

Studies in Cyperaceae in southern Africa 27: a contribution to knowledge of spikelet morphology in *Epischoenus* and the relationship of this genus to *Schoenus*

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Spikelet morphology in the endemic, southern African genus *Epischoenus* C.B. Clarke is considered and new information is given. Some problems of interpretation are discussed. The relationship of *Epischoenus* to the older and larger genus *Schoenus* L., which is predominantly SE Asian and Australian, is further emphasized by the new information provided. The question arises as to whether *Epischoenus* is separable from *Schoenus* by definite morphological discontinuity, or whether it is primarily on continental location that generic limitation rests. Species delimitation in *Epischoenus* is unsatisfactory and in need of revision. Field study of living organisms from stage to stage of development is required, but made difficult by habitats.

Aartjiemorfologie in die endemiese, Suider-Afrikaanse genus *Epischoenus* C.B. Clarke word oorweeg en nuwe inligting word aangebied. Sommige probleme in vertolking word bespreek. Die verwantskap tussen *Epischoenus* en die ouer en groter genus *Schoenus* L., wat hoofsaaklik in suid-oostelike Asië en Australië voorkom, word verder deur die jongste inligting wat verskaf word, beklemtoon. Die vraag ontstaan of *Epischoenus* skeibaar is van *Schoenus* deur bepaalde diskontinuiteite in morfologie, en of generiese beperkinge primêr op verskille in die ligging op die vasteland berus. Die afbakening van spesies in *Epischoenus* is onbevredigend en behoort hersien te word. Veldwerk op die ontwikkelingsfases in lewende organismes is nodig, maar word bemoeilik deur habitat.

Keywords: Spikelet morphology, *Epischoenus*, *Schoenus*.

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Introduction

Epischoenus C.B. Clarke, a genus of eight species, is endemic to southern Africa, particularly the western mountains of the Cape Province. Establishment dates to 1898 when *E. quadrangularis* (Boeck.) C.B. Clarke [= *Schoenus quadrangularis* Boeck.] became the type species, being segregated from *Schoenus* L. Significant generic differences were that in *Epischoenus* a single, bisexual floret occurred above others that were functionally male, whereas in *Schoenus* the one to several bisexual florets mostly preceded the nought to two that were functionally male. In addition, in *Epischoenus* it is the suprafloral axis that thickens and strengthens, ultimately drying, curving and, until abscission, remaining conspicuous in the spikelet. In *Schoenus* it is often the internodes between and above but adjacent to, the bisexual florets that enlarge to produce an anfractuose (zig-zag) spikelet rachilla.

There is no doubt of the close relationship between these genera, despite their mainly different continental locations. At the time of Clarke's initial separation of *Epischoenus* there must have been comparative evaluation. Subsequently, however, *Epischoenus* seems to have been studied in relative isolation. Observation and interpretation of spikelet structure in both genera are not straightforward. Of *Schoenus*, Kern (1974: 674) wrote: 'Specific delimitation is extremely difficult throughout the genus. Bentham's remark that further study from living plants or from specimens gathered in all the different stages of development of the flowers is required, is in force up till the present day.' It is no less applicable to *Epischoenus* now.

Levyns (1959: 72, Figure 1E) illustrated the florets of *Epischoenus* as non-axillary and interpreted the spikelet as cymose in construction. Haines (1967: 61, Figure 6N) for *Schoenus nigricans* L. interpreted each floret, of which there are up to five, as supra-axillary, that is as 'springing from the rachilla above the subtending bract rather than from the actual axil of the bract', and therefore considered the spikelet to be racemose with a

monopodial axis. The contentious topic of floral morphological interpretation has been extensively argued in the literature and will not be detailed here. It should be pointed out, however, that proponents of one or other structural interpretation have not necessarily had opportunity to dissect and comment upon a common set of critical species. Such procedure, together with study of changes from young to old stages of development, should be undertaken.

This article provides new observations on spikelet structure in *Epischoenus* and for comparison, *Schoenus*. Improved equipment and techniques not available to earlier investigators have made this more detailed information possible. An interpretation of spikelet structure that emphasizes the floral relationship existing in these two genera, is proposed. We also question the effectiveness of both the monopodial and sympodial interpretations, as these have been expressed up to the present time, as accurately explanatory of spikelet construction in these genera.

