Ann. Bot. Fennici 36: 81–97
Helsinki 30 June 1999
ISSN 0003-3847

The inflorescence in southern African species of *Bolboschoenus* (Cyperaceae)

Jane Browning & Kathleen D. Gordon-Gray

Browning, J. & Gordon-Gray, K. D., Botany Department, University of Natal Pietermaritzburg, Private Bag X01, Scottsville 3209, Republic of South Africa

Received 19 October 1998, accepted 2 March 1999

Browning, J. & Gordon-Gray, K. D. 1999: The inflorescence in southern African species of *Bolboschoenus* (Cyperaceae). — *Ann. Bot. Fennici* 36: 81–97.

Inflorescence construction within the southern African species of *Bolboschoenus* (L.) Palla, namely, *B. glaucus* (Lam.) S. G. Smith, *B. maritimus* (L.) Palla *s. str.,* and *B. nobilis* (Ridley) Goetghebeur & D. A. Simpson is discussed and illustrated diagrammatically and photographically. A glossary of terminology is given. [Note that *B. maritimus s. str.* excludes *B. glaucus*, which is often included by authors in *B. maritimus s. lat.*] The basic inflorescence pattern covers a considerable range from a solitary spikelet to complex, compound inflorescences with three orders of branches and hundreds of spikelets. For each entity, inflorescence limits are variable, correlated it would seem with plant robustness and growing conditions.

Key words: *Bolboschoenus maritimus s. str., B. glaucus, B. nobilis,* inflorescence construction, southern Africa.

INTRODUCTION

Within Cyperaceae inflorescence morphology is diverse and complex. In description in formal taxonomy misapplication of terms has led to examples incorrect in the organological sense; 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 (open), that is, with axes capable theoretically of indefinite growth (Troll 1964: 178, Weberling 1981: 278, 1992: 224, Kuk-

konen 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, were devised for determinate branching systems bearing dicotyledonous flowers, not spikelets, and are better avoided (Kukkonen 1994: 39).

Within a species of *Bolboschoenus*, for example *B. maritimus* (L.) Palla, 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* (Ridley) Goetghebeur & D. A. Simpson, 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 and Tivano (1991) and Vegetti (1992, 1994) investigated the inflorescences of *Schoenoplectus* and *Isolepis*, further broadening terminology. Our study of *Bolboschoenus* inflorescences has benefited from these earlier accounts. We 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 we found this necessary. We use the term anthelodium for the inflorescence of *Bolboschoenus*.

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

1) To become familiar with the structural morphology of *Bolboscoenus maritimus*, *B. glaucus* (Lam.) S. G. Smith, and *B. nobilis*, as these species are represented in southern Africa.
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 (Browning *et al.* 1998) — 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.
4) To determine whether any distinction in inflorescence construction might support the generic separation of *Bolboschoenus* from *Schoenoplectus*.

BASIC STRUCTURE AND TERMINOLOGY

A diagrammatic representation of part of a theoretical inflorescence of *Bolboschoenus* that bears rays is presented in Fig. 1. For explication, the most complex construction encountered during this study (a synflorescence) 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 given in the accompanying glossary (p. 14) that are based on earlier concepts of Troll (1964), Weberling (1981, 1989), Kukkonen (1984, 1986, 1994), Vegetti and 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, Fig. 1 and the glossary should be consulted when necessary.

Materials and methods

Fresh inflorescences of plants of *Bolboschoenus maritimus s. str.* 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 correspond-

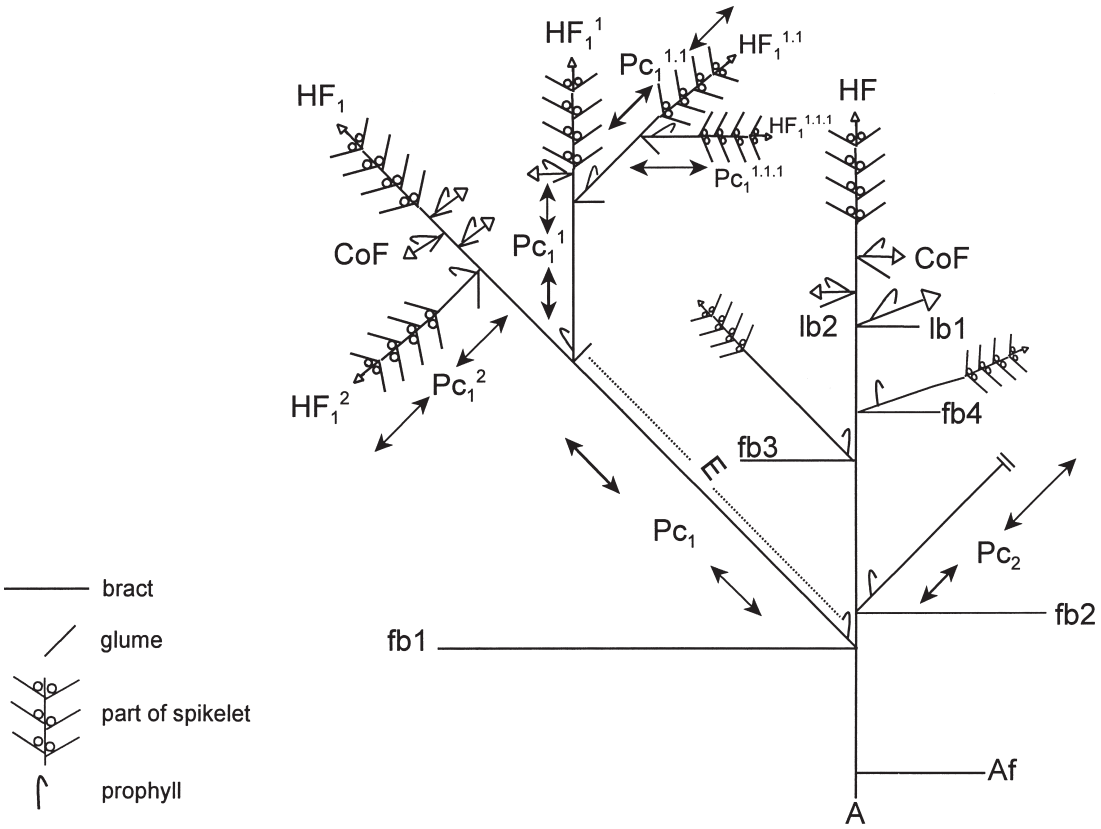


Fig. 1. *Bolboschoenus* inflorescence structure. A diagrammatic representation of a portion of the most complex construction encountered with branching of first to fourth orders. Note that for the purpose of simplification: (1) only four paracladia arising from the main culm axis have been shown; (2) the number of coflorescences arising from the main axis has been reduced to three; (3) paracladium 2 has been severed; it has a construction comparable with that of paracladium 1; (4) paracladia 3 and 4 from the main axis (not numbered in diagram) have been reduced in complexity. — A: culm axis. — Af: uppermost culm leaf. — fb1, fb2, fb3, etc.: foliaceous bracts. — lb1, lb2, etc.: laminar bracts. — HF: main, terminal, central partial florescence. — HF_1: main florescence of paracladium 1. — Pc_1: paracladium 1 (first order branch). — Pc_2: paracladium 2 (first order branch). — Pc_1^1: paracladium (second order branch). — $Pc_1^{1.1}$: paracladium (third order branch). — $Pc_1^{1.1.1}$: paracladium (fourth order branch). — E: epipodium (= ray or peduncle). — ◁▷: CoF = spikelet, prophyll + subtending bract. — △: spikelet bud. — ○: potential or developed bisexual floret. — ● or •: branch bud (both sizes). — ✚: abortive floret

ing 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 *Bolboschoenus 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 with a Nikon dissecting microscope with magnification adjusted as required, up to 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.

