other determinations that may have been given on the respective herbarium sheets.
2. The species for each country are listed alphabetically according to the initial letter of the specific epithet (*italics*; **bold typeface**).
3. Continents are not placed alphabetically, but follow the sequence of chapters in the text of the thesis (**capitals**; **bold typeface**).
4. Within a continent, countries are listed from west to east and north to south.
5. The Appendix should be read; column left followed by column right, then over to the back of the same page.

AFRICA AND ASSOCIATED ISLANDS

AZORES

Indeterminate

Gonan (?) *s.n.* (K)
In paludosis circa Traya da Victoria June 1838 "G"
(Gonan)

MOROCCO

Bolboschoenus glaucus

J. Ball s.n. (K)
Ex Regno Muroccano, prope Tetuan ad ostium
fluminis Ibn Hanesh. 6th June 1851.

Relique Maroccano ex herb. *Schoushoe* (BM)
Tanger.

J. Lewalle 11916 (BM)
Ex herb. Horti. Bot. Nat. Belg.

Locality; Tiflet. 19 Mar. 1988. Alt. 400 m.

E. Jahandiez 142 (BM)
Plantes Marocaines 1929.
Djebala; Ouezzan, bords de l'oued Mellah.

M.R.K. Lambert 190 (BM)
Loc: Tuisgui-Remz, 150 km E. of Tan-Tan. Prov:
Tarfaya. Oasis. Alt. 200 m. 19/3/1969. Abundant.
Dry cracked & hard, silty soil, among palms.

F. Schuhwerk 90/451 (NY - photostat)
Province de Tarfaya: Oued Aabar, ca. 7km N Abti
E der Straße P 44 von Tan-Tan nach Samara (Es
Semara); 40-60 m NN; salzig sandige Flächen am
Oued-Ufer, im Wasser, steinig-felsige Hänge der
Ost-/Westseite. 11°25'W, 28°00'N.

Bolboschoenus maritimus

E. Jahandiez 796. (BM)
Plantes Marocaines 1924. Noyer Atlas: Timhadit
[?], bords du Guigou 1800 m

c.f. *B. maritimus*, including putative hybrids

J. Lewalle 9008 (BM) Ex Herb. Hort. Bot. Nat. Belg.
Locality; Bouznika (Maroc) Alt. 60 m. 23/4/79. St. bor d'Oued

Dr. Font Quer - iter Maroccanum 1930 (BM)
Det. *Scirpus maritimus*. Hab. ad ripas fl. Lukos, juxta E. Araix. 3 March.

Michel Gandoger s.n. (MO - photostat)
Dj (?) Habibi 35 43N 1.08W

ALGERIA

Bolboschoenus glaucus

Faure, A. 1582 (LD)
Oued Timberl? (Oran). Bords du canal.

P. Jamin (BM) Pl. D'Algérie, 1851. (BM)
214 *Scirpus maritimus* L.
S. tuberosus, Desf.
(Durieu.)

Dely Ibrahim près Alger 13 Juillet. No 16 [in very old ink]

Davis 52242 (BM)
Algeria. K3: Lac des Oiseaux. c. half way between Annaba (Bone) and El Kala. 5--10 m. Marsh. Perennial 1 m. 12 May 1971.

Davis 59498 (BM)
Algeria. A1: Marshy area between Kolea and Ben Salah, near Pont des Zouaves. c. 40 m. Marshes and swamps. Perennial 28 June 1975.

Davis 52928 (BM)
Algeria. K2: Between Les Falaises and Tichi (Bejaia-Djiddjelli). Sea level. Marshy places behind the dunes. 28th May 1971.

Dr. R. Trabut s.n. (1892) (UC)
Algeria: Marais à Ain-Taya; 36.51N, 3.18E

Scirpus maritimus L. (BM)
le Calle. Alger 28.4.30 D'lypheus (illegible).

c.f. *B. glaucus*, including putative hybrids

A. Meyer s.n. (K)
Société duaphinoise 1878, No. 1870 bis. *Scirpus maritimus* L. Sp. ed. 2. p.74. Munb. Cat. Alg. ed 2. p. 34 - *S. tuberosus* Desf. Atl. 1. p. 50 (Visit Cosson). Rebeval à 18 kilom. de Dellys (Algerie): maré-cage dessèché, au bord de l'Oued-Ahlel, près du Sébao. 11 June 1877.

Bolboschoenus maritimus

Desfontaines s.n. (P)
Type of *Scirpus tuberosus* Desf.

TUNISIA

Bolboschoenus glaucus

C.J. Pitard s.n. (BM)
Gabès, in humidis. iv. 1909.

Davis & Lamond D 57828 (BM)
Tunisia. N: plain of Oued Kebir, south of Tabarka. 0--10 m. By irrigation ditches.

LIBYA

Bolboschoenus glaucus

R. Pampanini & R. Pichi-Sermolli 1189 (K)
Libia-Cirenaica el Gubba - U. Mara Scerscera. 6 May 1934.

EGYPT AND SINAI PENINSULA

Bolboschoenus glaucus

Ex. Herb. C.A. Wright F.L.S. (BM)
Plate MDC1. vol X [?]
Sea club rush. Pyramids Egypt. 12.4.77 [1877]

J. Bornmüller 11032 (BM)
Inter Aegyptiacum 1908. Kairo, in palmetis ad El-Marj. 1908.iv. 27 et 28.

R. Meinertzhagen s.n. (BM)
1928.

R. Meinertzhagen s.n. (BM)
Herbarium of Colonel R. Meinertzhagen
Dakhla Oasis, Egypt. Swamp, March.

Vivi Tackholm s.n. (LD)
Faiyum 26/3/1965

Tackholm, V. et al. s.n. (LD)
Abu Matamir, eastern Delta.

Gun Romee and Tackholm, V. s.n. (LD)
Faiyum Oasis, SW Cairo. S. beach of Lake Quarun. 5.5.1967.

Gun Romee 129 (LD)
Libyan desert; Dakhla Oasis, Mut 3 ?

Gun Romee 164 (LD)
Libyan desert; Dakhla Oasis, Budkhulu 1.

Gun Romee 174 (LD)
Libyan desert; Dakhla Oasis. El Qasr 2.

Gun Romee 221 (LD)
Libyan desert; Dakhla Oasis. El Qasr village fields.

Gun Romee 277 (LD)
Libyan desert; Dakhla Oasis. Hindawi.

Keller, Dr. A. 206 (NSW, PRE)
Kairo (ex Botanisches Museum der Universitat Zurich).

Amin, Amal et al s.n. (LD)
El Faiyum. 15/2/1974.

Imam, M., s.n. (LD)
El Faiyum 17/2/1971.

R. Meinertzhagen s.n. (BM)
Herbarium of Colonel R. Meinertzhagen
Kharoa Oasis, Egypt. Moist ground. March.

Amal Amin, Abdel Aziz & S. Sisi s.n. (NY-
photostat)
El Gedia, Rosetta. 9/7/1976

CAPE VERDE ISLANDS

Bolboschoenus grandispicus

W. Lobin 2021 (K)
Flora der Kapverdischen Inseln (Cape Verde Isl.)
Boa vista, im Ribeira do Agua an der StraBe van
Sal-Rei zum Flughalee.

MAURITANIA

Bolboschoenus glaucus

D.E. Johnson s.n. (NU)
Rosso, southern Mauritania. 24 Oct. 1997. Sample
1.
Border of irrigated rice fields.

SENEGAL

Bolboschoenus glaucus

3 on one sheet.
Right side plant with 1 mature nut. Seen for FWTA
Ex Herb. J. Gay (K)
Senegal. Roger didit Mayo 1825.

Roussillon s.n. (P) photo!
Herb. Lamarck.
(Type of *Scirpus glaucus* Lamarck)

Guido Bocker s.n. (GENT)
Boundary between St. Louis & Richard
Toll/Senegal.

J. & A. Raynal 5991 (P)
Darou (Senegal), cultures de la piste Pout-
Fouloume. bordure de lac salé (zone cultivable).
28/06/60. Ref. Maire Fl. Afr. N.

J. & A. Raynal 5925 (K, P)
Yankoba (Senegal) 9 km NNW of Rufisque, niaye
Derh Boumak (carte IGN 50000° 1956); bordure
de typhaie partiellement défrichée, près de cultures
maraichères. 05/06/60.

J. Audru 3048 (P)
Béthio Senegal. Depression 10 cm d'eau. Ceinture
exterieuse. 6.1.1966.

J.G. Adam 734 (P)
Environs de Dakar. Lac Tanma ?. 25 Feb. 1948
(Contrôleur Forestier -Niayes, Cap Vert, Dakar).

J. Audru 3044 (P)
Ross, Bethio Senegal 6.1.1966.

J. & A. Raynal 7069 (P)
Mbidjem (4 km SE Kayar, Senegal), cultures en
lisière du Lac Tanma, 4 km env. au N du village.
17.6.1961.

Berhaut 1101 (K) (MO - photostat)
Senegal, Tauma (?). Juill 1950.

D.E. Johnson Sample No. 1 (NU)
Fanaye, WARDA experimental farm, 160km from
St. Louis, Senegal.
Border of rice field, next to drainage canal. Dry on
the surface. Soil= Clay.
6 May 1997.

D.E. Johnson Sample No. 2 (NU)
Ndiaw (Richard Toll) 100 km from St. Louis.
Marginal rice area, between road and irrigation
canal, irrigated rice in rotation with vegetables.
Shallow flooding. 6 May 1997.

D.E. Johnson Sample No. 3 (NU)
Colonat Perimeter, 7--8 km from Richard Toll, 92
km from St. Louis, Senegal.
Rice field, marginal zone. 0--5 cm flooding. Soil:
clay, saline. 6 May 1997.

D.E. Johnson Sample No. 4 (NU)
Between Russ Bethio to Grande Digue, 52 km
from St. Louis.

Rice field. Shallow flood, 0–2 cm. Soil: clay,
saline. 6 May 1997.

D.E. Johnson Sample No. 5 (NU)
N'diaye (edge of WARDA experimental farm.
Irrigation canal. Surface dry. 6 May 1997.

D.E. Johnson Sample No. 6 (NU)
Pont Gendarme, 42 km from St. Louis.
Rice field under long fallow. Soil moist
Soil: clay, low to medium salinity. 9 May 1997.

D.E. Johnson Sample No. 7 (NU)
N'diaye, WARDA experimental farm.
Rice field, continuous rice cultivation.
Shallow flooding. Soil: heavy clay, weakly saline.
15 May 1997.

D.E. Johnson s.n. (NU)
N'diaye, WARDA experimental farm, N. Senegal
Oct. 23, 1997 Sample 3
Margins of rice fields; continuous rice cultivation.
Shallow flooding. Heavy clay, weakly saline.

D.E. Johnson s.n. (NU)
4km from Richard Toll, 95 km from St. Louis, N.
Senegal Oct. 23, 1997 Sample 2
Rice field margins. Soil, clay, saline.

Bolboschoenus grandispicus

C. Vanden Berghen 9529 (BR)
Loc: Basse-Casamance. Abéné. Lisieré de marigot,
sur une vose fortement humifere, encore humide.
28 Jan. 1992.

C. Vanden Berghen 9571 (BR)
Loc: Basse-Casamance. Mossor. Depression dans
les dunes benes fixies. Sol fortement humifere
vicemment inonde. Alt. 2 m. 3 February (?) 1992.

C. Vanden Berghen 7771a (BR)
Loc: Basse-Casamance. Abéné. Marigot a sec,
bordé de mangrove en vitabile reduite, isolé de
l'ocean. Sable humifere, humide. Deux stigmates.
Alt. 3 m. 21 July 1986.

Perrotet 838 (P)
Senegal. de 1824 à 1829. Isotype of *Isolepis*
grandispica Steud.

J. & A. Raynal 6087 (P)
Dési Biram Ndao (Senegal), extrémité NE du L.

Retba (rive N). bord de lac salé, en avant de la
ceinture de *Typha elephantina*. 24/07/60.

J.G. Adam 17627 (P)
Lac. Retba. 29.4.1960.

J.G. Adam 16857 (P)
Hann, 11.1958. Dakar, Senegal.

J.G. Adam 12.262 (P)
Lagune de Hann, 28/6/56.

J. G. Adam 17660, 17664 (P)
Mboro 18.5.1960. Senegal.

R.P. Berhaut 1021
Presqu île du Cap Vert Dakar - Niayes; Hann
Mbao Sangalkam, Nayar (Senegal). Mars 1950.

Berhaut 2697 (P)
Senegal 1950-51

J. & A. Raynal 5965 (P)
Hann (Senegal) à la hauteur du Parc forestier (locus
classicus!). bord de dépression salée coupée de la
mer. 22/06/1960.

MALI

Bolboschoenus glaucus

J.T. Davey 71 (K)
Mare near Toubel. 22/5/1952. Low lying area,
subject to flooding. Growing in water. Sedge, up to
4'6" in height.