Materials and Methods

Where possible, spikelets of different ages were removed from herbarium material, rehydrated, dissected and observed using an Olympus binocular microscope $\times 40$. Sterile lower glumes were removed and fertile glumes were cut or removed to expose details of floret position and rachilla structure. Toluidine blue was used to clarify, for illustration, positions on the spikelet axis from which glumes were removed. Rachillas, after removal of selected glumes and parts of the spikelet axis, were mounted on stubs using double-sided aluminium foil on double-sided cello tape, sputter-coated with gold-palladium using a Polaroid E 5100 sputter coater, and viewed under an Hitachi S 570 scanning electron microscope.

Spikelet morphology in *Epischoenus*

Levyns (1959: 72–80) gave a carefully observed and a thoughtfully interpreted description of spikelet morphology that covered the eight species known. Some points require comment.

- (i) The bracts (glumes) are 'more or less 2-ranked'. This wording satisfactorily accommodates the slight spiral twisting of the spikelet axis through its length that off-sets the apparently distichous glumes.
- (ii) Observation of the floret as non-axillary to the glume developed from the same node, is significant. It led Levyns directly to the implication that the spikelet axis was a branched pseudorachilla. However, anatomical or other satisfactory proof of such branching has never been provided, so that the interpretation of spikelet construction remains problematic (Eiten 1976: 86-89).
- (iii) Variability in numbers of spikelet parts both inter- and intraspecifically was recorded, but perhaps inadequately stressed. There is variability between and within species in the number of proximal, sterile glumes, the number of distal fertile glumes and the number of florets. The stable character in spikelet organization is that only *one* of the potentially bisexual florets developed ever sets fruit and that this is distal to the variable number of functionally male florets, most of which possess rudiments of a gynoeceal whorl. It is easy to assume that the functional bisexual floret is uppermost on the spikelet axis, but this is not absolute. Levyns (1959: 73) drew attention to the occasional presence of a male (usually abortive) floret in the vestigial bracts borne upon the suprafloral axis.
- (iv) The suprafloral axis bears 'one or more sterile bracts [glumes] at its tip'. This significant observation reported the heterogeneity of this uppermost portion of the spikelet rachilla. As ovary maturation proceeds, this axis, together with the glume(s) it may carry, enlarges and strengthens into a 'curved and cartilaginous' structure that may become a feature of older spikelets before they disintegrate by abscission.

For Levyns, the suprafloral axis provided a means of subgeneric grouping. She found it to be free from, or adnate to, the bract (glume) at its base and on this character recognized *E. gracilis* Levyns, *E. quadrangularis* C.B. Clarke and *E. villosus* Levyns with this axis free. *E. adnatus* Levyns and *E. dregeanus* (Boeck.) Levyns she found to show adnation, whereas in *E. complanatus* Levyns and *E. lucidus* (C.B. Clarke) Levyns she found adnation for a short distance only. *E. cernuus* Levyns, in which this axis is smaller than in any other species, she found also free, but to have grouped this taxon with *E. gracilis* and affiliates would have been to conceal differences that could become critical.

Present observations and interpretations

Suprafloral axis

In its most highly elaborated form we found the suprafloral axis to consist of two sections: (i) a proximal portion, stouter than the remainder, that directly by growth continues into (ii) a distal zone that is usually flattened and narrow. The apex of this distal zone carries a vestigial glume.