INFLORESCENCE STRUCTURE IN THE SOUTHERN AFRICAN SPECIES OF *BOLBOSCHOENUS*

In this account it was found easiest to proceed from the simplest (most reduced) inflorescence type and to elaborate progressively to the most complex. Note that in the diagrammatic representations A_2, B_2 etc. distances on axes have been (1)

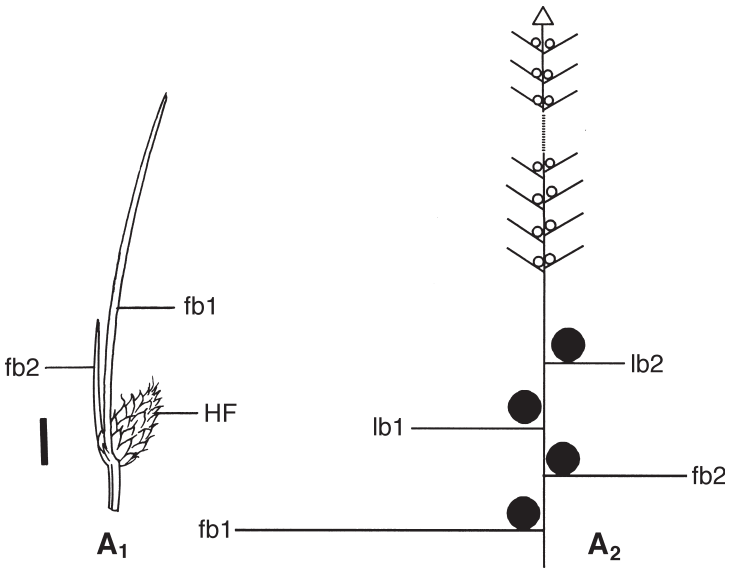


Fig. 2. *Bolboschoenus maritimus s.str.*: inflorescence of one spikelet. — A_1: in lateral view. — A_2: diagrammatic representation of dissection of this. A_1, *Browning 814* (NU). Scale bar = 20 mm.

exaggerated to accommodate structural features, and (2) a branch bud that has not grown out into a coflorescence or a paracladium is visible only on dissection (not to an observer of the inflorescence) and therefore has not been numbered; for example *see* Fig. $3B_2$.

The solitary spikelet
(Fig. 2)

Inflorescences of this type are occasional in *Bolboschoenus maritimus s. str.* The example illustrated was taken from *Browning 814* (NU).

The solitary spikelet terminates a shoot (culm) and appears pseudolateral (Fig. $2A_1$) because the main, lowest, foliaceous bract (fb1 in Fig. $2A_2$) continues in the line of the culm. A second smaller foliaceous 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 Fig. $2A_2$ 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 foliaceous bracts, which closely invest it. These are correctly part of the inflorescence.

The contracted head
(Fig. 3)

Inflorescences of this type are common in *Bolboschoenus maritimus s. str.* All the examples illustrated are of this species and taken from *Browning 814, 815* (NU).

The contracted head (Fig. $3B_1$) consists, in the case illustrated, of four closely associated sessile spikelets subtended by two foliaceous bracts (Fig. $3B_2$: fb1 and fb2). On dissection, it is seen to comprise a main axis carrying sequentially two foliaceous bracts, two laminar bracts and the main florescence. In the axil of the lowest foliaceous 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