J.T. Davey 22 (K)
Mare entre Tiouki et Selingourou. Mare dans la
plaine inondée. 9/2/1952.

MIDDLE NIGER

Bolboschoenus glaucus

O.B. Lean 62 (K)
Locality Diri (or Dire). Bands of swamp. Tangled
mass of dry vegetation. 3 ft high in seed.

ETHIOPIA

Bolboschoenus glaucus

J.W. Ash 723 (EA)
Koba Dam; near inlet of Aswan river. 90 km S. of
Addis on Main Rift Valley. Alt. 1,350 m - 9/7/76.

J.W. Ash 3729 (MO - photostat)
1 km north of Mataka or 15 km south of Gewani.
1010: 3408; 189 km south of junction of new
Trapp road and Ol Kombolcha-Assab road.

SOMALIA

Bolboschoenus glaucus

Peveling C1 (GENT)
Sidamo (Flora of southern Somalia) 22.12.87
Long= 44°51'E/2°3'N. Alt. 50 m. swampy roadside
along irrigation channel.

S.M.A. Kasmi, Elmi & Rodol 534 (EA)
Between Mudum & Sublalay - 18/6/78.

CONGO

Bolboschoenus glaucus

Schmitz, A. 8336 (PRE)
Katanga Prov. salines de Kalashi.

UGANDA

Bolboschoenus glaucus

G. Scheffler 220 (BM)
Brit. Uganda. Station Kibwezi. ...Steppe, .. 1000
m..

Scheffler, G 220 (PRE)
Station Kibwezi (b.c. 1000m Seehohe ?)

KENYA

Bolboschoenus glaucus

van Someren, EA16264 (EA)
Rift Valley 'Swamp', West Ngong Hills.

West, O. 5290 (PRE)
Lorian Swamp. Common.

Proctor, J. 3657 (PRE)
Lake Manka, Lushoto Dist. In lake shore
community. Alt. 1500 ft.

Mumiukha 157 (EA)
Lenker Swamp Loitokitok - 13/6/73. Grazed by
game & cattle

G.R. Cunningham-van Someren EA16264 (EA)
Rift Valley 'Swamp' West Ngong Hills - *Fuirena*
sp. major component of original swamp vegetation

appearing around June 1977 now spreading and
flowering. Many hectares of this species. Many
other spp. of Cyperaceae. 12/3/78

R.B. & A.J. Faden 74/1082 (MO - photostat,
PRE))
Kitwa, Pembe Hill and vicinity 2°27'S' 40°42'E.
Alt. 50 m
Marshes on landward side of dunes - glumes pale
brown.

TANZANIA

Bolboschoenus glaucus

B.D. Burt 2764 (BM)
Ex Herb. Hort. Bot. Reg. Kew.
Tanganika Terr.: Kikori, Sta. A. Alt. 4200 ft.
14/1/1930.

R.E.S. Tanner 2856 (UC - photostat)
Tanga Province; Mwera Chiefdom, Pangani
District; Chengeni Parish.

A. Peter 32878 (MO - photostat)
Ngogo, Gulwe (?) Kinagani (?), 800 m.

A. Peter 12376 (MO - photostat)
South.. Pangani, Buiko (?) 600 m.

E.A. Robinson 1642 (NY - photostat)
N. Rukwa valley; 2600ft.

Semsei 3976 (PRE)
Korogwe Distr. Tanga Region; Mkomazi Valley -
in abandoned native lands.

Wingfield, R. 1425 (NU)
Tanga-to Same Rd.c.100 m beyond Mkomazi river.

Fitzgerald, DV. 554 (NU)
N. Rukwa plain.

Greenway, P.J. 3976 (PRE)
Mkomazi (Flora of W Usambaras) Alt. 1500 ft.)

Siame, W. 312 (NU)
Central Rukwa; Kafukola. Alt. 2640 ft.

Siame, W. 570 (NU)
North Rukwa; Kavuu R., Nziga. Alt. 2602ft.

Whellan, IA. 1197 (PRE)
Ufipa Distr., 'Hembe'? Kapangombe plains, Rukwa
Valley.

ANGOLA

Bolboschoenus glaucus

H. Humbert 16397 (BM)
Mossamedes. Alt. 2--4 m. L'eau cultivate.

H. & E. Hess 51/19 (GENT)
Prov. de Benguela, 3km nördlich von Benguela in
Richtung Lobito. Ausgetrockneter Graben neben
abgeerntetem Zuckerrohr. 29.11.1951.

H. & E. Hess 51/26 (GENT)
Prov. de Benguela, 7 km nördlich von Benguela in
Richtung Lobito. Am Tümpel neben der
Katangbahn. Zwiebförmige Basis und
ausläufertreibend. 29.11.1951.

Torre, AR. 8345 (LISC)
Porto Alexandre, lagoa de S. J. do Sul

Welwitsch 6972 (BM)
Mossamedes: One of the most troublesome weed in
the cotton fields. Julio 1859.

Welwitsch 6974 (BM)
Distr. Mossamedes; Habit. in uliginosis non procul
Oceano atl. pr. Giraul. Julio 1859.

Welwitsch 6980 (BM)
Hab. freq as Lagoa da Funda prope Funda. Seth.
1857. "Glumacea 2--3 pedalis, radice tuberosa;
habitus Scirpi maritimi?"

Welwitsch 6992 (BM)
Habit in dunensis humidis (!) prope Quizembo,
longe ab Oceano et imo a flumine Quizembo
remotis, socialis cum Kyllingiis et Convolvul.
nolanoides. Dist Congo Quizembo. Novbr. 1853.

Welwitsch 7003 (BM)
Lagoa de Quizembo. Distr. Congo. Novb. 1853.

Welwitsch 7011 (BM)
Hab. in paludosis inundatis ad sinistram flum.
Bengo pr. Funda, nec alibi a me visa. Distr. Icolo e
Bengo. Septbr. 1854.

Bolboschoenus nobilis

Welwitsch 6975 (BM).
Angola, Mossamedes, Maiombo river, Oct. 1859.
Type of *Scirpus nobilis* Ridley, in Trans. Linn.
Soc. ser. 2, Bot., 2: 159 (1884).

Plantae Angolensium *Gossweileri 14129* (BM)

Huila, Ruacana. Cunene River. Alt. 900 m

Chapman & Baines s.n. (K!).
South West Africa. Syntype of *Scirpus*
laetiflorens C.B. Clarke, C.B. Clarke Cyperaceae.
2. In Flora of Tropical Africa (1902).

ZAMBIA

Bolboschoenus glaucus

P.J. Greenway & J.P.M. Brennan 7979 (PRE)
Katambora - Kasangula - 25/8/47.

van Rensburg, HJ., KBS2960 (MRSC) Photo!
Kafue floodplain, 4miles S. of Namabeshi,
Narubandu.

MALAWI

Bolboschoenus glaucus

I.H. Patel, J.H. Seyani & W. Nachamba 1624 (MO
- photostat)
Nambazo willage, North of Mulanje.

Vesey-Fitzgerald 4190 (NY- photostat)
L. Chilwa - Likungara R. Alt. 2000ft.

Seyani, JH. 701 (BOL (ex SRGH))
Malawi; Mulanje Distr., Malunguni Harbour, L.
Chilwa (3ft. dambo, clay- cattle)

MOZAMBIQUE

Bolboschoenus glaucus

Bond, W. W530 (LISC)
Chinde. Distr. Zambezia. (in 6in water, on saline
clays).

Torre, AR. 7878 (LISC)
Guija, Canicado, ao km. 20, estrada para
Chamusca.

Torre, AR. 8058 (LISC)
Vila Joao Belo, estrada para o Farol, Via Lumane.

Torre, AR 8061 (LISC)
Vila Joao Belo, estrada para o Farol, via Lumane.

Torre, AR. 8078 (LISC)
Vila Joao Belo.

Torre, AR & Paiva 12191 (LISC)
Manica e Sofala. Gorongosa National Park. Vern.

name Icoho (Sena).

Macedo & Macuacua 1111 (PRE)
Sul do Save-Chibuto- junto as Rio Changans.

Lea, A 23 (PRE)
Distr. Chemba (Mozambique) near Tambara.

Gomes Pedro, J. 28 (PRE)
Chinde Distr., Micaune S.A. Madal Est. Muanaiu.

Jan de Koning & C. Boane 8649 (BM)
Maputo: Maputo. Costa do Sol para Marracuene.
19.2.1981.

Borle, J 110 (PRE)
L. Marques. Catembe.

ZIMBABWE

Bolboschoenus glaucus

N.C. Chase 6961 (LISC, NU, PRE)
Zimbabwe - 30 miles south of Devuli Halt -
24/7/58.

Goldsmith, B (3 sheets) 21 (NU)
Gwampa Forest Reserve.

Drummond & Rutherford Smith 7598 (LISC, PRE)
Nuanetsi; Between Palfrey's store and Nuanetsi
drift.

BOTSWANA

Bolboschoenus glaucus

de Beer JS. & Yalala, AM. 4 (NU)
Bechuanaland, Ngamiland.

Mary Paterson 25 (NY- photostat)
Makarikari Pan.

J.F. Ngoni 521 (MO - photostat)
Nata River near Nata Village.

INHACA ISLAND

Bolboschoenus glaucus

Noel, ARA. 10989 (GRA)
Inhaca Island. Fresh water swamp.

MADAGASCAR

Bolboschoenus glaucus

Forbes 12 (BM)
Type of *Scirpus nobilis* Ridley

Peltier, M. 3406 (P)
Mangolovolo.

Kotavao, R.A. (Gov. forest) 4565 (P)
Soalala Distr. Anoranomavo (?) Canton; localite R
N(?) 8.

Bosser, J. 8332 (P)
Sur Sols .. les, Maroroay ? ouest.

Decary, M. 8026 (PRE)
env. de Lambohorano.

Morant, P. 760 (P)
Ponte de Soalala.

Perrier de la Bathie 2445 (P)
Ouest. Bords de la mer. Ambongo. Aout ? 1903.

N. AMERICA AND ASSOCIATED ISLANDS

CANADA

Bolboschoenus fluviatilis

Fr. Edmond Roy 3209 (NU)
Rigaud, comté de Vaudreuil. 9. juillet 1934.

F. Marie-Victorin, & F. Rolland-Germain 49307
(PH)
Canada: Quebec. Sainte-Rose, comte de Laval;
Rivière des Mille-Isles. 29 July 1932.

B. maritimus ssp. paludosus

M.L. Fernald, Bayard Long & Harold St. John
6987 (PH)
CAN: Prince Edward Island. Salt marsh, Bunbury.
28 Aug. 1912.

G.F. Ledingham 6465 (NLU)
CAN: Saskatchewan. ½ mile south of Tribune, 30
miles south of Weyburn. 4 Sept. 1979.

Fernald & Long 20214 (K)
Nova Scotia: Kidstone Island

Edmondson 6226 (K)
Quebec; Metis beach.

Marcel Raymond & James Kucyniak 2150 (K)
Quebec: Anse-au-Griffon, comté de Gaspé.

R. Cayouette & Père Louise-Marie. o.c.r. 51-309
(K)
Compté de Gaspé, près du quai.

Fernald, Bartram, Bayard Long and Harold St. John 6980 (K)
Prince Edward Island, Border of Salt-marsh, Mt. Stewart.

John MacCoun s.n. (K)
Ex Herb. Geol. Survey Dept. Canada.
Salt marshes Kamloops B.C. Aug. 16. 1889.

Dr. Richardson Drummond s.n. (K)
Saskatchewan to the Bodly (?) Mt.

Prof. MacCoun 1619 (K)
Flora Canadensis. Hab. Athabasca Plains.

Bro. Victorin s.n. (K)
Plantes du Canada. Bords de la mer à Trois-Pistoles Co. Rimouski. Juillet 1913. 18 Jan 1916.

H.J. Scoggan 11209 (K)
Oak Lake, 12 miles east of Virden Marsh, 3 miles south of village. July 8, 1953.

Bolboschoenus robustus* x *maritimus

F. Marie-Victorin, F. Rolland-Germain et al. 49382 (PH).
CAN: New Brunswick; College Bridge Lake, comté de Westmorland: rivage maritime. 21 Aug. 1931.

UNITED STATES OF AMERICA

Bolboschoenus fluviatilis

S. Galen Smith & Damon Smith 8505 (WIS)
USA: Rock Co; North side of U.S. Highway 59 ca. 1.5mi.s. of Lima Center, T.4 N, R.14 E, sect. 29. 26 Aug. 1993.
Common emergent in 1 m of water with *Scirpus heterochaetus*, *S. validus*, *S. heterochaetus* x *validus*, *Ceratophyllum demersum*, *Potamogeton zosteriformis*, *Najas flexilis*. Keetle depression in farmland; marsh developed during low water in 1988-92 after ca. 20 years of deep water following years of low water with marsh.

Peter Rubtsov 2033 (PH).
USA: Sonoma Co., Guerneville Marsh. 7 Aug. 1955.
Open, wet to damp ground.