The proximal portion lies closely adpressed to the glume adjacent to it in the region of the glume's lower midrib and usually becomes adnate. The distal portion is variable in length within spikelets of a clone and is usually directed inwards away from the glume at an angle of less than forty-five degrees. From the apex of this distal part arises the vestigial glume that is also variable in length from one spikelet to another. This glume is sterile and at best no more than a narrow strip of delicate tissue. Nevertheless, it may occasionally enwrap rudiments of a potentially male floret and perhaps a second glume, which is not easily identified. *E. gracilis* (Figure 1A, B) is representative of this elaborated form of the axis. Our interpretation of it differs from that of Levyns (1959: 75), who recognised it as 'free from the

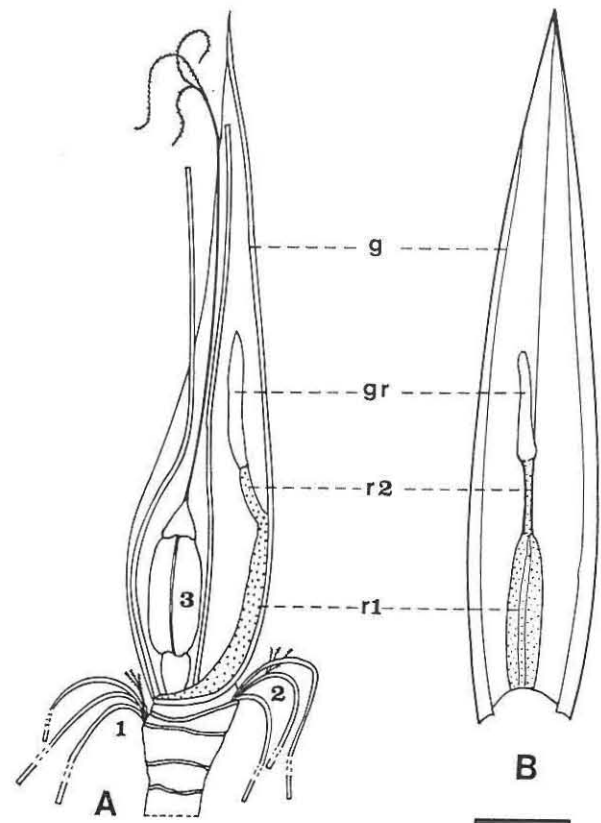


Figure 1 *Epischoenus gracilis*. A. Spikelet (distal portion), dissected to show two potentially bisexual, functionally male florets (1 + 2) (filaments severed) surmounted by the only functionally bisexual floret (3) (one stamen removed) and the suprafloral axis with proximal portion adnate to glume. B. Glume associated with maturing fruit (adaxial view) with adnate suprafloral axis. g, Glume associated with maturing fruit; gr, vestigial glume; r1, axis, proximal portion; r2, axis, distal portion. Levyns 9339. Scale bar: 1 mm.

bract', because she must have taken into consideration only the free portions, neglecting altogether the proximal adnate zone.

In its least developed form this suprafloral axis may be overlooked. It consists of a minute point, no more than a nub of tissue visible only under magnification, unless a slender, short, vestigial glume is produced from near its apex which occasionally is the case (Figure 2 with inset). *E. cernuus* is the only species in which such a scant, suprafloral axis occurs. In our opinion, it is also the only species in which this axis may be described as 'free'.

In species other than *E. cernuus*, for example *E. dregeanus* (Figure 3), this axis does not differ fundamentally from the structure described for *E. gracilis* (Figure 1), except that the distal, inwardly directed portion was seldom developed. There are differences in the size and robustness of the rachilla itself and in the vestigial glume, to give a range not only from species to species, but also within individual species, so that it is difficult to provide a generalized description for a taxon. These differences seem to correlate directly with enlargement (sexual maturation, or not), of the ovary of the bisexual floret. When there is no evidence of swelling of this ovary, the basal portion of the suprafloral axis undergoes little change. However, when this ovary reaches what appears to be a critical size, or stage in relation to chemical changes, there is growth of the proximal part of the rachilla in particular, which expands, elongates, curves and hardens. As maturity proceeds, the whole suprafloral axis dries, frequently curling over. As this curling takes place, the glume tissue adnate