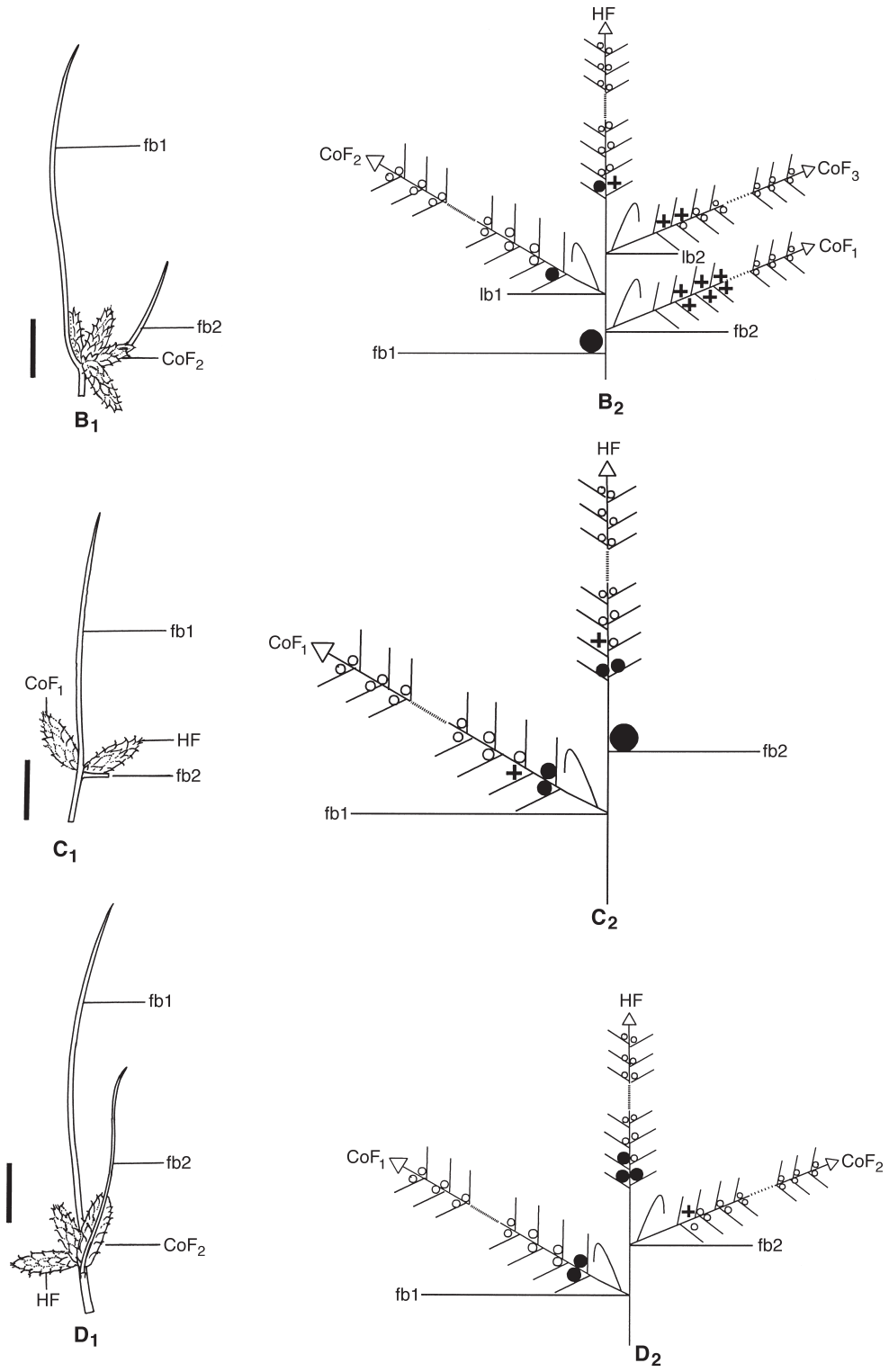


Fig. 3. *Bolboschoenus maritimus s.str.* Inflorescences representative of contracted heads of four spikelets (B_1), two spikelets (C_1), three spikelets (D_1). — B_2, C_2, D_2: diagrammatic representations of dissections of these. B_1, *Browning 815* (NU); C_1, D_1 , *Browning 814* (NU). Scale bar = 20 mm.

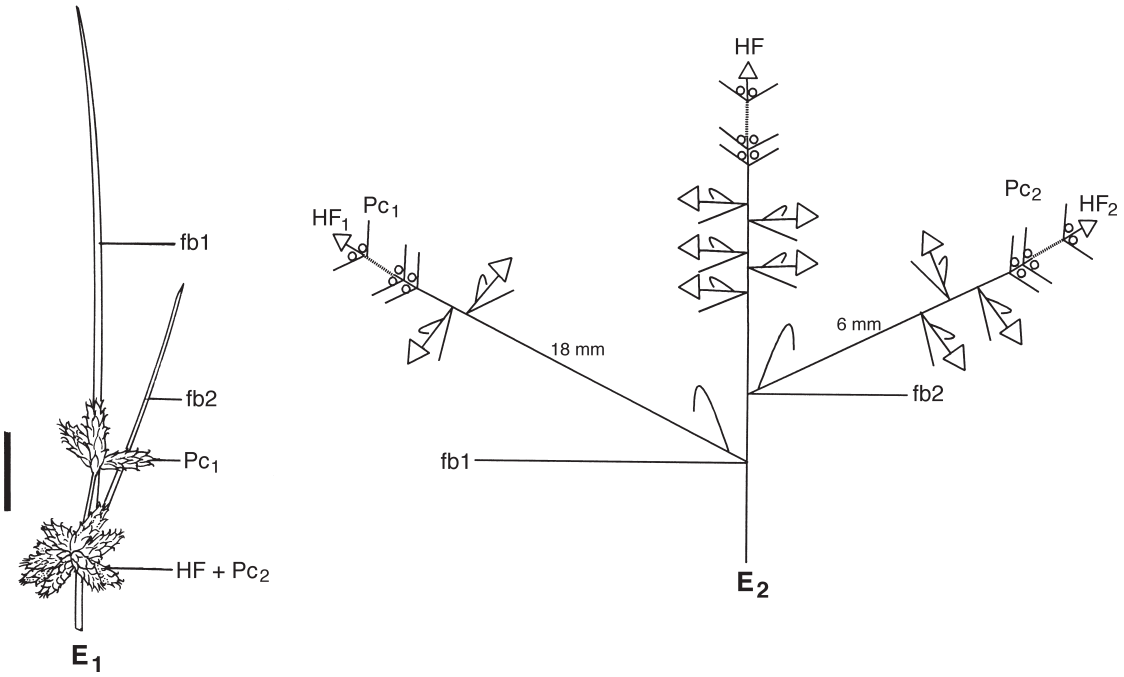


Fig. 4. *Bolboschoenus maritimus s.str.* Inflorescence representative of the few-rayed anthelodium. — E_1: example with two rays (short ray obscured). — E_2: diagrammatic representation of dissection of this. E_1, *Browning 817* (NU). Scale bar = 20 mm.

spikelets that differ from the main florescence only in that each is bracteated and prophyllate. These lateral spikelets are coflorescences (CoF_1, CoF_2, CoF_3). Their axes are first order branches from the main axis. Structurally, the contracted head (Fig. $3B_2$) is capable of development from the solitary spikelet shown in Fig. $2A_2$. Branch buds axillary to fb2, lb1 and lb2 in Fig. $2A_2$ have, in the case of Fig. $3B_2$, grown into coflorescences, whereas the bud axillary to fb1 has remained dormant.

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 coflorescence 2 (CoF_2). These axillary buds, if activated into growth, are theoretically at least, each capable of development into a coflorescence. (2) The presence of a number of aborted floral buds in the coflorescences (one only in HF). Aborted floral buds were observed in many inflorescences of *Bolboschoenus maritimus* from Verlorenvlei, South Africa. Note that in Fig. $3B_2$ the basal glumes of CoF_1 are denoted as empty; presumably the aborted floral buds had fallen away or were always lacking (*see* also Discussion).

Other examples of contracted heads consisting of two and three spikelets are shown in Figs. $3C_1$, C_2 and D_1, D_2 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.

The few-rayed inflorescence (anthelodium)

(Fig. 4)

Inflorescences with 1–3(–4) rays are also common in *Bolboschoenus maritimus s. str.* The example illustrated is of a two-rayed anthelodium of *B. maritimus s. str.* taken from *Browning 817* (NU). Note that in Fig. $4E_1$ the second short ray is obscured. This anthelodium consists of thirteen spikelets in all. Three of these are sessile distally