Sartwell 248 (PH)
USA: New York, Penn Yan. no date.

Steven P. Churchill 7772 (PH)
USA: South Dakota; Kingsbury Co. 5 miles s. of Arlington on Hwy 81. 23 June 1976.
Typha-Scirpus wetland marsh, plant occasional with *Beckmannia*, *Rumex*, *Sparganium*, *Alisma* etc.

A.E. Schuyler 4340 (PH)
USA: Minnesota; Wright Co., about 5 miles southeast of Buffalo, in wet depression between railroad and route 55 near Dickinsin Spring. 1 Sept. 1972.

E.B. Harger 6601 (PH)
USA; Lyme Co., Muddy shore of Connecticut R. at Selden's Cove. 18 Aug. 1915.

Reznicek 9675 (MICH)
Sandusky Co.; SW corner Junct. US 6 and Yorktown Rd., Riley Twp., ca 14.5 km NE of Fremont, SE 1/4 sec 1.
Wet, marshy banks of Strong Creek, along Yorktown Rd. Frequent but fruiting sparingly. *A.A. Reznicek 9675*, *B. Grese*, *T. Beavais*. Aug 4 1993.

c.f. *Bolboschoenus glaucus*

S. Galen Smith & R. Taylor 3134 (NY)
California, Merced County. Collected 5-6 Sept. 1958
"Species introduced prior to 1948 and now cultivated as food for wild ducks. Forming extensive stands in a field which was plowed in spring and then kept flooded to ca. 6 inches; also in drainage ditches. Somewhat alkaline soil on Los Banos Waterfowl Refuge, ca. 2 miles north of Los Banos."

Malcolm Nobs & S. Galen Smith 1883 (NY)
California, Glenn County: Collected 10 Sept. 1949.
"Rice fields about 1 mile south of Willows".

Bolboschoenus maritimus (the subspecies to be recognised in Flora North America, presently in preparation, have not been listed separately).

Ivan Cromwell 9 (K)
From Herbarium of the Catholic University of America. Det. *Scirpus paludosus* A. Nels.
San Ysidro, Dona Anna County, June 1937.

Ivan Cromwell 10 (K)
Plants of New Mexico. Det. *Scirpus paludosus* A.

Nels. Derry, Sierra County. June 27, 1937.

B.C. Tharp 43-518 (K)

Herbarium of the University of Texas. Plants of PECOS County, Texas. Det. *Scirpus paludosus* A. Nels. Stock tanks, Cunningham Ranch House. July 9, 1943.

Wiggins & Gillespie 3970 (MICH)

Near Rancho Salina, foot of Guatay Grade, about 4 miles south of Rio Guadalupe (Saline flats) Sept. 11, 1929. (ex Dudley Herbarium of Stanford University. Plants of Baja California. Det. *Scirpus maritimus* Linn. var. *paludosus* (A. Nels.) Kuekenenthal

Dunfee Minckley LD-8 (NLU)

USA: Arizona; Yuma Co., Mile 700 (approx.) on the Lower Colorado River. 21 Sept. 1974. Det. *Scirpus maritimus* L. var. *paludosus* (A. Nels.) Koyama.

Robert T. Clausen & Harold Trapido 4674 (PH)

USA: California. Riverside Co., Mud flat, mouth of creek, Oceanside. 18 June 1940. Det. *Scirpus paludosus* Nels.

S.E. Fellows 54 (PH)

USA: Minnesota. Pipestone. 12 July 1932. Det. *Scirpus maritimus* L. by S.G. Smith 1991 & 1993. Note appended "Some nuts 3-angles with concave sides."

L.A. Kenoyer & Francis W. Pennell 3470 (PH)

USA: Massachusetts. Barnstable Co; Salt marsh, North of Falmouth. 5 Aug. 1911. Det. *Scirpus maritimus* L. by A.E. Schuyler 1976 and S.G. Smith 1991, and 1993.

Francis Pennell 1135 (MICH)

Salt marsh near Polpis. August 23, 1921. *Scirpus campestris* Britton v. *paludosus* (A. Nels) Fernald - The Academy of Nat Sciences of Philadelphia - Nantucket County, Massachusetts. Det. *Scirpus maritimus* L. by S.G. Smith 1991.

Robert A. Norris 4778 (NLU)

USA: California: Marin Co., Tiburon Peninsula. [Muddy ditch (not evidently brackish)]. 10 July 1984. Det. *Scirpus maritimus* L. (includes *S. paludosus* A. Nels.) by S.G. Smith 1993.

A.N. Steward 7224 (NLU)

USA: Oregon. Harney Co., Harney lake, 1 mile off southeast shore. 11 July 1956.

Det. *Scirpus maritimus* L. (includes *S. paludosus* A. Nels.) by S.G. Smith 1993.

Bruce Baldwin 300 (UCSB)

USA: California. Santa Barbara Co., Coal Oil Pt. Reserve. 2 Nov. 1979. Det. *Scirpus maritimus* L. by S.G. Smith 1992.

W.R. Ferren 1720 (UCSB)

USA: California: Santa Barbara Co., Carpinteria Salt Marsh, Carpinteria. 15 Sept. 1978. Det. *Scirpus maritimus* L. by S.G. Smith 1992 & 1993.

J.M. Macfarlane & W.R. Taylor s.n. (PH)

USA: Maine: Peak's Island, Casco Bay. 8 Sept. 1916.

Det. *Scirpus maritimus* L. by S.G. Smith 1993. Note appended, 'Nuts lenticular to obtusely compressed - trigonous, sides often concave. Floral scales intermed. between *robustus* and *maritimus*. Leaf sheath summit as in *maritimus*'.

Hinds, H.R. 6626 (MICH)

Frequent. One or two forms the other long narrow spikelet. Salt marsh. Point au Carr. 23 oct. 1983. Flora of New Brunswick; Nothumberland County. Connell Memorial Herbarium, University of New Brunswick, Fredericton, New Brunswick. Det. *Scirpus maritimus* L.

Smyth, B.B. 16 (MICH)

Sea Club-Rush Hutchinson, Kansas. July 29 - 1890. From the United States National Herbarium. Herbarium Kent Scientific Museum Grand Rapids Mich. Det. *Scirpus maritimus* ! S.G. Smith 1991.

Bolboschoenus novae-angliae

Hotchkiss, N. & Uhler, F.M. 7143 (US)

Occasional in slightly brackish marsh about 2 miles south of Wide Water, Stafford Co. July 29, 1947. (Flora of Wahington-Baltimore area)

Svenson, H.K. 1642 (PH)

USA: Massachusetts. Barnstable Co. Salt marsh. 30 Aug. 1968.

Schuyler, A.E. 4477 (PH)

USA: Maine, Waldo Co: about 2 miles north of Prospect, scattered stands in extensive brackish to saline marsh (Howard L. Mandall Wildlife Management Area) 31 Aug. 1973.

Earle, Elizabeth, C. 5417 (PH)

USA: Maryland Talbot Co. Marshy area near bridge, Kings Creek, 5½ mi. e.x n. of Easton. 23 July, 1968.

Schuyler, A.E. 4417 (PH)

USA: Maine: Sagadahoc So. about 1 mile northeast of Woolwich, along rocky shore of Pleasant Cove. Growing at upper limit of tide above mixed zone of *Scirpus pungens* and *S. acutus* x *validus*. 16 Aug. 1973.

Fernald, M.L. and Baynard Long 18061 (PH)

USA: Massachusetts. Barnstable Co. Quivett Creek, East Dennis, Dennis. Rich swale bordering salt marsh. 18 Aug. 1919.

John M. Fogg, Jr. 3154 (PH)

USA: Massachusetts: Dukes Co., Margin of Typha swamp. E. end of island. Naushon. 1 Oct. 1927

M.L. Fernald and Bayard Long, 8934 (PH)

USA: Rhode Island, Newport Co., Dryish borders of salt marshes about Harbor Pond and Trim's Pond, Block Island. 19 Aug. 1913.

Miller, E.S. sn. (PH)

USA: New York; Wading River. 23 July 1877.

Bolboschoenus robustus

Dr. Edward Palmer 160 (K)

Vicinity of Tampico, Tamaulipas; altitude about 15 m.

J.N. Rovirosa 736 (K)

Flora Mexicana. Habitat in paludosis ad ripas fluminis Gonzalez prope La Ceriba (Ceiba?) Feb. 11. 1890.

Chase 2523 (MICH)

Chesapeake Beach - brackish marsh. 8-2-04. Herbarium of Agnes Chase. Herbarium of Frank C. Gates 1985 Ex Herbarium University of Illinois. Herbarium of Michigan.

Joseph Ewan 17966 (NO)

USA: Louisiana: Salt marsh, Delta Wildlife Refuge, delta of Mississippi R. above Pilottown, Plaquemines Parish, 26-27 Nov. 1948.

A.R. Hodgdon & F.L. Steele 19810 (PH)

USA: New Hampshire; Rockingham Co., Newfields, along Squamscott River. 8 Aug. 1973.

Glen N. Montz 3870 (NO)

USA: Louisiana. St. Mary Parish; Atchafalaya Bay on dredged material [Coast of Gulf of Mexico] 1 Sept. 1975.

M.L. Fernald & Bayard Long 18057 (PH)

USA: Massachusetts; Barnstable Co. Springy swales bordering the Great Marshes, West Barnstable, Barnstable. 26 Aug. 1919.

Thomas C. Porter s.n. (PH)

USA: New York. Staten Island. [adjacent to New York city; probably in salt marsh.] no date.

W.R. Ferren et al 2336 (PH)

USA: California: Orange Co. Salt marsh, Newport Beach. 27 Aug. 1980.

Putative *Bolboschoenus robustus* x *maritimus*

Rodney H. True 315 (PH)

USA: Maine: Casco Bay; near high tide line, east side of Beal's Cave.. 8 Sept. 1923

Det. *Scirpus robustus* x *maritimus* Hybrid? S. Galen Smith 1991 & 1993.

W.R. Ferren 2686 (PH)

USA: California; Santa Barbara Co., [Coastal] lagoon margin ca. 5 mi W of Goleta. 6 Oct. 1983. Det. *Scirpus robustus* Pursh x *maritimus* L. ? Hybrid. by S. Galen Smith 1991, with note 'Habit like *S. cylindricus* (Torr.) Britt. or *S. robustus* x *fluviatilis*.' also 1993.

W.R. Ferren, S. Whitmore, B. Millett 2339 (PH)

USA: California; Orange Co., Tidal ditch in salt marsh of Newport Backbay, just W. of Backbay Drive, ca. 3km NE of Rt. 1, Newport Beach. Associated with *Scirpus robustus*..27 Aug. 1980. Det. *Scirpus* *maritimus* x *robustus* by S.G. Smith 1992; with note 'sheath mouth as in *maritimus*' and 'This specimen differs somewhat from "duplicate" at U.C. Santa Barbara.

Indeterminate

H. Walton Clark s.n. (K)

California Academy of Sciences. Flora of California. *Scirpus pacificus* Britton Indio Riverside Co. June 1926. (Det. by Schuyler 1974 as *S. paludosus*.)

HAWAII

Bolboschoenus maritimus ssp. *paludosus*

Otto Degener 31.113 (GENT, K)

Salt lake, Oahii, Muddy edge of drying lake.
Sept. 15, 1966.

Dr. Hillebrand 529 (K)
Sandwich Islands. Received July 1865. Salt lake
..?

Herb Forsyth (K)
Purchased 1835. Sandwich Isles. *Scirpus affinis*
Rth. Clarke 1887 writes, "*Scirpus maritimus* Linn.
This is not exactly = the Indian *affinis*, which has a
remarkably small nut = this is exactly = the
Australian 'digynus' i.e. the 2-fid style form of the
Australian *fluviatilis* var. *macrostachys* Mich."

J.F.G. Stokes s. n. (K)
Flora Hawaiiensis. *Scirpus maritimus* var. *digynus*
Boeck. June 1-2-1920.
Kaelepulu Stream, near Kailu Oalu.

C.N. Forbes 408 (K)
Flora Hawaiiensis. Collected by C.N. Forbes on
Molokai Pukoo. Aug. 1912.

REVILLAGIGEDO ISLANDS

Bolboschoenus maritimus subsp. *paludosus*

Herbert L. Mason 1580 (K)
California Academy of Science. Expedition to the
Revillagigedo Islands 1925
Clarion Island. *Scirpus robustus* var. *paludosus*
(Nels.) Fern.
Growing on the margins of a fresh water pool
behind sand dunes. Plant 4-8 ft high. April 29,
1925.

SOUTH AMERICA

VENEZUELA

Bolboschoenus robustus

'Steyermark, Liesner, & Delascio 114914 (MO, VEN).
Venezuela, Territorio Federal. Delta Amacuro,
Depto. Pedernales (boundary with Depto.
Tucupita): sand beach bordering open sandy mud
flats and wet depressions, mouth of Ca~no
Guiniquina, between Punta Araguabisi and Punta
Baja, at Barra Guiniquina, Lat. 9 degrees 30
minutes N, 60 degrees, 58 minutes W, 50 meters
elev. 18 Oct. 1977.

