

Studies in Cyperaceae in southern Africa. 28: Spikelet morphology in *Rhynchospora gracillima* ssp. *subquadrata*

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An account of spikelet structure of young, mature and old spikelets of *Rhynchospora gracillima* Thwaites subsp. *subquadrata* (Cherm.) J. Raynal, which has an anfractuose rachilla, is given. Electron micrographs of spikelets and drawings from specimens collected in Zimbabwe are used in illustration. Spikelet construction is discussed with reference to positions occupied by florets and glumes (floral scales) and monopodial and sympodial branching systems. It is concluded: (1) that the florets are not axillary to the glumes; (2) that an interpretation of sympodial construction for the spikelet is not acceptable; (3) that a more convincing explanation should be sought.

Die aartjie-samestelling van jong, volwasse en ou aartjies van *Rhynchospora gracillima* Thwaites subsp. *subquadrata* (Cherm.) J. Raynal, wat 'n gegolfde ragilla besit, word beskryf. Illustrasies maak gebruik van elektronmikroskoopfoto's van aartjies en tekeninge van eksemplare wat in Zimbabwe versamel is. Aartjie samestelling word bespreek met betrekking tot die posisies wat blommeltjies en graandoppies (blomskubbe) beset, sowel as monopodiale en simpodiale vertakkingstelsels. Die slotsom word bereik: (1) dat die blommeltjies nie okselstandig tot die graandoppies is nie; (2) dat die interpretasie van simpodiale samestelling nie aanvaarbaar is vir die aartjies nie; (3) dat 'n meer oortuigende verklaring gesoek moet word.

Keywords: Cyperaceae; *Rhynchospora gracillima*; spikelet structure.

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Introduction

Rhynchospora gracillima (Thwaites) [Type: *Thwaites C.P. 3818* (K) according to Koyama 1985: 340] was established in 1864 for an entity from Ceylon (Sri Lanka). *R. subquadrata* Chermeson [Syntypes: *Perrier de la Bâthie 920*; *Viguiet & Humbert 397* (P) as designated by Chermeson 1922] was described to accommodate plants from Madagascar that differed from *R. gracillima* in features of the inflorescence and floral organs. Robinson (1961: 40) reported *R. subquadrata* for Africa and distinguished this species from *R. gracillima* on the number of transverse ridges to the face of the achene. He remarked upon '... the markedly sinuous or serpentine rachilla [rachilla] which after maturity turns black and is about the only conspicuous feature of the plant.' Earlier Kükenthal (1951: 274) had mentioned the unusual zig-zag axis of the spikelet ('*rhachilla anfractuosa*') in *R. subquadrata*, but Chermeson's (1922: 720/721) protologue entirely omitted this feature, as did his comparison of this species with *R. gracillima*. Raynal (1967: 321) reduced *R. subquadrata* to a subspecies under *R. gracillima* on the basis of the achene sculpturing reported by Robinson (1961: 40).

There have been differences of opinion in the interpretation of spikelet structure in *Rhynchospora* and its allies. Some authorities from Pax (1886, 1887) to Schultze-Motel (1964) accepted the branching as cymose and the rachilla as sympodial, while others, especially later workers (Koyama 1961; Haines 1967; Eiten 1976), believed it to be racemose and the rachilla monopodial.

These differences have not yet been fully and satisfactorily resolved. Those who envisage the floret as terminating a branch of the rachilla (cymose branching of the spikelet), interpret the next rachilla internode as a branch of higher order. This branch is again terminated by a floret. According to this pattern, the florets are terminal, that is, not axillary to a glume. It is the rachilla of higher order that is axillary to the associated glume (Figure 1A).

In spikelets that have been interpreted as sympodial, the basal glumes are often sterile, and the internodes not elongated. Such sterility of the lower glumes is evident in *Rhynchospora gracillima* ssp. *subquadrata*.