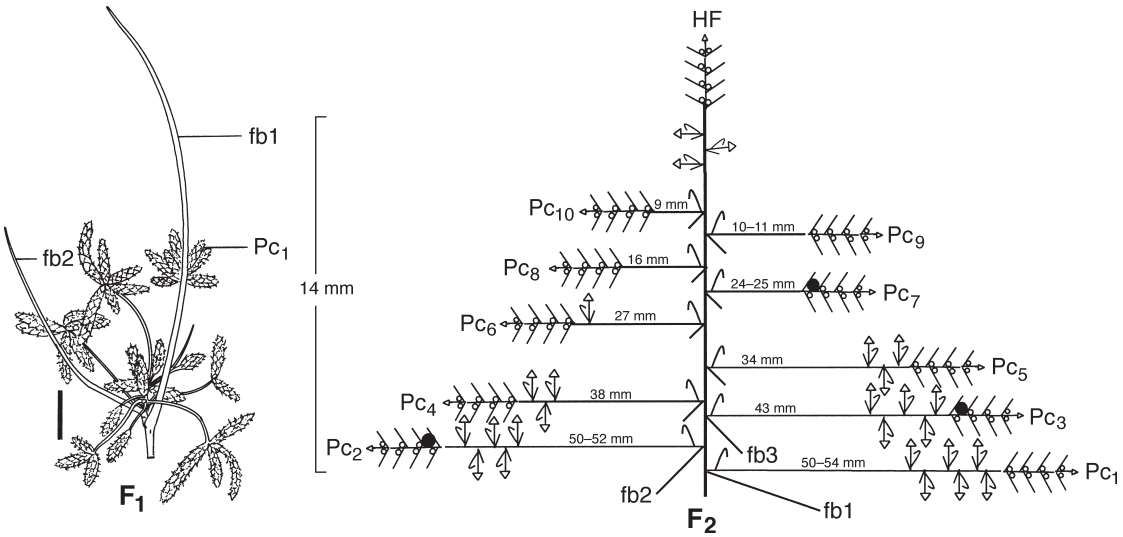


Fig. 5. *Bolboschoenus glaucus*. Inflorescence representative of the many-rayed anthelodium. — F_1: example with ten rays: — F_2: diagrammatic representation of dissection of this. F_1, *Johnson s.n.* (NU) Senegal, West Africa. Scale bar = 20 mm.

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 Fig. $4E_2$. Consider first the main central partial florescence. This comprises a central spikelet HF that lacks bract and prophyll, closely accompanied by five coflorescences (sessile spikelets each bracteated and prophyllate). From foliaceous 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 foliaceous 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.

The many-rayed inflorescence (anthelodium) (Figs. 5 and 6)

Inflorescences with ten and often more rays are usual for *Bolboschoenus glaucus*. The examples illustrated are two ten-rayed anthelodia, one from Senegal taken from *Johnson s. n.* (23 Oct. 1997, NU), F_1, F_2; the other from Mzinene, KwaZulu/Natal, South Africa and taken from *C. J. Ward 14201* (NU), G_1, G_2. The Senegal example is included for comparison as its location is northwestern in Africa in contrast to the southeastern African position of the Mzinene example.

Essentially these more complex anthelodia characteristic of *Bolboschoenus glaucus* differ only in degree from the few-rayed type that is of frequent occurrence within *B. maritimus s. str.* In Fig. $5F_1$ 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 Fig. $5F_2$). 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 con-

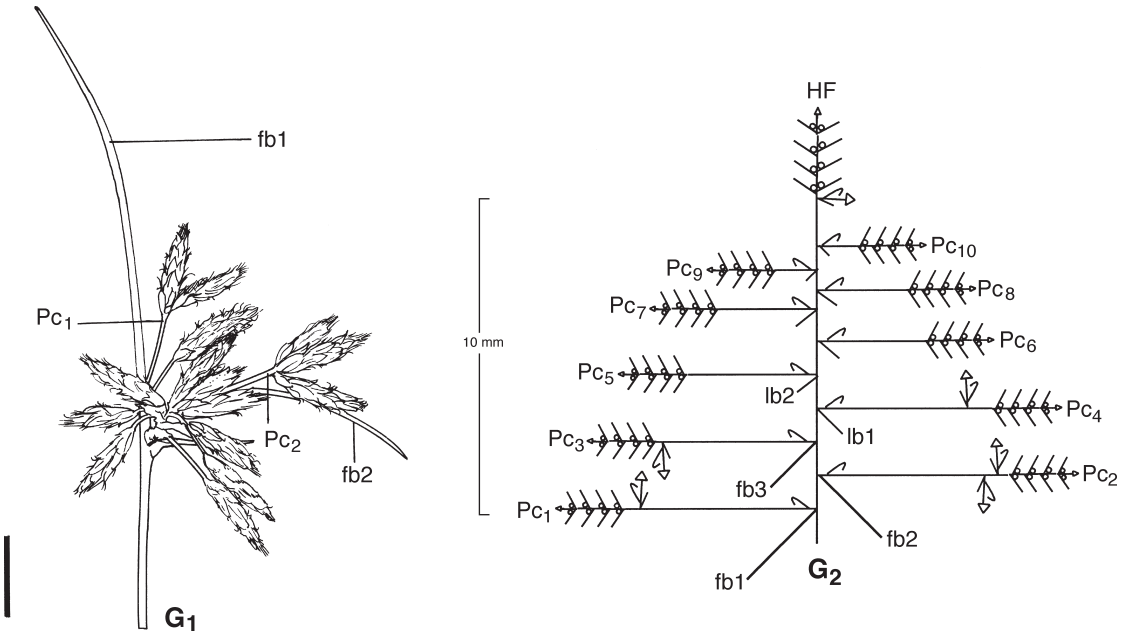


Fig. 6. *Bolboschoenus glaucus*. Inflorescence representative of the many-rayed anthelodium. — G_1: example with ten rays. — G_2: diagrammatic representation of dissection of this. G_1, *C. J. Ward 14201* (NU) KwaZulu/Natal, South Africa. Scale bar = 15 mm.

sist of a solitary spikelet only, unaccompanied by coflorescences. 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 foliaceous 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 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 (Fig. 6), is built on a similar plan, and differs from the example from Senegal (Fig. 5) 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, paracladia bearing solitary spikelets predominate (6 out of 10), whereas in the example from Senegal paracladia bearing clusters of spikelets are in the majority (6 out of 10).

The compound anthelodium

(Figs. 7–10)

This expanded, many spikeletted inflorescence is borne by the tall, leafy shoots of *Bolboschoenus nobilis*. The example illustrated is from Namibia and taken from *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 Fig. $8H_3$ and diagrammatically in Fig. $7H_2$) 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) that collectively form the main central partial florescence. 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