Steyermark, Liesner, & Delascio 114866 (VEN)
Venezuela, Territorio Federal. Delta Amacuro,

Depto. Pedernales (boundary with Depto.
Tucupita): sand beach bordering open sandy mud
flats and wet depressions, mouth of Ca~no
Guiniquina, between Punta Araguabisi and Punta
Baja, at Barra Guiniquina, Lat. 9 degrees 30
minutes N, 60 degrees, 58 minutes W, 50 meters
elev. 18 Oct. 1977.

GUYANA

Bolboschoenus robustus

Rambaran 4 (K)
Vreeden-Hoop Foreshore.

BRAZIL

Bolboschoenus robustus

Coll ? 1205 (K)
Common in fresh water marshes .

Gardner 1838 (K)
Pernambuco.

Tweedie s.n. (K)
Rio Grande.

PARAGUAY & ARGENTINA

Bolboschoenus robustus

A. Burkart 15670 (K)
Prov. Buenos Aires. Gral. Lavalle

G. Clavay 170 (K)
Laid in for J. Ball
Valle du Rio negro & Patagones en Tezarier
"On l'appelle 'Estero'.

Theodora Rojas 311 (K)
Fluminis Pilcomayo.

Theodoro Rojas 608 (BM, K)
Comision argentino-paraguaya de limites 1906
Plantae Pilcomayenses
a custode herbarii Hassleriani.
In regione cursus inferioris fluminis Pilcomayo
mens Aug.

R. Guaglianone et al 1291 (SI)
Argentina: Prov. Buenos Aires, Pdo. Magdalena,
Pipinas. Bañados de la costa. 15-xii-1985.

B. maritimus ssp. *paludosus*

Walter Fischer 1760 (BM, K)
Sept 1914 Feb 1915. Vicinity of General Roca,
Rio Negro. Alt. 250–360 m.

Hicken 3153 (SI)
Argentina: Prov. Buenos Aires, Sierra de la
Ventana.

P. Steibel & Troiani 5359 (SI)
Argentina: Prov. La Pampa; dpto. Puelén. Colonia
25 de Mayo. 13-xii-1977.

W.J. Eyerdam, A.A. Beetle & E. Grondona 23589
(K)
Argentina: Gob. Chubut, Depto. Rawson 2 km
south of Trelew, bank of Rio Chubut. Shallow
water, rooted in sandy mud. Alt. 30 m. Not
common or abundant. Dec 22. 1938

Pedersen 9981 (K)
Shores of mar Chiquita. Miramar 25/10/1971.
Dep. San Justo. Prov. Cordoba.

URUGUAY

Bolboschoenus robustus

Gilbert (or Gibert ?) 1282 (K)
1874. Montevideo.

Tweedie ? s.n. (K)
Saint Lusie.

AUSTRALIA, NEW ZEALAND AND ASSOCIATED ISLANDS

AUSTRALIA

Bolboschoenus caldwellii

B.J. Lepschi & T.R. Lally 1758 (PERTH, CANB,
NU)
W. Australia: NW bank of Swan River at Garratt
Road Bridge, Bayswater Perth. 11 March 1995.

J.J. Bruhl 60 (CANB, NE, NU)
NSW 34° 50'S; 150° 43'E; Berry-Shoalhaven Rd.
E. of Far Meadow, Coolangatta Rd. 09/06/1985.
Tufted perennial herb. Habitat: In drainage ditch
leading to swamp, dairy pasture with Juncaceae.

M. Fagg & J. Pulley 1180 (NSW)
Canberra Dist. A.C.T. between Lyneham &
Gungahlin. Abundant in swamp. 9.1.1973.

K.L. Wilson 7576 (NSW)

Queensland. Buckinbah Weir, SE of St. George.
28° 10'S, 148° 50'E. Man-made reservoir (not very
large) for irrigation scheme - *Typha domingensis*
and *Persicaria attenuata* frequent on margins - in
bimble box country (mostly cleared). Occasional
patches over little bridge on E side of water. 10
Jun. 1987.

P.K. Latz 8698 (NSW)
Northern territory. Palm Valley. 24° 03'S, 132°
42'E. Clonal perennial. Rare in sand over rock bed.
Seepage area. 17/05/1981.

W.F. Kenneally 7181 (NSW)
Western Australia. S. bank of Swan River at Alfred
Cove Nat. Res. approx 6 km upriver from
Freemantle. Lat. 32° 01'S, Long. 115° 48'E. 2
April 1980. Rhizomatous sedge. Common along
foreshore of river with *Juncus kraussii* in coarse
white shelly sand.

R. Pressey s.n. (NSW)
Victoria. 15 km SSE of Monak. Lat. 34° 25'S,
Long. 142° 20'E. 9.2.1985.

S. McIntyre & M. Newnham 504 (NSW)
Drainage channel near farm 263 near Beelbanger.
Lat. 34° 15'S, Long. 146° 07'E. Large population
(1000+); up to 1.5 m high. 7 Feb. 1985.

S.T. Blake 23073 (NSW)
Queensland. Brisbane. Pinkenba. Broad roadside
ditch, unseasonably dry. Erect culms, green leaves.
04 Apr. 1969.

A.C. Beaughtole ACB37839 (NSW)
Lake Tyers. East Gippsland, Vic. Boundary road
area. 7.4.1971

S.M. McIntyre & M. Newnham 502 (NSW)
M.I.A. farm 1653, SW corner; just North of
Beelbanger. Lat. 34° 15'S; 146° 07'E. 7 Feb.
1985. Mostly in clumps throughout rice crop, but
mainly near edges.

K.L. Wilson 1677 (NSW)
Southern margin of Lake Cargelligo. lat. 38° 18'S;
long. 146° 23'E. 27.9.1983. Abundant in ditch
behind levee bank beside road. Also *Typha*, *Rumex*
crispus, *Cyperus gymnocaulos*.

P.L. Milthorpe & G. M. Cunningham 5066 (NSW)
"Thurloo Downs" Lat. 29° 17'S; Long. 143° 29'E.
2/12/1976. Bore drain, tall sedge to 90 cm tall.
Seeding.

K.L. Wilson 6019 (NSW)

2.5 km E of Macquarie R on Willie-Sandy Camp Rd. Lat. 30° 53'S; Long. 147° 31'E. 14/11/1984. Frequent in mud & water to 10 cm deep, in open swampy area beside road. With water couch, *Eleocharis plana*, *Ranunculus*, *Azolla*.

N.V. Fitzgerald s.n. NSW 51759

Swan River near Perth (West Australia). 4 -1901.

K.L. Wilson 4607 (NSW)

31 km SE of William Creek on Marree Road. lat. 29° 04'S; Long. 136° 31'E. 10/4/1983. Man-made lake between red sand dunes with hot bore water running in from a pipe. Occasional in mud (but obviously more common from abundant tubers lying around).

H.B. Williamson 124 NSW1760 (NSW)

Warrnambool. Vic.

Bolboschoenus fluviatilis

Geoff Sainty 2105 (NU)

Australia: NSW. Botany Wetland, Pond 5. 2/3/1996.

Skinner, S. s.n. (NE)

Bushells Lagoon, Freeman's Reach. Hawkesbury River, N.S.W. 13.12.71. Soil- gray alluvial. Community - reedbed at lagoon margin. Remarks: Rather tall sedge - to 8 ft - 2 ft. in water.

R. Coveny 4034 & R. Bisby (NSW)

9 miles (14.5 km) S. of Dapto on the Prince's Highway. 34°36'S; 151°51'E. 13.3.1972. Erect sedge 1.5-2 m high with dark brown spikelets and creeping rhizome growing with *Phragmites australis* etc.

R.A. Buchanan s.n. NSW 373818 (NSW)

Ellalong Lagoon; W of Cessnock. 16.2.1979. Swamp.

S.T. Blake 18261 (NSW)

Sandgate. 30 Nov. 1948. Associated with *Typha* at edge of lagoon. Evidently with creeping rhizome; stems erect \pm 1.5 m high; leaves green; spikelets brown.

A. Gray 3921 NSW 72952 (NSW)

Near Kempsey NSW. 31°04'S; 152°49'E. viii. 1974. Swampy area near roadside.

K.L. Solling 582 (NSW) Drawn for Flora of NSW Centennial Park, Sydney. 22.xi.1973. Erect c. 2 m

tall. Growning at edge of Lakes.

K.L. Wilson 995 & L. Johnson (NSW)

½ km E of Mt. Alfred Creek, c. 8 km W of Jingellic crossing on Tallangatta road. Vic. Lat. 35°57'S; Long. 147°38'E. 14.2.1975. In mud at edge of big lagoon beside Murray R.

A.C. Beaulehole ACB 70665 (NSW)

Hughes Creek Flora Reserve, Vic. 6. xii. 1982. Melbourne Study Area, Sector F. Sub-block 31C. Dupl. MEL.

L. Johnson 9028 NSW 373819 (NSW)

Black Creek, Kinchela (Lower Macleary R.) Lat. 30°58'S; Long. 153°00'E. Alt. 2 m. 28.1.1985. Abundant in dry creek bed on extensive alluvial flat forming pure dense stands. Also on part of creek bed along Kinchela-Hat Head road in similar situation.

Apeo Pty. Ltd. per District Agronomist NSW 77413 (NSW)

Maitland District. Lat. 32°43'S; 151°33'E.

K.L. Wilson 5714 NSW 373816 (NSW)

S.E. bank of Tweed River at Jumbulgun ferry. Lat. 28° 17'S; Long. 153° 27'E. 22.xii.1983. One large patch near ferry in shallow water (water at least brackish - scattered mangroves along banks). Also *Schoenoplectus* (5713) and *Cyperus laevigatus* (5715).

S.T. Blake 23573 (NSW)

S. of Coolum, E. of Bli Bli; 26° 37'S; 153° 05'E. Side and bottom of drainage ditch at roadside through wallum flat, forming communities. Rhizome slender with tubers....

C.T. White s.n. NSW 72946 (NSW)

Sandgate (Moreton Bay). Oct. 1915.

K.L. Wilson 6020 (NSW)

Monkeygar Creek, 3.5 km E of Macquarie R on Willie-Sandy Camp road. Lat. 30° 53'S; Long. 147° 32'E. 14.xi.1984. Abundant with *Phragmites* and *Typha* at edge of marsh. c.f. smaller 6019 (*B. caldwellii*) from nearby locality.

K.L. Wilson 2248 (NSW)

Boydton turn-off from Princes Highway c. 7½ km S. of Eden. 8.11.1979. In large ditch beside road with *Typha*.

Bolboschoenus medianus

A.C. Beauglehole ACB 63095 (NSW)

Victoria. J40. Corangamite Study Area. Sector B.
Sub-block: 6I. Lake Jollicum Wildlife Reserve. 3
km NE of Nerrin Nerrin P.O. 11.1.1979.

R. Coveny 11583 & P. Hind (NSW)

Coffins Crossing on Molonglo River, 3.6 km SSW
of Cook, P.O. A.C.T. Lat. 35°17'S; Long.
149°02.30'E. Alt. 510 m. 22/1/1983.

Perennial sedge up to 1 m high with creeping
rhizome & brown spikelets. Locally common in
shallow water..

M & B Gray 4002A (NE, NSW)

Molonglo River, Canberra A.C.T. 25.11.1956.
Anaerobic & gravelly mud. Growing with base in
water.

B.J. Lepschi 1598 (NU)

Molonglo river at "Burbong" Hstd., 8km ENE of
Queanbeyan Post Office. 35°21'S 149°18'E.
Blackish-brown mud in water to c.40 cm deep at
rivers edge. With *Eleocharis* spp., *Phalaris*
aquatica, *Poa labillardierii*, *Persicaria* spp. and
Salix alba. Fairly common in patches. Dupl. to A,
BRI, CTES, G, L, MBM, NE, NSW, NU, OSBU,
US. 1 Apr. 1994.

B.J. Lepschi 1604 (NU)

Mulwaree River, c.2km N of Tarago. 35° 04'S
149° 39'E. silty clay in slow-flowing water to c.
40cm deep. With *Eleocharis* sp. and *Myriophyllum*
sp. Fairly common. Dupl. to NE, NSW, NU. 3
Apr. 1994

A.C. Beauglehole ACB44296, G.W. Carr & D.G. Cameron (NSW)

Victoria -South west. Grid K42. ca. 3¼ mls. (5.2
Km) N.W. of Cape Otway lighthouse, along Aire
River. 13 Mar. 1974.

K.L. Wilson 3149 (NSW)

Finniss R, 15 km S of Strathalbyn on Goolwa Rd.
SA. Lat. 35°23'S; Long 138°48'E. 11.May 1980.
Frequent at edge of water.

