Introduction
The sedges of the family Cyperaceae are predominantly wetland plants ranging from tall perennials like *Cyperus papyrus* to delicate, low-growing, inconspicuous, short-lived herbs such as *Isolepis* species. Mostly widespread on all continents, the structural features of their sexual reproductive parts (inflorescences, spikelets, florets) are varied, and sometimes variable within individual plants. For longer than two centuries these organs have been difficult to interpret in keeping with patterns evident in groups that, from time to time, have been considered closely related (lilies, grasses, rushes). This led to incongruous systematic arrangements and confusion in naming. It is now confidently accepted that the rushes (family Juncaceae) are the closest living relatives of the sedges and that grasses and especially lilies be dismissed as possible early ancestors.

Linnaeus in 1753 knew of Cyperaceae. He established the genus *Scirpus*; its limits were wide and its components heterogeneous. Today *Scirpus sensu stricto* (that is in its restricted sense) is limited to the northern hemisphere (apart from introductions that have become naturalized). The story to be told here is of one of the segregant groups from *Scirpus*, namely *Bolboschoenus* - ‘bolbos’ (Greek = bulb) because of the hard underground swellings (corms, but often less correctly called tubers) on the underground stems (rhizomes); ‘skoinos’ (Greek = rush-like) because of superficial resemblance to such plants. (Note that the name change from *Scirpus* to *Bolboschoenus* (Palla 1904) was only slowly adopted in South Africa.)

The plants
Plants of *Bolboschoenus* are recognizable by their noded, three-angled stems (culms) bearing numerous leaves that are rough with fine hairs. Apically on the culms are borne flowering branches (collectively inflorescences) bearing numerous spikelets. The inflorescences may be branched, or unbranched with the spikelets aggregated into a head; very occasionally the spikelets are solitary. The spikelets are cyindrical with floral scales (glumes) spirally arranged, their tips irregularly prolonged and generally directed outwards. Within each floral scale is a floret (a reduced flower) usually of three stamens, ovary with three style branches (sometimes only two), and some bristles that fall easily and are interpreted as remnants of a perianth.

In South Africa
Returned from war service in North Africa and Europe, my husband to be expressed a fervent wish “Never to see Europe again. Let us get to know our own country!” As a botanist I was delighted to concur. This saw us set out in October 1959 for a month of travelling what are now the Eastern and Western Cape Provinces. We kept to less frequented roads and stopped often to look and to learn. Sedges and grasses were my particular interest. Early one evening while parking at a small country inn for a night’s lodging we noticed a car already there had plant presses and drying sheets bundled on the back seat. Whoever? A little later the experienced ecologist John Acocks was advising us of the need for time to be spent along the western coastline where stands of sedges and some unusual grasses were prominent. Then to proceed to the Olifants River, Clanwilliam and Nieuwoudtville where sedges had gone almost unnoticed. Enquiries about a permit to collect these plants had elicited the answer that there were no restrictions on collecting “those weeds”!

Along the western coastline I saw for the first time populations of *Bolboschoenus maritimus* growing naturally. This was the only species of the genus recorded for South Africa and from these plants I was able to appreciate some of the habitat requirements of the species in relation to associated wetland plants, especially *Phragmites australis* (Reed Grass) and *Typha capensis* (Bulrush). The main center of distribution of *Bolboschoenus maritimus* is Europe, particularly Scandinavia. So how did populations come to be growing along the western and south-eastern coasts of the Cape of South Africa?

Later, back home, I began to be asked questions I could not adequately answer. Were the western coastal plants identical to those of St Lucia and further north? And what of those tall plants growing in streamlets on the Brandburg mountains in South West Africa (now Namibia)? At best, literature reflected these entities to be varietal expressions of *B maritimus*, the St Lucia plants perhaps var. *macrostachys*? the Brandburg ones more definitely var. *nobilis*. The latter variety was later recognized as distinctive (Goetghebeur & Simpson 1991) and accorded specific status as *B. nobilis*. This specific name had first been given to plants collected by Welwitsch at the Maiombo River, Mossamades, Angola prior to 1884 and named *Scirpus nobilis* by Ridley.

Marek, a Polish botanist, had studied the anatomy of the walls of some sedge fruits including those of *B. maritimus*. His account, written in Polish with an English summary, was not much read because of language differences. His work was taken up by Oteng-Yerboah in the early 1970’s and subsequently, with development of the technique of scanning electron microscopy, it provided a suite of additional criteria by which to distinguish some sedge species. An explanation of fruit structure is needed here. It is given for *Bolboschoenus* only (Figures 1–4).
Figures 1–4. Scanning electron micrographs of fruits.