The alternative interpretation, according to which the floret does not terminate the rachilla (racemose branching of the spikelet), recognizes the rachilla as continuing growth to produce further glumes and florets. Each floret is situated in the axil of the subtending glume, that is, between the glume and the rachilla

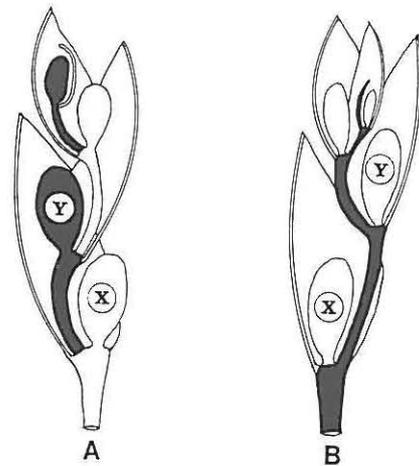


Figure 1 Branching patterns of spikelets. A, according to sympodial hypothesis: florets X, Y and upwards are terminal and each limits a successive portion of spikelet rachilla; each portion is interpreted as a branch of higher order (uncoloured and blackened alternately for clarity). B, according to monopodial hypothesis: florets X, Y and upwards are axillary; the axis is interpreted as being of continuous growth throughout (blackened).

(Figure 1B). Eiten (1976: 82) accepted the spikelet in *Rhynchospora* as a 'racemously branched structure consisting of an axis (rachilla) of potentially indefinite growth bearing lateral, true flowers. Each flower arises in the axil of a glume (scale like bract) which covers it'.

Haines (1967: 62) stated 'The peculiarity of the tribe [Rhynchosporae] lies in the enwrapping glumes, not in a cymose structure'.

Neither Haines (1967), nor Eiten (1976), included *Rhynchospora gracillima* among the taxa they discussed. This species, although widely distributed through the Old World, is not well studied. Because of its anfractuose rachilla, it is worthy of detailed investigation.

This article provides an account of young, mature and old stages of spikelet morphology, excluding anatomy, in *R. gracillima* ssp. *subquadrata*. Electron scanning of portions of the spikelet axis, with achenes attached, provides improved understanding of structure in this species of a genus that, in aspects of plant size and inflorescence form, is heterogeneous.

Material and Methods

Plants of ssp. *subquadrata* are infrequent, slender, delicate elements of moist grassland, and therefore not easy to locate. A gathering in eastern Zimbabwe in 1991 (*Browning 356*, NU) provided a range from young, to mature, to old spikelets. Examination of the rachilla was carried out by careful removal of glumes from the spikelet base upwards, after regeneration by hydration. Representative portions were mounted on stubs using double-sided aluminium foil on double-sided cello tape, sputter coated with gold-palladium using a Polaron E 5100 sputter coater and viewed under an Hitachi S 570 Scanning Electron Microscope. Comparisons were made against specimens from Zambia [*EA. Robinson 223, 1754, 2396, 3318, 3408* (all NU), cited E.A. Robinson (1960/61: 410)].

Observations

Reliable descriptions applicable to the typical subspecies (Kern 1974: 721) and to ssp. *subquadrata* (Robinson 1961: 40, as *R. subquadrata*; Haines & Lye 1983: 315) are available, and as this article deals only with spikelets, formal description of whole plants has not been given. Some additional information relating to floral organs and derived exclusively from the *Browning* and *Robinson* specimens cited earlier, follows.

Spikelets

The central and lateral spikelets in each anthelate group of the narrowly branching, paniculate inflorescence are solitary on slender, short (central) or longer (lateral) peduncles. Each spikelet is distant from the prophyll and subtending bract of the rachilla axis (spikelet type 1 of Eiten 1976: 86); therefore from the base of the spikelet upwards, the spirodistichous, reduced and flattened leaf-like overlapping appendages are glumes (floral scales). Table 1 gives a summary of general spikelet structure (Figure 2) and the variability encountered in these spikelets. It should be noted that 50% of the spikelets we dissected had four sterile glumes (represented in Figure 2); while 50% had five sterile glumes (represented in Figure 3). We were not able to find a correlation between the number of sterile glumes and the positioning of the spikelet as central or lateral in an inflorescence. When the glumes are in position, the rachilla is not visible. Each fertile glume partially enwraps the one above it. This enwrapping is more complete in the immature apical zone.