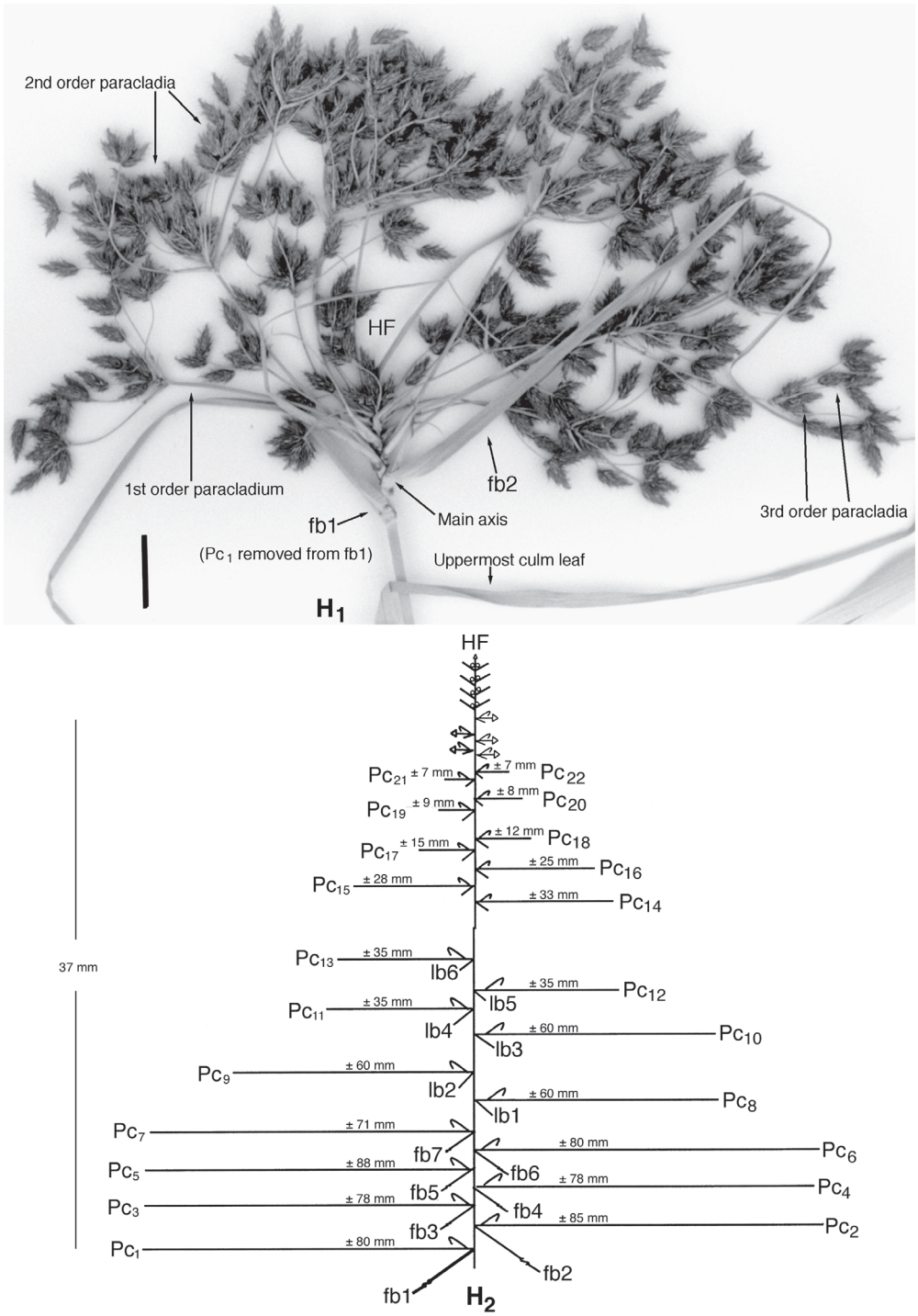


Fig. 7. *Bolboschoenus nobilis*. Inflorescence representative of the compound anthelodium. — H_1: example (lowest paracladium removed to permit better positioning). — H_2: diagrammatic representation of main axis of this example showing first order paracladia in sequence (Pc_1–Pc_{22}) followed by five coflorescences (CoF) and main florescence (HF). The coflorescences and main florescence collectively constitute the short, compact cluster central in the synflorescence. This cluster appears sessile terminating the main axis. H_1, *C. J. Ward 13245* (NU). Scale bar = 23 mm.

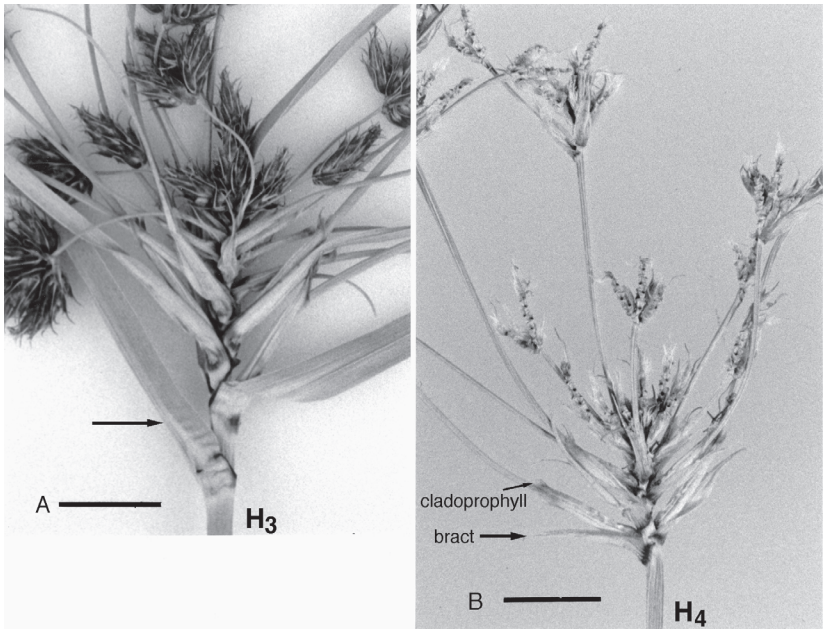


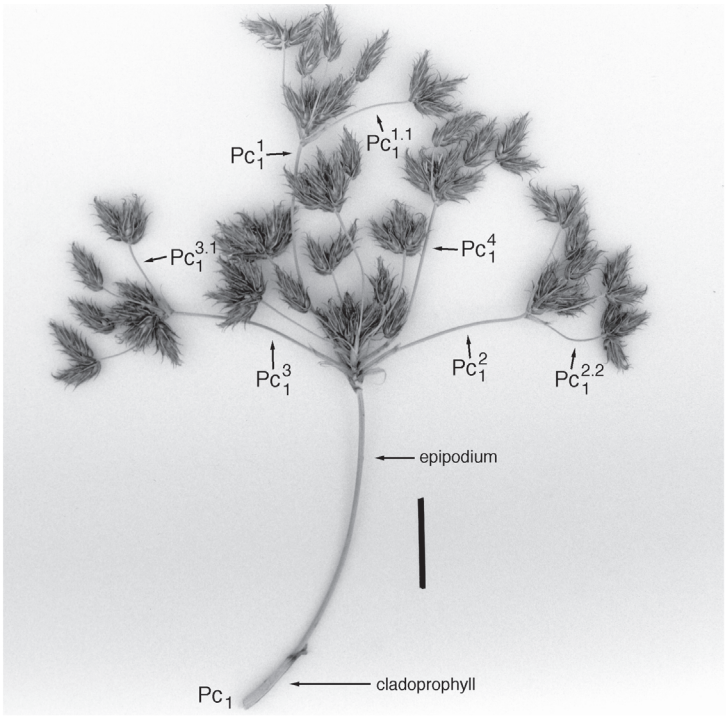
Fig. 8. *Bolboschoenus nobilis*. Inflorescence representative of the compound anthelodium. — H_3: main axis enlarged to show spirality and parts in greater detail; note cladoprophyll within first foliar bract (arrowed). — H_4: partial florescence of one first order paracladium after glumes had abscised naturally; note bracts, cladoprophylls, and presence of second order paracladium on uppermost centrally placed first order paracladium. H_3, H_4, *C. J. Ward 13245* (NU). Scale bar = 10 mm.