Figure 1: Bolboschoenus maritimus, Lubke 93, Riet River mouth, near Grahamstown.

Figure 2: B. glaucus, de Beer Yalala 4, Sowa Pan, Botswana. Compare these two figures.

Figure 3: B. nobilis, Giess 9564, Uis, Omararu River, Namibia. (Figures 1–3: A – nutlet, scale bar = 500 μm; B – nutlet surface, scale bar = 25 μm; C – nutlet in section, scale bar = 500 μm; D – pericarp in section, much magnified, scale bar = 25 μm).

Figure 4: B. nobilis, Story 5873, Kapupa Valley, Southern Angola (Note (a) breaking down of external walls of nutlets; (b) outer cell walls gone, showing silica bodies in the cell spaces (scale bars = 25 μm).

Fruits are small nutlets (frequently, but less correctly, called achenes) that in South Africa range from 2.3–3.4 × 1.3–2.4 mm long and wide. Prominently to less definitely three-angled, with one face more rounded than the other two, they are grey to black, blotched and poorly light reflective, or light to dark or golden brown and light reflective, sometimes shining. In transverse section the fruit wall (called pericarp) consists of three layers (known as exo-, meso- and endocarp, from outside inwards). Meso- and endocarp both consist of closely-packed thickened cells that run longitudinally down the fruit in the mesocarp, but round the fruit in the endocarp. Apart from variations in the thickness of these layers, they are fairly uniform and so assist little
in differentiating species. It is the exocarp that differs, the individual cells being sometimes no deeper than wide, sometimes two to three times as deep as wide. These epidermal cells play a part in fruit distribution, as at death they become air-filled. The heavier the fruit, the less time it floats and is carried by water before sinking. (Hroudova et al. 1997). All sedge fruits contain only a single seed.

My friend and co-worker, Jane Browning, became very interested and together we decided to get to know more of these plants. Jane spent a week at Verlorevlei to see what I had earlier noted of B. maritimus. She sampled plants from the length of this coastal lake and from shoreline and its inland limit to cover differences in salinity of ambient water. Such differences are difficult to assess accurately and no attempts to do this were made. Wherever domestic animals had been excluded Bolboschoenus plants bore fruit. Otherwise, plant apices had been browsed. Some cultivation had taken place; evidence of ploughing was indicated by circles of white tissue in the disturbed soil that were fragments of the carbohydrate-rich sedge rhizomes. Left undisturbed, these underground perennating organs are able to remain viable without aerial parts for two to three years. For comparison we also had nutlets from eastern coastal plants and some from Namibia. Work began. Jane took charge of scanning fruit procedures, while I studied the plants, looking at living examples and as much dried material as was available in several herbaria.

Our results
(For those interested, details are given under the references for papers by Browning and others. Only final conclusions are outlined here).

Verlorevlei (B. maritimus – Figures 5, 6)
From study of plants of B. maritimus in the area, clear differences were found between coastal plants and those from inland limits of the lake.

Coastal plants were altogether less robust; inflorescences were less branched and comprised fewer spikelets that, in many cases, were clustered into a head; occasionally an inflorescence was a single spikelet only (Figure 5). Sectioned fruits showed an exocarp of a single layer of cells radially extended so that cell depth exceeded cell width. Mesocarp was only approximately half the depth of the exocarp (ratio exocarp: mesocarp 2:1).

Inland plants were generally taller, carried larger inflorescences that were branched and consisted of many spikelets. The nutlets sectioned showed an exocarp of less radially deep cells and a thicker mesocarp, so that exocarp:mesocarp ratio was 1:2, that is a reversal of coastal form.

What did these differences signify? No conclusive answer came to mind at this stage. Comparisons were made with plants and nutlets from St. Lucia and the Brandberg Mountains.
Figure 6. Representative inflorescences of the three species. 
The eastern entity (B. glaucus – Figures 2, 6, 8)
(This included plants from St Lucia, the Orange River mouth area and Nieuwoudtville (presumably all less saline habitats than coastal Verlorevlei)).

These plants were yet more robust than those of Verlorevlei. Spikelets were longer (var. macrostachys?) and nutlets sectioned transversely showed exocarp cells more or less iso-diametric (not radially extended) and a wide mesocarp, so that exocarp:mesocarp ratio was approximately 1:5.