Young stage of development (Figure 2B; four sterile glumes)

Removal of glumes at this stage of spikelet development shows the rachilla internodes to be short and straight, with the internode

Table 1 *Rhynchospora gracillima* ssp. *subquadrata*. Summary of general spikelet structure including variability encountered in central and lateral spikelets of *Browning 356* (NU)

Glumes	Total no. per spikelet	Lowest 1-3	Next 4-5	Next 6-9	Terminal 10-11
Number fertility	7-8(-11) usually ca. 5 maturing achenes	All sterile (empty)	No. 4 sterile; no. 5 sterile or fertile	All potentially fertile, usually maturing achenes	All potentially fertile, often not developing fully
Length		2.0-2.5	3.2-3.7	3.2-3.7	1.0-2.5
Width		0.5-1.5	1.8-3.5	1.8-3.5	Not measured, tightly rolled
Rachilla spiral throughout		Narrow, straight, barely twisted	Well developed, markedly twisted, enlarged, curved, flattened to accommodate achenes		Poorly developed, sometimes tabescent
Stamens	2 per floret				
Style branches	2 per floret, well developed				

between glumes 4 and 5 (4/5) only slightly longer than those below. Floret X (arising from node 5) is at, or just past, anthesis with filaments elongate and the ovary commencing enlargement. The surface of node 5 is almost straight with a slight depression under the floret. Internode 5/6 is longest, having grown up behind and around floret X. Node 6 carries the already well-initiated, but still immature, floret Y. Node 7 carries glume 7 that totally envelops the as yet meristematic, terminal section of the rachilla. Note: In Figure 2B, as in others of this article, the continuous black line that indicates the abscission line of the glume over-emphasizes this feature at the expense of the continuity of the rachilla.

Mature spikelets (Figures 2C, D, E & 3)

Removal of glumes at this later stage shows the rachilla internodes between glumes 1 and 4 still short and straight. The achene of floret X is mature and is about to abscise from the slightly raised cushion of tissue on which it developed, or it has abscised during glume removal. This surface of node 5, now marked as an abscission line by the removal of glume 5, is no longer straight, but sloping. This alteration has come about by upgrowth of part of internode 4/5 behind and around the developing achene of floret X. The inner surface of this internode, where it has contacted the enlarging achene, is flat, smooth and polished. Glume 5 has not abscised along its complete line of nodal attachment. Behind the rachilla, the glume breaks away cleanly along this line, but adjacent to the achene, two lateral, short flaps of glume tissue persist (Figure 2D, arrows).

The remainder of the rachilla shows successive development of flattened, twisted internodes, longer and more pronouncedly curved than internode 4/5. The curves accommodate the florets, not all of which may fully mature a fruit. The uppermost terminal portion of the rachilla is still meristematic, occasionally tabescent (Figure 2E 10, 11). The spiral twisting of the fertile portion

of the rachilla causes the achenes to lie in different longitudinal planes (Figures 2C & 3).

Old spikelets (Figure 3 and inset)

Spikelet maturation proceeds acropetally, the lower glumes and achenes falling while the more distal ones are immature. The

meristematic apex remains intact with a glume, usually number 9 or 10, surrounding an immature bisexual floret that does not set fruit, and a rudimentary uppermost glume. At this stage the mostly naked, usually blackened rachilla is still attached to the inflorescence. Its zig-zag, spirally twisted, somewhat shrivelled structure is then easily discernible.