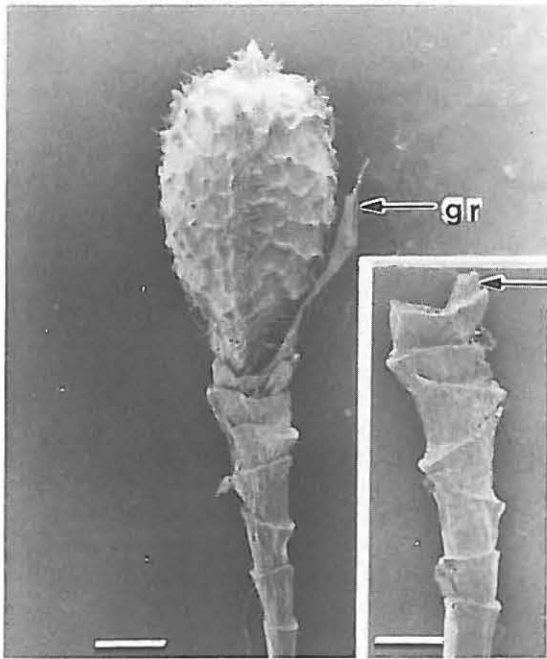


Figure 2 *Epischoenus cernuus*. Spikelets with glumes removed to show almost mature achene and suprafloral axis with slender, vestigial glume and (inset) suprafloral axis with undeveloped vestigial glume. gr, Vestigial glume. Esterhuysen 17982. Scale bar: 0.5 mm.

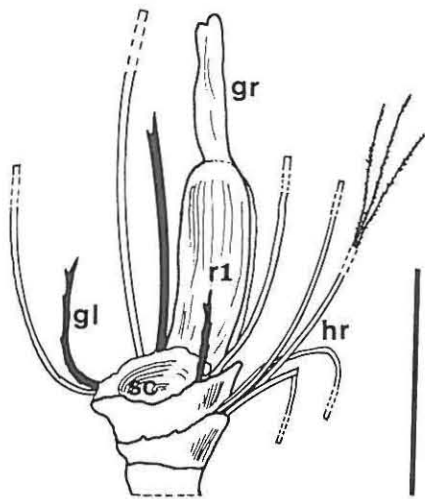


Figure 3 *Epischoenus dregeanus*. Spikelet (distal portion only) dissected to show one potentially bisexual, functionally male floret and scar indicating position of attachment of matured achene (removed). Note rudimentary glumellae arising from margin of gynophore which has remained *in situ*; also robust suprafloral axis consisting of thickened proximal portion and more slender, vestigial glume (no intervening middle zone developed). gl, Glumella; gr, vestigial glume; hr, potentially bisexual floret; r1, rachilla; sc, scar. Esterhuysen 15213. Scale bar: 1 mm.

to the proximal section is pulled away leaving an arched-shaped hole in the glume, and clearly marked superimposed tissue with a ragged margin on the axis (Figure 4).

Glumes

The proximal sterile glumes are typically boat-shaped, with a curved, almost horizontal, truncate base after abscission from the

spikelet axis (Figure 5A). This is also the structure of the lower fertile glumes associated with the florets that are functionally male. The glume to which the proximal portion of the suprafloral axis becomes adnate, differs in that after abscission an arch-shaped cavity is present. This cavity breaks the continuity of the