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 cladoprophylls. The second series has shorter epipodia (all approximately 60 mm) and also with well developed cladoprophylls. The third series has epipodia of approximately 35–25 mm 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 Fig. $7H_2$ and less obviously in Fig. $7H_1$. It results in a "spread" of spikelets through the extent of the synflorescence which should be advantageous in a wind pollinated plant.

Paracladium (Pc_1), the lowest, was detached and analysed. It is shown in Fig. $9H_5$ and diagrammatically in Fig. $9H_6$. The paracladia of paracladium Pc_1 were then detached sequentially and each illustrated diagrammatically (Fig. 10: Pc_1^1–Pc_1^{12}). 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 (Pc_1^{10}–Pc_1^{12}) lack coflorescences and consist each of one peduncled (rayed) spikelet only (the main florescence HF of that paracladium). Fig. $8H_4$ 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 cladoprophylls 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 southern 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 col-



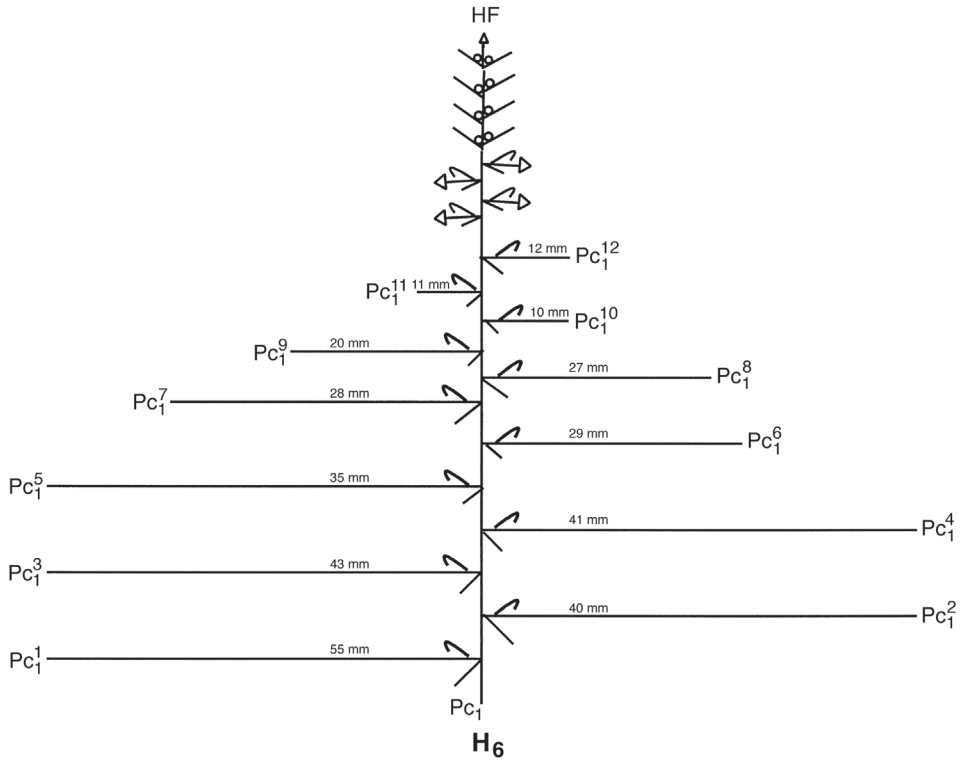


Fig. 9. *Bolboschoenus nobilis*. Inflorescence representative of the compound anthelodium. — H_5: structure of first order paracladium (Pc_1) removed from synflorescence (remainder shown in Fig. $7H_1$). — H_6: diagrammatic representation of dissection of this. H_5, *C. J. Ward 13245* (NU). Scale bar = 20 mm.