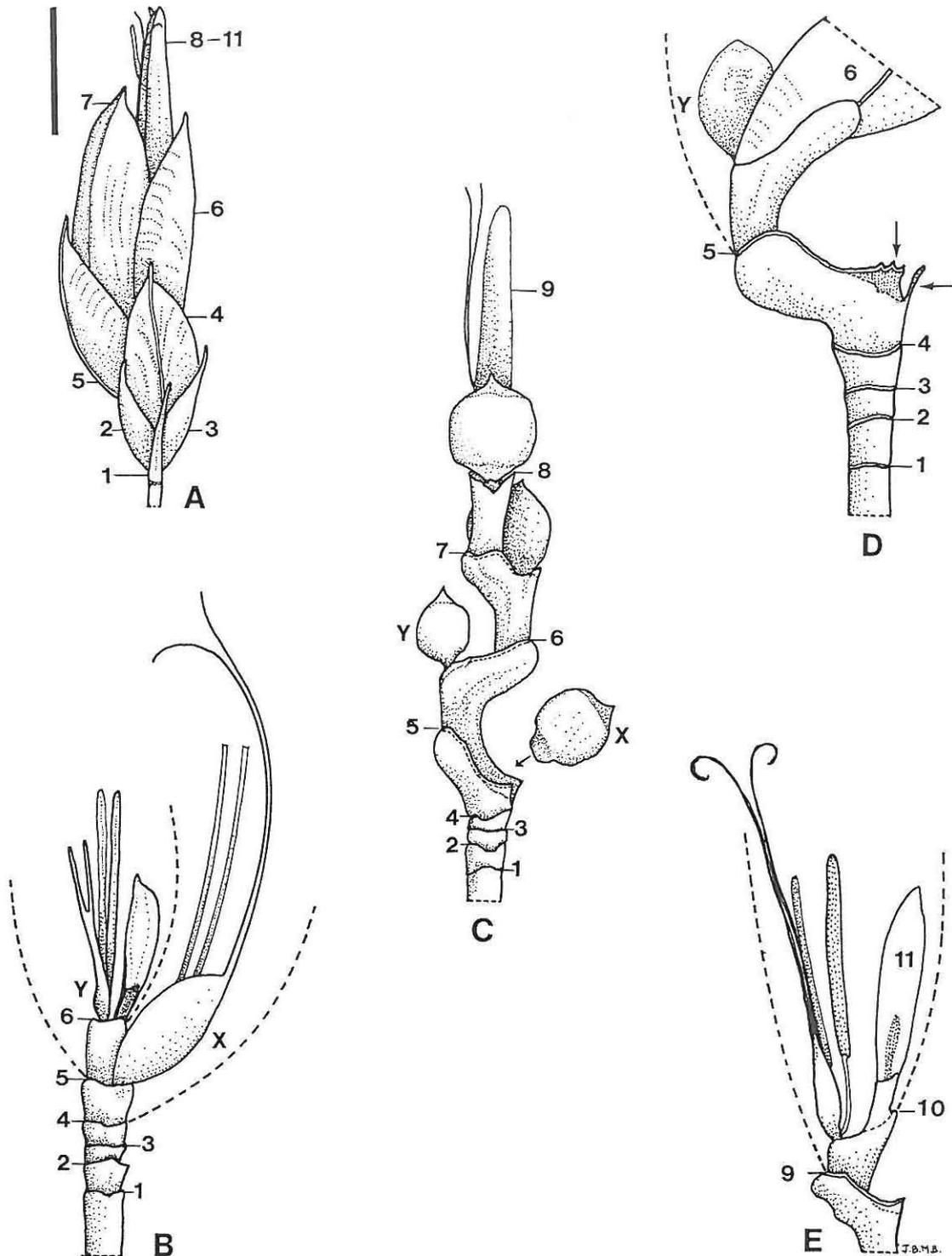


Figure 2 *Rhynchospora gracillima* subsp. *subquadrata*, Browning 356 (NU). A, entire spikelet, with lowest four glumes sterile; B, young spikelet with all except terminal glume (7) removed, showing two lowest florets (X, Y); note length and shape of rachilla internodes; C, rachilla of mature spikelet with terminal glume group posterior to uppermost fruit; note twisting of rachilla; D, detail of rachilla after abscission of lowest fertile glume and lowest achene; note fragments of glume persistent on rachilla in front of position of attachment of fruit (arrows). Glume 6 still attached; E, detail of apex of spikelet with glume 10 removed. In B, D, E positions from which some glumes arose are indicated by broken lines. Scale bar for A = 2 mm.

This study has revealed the following significant features of spikelet construction in *R. gracillima* ssp. *subquadrata*.

- (1) The proximal portion of the rachilla comprises short internodes that are straight, with only slight twisting. The nodes carry sterile glumes, four or five in number that are slightly spiralled.
- (2) The distal portion of the rachilla is the fertile zone, except for the immature apical zone that seldom sets fruit and may

become tabescent. Rachilla internodes in the fertile zone are enlarged, flattened, curved and internally smooth and polished. There is spiral twisting, so that the glumes and florets developed upwards on successive nodes lie in different longitudinal planes.

- (3) Enwrapment of a matured achene by the glume which developed from the same node is not complete, in fact it is scarcely partial. This may be seen quite clearly in Figure 3, where the upper achene, developed at node 7, is only slightly en-