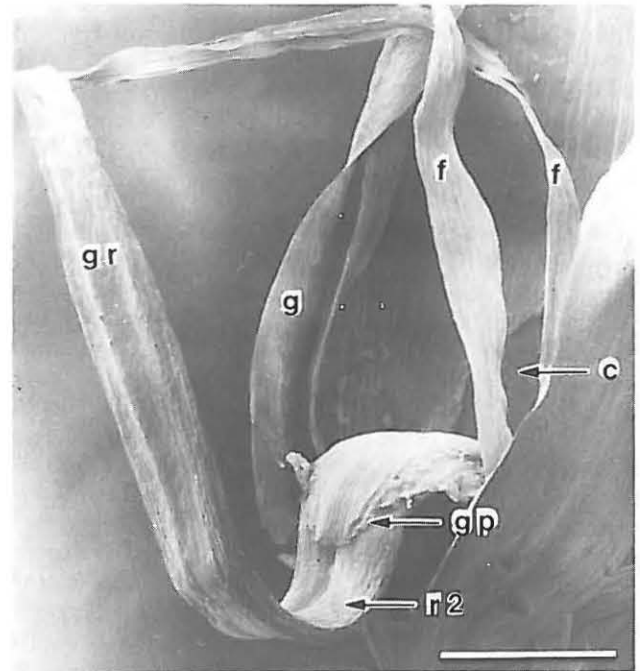


Figure 4 *Epischoenus gracilis*. Spikelet (distal portion only) dissected to show curling of cartilaginous, dry suprafloral axis. c, Arch-shaped cavity in glume torn away by contracting axis; f, filament; g, glume; gp, margin of glume tissue persistent on axis; gr, vestigial glume terminating axis; r2, suprafloral axis above proximal thickened portion. Levyns 9339. Scale bar: 0.5 mm.

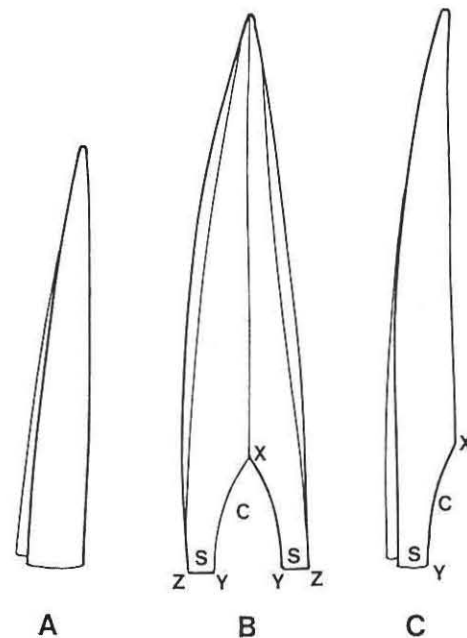


Figure 5 *Epischoenus*. Glumes, diagrammatic. A. Proximal sterile (profile). B. Distal fertile (adaxial view). C. Distal fertile (profile). c, Arch-shaped cavity; s, lateral strip; lines Y-X-Y and X-X, margin of arch-shaped cavity; Z-Z, line of base.

basal glume tissue leaving two narrow lateral strips. These strips are all that remain of the two flanks (Figure 5B). Clarke (1909, Table 88, Figures 5–7) illustrated this arch-shaped cavity for the fertile glume of *Epischoenus quadrangularis*.

Relationship to *Schoenus*

Spikelet structure in *Schoenus* differs from that of *Epischoenus* in that the number of bisexual florets that mature fruit often, but not always, exceeds one. The first-formed (most proximal) of these florets may set fruit, followed sequentially by other fruit-setting florets, so only the most distal one or two, or none, may be functionally male. In *Epischoenus* the maturing bisexual floret is distal to a variable number of potentially bisexual florets that either function as male only, or remain rudimentary and are sterile. Bruhl (1992), in a recent assessment of *Schoenus*, reported spikelets as consisting of 1–12 small sterile glumes followed by 1–6 that are larger and fertile and associated with 1–6 bisexual florets of which only the distal 0–2 may be functionally male. Glume arrangement is generally described as distichous (Kern 1974: 673), but in the five species we have examined there is some evidence of a slight twisting of the spikelet axis through its length, as is present in *Epischoenus*. This can be difficult to assess. In the history of the two genera, attention has focused on the spikelet rachilla which in *Schoenus* is strikingly anfractuose between and adjacent to the maturing bisexual florets. In *Epischoenus*, in contrast, it is only the suprafloral portion adjacent to the solitary bisexual floret that lengthens, thickens and curves. Mature spikelets of *Schoenus* (Figures 6B, 6D), because of the growth and curvature of the rachilla between and adjacent to the fertile bisexual florets, may appear to differ from mature spikelets of *Epischoenus* (Figures 6A, 6C). The basic pattern of spikelet morphology is, however, the same in both genera.

Discussion

Difficulties of interpretation of spikelet structure in *Schoenus* and *Epischoenus* are basically the same and hinge upon several features that are difficult to observe.