R. Pressey s.n. (NSW)

9km NE of Mildura [Div NSW SFWP] Lat
34°08'S; Long 142°14'E. 7.1.1985.

A.C. Beauglehole ACB 67553 (NSW) ex MEL
Victoria W9. Snowy River National Park S. of
McKillop Bridge, Snowy River 15 km W of
Tubbut P.O. 22.1.1980.

M. Gray 6035 (NSW 120794) (NSW)

Shores of Lake Burley Griffin, Canberra ACT
opposite Canberra Botanic Gardens, Black
Mountain. 25 Mar. 1967. In ca. 3--6 inches of
water. Rhizomes with globular tubers, common.
Dup. to E. Edgar.

S.J. Griffith s.n. NSW 242866 (NSW)

Khappinghat Creek area, 30 km SE of Taree,
Australia's NSW North Coast. Lat 32°02'S; Long.
152°32'E. Alt. 0 m. 24 Feb 1991. Creek bank in
Melaleuca quinquenervia woodland with scattered
Eucalyptus tereticornis. Soil derived from recent
sediments of estuarine origin. Herb. 1--2 m high.

Evan A. Chesterfield s.n. (NSW)

Barmah adjacent to Murray River upstream from
Echuca. 15.2.1979. Has large root swellings -
tubers.

L.A.S. Johnson s.n (NSW)

Snowy River NSW, at Vic. border 300 m.
15/iv/1968. Patches on river bank amongst sand
and silt.

K.L. Wilson 8612, J. Roberts & G. Sainty NSW 265132 & 273023 (NSW)

Baroona/Tillaloo Waterhole, S. of Gingham road,
c. 40 km directly NW of Moree. Australia NSW
N.W. Plains. Lat. 29°15'S, Long. 149°29'E. Big
open lagoon, about half full, fringed with coolibah
and some *E. camaldulensis*. Grey cracking clay
soils. One stand, at least 10 m long, on northern
shore. Also *Cyperus exaltatus*, *C. pygmaeus* C. ?
bifox (imm.); *C. gracilis* in surrounding woodland.
Dups to NE.

E. Betchi 122 (NSW)

Narromine, on river banks NSW.
Det. *S. maritimus* var. *fluviatilis* Torr. Kük 9/2/13.
Det. *S. medianus* by A. Gray 1974.

B. Semple 1663 (NSW)

"Glen Avon" - 10 ml N of Balranald. 5.1.1984.
Channelised flood plain with River Red Gum.
Sedge of over 1 meter. Localised areas only.

M.D. Fox 8304074 & H. Fallding (NSW)

Murray River bank at Curlwoa, just east of bridge.
Lat. 34°07'S, Long 141°59'E. 28.April 1983.
Frequent herb to 0.6 m high brown fruit, growing
in small lagoon beside main water course of
Murray River.

TASMANIA

Bolboschoenus caldwellii

Coll: M? 1592 (NSW 72977)
ex W.H. Archer's Herbarium of Tasmanian Plants.

L. Rodway s.n. NSW 72978 (NSW)
Tasmania

PAPUA NEW GUINEA

Bolboschoenus fluviatilis

Walker ANU 536 (K)
Sirunki, Western highlands. Swamp beneath the village of Nanguris.
Tall reed swamp area within major swamp. Alt. 8400 ft. Average height of spike head 180 cm and to top of flowering bract 205 cm... small tubers at base..

NEW CALEDONIA

Bolboschoenus fluviatilis

M. Bernier 1234 (K)
Conservateur du Musée Colonial de Nouméa
Nouvelle-Calédonie. Ex Herb. Paris.
Mi Nau (illegible).

K.L. Wilson 7809 NSW 237315 (NSW)
2 km W of Rivière de la Coulée bridge on Mont Doré-Nouméa road. Lat. 22°14'S; Long. 166°33'E. Alt. 5 m. 09 Feb. 1991. Open swamp at roadside behind *Melaleuca quinquenervia* swamp, which is itself behind mangroves. Alluvium. Dominant in open swamp (nearly dry- rains late this year) Dups to GENT, P.

NORFOLK ISLAND

Bolboschoenus fluviatilis

John MacGillivray 774 (K)
Voyage of H.M.S. Herald. Isle of Pines. Swampy ground Oct./53.
Clarke, 1887, wrote '*Scirpus maritimus* Linn (the Australian form)'.

Milne 161 (K)
Voyage of H.M.S. Herald. Isle of Pines.
Backhouse Oct. 53.

J. McCornish 179 (NSW)
Date: 3/39. Det. S.L. Blake as *B. medianus*. Det. K.L. Wilson as *B. fluviatilis*.

NEW ZEALAND

Bolboschoenus caldwellii

Cook 542 (AK)
Locality: Waitakaruru, near Thames. Jan. 1944.
Herb. No. 59206: Isotype, *Scirpus caldwellii* Cook

V.J. Cook s.n. AK 61772. (AK)
Kaikoura Ecological Region. Jan. 1947.

Bolboschoenus fluviatilis

Herbarium of V.J. Cook. (AK)
Locality: Port Waikato
Herb No. 59189 Isotype, *Scirpus perviridis* Cook

R. Mason 10,115 (Herb. No. 169344) (NSW)
Channel near paper mills, Whakatane. Dupl of No. 169344. 31.1.1963.

R.O. Gander 1003 (NSW)
Island Block, Waikato Basin. 9.3.1975. Alt. 150 ft.
In seepage at road edge.

R. Cooper s.n. Herb. No. 119873 (AK)
Tokatoka, 489563 on Map N 27, Hobson County.
22.2.1968.

Bolboschoenus medianus

V.J. Cook 463 (AK)
Locality: Waitakaruru nr. Thames. Jan. 1940
Herb No. 61798 Isotype, *Scirpus medianus* Cook

c.f. *B. glaucus* (introduction ?)

A.J. Healy & B.G. Hamlin 50/70 (K)
Botany Div. DSIR Christchurch N.Z. Duplicate of 82080.
Det. *Scirpus medianus* V.J. Cook
Loc. Near Puketapu, Hawkes Bay, North Island.
Abundant on verges of Typha swamp.
Date 12/2/1950 and 7/9/1953. Plants to 1 m tall.

EUROPE

SWEDEN

Bolboschoenus maritimus s.s.

L.A. Nilsson s.n. (NU)
Sweden, Gotland, Oestergarn parish, Herrvik,
Natviksudden. lat./Long. 77:24N 18:55E. 3 Sept.
1991. On sea shore of the Baltic (brackish water).

Örjan Nilsson s.n. (H)
Sweden. E Uppland (Roslagen), par. Börstill, 2 km

W kallö, near Husbacka. Along stoney and muddy seashore, in very shallow brackish water. 14. Oct. 1995.

FINLAND

Bolboschoenus maritimus

Sakari Hinneri & Unto Laine s.n. (NU)
Finland. Region aboënsis (Ab), Askainen. Small bay with brackish water near Lempisaari estate in Lemsjöholmen. 16 Aug. 1972. (ex Turku University Herbarium)

RUSSIA FEDERATION (west)

Bolboschoenus glaucus and *B. yagara*

Two on one sheet (K)
Left = Museum botan. Acad. Petrop.
Songaria (the locality ?) Exp. AG. Schrenk. Com., A. Bennett Nov. 1890
This confirmed from fruit = *B. glaucus* (J.B. 1997)
Right = Ex. Herbario horti Petropolitani
Illegible, may be *Ufrunis* ? and *Maarku* ?
This is confirmed by fruit = *B. yagara* (J.B. 1997)

c.f. *Bolboschoenus maritimus*

TH. Henru and Jll. Eropoba 967 (K)
Russian label- ex Herb. Inst. Bot. As. Sc. URSS.
Apparently Volgograd distr. 19/vii/1952.
Det: *B. maritimus* by T. Egorova in 1967.

BRITISH ISLES

Bolboschoenus maritimus

A.R. Horwood s.n. (K)
Benacre Broad. Saltmarsh next to shingle. 21/July/1928.

F.M. Day s.n. (K)
Walberswick. Suffolk. 6/9/38.

E. Milne Redhead & HKA. Shaw 1613 (K)
Dykes between Woodbridge and Melton. 29.9.1931. In brackish water.

AR. Horwood 9 (K)
Edge of shingle, reed swamp Easton Broad, Wrenthan, Suffolk. 17.ix. 1934.

J.T.L. Boswell-Syme s.n. (BM)

Battersea. Surrey. July-Aug. 1882.

Herbarium Churchillianum Proprium (K)
Bequeathed 1906. Collector (?).
By side of ditch along road from Rye to Winchelsea Sussex Oct. 25. 1865.

FN. Hepper 825 (K)
E. Yorks. Kilnsea. in sand at high water mark. 14 Aug. 1955.

MD. Ker 156 (K)
Mouth of Beaulieu River about 1 m W of Lepe. Swampy ground just above high water mark. Sea level 17.9.36.

FY. Broeas 1190 (K)
Ditch parallel with the coast between Queenboro' and Sheerness, Isle of Sheppey. 8-1855.

AA. Bulloch 519 (K)
N. Lincolnshire. Humberstone Foreshore; 2-3 miles S. of Cleethorpes. Brackish ditch behind St. Anthonys Bank. Also in one part of salt marsh with fresh water outflow from spring. Abundant; up to 3 ft. high.

JH. Chandler & JL. Gilbert 363 (K)
S. Lincolnshire. Around a pond at Gedney Drove 19.viii.1959.

M.B. Gerrans 700 (BM)
E. Kent. V.C. 15. Marshes at edge of Thames between Cliffe and Higham. 22 Sept. 1958.

E.C. Wallace 1297 (BM)
Kent. Dyke. Higham Marshes 5.10.1924.

S.T. Jermyn 302 (BM)
Essex: Foulness Island V.C. 18. 4 Sep. 1954.

Bolboschoenus yagara and putative hybrids

P.C. Hall s.n. (BM)
SALOP: in pond in grounds of Field Study V.C. 40 Centre, Preston Montford. Nat Grid 33/433143. 14 July 1961.

V. Summerhayes 1363 (K)
Somerset. King's Sedgemoor, below Walton Windmill, in partially dried up ditches - very abundant.ii.viii.1943. Alt. 17 ft. (6 North Somerset)

F.M. Day s.n. (K)
Somerset. Marshes near Glastonbury. 12/8/48.

EC. Wallace s.n. (K)
Surrey. By pond on Shalford Common.

Herb. *P. M. Hall* (BM)
Flora of Surrey. Br. Pl. List 746/2
By a pond on Shalford Common. E.C. Wallace ii.
vii. 1934.
Accompanied by a typed note "*Scirpus maritimus*
L. By pond on Shalford Common, Surrey. V.C. 17,
in abundance, August 11, 1934. A rare species
inland, recorded for adjoining county of Berkshire,
see Druce's Flora of Berks. There is no trace of
this species now at Iville Farm, the station
recorded in the Flora of Surrey - E.C. Wallace".

Ex Herb *JE. Lousley s.n.* (BM, K)
Margin of Lake. Grounds of Buckingham Palace.
v.c. 21 Middlesex 4- Sep. 1956.

DENMARK

Bolboschoenus maritimus

E. Coppejans 5782 (GENT)
Denemarken, Djursland; Ebeltoft. Alt. 0 m.
Standplaats: Strandvegetatie of 2 m un de sand von
de Baltische Zee. In groepen groeninol (?).
14.08.1985.

A. Hansen 11099 (GENT)
Ishøj, SW of Copenhagen (Denmark, isle of
Zealand, TBU.- district 45a), scattered among
normal plants in salt marshes near the sea, August
10th, 1980.

Kai Larsen s.n. (NE)
West Lolland, Kragenaes meadows near the sea.
6.9.1964. dist 35.
Botanisk Institut Aarhus Universitet. Denmark.

A Jäger s.n. (NU)
Denmark; Lolland; Nakskov; Albuen. 7 July 1997.

THE NETHERLANDS

Bolboschoenus maritimus

T. Ongena s.n. (GENT)
Nederland, Zeeland, Terneuzen, natuur, Westgeul
[FBL : B3.42.13. augustus '82. Alt. 0.50 m. Hab.
kalkrijk, zandig, vochtig substraat met zout
invloed, plaatselijk tijdelijk geïnundeerd (cf. lic.
verh.)

J. Duvigneaud 70 H 800 (12024) (GENT)
Hulst (Pays-Bas, Flandre zélandaise), au nord du

Hedwige Polder, schorre en bordure de l' Escaut, 5
september 1970.

'Rem. : La plupart des phytosociologues
distinguent souvent ce taxon au range variétal.

GERMANY

Bolboschoenus maritimus

A. Kneucker 219 (GENT, WIS)
Am Strande des Kieler Hafens unweit des Bülcker
Leuchtturms am Rande des Wassers in Schleswig-
Holstein. October 1908 und 1910.

putative hybrid

Herbert Fritze s.n. (NU)
Germany; North Germany; Lower Saxonia; Granz
on the River Elbe 18.7.1976.
During the flood of the river standing in the
brackish water. Distance from the North-sea : ab.
100 km.