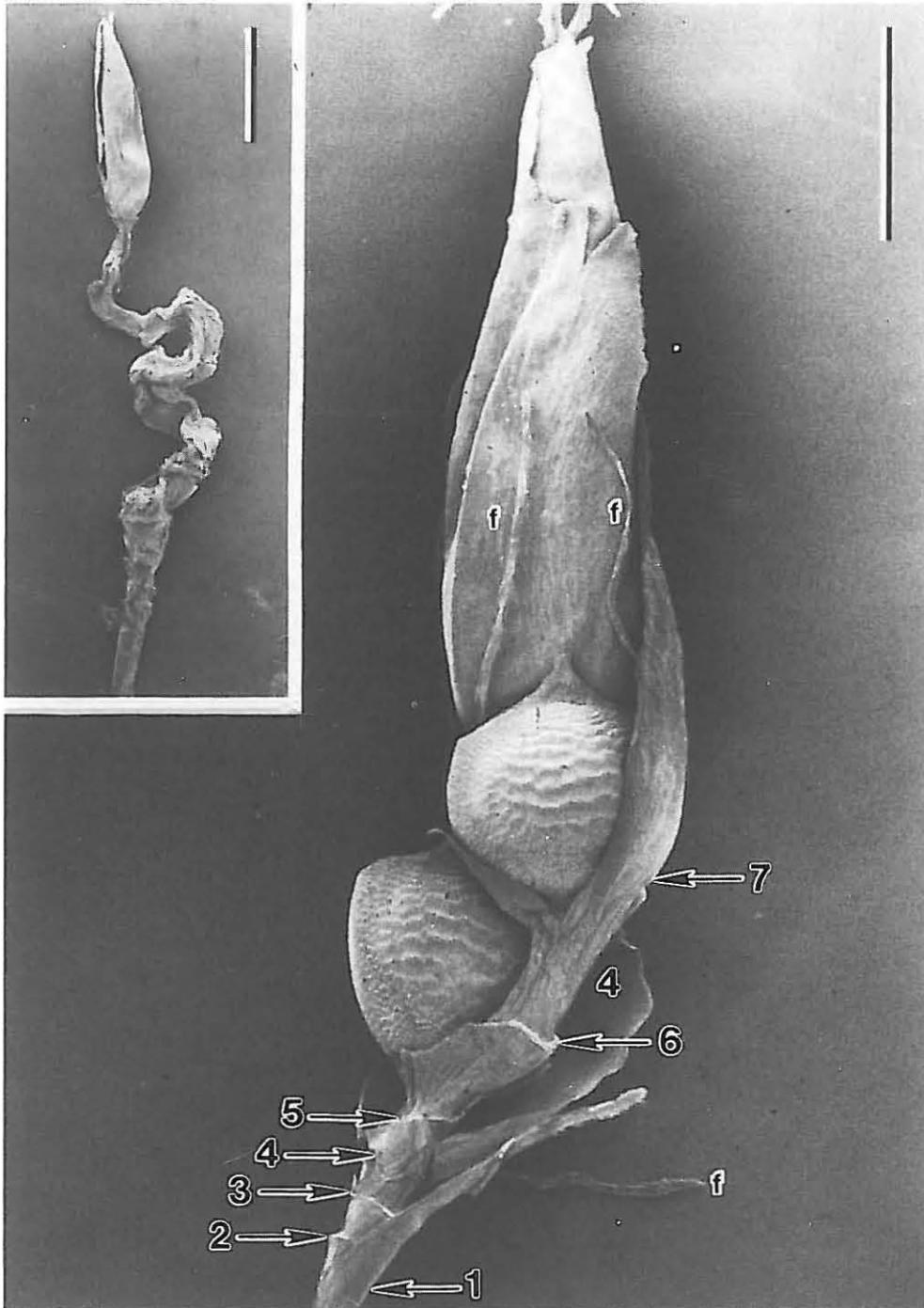


Figure 3 *Rhynchospora gracillima* subsp. *subquadrata*. Structure of mature and (inset) old spikelets revealed by SEM, *Browning 356* (NU). Spikelet with five sterile glumes. Glume 1 intact; 2 and 3 removed; 4 in position but partially detached; 5 and 6 removed. Note sloping line of detachment of 6 and its situation right of rachilla and lower achene. Glume 7 in position behind rachilla and upper achene. Note two filaments of upper floret and detached filament of lower floret (f). Apical portion of spikelet consists of glumes 8, 9, 10, 11, enwrapping one another. Inset: Old spikelet with glumes and florets abscised naturally, except for terminal tip where glumes have persisted. Note. Straight basal, sterile section of rachilla, in contrast to the spirally twisted, elongated fertile section. Scale bar = 1 mm.

wrapped by the glume arising from node 7. In the same way, the relationship between the lower achene and glume 6 (removed) may be visualized. The midline of glume 6 lies at the point of arrow 6, so it is this glume and not glume 7 that enwraps the upper achene, but the enwrapment is outside glume 7.

- (4) From Figure 3 (lower achene and glume 6) it may be seen that the matured achene, and therefore the floret, is not axillary to the glume developed from the same node. The arrangement is that the floret and glume developed from a node are separated from one another by the rachilla internode which lengthens, curves and flattens to accommodate the increasing bulk of the swelling ovary. If, in Figure 3, it is argued that the lower floret does not arise from the node producing glume 6, but from the node below, the lower