- (i) Internodes of the rachilla may be so short that the glumes appear to arise from the same level. The only accurate way to determine their sequence is to follow their enwrapping. The outer glume must arise from below the inner (Eiten 1976; 81).
- (ii) The stage at which adnation of the adpressed, proximal portion of the rachilla to its associated glume commences is not easily assessed and is variable. We believe this is linked to its elongation, thickening and curvature, all of which appear to depend upon development of the ovary of the bisexual floret. What this specifically provides is not understood. We speculate it may be a chemical released, perhaps after fertilization, that stimulates growth of that portion of the rachilla adjacent to it, causing its adnation to the glume. It seems likely this adnation results from pressure that causes adhesion of adjacent tissue layers, but this is speculative and has not been determined. It is unlikely that anatomical investigation will provide proof of the presence of glume tissue abaxial to the elongated rachilla, because of the extreme reduction and specialization that has taken place. We have not undertaken examination. It should be attempted.
- (iii) We believe it is only adnated glumes that abscise with an arch-shaped cavity between two elongated strips of tissue (Figures 5B, 5C, 6C, 6D). Our interpretation of Figure 4 is that with drying of the rachilla following fruit maturation there is tearing away from the main body of the glume, of the portion that was adnate to the rachilla, causing the arch-shaped hole and leaving the two lateral strips attached to the

node from which the glume developed. Later, abscission of the whole rachilla takes place.

Careful observation of these problematical features in young and older spikelets of five species of *Schoenus* and in all described species of *Epischoenus*, has led to certain conclusions that we believe more effectively explain spikelet construction in *Schoenus* and *Epischoenus* than was possible earlier.

Conclusions and Summary

By following the enwrapping of the fertile glumes, we conclude, as did Levyns (1959: 72), that florets in *Epischoenus* are non-axillary. The same floret positioning occurs in *Schoenus*.

We did not find, however, that each bisexual floret fully terminates growth of the main spikelet axis, as would be if the spikelet construction were cymose. This deduction is based on the formation of the rachilla *below* the potentially maturing bisexual floret in *Epischoenus*. In this zone the potentially bisexual florets that become functionally male or remain rudimentary, are developed from successive nodes. Here the internodes are short and straight-sided with very slightly increased development immediately under the floret only, or not at all (Figures 6A, 6C). In *Schoenus* where each bisexual floret is potentially capable of maturing a fruit, usually several internodes are elongate, thickened and curved (Figures 6B, 6D). If the bisexual floret does indeed terminate the spikelet rachilla, why should the functionally male florets in *Epischoenus* appear so markedly laterally placed in relation to the rachilla, and why should the rachilla appear to continue growth directly, without evidence of growth of a branch of succeeding order? There is no trace of a prophyll, which is said to be indicative of a branch of succeeding order. But in so reduced a structure as a spikelet, it is not surprising if no prophyll develops. We can only conclude that the spikelet axis is not sympodial, but monopodial. However, this deduction remains speculative and unproven.

We cannot accept the interpretation of spikelet construction which incorporates a monopodial axis, as put forward by Haines (1967: 71, Figure 6N) for *Schoenus nigricans*, because our observations of glume enwrapping and attachment provide evidence that the glume that is associated with a maturing ovary becomes adnate to an elongated, thickened curved section of the rachilla and is holed by this rachilla as it curls with drying-out at maturity of the fruit or immediately after. This tearing results in glume tissue being visible as an irregular margin on the dry rachilla (Figure 4). The narrow strips of the glume flanks that remain (Figure 5B) are often irregular, as the line of tearing is usually not smooth. They, and the irregular 'frill' of glume tissue that remains along the edges of the thickened portion of the rachilla, provide the reasoning whereby the glumes in *Schoenus* have been described as 'decurrent on the rachilla' (Kern 1974: 673) or the rachilla 'winged adjacent to flowers' (Bruhl 1992). This interpretation has been strengthened by what we believe to be the incorrect assumption that the line of glume attachment is at the point where adnation of the rachilla ceases, running therefrom down the line of attachment to the node from which the glume actually arises (Figures 5B & 5C, line X–Y). This line, instead of the line of actual attachment which is the almost horizontal, slightly curved base (Figure 5B, line Z–Z), shows the glume to be initially the same in form as are the sterile proximal glumes (Figure 5A). In addition, by unwrapping of the glumes and careful observation of their lines of attachment, we found, for example, that in Figure 6D node 3 carries glume 3 (sterile); node 4, glume 4 (fertile); and node 5, glume 5 (fertile). This does not support the interpretation given by Haines (1967: 71, Figure 6N) for *Schoenus nigricans*. According to his reasoning, glume 3 would axillate floret 4; glume 4, floret 5; and so on up the length of the spikelet axis.