Bolboschoenus yagara including putative hybrids

Baenitz, C. II 109 (MO)
North and middle Germany. 1865
Coll. by Gortitz ?

F. Schuhwerk 86/490 (NY)
Germany, Bavaria, Donauebene, etc... 25 July
1986.
Herbar F. Schuhwerk No. 86/490

R. Gross s.n. (NY)
Germany, West-Prussia. Tiegenhof an Gräben. July
1900.

Karl Kiffe s.n. (NU)
Im trockengelegten KÜ bei Münster-Gimbte auf
ausgetrocknetem Schlick. 17.8.1995

Karl Kiffe s.n. (NU)
Schübelsweiher ö. Hemhofen, nw. Erlangen,
Bayern.

Buchwald s.n. (BFN)
Jeverland/Ostfr. Binnenderchs. 5. Juni. 1955.

Meide s.n. (BFN)
Flora von Niedersachsen. Grohnde bei Göttingen.
1876.

Herzog s.n. (BFN)
Flora von Niedersachsen. Hildesheim. ?? de

Innerste. August 1879.

Flora von Niedersachsen (BFN)
Hannover; ad fossas. Mai 1830.

POLAND

Putative *Bolboschoenus yagara* x *maritimus*

J. Madalski 191 [?] (K)
Plantae Poloniae Exsiccatae
191 *Bolboschoenus maritimus* L. Palla
- Sitowiec nadmorski (= *Scirpus maritimus*)
Kotlina Naddniestrzanska (in convalle super. flum
Tyrae): Babina K. Sambora (pr. Sambor). In fossa
pr. locum "Zakutyna" dictum. -5- vii-1932.

BELGIUM

Bolboschoenus maritimus

M. Gryseels 645 (GENT)
België, Prov. West-Vl., Stuivekenskerke, vroegere
kleiputten, nu brakwater-plassen. Langs de oevers
van de plassen in dominante vlekken tussen
rietkragen e.a. oevervegetatie. 24/8/1978.

Putative *Bolboschoenus yagara* x *maritimus*

Ch. Firket s.n. (WIS)
Belgium; Meuse River. 3 Sept. 1872

GUERNSEY

c.f. *Bolboschoenus maritimus*

D. McClintock and Mrs P. Ryan s.n. (BM, K)
Portelet. Wet salty patch at foot of cliff 2nd Sept.
1994.

D. McClintock and Mrs P. Ryan s.n. 23 SeptAug.
1997 (NU)
Pleinmont, Guernsey. Rocks washed by the tide.

Mrs P. Ryan s.n. (BM)
3 sheets - all same collector and locality; one sheet
collected 1971.
Pleinmont- rocks washed by sea below seawall
below Imperial Hotel 29. ix. 1973.

Mrs P. Ryan s.n. 3 Aug. 1997 (NU)
Pleinmont, Guernsey. Rocks washed by the tide.

FRANCE

Bolboschoenus maritimus

Verdcourt & Wilmot-Dear 5378C (K)

Flora of France (Bouches du Rhône). Camargue
Reserve House S. of Mas de Capelière. 7.vii.80.

c.f. *B. maritimus* including putative hybrids

C.J. Ward 8390 (NU)

Southern France; Herault (province); Le Graue-du
Roi area; Etangdu Repausset. 15 July 1973.
Rhizome black, horizontal, in lower moist part of
drainage ditch at side of road in gravel and silt.
Low lying area, common. 150 cm tall.

Dr. Ed. Bonnet s.n., July 10th 1873 (K)
Herbarium Warleyensis. Loc. Marecages entre
Genlis et Magny. Cote d'Or. [This on original
handwritten label accompanied by printed label
with 'E.A. Willmot'.]

Dr. Ed. Bonnet s.n., July 20th 1873 (K)
Herbarium Warleyensis. Loc. Pontailleur sur Laone.
Cote d'Or. [This on original handwritten label
accompanied by printed label with 'E.A. Willmot'.]

Dr. Ed. Bonnet s.n., July 17th. 1864 (K)
Herbarium Warleyensis; ex Herb Gaudefroy. Loc.
Bords de la marne pres Paris.

E.A. Willmot collections of approx. 6 sheets (K)
from South of Montpellier - Littoral de Mediterr.

CZECH REPUBLIC AND SLOVAKIA

Bolboschoenus maritimus

Sojak, J. 112 (M)
Bohemia, Milnick district, saline marshes.
(Czechoslovakia)

ROMANIA

c.f. *Bolboschoenus affinis*

Sanka (?-illegible) January 1863 (K)
Scirpus maritimus var. *digynous*. Pr. pag. Gancs.

Bolboschoenus maritimus

Al. Borza 1190 (K)
1190 *Bolboschoenus maritimus* (L.) Palla in Koch
Syn. III. Aufl. p. 2531 (1907).
Transsilvania; distr. Turda. In lacu salso ad balneas
urbis Turda. Alt. ca 300 m.s.m. 24. Aug. 1925.
"Adn. Flores maxima ex parte duobus stylis
instructae: ideo plantae huc editae ad var digynous
Godr. Fl. Lorr. III p. 91 (1844), ad numerari

possunt."

Putative *Bolboschoenus maritimus* x *yagara*

J. Barth s.n. (K)
Herbarium Churchillianum Proprium, Bequeathed
1906.
Transsylvania, in paludosis ad Ionnersmarkt
(?)[Donnersmarkt ?].

MEDITERRANEAN EUROPE

SPAIN

Bolboschoenus glaucus

N.Y. Sandwith 6265 (K)
Flora of Spain: prov. Sevilla
Loc. Isla Mayor in salt marshes. June 15th 1963.

c.f. *B. glaucus*

J. Mendes Pinheiro 1580 (K)
Flora Lusitanica (Soc. Bot. 16° anno). *Scirpus*
maritimus L. α *geniunus* Godr.
Arredores de Coimbra : Ademira.

c.f. *Bolboschoenus maritimus*

P. Chouard, P. Montserrat, P. & L. Villar No.
JACA 455770 (GENT)
Las Penas de Riglos, Trieste (Espangne, prov.
Huesca), bord du barrage de La Pena, sur la rivière
Gállego, UTM/30T XM 8995, alt. 550 m sur limon
grisâtre marneux, bords inondés du lac artificiel,
avec *Phragmites australis*, 1 août 1970.
Rem.: Plante rare dans les Pyrénées mais
abondante aux Monegros et dans la partie centrale
de la vallée de l'Ebre.

CORSE

Bolboschoenus maritimus

1228 *Flora von Corsica* - *Paul Aellen* s.n. (WIS)
Stango di Palo. Augestrockener Wassergraben.
20.7.1933.

ITALY

Bolboschoenus glaucus

Collector ? (K)
Bequeathed from Churchillianum Proprium 1906
Venetia dist. patavina in luganus vol. cal. alt. 1--

300; 17/6 1867.

Bolboschoenus maritimus

Porta (?) s.n. (K)
Scirpus maritimus L. β *compactus* Kroch
Venetia dit. Patevino ad fontis thermales in luganes
(?) salvala alt. cub. 80--100; 25/6 1868.

SICILIA

Bolboschoenus glaucus

Poulorkin (illegible) s.n. (K)
Ex Herb Hook. Sisilia

Todaro s.n. 12/81 (K)
Todaro Flora Sicula Exiccata.
In paludosis - Palermo. Junio.
Mixed gathering ?

MALTA

Bolboschoenus glaucus

B.E.J. Wheeler 271 (K)
Flora of Malta. *Scirpus maritimus* L.
Loc. Malta: Gnejna. 1.7. 1957.

ALBANIA

Bolboschoenus glaucus

N.Y. Sandwith & A.H. G. Alston 2811 (K)
Flora of South Albania, 1935.
Loc: Vlorë (Valona). Sep 5th 1935. Alt. Sea level.
Hab. Ditches in salt marshes.

MACEDONIA

Bolboschoenus glaucus

H.G. Tedd s.n. (K)
Flora of Macedonia. Lake Kerkinis. 28 June 1933.
Habitat. In and near water of ditch of embankment
of Stuma R.

H.G. Tedd 281 (K)
Flora of Thrace. Locality. Boyadjiler. 15/5/1930.
Wet grassy places and standing in water (dry in
summer).

Collector *Imperial College* 144 (K)
Isle of Euboea. Alt. 500 ft. Aug 59. Beside
constant streams.

Capt. G.W. Harris 319 (K)
Greek Macedonia. Struma Plain and northern slopes of the Krusa Balkan. May 1918. Comm. W.B. Turrill 18th July 1918.

GREECE AND ASSOCIATED ISLANDS

Bolboschoenus glaucus

Sir. Colville Barclay 3376 (K)
Flora of Thasos. Loc. Thasos town. 9.9. 1975. Sea level. Damp sand near fresh water drain. Up to 1½ m. Brown fl. heads.

Snogerup & Gustafsson 44257 (LD)
Skiros: the plain between Kalamitsa and Ag. Mammias, 0–2 m.

Snogerup & Bothmer 32910 (LD)
Andros: 1 km NNW of Gavriou, ditches and wet fields, 0–5 m.

Runemark & Nordenstam 16711 (LD)
Rodas: NE of Yannathi.

Runemark & Nordenstam 16199 (LD)
Mikonos. St Anna Bay. Siliceous rock. Meadow at the sea.

Runemark & Bentzer 30014 (LD)
Serifos: the shore at the harbour..

c.f. B. glaucus

Carlstrom, A. 1426 (LD)
Rodhos. 1 km S of Kattavia

Bolboschoenus maritimus

Snogerup & Bothmer 33312 (LD)
Andros: Korthion, sandy seashore and sandfields, 0–10 m.

Runemark & Snogerup 9872 (LD)
Naxos. The shore 2.5 km W of Mitria.

c.f. B. maritimus

Carlstrom, A. 5645 (LD)
Rodhos. Kremasti, near sea level.
Material too young for certain identification (J.B. 1997).

Runemark & Engstrand 36125 (LD)
Mikonos. 2 km M of Ag. Stefani.

CRETE

Bolboschoenus glaucus

K.H. Rechinger fil. 14101b (K)
Inter Aegaeum VI., 1942. of 28.vi.1942
Creta Distr. Pyrgiotissa. In paludosis ad ostium fluvii Hieropotamos prope Tymbakion.

TURKEY

Bolboschoenus glaucus

McNeill 699 (K)
Turkey Prov. Van: Baskale Hakkari (Colemerik) c. 50 km from Baskale. 1800 m. Marsh ground. 30 Aug. 1965.

Davis & Hedge D32757 (K)
Prov. Kayseri. Kaseri - Incesu. 1200 m. Marsh. 29.8.1957.

PH. Davis 14759 (K)
Turkey. Between Konya & Kashanam dyke. 7/9/1947

MJE. Coode & BMG. Jones 256 (K)
C5. Adana. Adana to Karatas. 5 miles S of Adana. Near sea level. Roadside ditch. 1 st. May 1965.

E. Hennipman, P. Nijhoff et al 1392 (K)
Flora Turcomanniae Asiaticae. Inter Leydense 1959. Date 24-5. Alt. ca. 750 m
Prov. Maras. Loc. ca. 5 km S. of Maras. Reed-land along the river Aksu.

E. Hennipman et al. 1332 (K)
Flora Turcomanniae Asiaticae.. Date 22-5. Alt. 1 m.
Prov. ?cel Local. ca. 3 km E of Mersin. In shallow ditch. Clayish soil ca. 1 km from the sea.

Baki ? 431 (K)
Herbarium Turcicum. Ankara. 30.v.1945.

D.E.S. Truman 238 (K)
Antalya. Alt 10 ft. 26.6.1958

Dr. TA. Tengwall 551 (K)
Between Serik and Karanlik. Alt. 150 m 10.5.36

c.f. B. glaucus and putative hybrids

Hikmet Birand 52 (K)
Turkey. Izmir. 1943.

P. Sentis 4929 (K)

Inter Orientale 1892. Paphlagonia. Wilajet Kastambul.

Tossia. Sabadja, ad versuras 4/8.

Two mounted on this sheet - Right = *B.*

glaucus (J.B. 1997)

Left with narrow mesocarp, triangular, c.f. *B.*

glaucus x ? *yagara* (J.B. 1997)

MJE Coode & B.M. Jones with Yusuf Dönmet

2872 (K)

1st July 1965. Kesan; Akhoca to Beylik Mera

Koyu. Near sea level. Extensive marsh dominated by Phragmites. From 1-2.5 m tall.

Bolboschoenus maritimus

Simon & Hawkins 56 (K)

East Turkey. Bitlis Prov. 34 km West Ergis [villow van Gond ?]. Alt 1700 m. Salt marsh. Tall 8-15 high. v. common close to Lake Edge.

EM. Rix 298 (K)

Loc. Van Ercek göhn. Alt. 6000 ft. Salt marsh.