floret would then be axillary to glume 5. In accepting this, the upper floret should be axillary to glume 6; but this upper achene definitely cannot have been developed from the node from which glume 6 arose, because it is separated from that node by internode 6/7.
- (5) From the young spikelet with its glumes removed (Figure 2B), it is seen that a floret occupies only a portion of a rachilla node; it is accompanied by rachilla tissue (the next internode above). The fertile internode, at first (for example Figure 2B 5/6), is short and straight, no different from any of the sterile proximal internodes. It is with enlargement of the developing ovary that the fertile internode enlarges, changes shape, twists and modifies to accommodate the greatly increased volume of the matured ovary (compare Figure 2B 5/6 & C 5/6).
- (6) It is not proven whether the next-higher internode that continues growth of the rachilla is a direct continuation (a monopodial axis), or whether it is developed from a separate bud and therefore is a branch of higher order (a sympodial axis). No prophyll is detectable to suggest branching, but this may be lacking because of the extreme reduction and specialization of the spikelet. The fertile rachilla internode enlarges unevenly, flattens and twists during development of the floret, which indicates that the floret does not fully terminate the internode. If there is not full termination, then why should a separate bud be developed to continue growth of the rachilla? Surely it is probable that the axis is monopodial, continuing growth in a sinuous, anfractuous manner where space permits, that is, between florets and successively enwrapping glumes.