We conclude that for perfect development of the proximal zone of the suprafloral rachilla in *Epischoenus* (excepting *E. cernuus*) and for comparable growth of its internodes in *Schoenus*, there must have been enlargement to a critical size of the ovary

of the associated floret. (Note that *E. cernuus* is atypical of other species of the genus in some vegetative features and in its hairy achene.) Fruit set is not prolific in *Epischoenus* and this appears to be the case in *Schoenus* also, but this requires confirmation

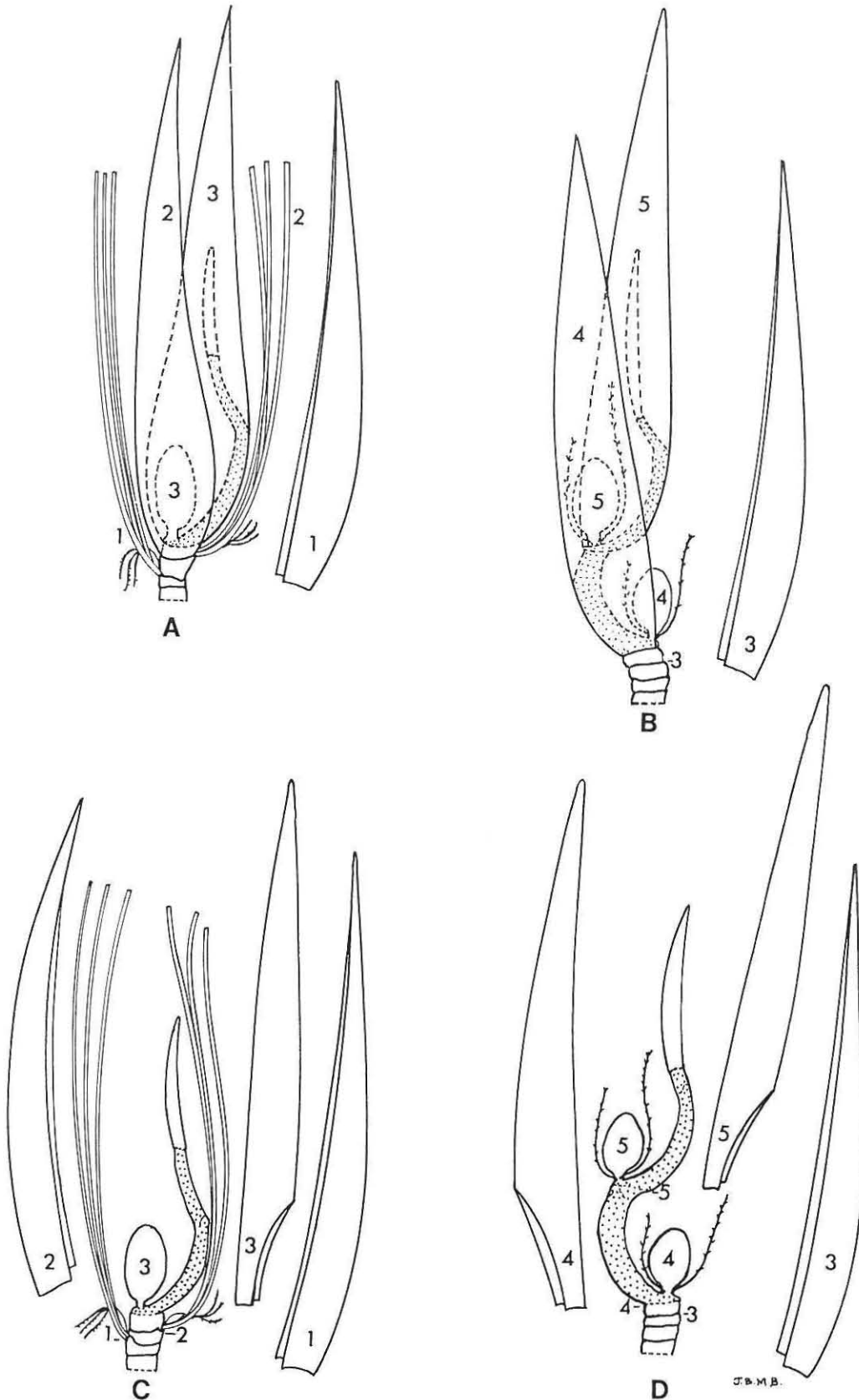


Figure 6 A, C. *Epischoenus gracilis*, Levyns 9339. B, D. *Schoenus ferrugineus*, van Wessem 129. Spikelets (distal portions only): A,B, glumes mostly intact; C,D, glumes mostly removed and placed to show relationship with spikelet axis. Numerals relate glumes and florets.

from a more extensive study of species. The herbarium specimens of both genera that lack good fruit set, show variability in the rachilla axis from unthickened to partially so and no, or imperfect, adnation of portions of it to the associated glumes. This may explain Levyns's (1959: 78, 79) interpretation of the suprafloral axis as 'shortly adnate to bract' and 'slightly adnate to bract' for *Epischoenus lucidus* and *E. complanatus*, respectively.

In *Schoenus* there are a number of species reported in which the spikelets may vary in the number of flowers produced, one per spikelet being not uncommon (Kern 1974). How such examples may be conclusively distinguished from examples of *Epischoenus* is not known. Comparisons are needed. Certainly, from young stages of floral development alone, elements of the two genera cannot be distinguished.

Glumellae (bristles) are potentially present in both genera. In *Epischoenus* they are usually only rudimentary and may be lacking. In *Schoenus* their development is from completely reduced (lacking) to fully grown and as long as or surpassing the fruit.