Baki ? 427 (K)

Herbarium Turcicum. Ankara - Mohan [ogolii henarinda ?]

Davis & Hedge D31877 (K)

Prov. Erzincan; plain E. of Erzincan. 1250 m. By warm spring in saline marsh.

MIDDLE EAST

ISRAEL

Bolboschoenus glaucus

Carne, WM. 42 (NSW)

Jordan Valley (Collected 23/7/1918)

IRAN

Bolboschoenus affinis

Jan Steen Andersen and Ivan Cornelius Petersen

121 (K)

Iran, 30 km south on Minyah. In the lake 50 cm water. Alt. 1600 m. 29/6/69.

c.f. *Bolboschoenus affinis*

K.P. Buttler 23040 & *R. von Bothmer* (H) (Herb

No. 11(?)53309

Iran. Prov. Hamadan. TU2. O, Matayer -42-

Hamadan, 84. 300 m S Zamanabad an der Strasse nach Jovkar, 1940 m. Date: 04.09.1977. Dups. H.M, ANK.

Bolboschoenus glaucus

Kukkonen 7626B (H 1654707)

Iran. Khorasan, Mashad, Camping area in the SE side of the town, waste land.. Aug. 1, 1972. Alt. 1150m.

Kukkonen 7626A (H. 1654358)

Iran. Khorasan, Mashad. W of Chenaran village ca. 60 km W. of Mashad. Waste land between wheat field and highway. Irrigation ditch.. Aug. 1, 1972. Alt. 1200 m.

Mohammera 1850

Herb Noeanum No 397 (K)

Clarke has noted on this sheet from Iran. 'S. *maritimus*, 3 styles, but nut not reticulate'

c.f. *B. glaucus*

Jan Steen Andersen and Ivan Cornelius Petersen 356 (K)

Danish Botanical Trans Asia Exp. 11. 1969.

Iran, 59 km West of Mashhad swamp in semi desert. 90 cm high. Alt. 1300 m. 10/7/1969.

OMAN

Bolboschoenus glaucus

MD. Gallagher 7966 (K)

Flora of Oman - Arabic name = Ath'mihr

Locality; Jawbah, 2km N. of junc. with road to

Hajj. 20°55'N; 58°13'E. Alt. 30 m. 15 May 1987.

Muddy ground between low rises in line with wadi Halfayn. A broad area 3 x 6 km, no animals except at edges, where also Aeluropue etc grazed by sheep and goats. Boy says this also eaten.

ASIA (Caspian area to Afghanistan)

KAZAKHASTAN

Bolboschoenus yagara

G. Paulenko supra no. 2791 (K, M)

Prov. Chabarovsk, lacus in valle in fluxu medio fl.

Amur prope p. Petropavlovka, 60 km orientem

versus ab. opp. Chabarovsk. (Kazakhstan)

c.f. *Bolboschoenus glaucus* including putative hybrids

Roshewitsch, R. & Heinrichson, A.S. s.n. (H 1594432)
Kazakhstan, E. Ust-Urt. Between Caspian Sea and Aral. 1.10.1926. Ex Herb. Inst. Bot. Ac. Sc. USSR.

P. Sentis 1962 (K)
Inter transcaspico-persicum 1900–1901
Regio transcaspica: Kisil Arwat; Karakala prope Nurgeli Chan, ad ripas fluvii Sumbar.

P. Sentis 1996 (K)
Inter transcaspico-persicum 1900–1901
Regio transcaspica: Kisil Arwat; Karakala prope Nurgeli Chan, ad ripas fluvii Sumbar. 28.vi.1901.

AZERBAIJAN

Bolboschoenus affinis

I. Kukkonen 12720 (H) (Herb. No. 1498755)
USSR, Azerbaijan SSR, Hanlar, C. 10 km. S of Baku on Caspian coast. In muddy depression near shore line with *Phragmites* and *Schoenoplectus litoralis* in large stands. 2nd. June 1983. UTM grid.

I. Kukkonen 12727 (H) (Herb. No. 1498758)
USSR, Azerbaijan SSR, Bejuk Sor 8–10 km N of Baku. Large pool in disturbed area just above the shore line, in stands. 3rd June 1983. UTM grid:-

B. affinis and *B. glaucus* (mounted together on same sheets)

TYPE of *S. maritimus* var. *compactus* (K)
1. Left side - short plants, ca. 30 cm high.
Ex herbario horti Petropolitani; recd. 12/1885.
Scirpus maritimus L. β *compactus*
Chiva 1873. Turkestan. Korolkow et Kranpe.
Clarke has noted Nov. 1887 'The Chiva plant is *Scirpus affinis* Roth'
= *B. affinis* (J.B. 1997).

2. Right side
Ex herbario horti Petropolitani; recd. 12/1885.
A. Regel, Inter Turkestanicum 1877 & 8
Scirpus maritimus L. β *compactus*
Tschimpansi prope Kaldscha.
Clarke has written 'the Karldscha plant is *Sc. maritimus* Linn.
No nuts, but on facies this plant = *B. glaucus* (J.B. 1997).

A. Regel Inter Turkestanicum ex Botanical & Forestry Dept. Hongkong Herbarium no 30416

(K). Det. as *S. maritimus* β *compactus*. ix. 77.
There are 3 on the sheet. Two left = *B. affinis*; one on right = *B. glaucus*. All confirmed by fruit in section (J.B. 1997).

A. Regel Inter Turkestanicum (K)
Details illegible. Left = Kasch 3–4000 ft. 30/vi/1879 = *B. glaucus* (J.B. 1997).
Right = Pilutschi..? 3–5000 ft. 24/iv/1879 = *B. affinis* (J.B. 1997).

Two on one sheet; (K)
Left one - in locis inundatis prov. Aderbeid = s?ehan circa Khoi. From fruit = *B. glaucus* (J.B. 1997).
Right one - *D. Fischer* s.n. (K). Desertum Kingisicum = *B. affinis* (J.B. 1997).

c.f. *Bolboschoenus affinis* and *Scirpus biconcavus*

Pertti Uotila No. 19480 (H) (Herb. No. 1653319)
Finnish Botanical Expedition to West-Central Asia 1972.
Iran; East Azerbaijan (Loc. 275) Ca. 60 km SE of Tabriz on the road from Zanjan to Tabriz. Shallow lake shore. Alt. 1900 m. Aug. 19, 1972.

Bolboschoenus glaucus

Kukkonen 12724 (H 1498757)
USSR, Azerbaijan SSR, Bejuk Shor, Large pool in disturbed area c. 8–10 km N of Baku. Common in shallow water and near pool. 3rd June 1983.

UZBEKISTAN

Bolboschoenus affinis

N. Androssow et M. Kelow s.n. (K)
Herbarium Florae Rossica
Bucharae, in paludosis pr. Farab (ad. fl. Amu-Darja) 20. Aug. 1901.

Herb. Fl. Ross 994 (H) (Herb. No. 1220705)
Bucharae, in paludosis pr. Farab (ad. fl. Amu-Darja) 20. August. 1901. Legerunt. N. Androssow et M. Kelow.

Bolboschoenus glaucus

Z. von Minkwitz 635 (or 636 ?) (H 1485719)
North of Tashkent; Syr-Darya, distr. Tschimkent, Lake Chuvuka-Kul (?) 12 west towards Chilikes(?) Ex Herb. Inst. Bot. Ac. Sc. URSS.

Russian label (K)

Apparently from Samarkand Distr. Uzbekistan.

Received from (H) 2794a Hrb. Fl. Rossicae. (H 1220702) [see below]

Prov. Fergana, distr. Kokand, In arenosis salsis pr. Melnikowo 1916. V.19.

sub *Scirpus affinis* var. *maritimoides*. Drobov, V.P.

c.f. *B. glaucus* perhaps putative hybrid

2794b ex Herbarium Florae Rossicae (M, WIS)
Bucharu, in palude pr. Farab a d f. Amu-Darja.
1901.viii.14.

AFGHANISTAN

Bolboschoenus affinis

I. Kukkonen 6437 (H) (Herb No. 1654702)
Finnish Botanical Expedition to West-Central Asia
1972.

Afghanistan. Baghlan (Loc. 149). Ca. 6 km. S of
Pule-Khumri. Pond at the river of Pule-Khumri.
Alt. 650 m. May 21, 1972.

Bolboschoenus glaucus

Kukkonen 7570. (H 1654706)
Afghanistan, Kandahar. Ca. 45 km E of Kandahar
along the highway. *Artemisia-Chenopodiaceae*
semidesert, gentle towards E facing slope. July 28,
1972. Alt. 1200m.

Afghanistan Griffith (this written on sheet itself)
This may be no. 60
Cited by Clarke in Fl. Brit. India VI p. 658 as
Scirpus maritimus L.

ASIA (eastern)

RUSSIAN FEDERATION (east)

Bolboschoenus affinis

Eric Hulten 303 (K)
Expedition Suecica ad Peninsulam Kamtschatka
Kamtschaka australis: Near Natchika Village at the
hot spring 350 m sept. 2nd. 1921.

Exped. Explor. TH.P. Riabouchinsky (K)
Peninsula Kamtschatka (Kamtschatka) 1908--1909
V.L. Komarov
6 March 1913.

Bolboschoenus yagara

ex herbario horti Petropolitani (K)
Amur, and illegible = Maximovic?. No herbarium
number, but Herbarium Hookerianum 1867.

CHINA

Bolboschoenus affinis (and *Scirpus biconcavus* Ohwi)

D. Litvinov 1624 (K)
Museum Botanicum academiae Scientiarum
Petropolitanae
1902. vii.19. Loc: Manchuria.

M' l'abbe A. David No. 1909 (K)
Ex Herbario Musei Parisiensis. Rec. 12/82
Chine (Mongolie Orientale).

On same sheet.

Left - Bretschneider 784 (K)
Ex Herbario horti Petropolitani - Rec 3/80.
Loc:- illegible, but perhaps Il. Perinensis.
Right - Perry 7/83 (K)
Loc: Chefoo [Cheefoo]
Clarke "this is *B. affinis* and the one above is
young and probably *B. maritimus*"

Abbe E. Licent 6428 (K)
Flora of China
Loc: Vers le Miao tao. 29.8.21.

C.Y. Chiao 2412 (K)
Plants of Shantung Province, June 7, 1930.
Loc: First Park Tsingtao [Qingdao?]. Erect herb in
pond.

C.Y. Chiao 2515 (K)
Plants of Shantung Province China. Herbarium of
the University of Nanking.
Loc: First Park. Tsingtao. June 15, 1930. Herb
along ditches, near seashore.

E.H. Wilson 4541 (K)
Loc: Gangtze Banks.

Abbe E. Licent 8334 (K)
Flora Northern China and Manchuria
Flora of Tientsin.

George Forrest 2032 (K)
Collected for A.K. Bulley of Ness, Neston,
Cheshire.
Plants of E. Tibet and S.W. China.
Loc: Plant of 9--16 inches. Clayey, boggy

pastureland on the Lichiang plain to the south of the city. Lat. 26° 50' N. Alt. 8 200 ft. May 1906.

Harry Smith 5988 (K)

Plantae Sinensis

Loc: Prov: Shansi, austr., Yün-cheng. Salt Lake in uliginosus salsiforis (?) ca. 600 m. 1/7/24.

Bolboschoenus yagara

Plants of China (K)

? Simm & Sippr WHO code X- 334

Collector *Huang Xiulan, Wang Xingwu*; Date 7. 1982

Loc: Liaoning Province. Alt. 100m. Swamp.

E.D. Merrill 11426 (K, NY, NSW)

Nanking, Kiangsu Province. June, 1922.

Y.C. Wang 325 (K) and also *L.C. Wang 287 (K)*

Loc: Nanking, Kiangsu Province.

c.f. *B. yagara*, perhaps putative hybrid

A.N. Steward 2054 (K)

Flora of Kiangsu Province China. Herb. University of Nankin.

Loc: Nanking. Lotus lake. Edge of Water v/4/22.

KOREA

Bolboschoenus yagara

V. Komarov 230 (K)

Ex herbario Horti Botanicis Imper. Petropolitani.

Loc: Korea septentrionalis. Flum. Talu.

JAPAN

***Bolboschoenus affinis* (and *Scirpus biconcavus* Ohwi)**

Ex. Herb. horti. bot. Petropolitani (K)

Com. A. Bennett, Nov. 1890

Maximowicz. Intersecundum

Japonia Yokohama 1862.

In Russian language; in cover for Japan (K)

Collectors ? N. Kyznexo and Tn. Ecopoba ?

Herb. Instituti Botanici Academiae Sc. URSS.

Det. as *Bolboschoenus planiculmis* (Fr. Schmidt) Egorova

G. Murata and H. Koyama 436 (K, NSW)

Plantae Japonicae Exsiccatae No 436 ex Herbario Universitatis Kyotensis

Loc: Honshu, Pref. Kyoto (Prov. Tango); in Kumihama-bay, Kumihama-cho, Kuma-no-gun. June 26. 1965.