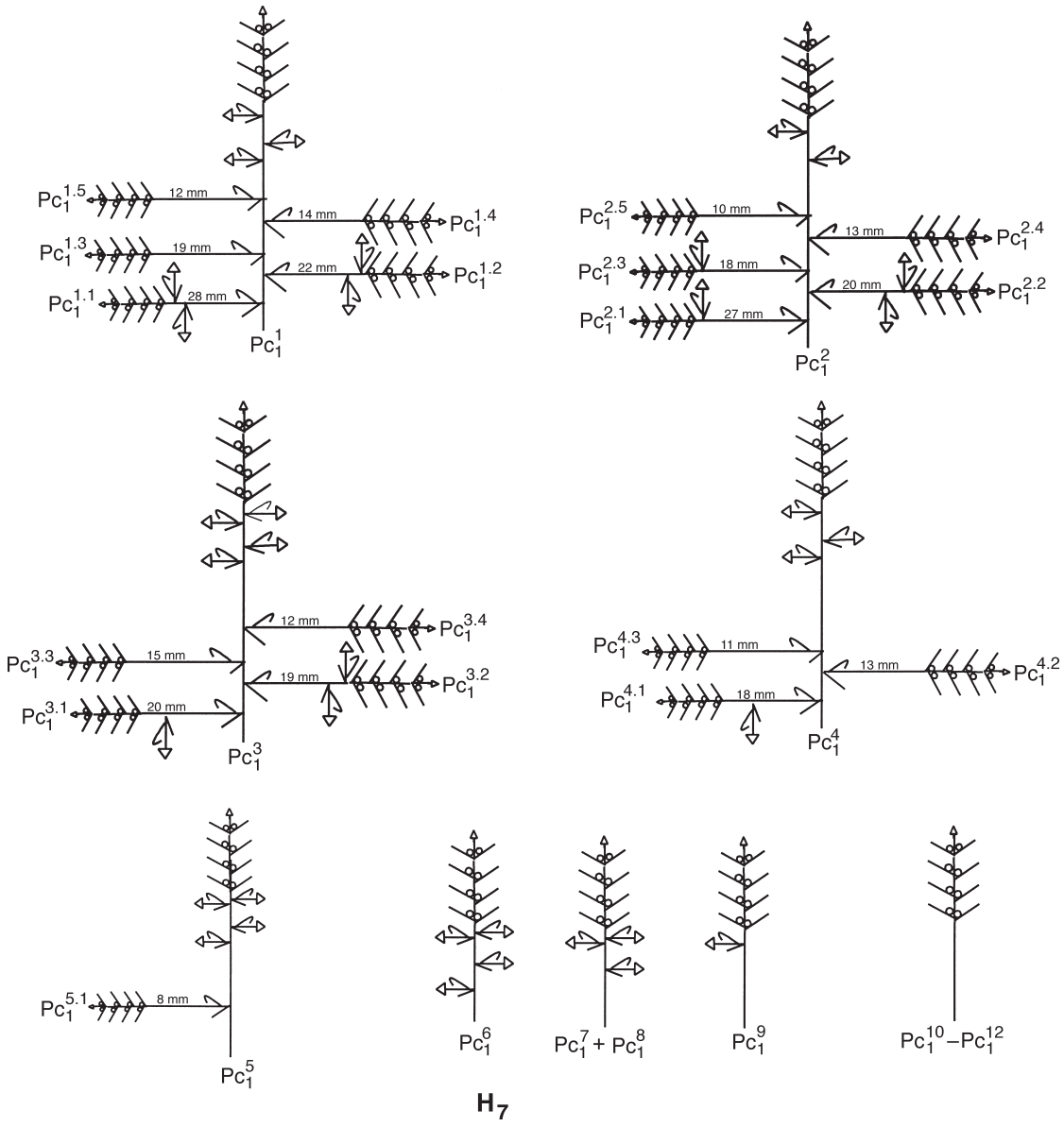


Fig. 10. *Bolboschoenus nobilis*. Inflorescence representative of the compound anthelodium. — H_7: diagrammatic representations of dissections of second order paracladia (Pc_1^1–Pc_1^{12}); note that Pc_1^6–Pc_1^{12} show no development of third order branches, and Pc_1^{10}–Pc_1^{12} lack third order branches and coflorescences. H_7, *C. J. Ward 13245* (NU).

lectively upwards of 400 spikelets. In the account given it is shown how an inflorescence comprising a solitary spikelet only possesses 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), is 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 southern African (and world) species of the genus. This species, which grows along inland water bodies 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 *Bolboschoenus maritimus s. str.* has had repeated mention in literature. Our 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 corms. 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 the deductions from them 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 southern African (and world) 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. str.* 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 is the outcome of many interacting factors.

In Table 1 the important features of inflores-

Table 1. Important qualitative and quantitative inflorescence parameters representative of southern African species of *Bolboschoenus* (all measurements in mm).

Character	*B. maritimus s.str.*	*B. glaucus*	*B. nobilis*
Number of foliaceous bracts	2(–3)	2–3	1–4(–7)
Inflorescence width (at widest point)	(7–)10–60	55–98	100–283
Inflorescence depth (apex to first foliaceous bract)	15–55	42–65	55–180
Inflorescence form	solitary spikelet or compact head or head with few first order rays	anthelodium of first and sometimes second order rays	compound anthelodium of first to third order rays
Number of spikelets	1–5(–20)	(16–)20–35(–62)	(60–)100–200(–450)
Number of first order rays	1–4	7–10(–14)	10–15(–22)
Epipodia: length of first order rays	18–30(–50)	20–35(–45)	(7–)40–80(–100)
Angle of first order rays to main axis	usually less than 90°	some 90°	some 90°
Main axis: length from first foliaceous bract to base of main florescence	1–5 mm; not easily observed because inflorescence compact	10–14(–16); generally obvious in mature inflorescences	18–30(–37); generally obvious in mature inflorescences

cence structure and size for inflorescences of the southern African species of *Bolboschoenus* as derived from the present study, are summarised. Significant discontinuities are lacking, but when extremes, for example *B. maritimus s. str.* 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. str.* This is merely a guide in identification and should never be relied upon in isolation.

In connection with inflorescence construction, it was noted that in southern African species occasional axillary floral buds (potential florets) within spikelets had aborted (failed to attain full structural development). Few such aborted buds were observed within *Bolboschoenus nobilis*. However, in *B. glaucus* they were prevalent and often numerous in individual spikelets and were encountered also in *B. maritimus s. str.*, 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. *Bolboschoenus glaucus*, in southern Africa, and as far as we 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.

In the southern African species of *Bolboschoenus*, axillary buds in the axils of the prophylls of the basal paracladia that 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 & 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.

In our study of the inflorescence of southern African species of *Bolboschoenus* we found no specific feature represented to support the differentiation of this genus from *Schoenoplectus*.

GLOSSARY

(cf. Fig. 11)

(abbreviation: *q.v.* = *quod viva* = which see)

Anthelodium (pl. *anthelodia*): an indeterminate, polytelic inflorescence that in *Bolboschoenus* is crateriform with a compressed main axis terminated by an indeterminate spikelet (the main terminal central partial florescence HF... *q.v.* florescence 1.) that is closely surrounded by sessile or subsessile spikelets (each a coflorescence CoF... *q.v.*) to form a central compact group (the main central partial florescence ... *q.v.* florescence 2.). This compact group (HF+1–many CoF's) is overtopped by lateral partial peduncled florescences (paracladia ... *q.v.*) that are first order branches of the main axis, which in turn may produce second and third order branches. Therefore in its most developed expression in *Bolboschoenus* (as in *B. nobilis*), the anthelodium is compound, a synflorescence that comprises the main central florescence (the abbreviated main axis) surrounded and overtopped by lateral partial peduncled florescences (paracladia).

Bract: a leaf (often reduced) 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:

- — foliaceous (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.