Discussion

The major points already stated require testing against concepts expressed by other investigators, who have examined species that show comparable spikelet organization. We believe the following to be particularly relevant.

Haines (1967: 61) discussed the structure of a terminal spikelet of *Rhynchospora corymbosa* (L.) Britton. Of his illustrations (Figure 5G, H) he writes:

'A terminal spikelet... has three empty glumes 1, 2 and 3 at the base and removal of glume 4 ... does not expose a flower. But the next glume 5 which hides the lowest flower from view does not subtend it, for the glume and flower lie on opposite sides of the rachilla. In fact this flower is subtended by 4, but is closely enwrapped by the overlapping membranous margins of 5'.

If the lowest flower is subtended by glume 4, as is said, then glume 5 lies completely within glume 4 and both surround the lowest floret (Figure 5J). This is evident in Haines's ground plan of the spikelet and in his Figure 5H, where no part of the lowest floret is visible. This is in accordance with Haines's statement

(1967: 62) 'The peculiarity of the tribe [Rhynchosporae] lies in the enwrapping glumes, not in a cymose structure'. But it means that the lowest floret arises from the node above that which gives rise to glume 4, because it is completely enveloped by glume 5 (Figure 5G, H, I, J), namely, it must arise from the same node from which glume 5 developed, therefore it cannot be subtended (axillated) by glume 4, but merely enwrapped by it, outside of glume 5.

Eiten (1976: 110) concluded with a list of problems still unresolved. The last of these related to spikelet rachillas. She wrote 'Are the apparent rachillas (lacking recognizable prophylls along their length) monopodial (true rachillas) or sympodial (pseudorachillas)?' This was after intensive study of species in which a pistillate floret appeared to terminate the spikelet rachilla (for example *Lagenocarpus rigidus* Nees). She drew the conclusion that '...an apparent terminal position of a flower in the Cyperaceae is no indication that it really is so; rather, it may well be pseudoterminal, that is lateral'. And after thorough examination of species of *Scleria*, she stated some of her observations 'furnish direct evidence from the genus *Scleria* itself that the pistil in a bisexual spikelet-like structure is lateral, that is, that there is only one axis and so the structure is a true spikelet'. She also stated (Eiten 1976: 98) 'The bisexual spikelet in *Scleria* is similar in its branching pattern to that of *Rhynchospora*'. It is certain that Eiten accepted some species at least, of both *Scleria* and *Rhynchospora*, as possessing spikelets with a monopodial axis, that is, a racemose construction. However, it cannot be assumed that comparable structural features in different genera have been arrived at by identical routes.

The points that are significant to us and which we wish to stress are:

- (1) We, and Haines (1967), independently observed the positioning of the florets in spikelets of *Rhynchospora*. Haines was concerned with *R. corymbosa* in which there is no elongation of those internodes associated with fertile florets; we studied *R. gracillima* ssp. *subquadrata* in which elongation of such internodes does take place. These independent observations of basic spikelet construction are not discrepant (compare Figure 4A & B). It is the interpretation of the structures represented that is different. We find it difficult to accept that a floret that is 'closely enwrapped by the overlapping membranous margins' (Haines 1967: 61) of a superior glume can, in fact, arise from the node from which the immediately inferior glume developed. We cannot accept the sympodial (cymose) interpretation of spikelet construction, as this has never been proven, and we found no evidence to suggest each floret completely terminates the axis upon which it is borne so that no meristematic tissue of that axis remains to continue growth. Therefore we have looked for alternative explanations.
- (2) From Eiten's (1976) study there appears to be no hindrance to the concept that an apparently terminal floret may be in fact lateral. Likewise, there appears to be no hindrance to an apparently terminal floret being located in a true spikelet, that is, a racemose spikelet in which the rachilla axis is monopodial (for example some *Scleria* spp.).
- (3) If Figure 1A and B are compared, the fundamental difference between them lies in the positioning of the rachilla internodes in relation to glumes and florets developed from the nodes. In Figure 1A, for each node and the internode above, the internode (rachilla) is positioned between the glume and floret developed from the node below; that is, the floret is non-axillary and is not subtended (axillated) by the glume developed from the same node. In Figure 1B, this is not so, the floret is clearly axillary to the glume and it is the rachilla that is in a non-axillary position.

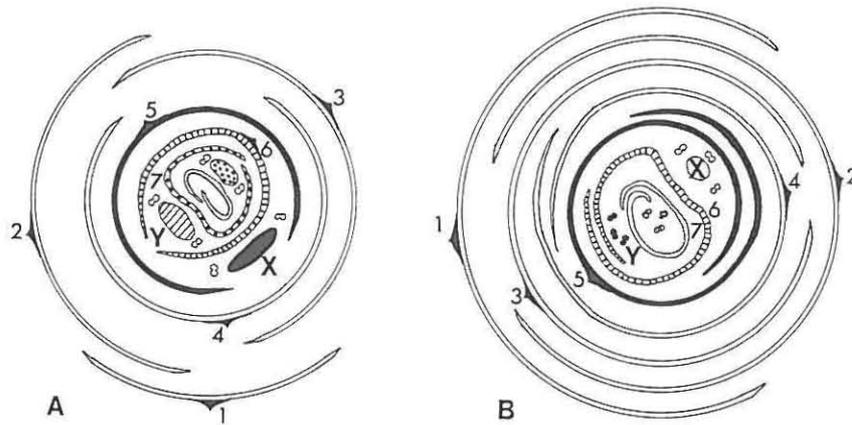


Figure 4 Diagrammatic ground plans of spikelets. A, *Rhynchospora gracillima* ssp. *subquadrata*: lowermost (outermost in diagram) four glumes are sterile; remainder fertile, except for uppermost portion, which may become tabescent (only enveloping glume shown, uncoloured). B, *Rhynchospora corymbosa*, as illustrated by Haines 1967, Figure 5J, except that shading has been introduced and bristles omitted. Note: in A and B the shading indicates the interpretation applied; therefore in A, outer four glumes (sterile) are uncoloured, blackened glume and floret X arise from same node, the floret being non-axillary to glume, and successively upward for striped and dotted glumes and florets; in B, following Haines, lowest three sterile glumes uncoloured, fourth said to subtend (axillate) floret X (also uncoloured), fifth said to subtend floret Y which is usually reduced to male condition, and so upwards for striped glume which is said to subtend male floret which lies enwrapped within glume 7.

Conclusion

If the man-made, and so far unproven, concept of sympodality is set aside, then the fundamental difference between the spikelet structures depicted in Figure 1A and B may be explained very simply by suggesting that with initiation of a floret and glume from a node, the meristematic tissue remaining is activated and grows where space permits. This growth may take place so that the floret lies in an axillary position in relation to the glume, or it may be between floret and glume, so that the rachilla itself is axillary to the glume. We suggest that further detailed study of spikelet construction should be undertaken, making use of equipment and techniques not available to many workers in Cyperaceae who observed the non-axillary positioning of florets and attempted an explanation. In other words, further species of *Rhynchospora* and species of other genera exhibiting non-axillary florets, according to the findings of earlier workers, should be critically re-examined from young to mature stages of growth and then reassessed structurally.

Acknowledgements

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