Miyoshi Furuse 6912 (K)

Loc: An inland sea lake - the lake shore of Noto-ko Noto Abashiri-shi, Prov. Kitami Hokkaido (YEZO) 26 Aug. 1974. By wet sandy place (a little muddy).

Two collection sheet from 1888. (K)

Left=Collections from Japan by *Rev. Père Faurie* 2736. Honai. This equates with *B. affinis* (J.B. 1997).

Right=Collections from Japan by *Rev. Père Faurie* 827 ? This equates with *B. yagara* (J.B. 1997).

Bolboschoenus planiculmis

Collector ? No. 3197 (NY)

Ex. New York Botanical Garden; ex Herbarium of Tetsuo Koyama.

Locality - in Japanese. Date: Aug. 13, 1982.

Det. *Bolboschoenus planiculmis* (F. Schm.) T.

Koyama by T. Koyama

Bolboschoenus yagara

See above, as two mounted on same sheet: *Rev.*

Père Faurie 827 ? This equates with *B. yagara* (J.B. 1997).

Rev. Père Faurie 962 (K)

Noeji ? 1886.

Shigetaka Suzuki s.n. (K)

Ex Herb. Shigetaka Suzuki 393008. May 15. 1949.

Loc: Mukoga-oka, Kanagawa-pr. Honshu. Alt. 50

m. Jap. name = Ukiyagara

N 35° 37'; E 139° 33'

c.f. *B. yagara*, perhaps putative hybrid

Plantae Florae Japonicae ex Herbarium T. Terasaki (or Jerasaki ?) (K)

Loc: Tokyo, Japan, viii/1906

OKINAWA

Bolboschoenus affinis

Miyoshi Furuse 2892 (K)

Hoshidate. Is. Iriomote Prov. Ryukyu. *Yaeyama Islands* (Pref. Okinawa)

10 April 1973 by waste rice paddy.

TAIWAN (Formosa)

Bolboschoenus affinis

Note: according to Koyama (1978: 207) there is only one species recorded for Taiwan, namely *B. planiculmis* (J.B. 1997)

A. Henry 1818 (K)

Loc: Formosa. Takow - in moist place.

ASIA (south eastern)

PAKISTAN and KASHMIR

Bolboschoenus affinis

Dr. F.A. Perrott (née Street) 18 (K)

Flora of N. Pakistan

Loc: Borit Jil (a small saline lake, pH 8.9) Hunza Valley, Kara Koram Mountains. Alt. 2500 m. 31/Aug. 1980. On marshy lake edge.

Mrs. A.S. Beil 395 (K)

Flora of Banda N.W.P. [=Uttah Pradesh] May 15/1901.

Vernac. name= Ghundela

Habitat - riverside.

R.R. Stewart 12501 (K) Sheet 1

Plants of North west Himalaya

Loc: Khauna near Rawalpindi. Oct. 1928

Two on one sheet (K)

Left = Herb Ind. Or. Hook. fil & Thomson

Hab. Punjab. Regio Trop.

Coll: T.T.

On the same side another hand written label

"*Scirpus* Deobund Oct. 1845

Clarke det. as *S. maritimus* var. *affinis* - Fl. Br. Ind. VI: 659.

right = Herb Ind. Or. Hook. fil & Thomson

Hab. Plan. Ganget Sup. Regio Trop.

Coll: T.T.

On the same side another hand written label

"Lahore, March 1846"

J.R. Drummond 24934 (K)

India; Punjab

J.R. Drummond 24935 (K)

India; Punjab

c.f. *B. affinis* including putative hybrids

Jafri & Atchar 1938 (K)

Balochistan. Kalap Ziaraf [?] Alt. 7000 ft.

20/06/57. Common.

On one sheet (K)

Left = N.W. India, *Ab. Royle s.n.*

right = 2 plants; Wall Cat 3463B, cited by C.B.

Clarke VI: 659. S. Balma *W. Ham* [?] - Monghir. B Aulsufghur [?] 1825.

Bolboschoenus glaucus

Koelz, W. 7562 (US ; No. 1609702)

Kinghar Lake (Kinghar Dhand), Karachi District, Topographic Sheet No. 40 D/1, A-1. 20 Jan. 1934. Botanical Collections in Sind, India under the Auspices of University of Michigan.

H. Freitag & G. Kothe 18,502 (sent to I. Kukkonen for ID)

G.2. Makran Coastal Plain, 20 km WNW of Pasni at road to Gwadar.

Plants of Baluchistan & Sind.

Hab: throughlike flat artificial depression moist soil, *Scirpus*-comm. Alt. C. 15m NN. Date 29.9.1986.

Notes: rhizomatous, dense stand.

Siddiqi & Zaffar 3759 (K)

Stewart Herbarium

Gordon College of Rawalpindi - Plants of Pakistan

Loc: Bannu to Tajazai - along water. 6.4. 1966.

Wm. T. Stearn 47 (K)

Flora of Sind

Near Drigh Road within 7 miles of Karachi.

Abundant in water logged soils. Feb. 1945.

Sheets I, II, and III. Plant ca. 26-35 cm.

S.M.H. Jafie 1010 (K)

Flora of W. Pakistan

Plants of Khaupur [?] Div. (Sind ?)

Loc: Khaupur. Very common also in water logged areas. 25.10.55

Dr. Salim No. 22 (K)

Timorgasha [near Peshawar]. Alt. 3000 ft. April 1963.

Growing in stony soil.

Bashir Ahmad Suhail 272 (K)

University of Peshawar

Loc: Mordon [Marden?]

J.R. Drummond (K)

Punjab

J.R. Drummond 24931 (UC - photostat)

Rania, Hissar Dist. [India - Punjab]

J.R. Drummond 24932 (UC - photostat)
No locality [India - Punjab]

Kabir 15231 (ex Herb J.R. Drummond) (UC - photostat)
In paludosis e 700 prope oppidum Hansi in dist. Hissar.

J.R. Drummond 24026 (K)
Punjab, Hissar. 17/1/86

J.R. Drummond 24932 (K)
No locality other than Punjab.

J.R. Drummond 932 (K)
in paludosis c. 1100 ft. in dit Kohat.

J.R. Drummond 15231 (K)
Prope oppidum Hansi in dit Hissar.

J.R. Drummond 23595 (K)
Karnal Jungle.

J.R. Drummond 24931 (K)
Rania, Hissar Dist.

c.f. *B. glaucus* perhaps putative hybrid

Thomson s.n. (K)
Herb. Ind. Or. Hook. fil & Thomson
Hab. Punjab. Regio Trop
Also an extra label - Lahore. March 1846 or 1845.
Cited by Clarke Fl. Brit. Ind. Vol VI p. 658.

INDIA (northern) and ASSAM

Bolboschoenus affinis

Coll...? 26203; 24/April 1875 (K)
Churs of Pudda Moorshedabad

Herb Griffith (K)
Herb of the late East India Company 6263

Griffith 1745 (K)
Assam

Bolboschoenus glaucus

Inayat 22892 (K)
Flora of Upper Gangetic Plain
Dist. Kheri. 15/4/98

Collector ...? 6504 (K)
Flora of North Western India.

Barwar Sagar
Jhansi Distr.. 9.12.86.

Collector ...? 6504a (K)
Mustaffabad.
Manipuri Distr. 18.4.86

Voyage de V. Jacquemont aux indes orient 98 (K)
Ex Herb. Mus. Paris 503
Cited by Clarke in Fl. Brit. India VI p. 658 as
Scirpus maritimus L.

RR. & ID. Stewart 1335 (K) Sheet I, II
Gurdaspur near Beas [Beas is a river in Prov.
Himachal Pradesh]

INDIA (central and southern)

Bolboschoenus affinis

Stocks, Law etc.s.n. (C)
Hab Malabar, Concan etc., Regio trop. Herb. Ind.
Or. Hook. fil & Thomson
Neotype *Scirpus maritimus* subsp. *affinis* (Roth in
R. & S.) T. Norlindh - Bot. Notiser 1972, vol 125:
397-405. (Fig 1G, H)

V.D. Vartak 8225 (K)
Flora of Maharashtra State
Mutha River, Poona. 1800 ft.

H.F. Mooney 3004 (K)
Bed of Mahanadi at Sonapur Orissa in slightly
moist sand. 7/April/48.

H.F. Mooney 1682 (K)
Narsinghpur [Narsimhapur], State Orissa

C. Maries 297 (WIS)[see also 285 (K) -from same
locality = *B. glaucus*]
India; Gwalior. April 1890.
Donated in 1994 to WIS from Vern E. McNeillius
Herbarium.

Mr Law [?] (K)
Bombay
Cited by Clarke VI, p. 659

Dr. T. Thomson s.n. (K)
Meenit [? = Meerut ?]

A Fischer [illegible] (K)
Flora of Madras
Malabar. 22.IX.1930

Bolboschoenus glaucus

Bombay Herbarium of the late N.A. Dalzell (K)
Cited by Clarke in Fl. Brit. Ind. Vol. VI P. 658
Loc: [illegible]
Plant ca. 26 cm

Wallace, E.C. 9224 (BM)
Flora of India. margin of pond. Andherbi, Salsette
Island, Bombay 31.12.1945

Very old sheet (K)
In ancient ink is "*Scirpus cylindraceus* Koenig".
On another "*Scirpus cylindric*
ab amicifs (?) Heyne
Mayvore (?) 1801 [= Mysore]

W.A. Talb 2226 (K)
Flora of Dharwar Dist. Haveru [?=Haveri ?] Jan.
2, 1890.
Ex Herb J.S. Gamble

Henry Chisholm Davidson s.n. (K)
Around Bombay and Poona. VIII 1893.

H. Santapara S.J. 16941 (K)
Gondal.

Growing in dense masses in water at irrigation lake
and dam.

H. Santapara S.J. 16612 (K)
Dwarka nr. station Saurashtra.

V.D. Vartak 20489 (K)
Kalyan. (Kalyandurg ?). Alt. 20 ft.

C.D.K. Cook and B.J. Gut 5 (K)
Rajasthan State; Kota. In fallow rice field, water
depth 10 cm. UNDP Research Farm, 8 km NW of
Kota.

C.D.K. Cook and B.J. Gut 56 (K)
Rajasthan State; Kota.

Hooper & Gandhi K.N. (K)
Cited H.F.P. 2394. Cited, SS. Hooper in Flora of
Hassan, p.658, under *B. maritimus*.
Addahalla on Channarayapatna road. 11 Nov.
1971.

C.J. Saldanha 13747 (K)
Arsikers.
Cited, SS Hooper in Flora Hassan p. 658, under *B.*
maritimus.

Herb. Wight. (K)
propr. Peninsula Ind. orientalis

Seen by Clarke Vol VI, 658. Written on a piece of
paper below "1897 *Scirpus maritimus* var. *glaucus*
NE; *S. tridentatus* Roxb - Wall. L.n. 3504".

C. Mareis 285 (K)
Gwalior.

Unlocated

Bolboschoenus affinis

On one sheet (K)
left= R. Thompson. No 359 Com. Dr. Brandis 1873
Forests north Oudh 1870.
right = Wallich 3463B (but see previous same
number!)
Agufghur.

Harsukh 22865(K)
Garakhpur

Inayat 22865a (K)
Pilibhit

c.f. *B. affinis* including putative hybrids

A very old sheet
Top right = Flora Amager and...
Julio 1783 (Seiddia ? - illegible)

Bottom left =
Scirpus maritimus Herb Rottlerianum
Prof. Willden Penins. Indiae Orientalis
Presented by the Council of
Kings College, Feb 1872.

Scirpus maritimus
Prof. Herman

Bolboschoenus glaucus

J.R. Drummond 24823 (K)
Inter Khumanon et Morinda 17/3/1885

THAILAND

Bolboschoenus affinis

Kerr No. 21409 (BM, K)
Locality: Tat Hanon. Nalchon Phanom ?(Nakawn
Panom according to Koyama 1979: 284). alt. 200
m. May. 11. 1932. In damp ground at edge of
water.
Cited by J.H. Kern, Cyperaceae of Thailand.

VIETNAM

Bolboschoenus affinis

B. Balansa 4824 (K)
Pl. du Tonkin 1890--1891. Hanoi 11/Jan/1891.
(Cited Koyama 1979: 284)

APPENDIX 3

Author's

Publications on *Bolboschoenus*

APPENDIX 3

Author's publications on *Bolboschoenus*, arranged chronologically.

Browning, J. and Gordon-Gray, K.D. 1992. Studies in Cyperaceae in southern Africa. 19: The genus *Bolboschoenus*. *South African Journal of Botany*, 58 (5): 380--385.

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Author's publications on Cyperaceae, excluding the genus *Bolboschoenus*, arranged chronologically.

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National Herbarium of Namibia, Windhoek (WIND)

South African Museum Herbarium, Kirstenbosch (SAM)