The Angolan/Namibian entity (B. nobilis – Figures 3, 4, 6, 9, 10)
Here these sedges, when protected from browsing animals, were from 1.5–4.1 m tall. Inflorescences, again on protected plants, were very large and much branched (55–180 × 100–283 mm long (i.e. deep) and wide, and carrying up to about 450 spikelets. Nutlets were smaller than those of the other two species, 2.2–2.8 × 1.3–1.7 mm long and wide, grey to black often spotted or blotched. Those sectioned showed the exocarp to be a single layer of iso-diametric cells and that the exocarp:mesocarp
ratio could vary from 1:4 to 1:10. Figure 4 shows clearly that the outer walls of the epidermal cells eventually break down to expose the cell contents – at this stage silica bodies formed from silica dissolved in the water absorbed and are deposited in crystalline form with water loss in transpiration.

There was no doubt any longer that three species were present in southern Africa. An authoritative name had to be found for the ‘St Lucia entity’. Willing cooperation in this task came from foreign botanists and in due course Bolboschoenus glaucus (Lam.) S. G. Smith was established. (Note that the author names that follow genus and species are essential to specify who published the binomial). Lam. is for Lamarck in whose herbarium in Paris plants collected by Roussillon in 1791 in Senegal are preserved. These had first been named Scirpus glaucus then transferred to Scirpus maritimus var. macrostachys. Prof. S. Galen Smith was, at the time, in Wisconsin and busy with a revision of Cyperaceae for the latest edition of Flora of North America. His able assistance was greatly appreciated.

From our own work and that of others, particularly a group centred in the Czech Republic (Hroudova et al. 2007), we now know that B. glaucus has extensive distribution. It is present through suitable, mostly riverine, situations in east tropical and north Africa, the Mediterranean as far north and east as Portugal, Greece, the southern Ukraine and Russia, central Asia, Iran, Iraq, Afghanistan, Pakistan and India. It is astonishing that for so long it continued as a sub-unit of B. maritimus. There were odd attempts to recognize it as a distinct species, but none of these was maintained. It is a thermophilic plant that requires sunlight and summer temperatures sufficiently high to induce flowering (low temperatures keep the plants growing, but sterile). It requires water with low salinities. Actual records from natural stands indicate salinities mostly of two parts per thousand, that means water slightly brackish to human taste (pers. comm. C.J. Ward). Plants cannot survive strong competition from taller plants; they may be ousted by either, or both, Phragmites and Typha.

The Czech group has also much refined the concept of B. maritimus sensu stricto. It is a halophyte mostly inhabiting saline (alkaline) habitats, particularly along seashores and in inland saline pans. But the species is also able to flourish under non-saline conditions. Its aerial parts can withstand salinities lethal to many freshwater requiring plants and its rhizomes survive dry periods where salt levels remain high. Records from Morgan’s Bay indicate stands grow where salinities are about fifteen parts per thousand, increasing to 28 parts per thousand at high tides (pers. comm. C.J. Ward). Seed germination is good where salt levels are fluctuating. The main center of distribution of the species is Scandinavia.

Conclusions

It seems the most likely supposition that migrating birds from the north did bring B. maritimus to the western and south-eastern Cape coasts, but there is no knowing precisely what was brought and when B. glaucus fruits could also have been deposited by birds having rested in southern France (the Camargue?) or by ducks migrating seasonally round sub-Saharan Africa. And B. maritimus is not the only species in Europe; there are now known to be three others in addition to B. maritimus and B. glaucus. What is conclusive is that the B. maritimus plants along the Cape coasts are not uniform morphologically. It must be concluded that habitat conditions have been gradually selective, so that clones more closely representative of B. maritimus sensu stricto are along the sea-shore, while those less representative are in more inland situations where lessened salinity is probable. We do know that within the genus natural hybrid speciation is possible. Some American, some Australian and some European species give evidence of this. It requires generations and the fulfillment of many requirements to succeed, but occasionally the hybrid progeny are better adapted

Figure 9. B. nobilis, riverine stand in streamlet in granitic Brandburg Mountains, Namibia (note that culms measured up to 4.125 m in height).
to changing habitat conditions in a fluctuating climate than are the parental species, which may, or may not, disappear.

In southern Africa where attention to water supplies is of vital importance for a burgeoning population, B. glaucus is valuable. Its riverine stands help to resist river-bank erosion, especially during flooding; they aid in slowing floodwaters and promote siltation and have a purifying effect on water quality. What is perhaps most needful is to maintain the natural habitats of the species. Without this, stands are likely to disappear. In eastern Australia where water availability is already a problem, plant nurseries are now growing from seed quantities of B. fluviatilis, a species allied to B. glaucus, to supplement estuarine vegetation along important rivers where previous pollution has severely reduced natural stands (pers. comm., Australian botanists to J. Browning).

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References