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

- — branch bud (●) or (•) axillary to a bract

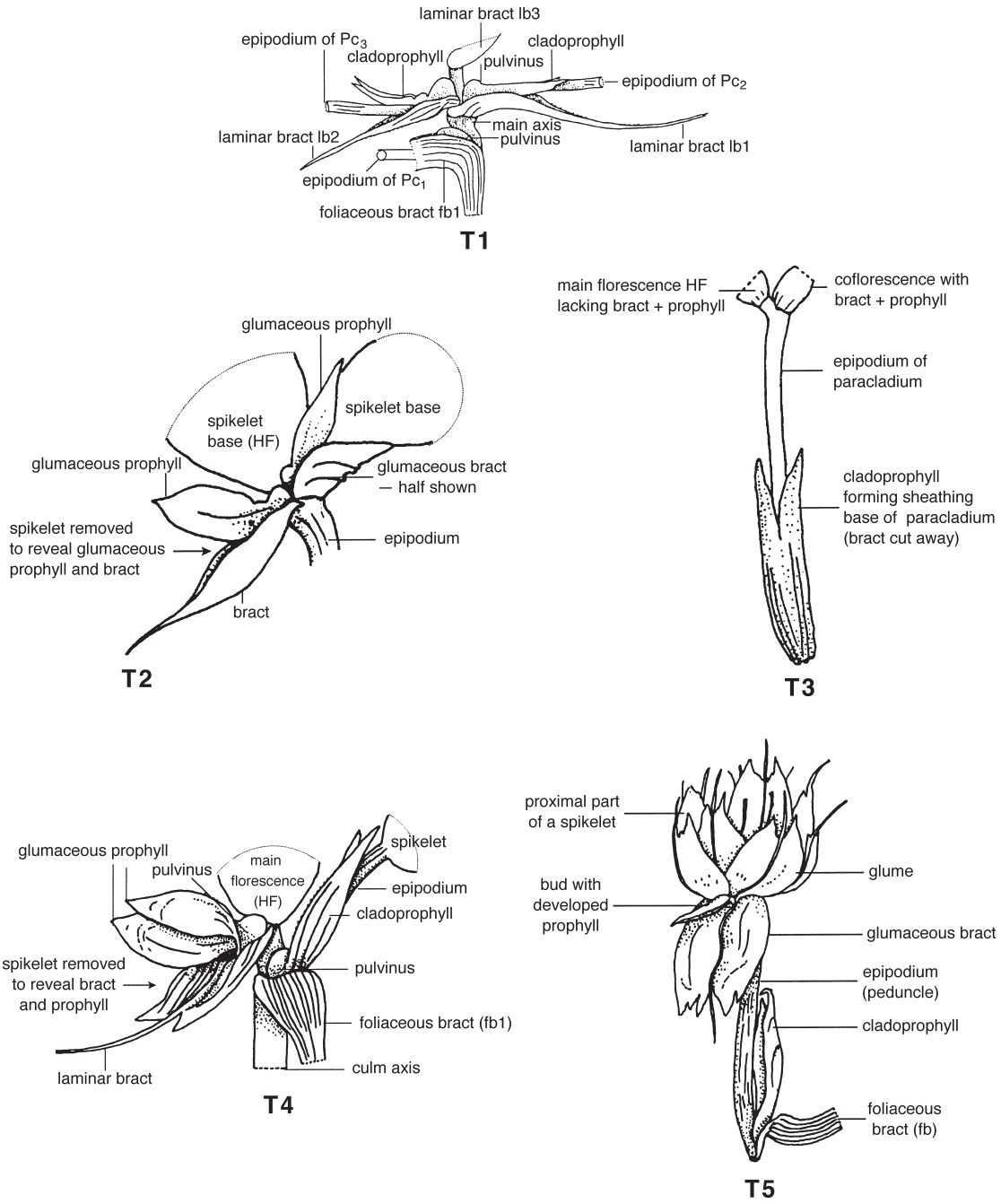


Fig. 11. *Bolboschoenus*. Graphic representations of inflorescence morphology for use with glossary. — T1: *B. glaucus*: proximal part of main axis of inflorescence showing one foliaceous and two laminar bracts, three epipodia (severed) and associated pulvinate cladoprophylls. Note epipodia lie at right angles to main axis (usual in *B. glaucus*). — T2: *B. glaucus*: partial lateral florescence of paracladium, showing main florescence HF and two coflorescences (one removed) with associated glumaceous bracts and prophylls. — T3: *B. glaucus*: paracladium showing cladoprophyll, epipodium, main florescence and one coflorescence. — T4: *B. maritimus*: inflorescence consisting of main florescence HF, one coflorescence with laminar bract and prophyll and one paracladium with cladoprophyll and epipodium. Note angle of epipodium = less than right angle (usual in *B. maritimus s.str.*). — T5: *B. maritimus*: paracladium bearing one spikelet; glumaceous bract turned back to reveal axillary bud with recognisable prophyll. Drawings not to scale.

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

Coflorescence: in *Bolboschoenus*, a sessile or subsessile 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  incorporates the subtending bract which, in reality, is not part of the bud giving rise to the coflorescence.) A coflorescence may be considered as a reduced, sessile paracladium.

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

Florescence: a floral-bearing part of the total synflorescence ... *q.v*. Used in denoting any of the following: (1) the main, terminal, central partial florescence HF (a spikelet that lacks subtending bract and prophyll (these basal on main axis) and therefore different from a coflorescence. (2) The main central partial florescence: the main terminal spikelet together with the lateral coflorescences below. (3) A lateral peduncled partial florescence = a paracladium ... *q.v*.

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.

Inflorescence: a collective, general term applied to the arrangement of flowers or spikelets on their supporting branches.

Paracladium (pl. *paracladia*): a lateral, peduncled partial florescence 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 (spongy) basally (cladoprophyll), an elongate peduncle (epipodium E), and distally, the spikelets and their supports.

Prophyll: the first leaf on a branch recognisable by two main keels facing the axis that extend into acuminate apices. Within the inflorescence of *Bolboschoenus* of two kinds, namely:
— cladoprophyll: a tubular sheath enveloping a proximal portion of an epipodium.
— glumaceous prophyll: membranous and glume-like, but differing from a glume in the two adaxial keels that extend into acuminate apices.

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

Synflorescence: in *Bolboschoenus* the total of flower-bearing spikelets on a culm together with the branches and branchlets that bear them = a compound anthelodium comprising a central contracted unit (the main central partial florescence) surrounded and overtopped by lateral peduncled partial florescences (paracladia).

Acknowledgements: We gratefully acknowledge the assistance of Rogan Roth who took the photographs, and the reviewers for their helpful remarks. Publication would not have been possible without financial aid from the University of Natal Research Fund.

REFERENCES

Browning, J., Gordon-Gray, K. D., van Staden, J. & Ward, C. J. 1998: Studies in Cyperaceae in southern Africa. 35: A field study of *Bolboschoenus maritimus s. l.* in a western Cape wetland. — *South African J. Bot.* 64: 70–81.

Kukkonen, I. 1984: On the inflorescence structure in the family Cyperaceae. — *Ann. Bot. Fennici* 21: 257–264.

Kukkonen, I. 1986: Special features of the inflorescence structure in the family Cyperaceae. — *Ann. Bot. Fennici* 23: 107–120.

Kukkonen, I. 1994: Definition of descriptive terms for the Cyperaceae. — *Ann. Bot. Fennici* 31: 37–43.

Norlindh, T. 1972: Notes on the taxonomy and variation in the *Scirpus maritimus* complex. — *Bot. Notiser* 125: 397–405.

Troll, W. 1964: *Die Infloreszenzen*. — Gustav Fisher Verlag,

Jena. 615 pp.
Vegetti, A. C. 1992: Typology of the inflorescence in species of *Schoenoplectus* (Cyperaceae) of Austral America. — *Beitr. Biol. Pflanzen* 67: 241–249.
Vegetti, A. C. 1994: Typology of the inflorescence in species of *Isolepis*. — *Beitr. Biol. Pflanzen* 68: 21–26.
Vegetti, A. C. & Tivano, J. C. 1991: Inflorescence typology in *Schoenoplectus californicus* (Cyperaceae). — *Beitr. Biol. Pflanzen* 66: 323–345.
Weberling, F. 1981: *Morphologie der Blüten und der Blütenstände*. — Ulmer, Stuttgart. 391 pp.
Weberling, F. 1989: *Morphology of flowers and inflorescences*. — Cambridge Univ. Press, Cambridge. 1st paperback edition 1992. 405 pp.