Attention is drawn to the presence, in both genera, of two forms of glumes, namely, ones not associated with mature fruits that appear typical of Cyperaceae, and others associated with maturing fruits that are similar except that in the region of the lower mid-vein, there is an arch-shaped cavity. We believe these are fundamentally alike, but owe their difference to adhesion of the area of the arch-shaped cavity to the closely adpressed portion of the rachilla, which, when the rachilla dries, is torn out.

These conclusions emphasize relationship between the two genera and suggest that the endemic African status imposed upon *Epischoenus* by its segregation from *Schoenus* overstates differences between them.

Specimens examined

Epischoenus (BOL)

E. adnatus Levyns

Esterhuysen 12938 TYPE, 15222, 33112; *Levyns* 9642; *Stokoe* (BOL 58473).

E. cernuus Levyns

Esterhuysen 17982; *Levyns* 8873 TYPE.

E. complanatus Levyns

Esterhuysen 8181, 11593, 17776, 26496 TYPE, 27610, 33808.

E. dregeanus (Boeck.) Levyns

Esterhuysen 15213; *Levyns* 8111, 9367.

E. gracilis Levyns

Esterhuysen 7457, 8255, 11812, 12443, 19883, 35321; *Levyns* 7389 TYPE, 9339.

E. lucidus (C.B. Clarke) Levyns

Levyns 8142 TYPE, 9362A.

E. quadrangularis (Boeck.) Levyns

Esterhuysen 6861, 27538.

E. villosus Levyns

Esterhuysen 16927; *Levyns* 8884.

Schoenus (NU)

S. apogon Roem. & Schult.

R.O. Gardner 924

S. brevifolius R. Br.

R.O. Gardner 920

S. ferrugineus L.

R. van Wessem 129, *H. Fritze* s.n.

S. melanostachys R. Br.

E.F. Constable 5117

S. nigricans L.

J.B. Phipps 1388, *G. Potts* 6386, *R.G. Strey* 7739, *Montford & Turrill* 552, 2592, *Hekking* 191, *Hubbard* 11024, *Ward* 8259, *H. Fritze* s.n.

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