FIMBRISTYLIS AND BULBOSTYLIS: GENERIC LIMITS AS SEEN BY A STUDENT OF SOUTHERN AFRICAN SPECIES

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SUMMARY

A brief history of the genera *Fimbristylis* VAHL and *Bulbostylis* C. B. CL. is given. Fourteen species of *Fimbristylis* and seventeen species of *Bulbostylis* are listed for southern Africa together with more important synonyms, known world distribution and notes on their habitat preferences and growth forms. The main variation patterns in morphological and anatomical form manifested among these species are described. It is suggested that the species represent (in general) an adaptive sequence from a tropical, fairly diverse, waterloving stock to a more temperate, more uniform, dryland element developed in response to more extreme environments in more temperate latitudes. The suggestion is made that if *B. schlechteri* is excepted until better known, the southern African species fall into three natural groups within this adaptive sequence, which can be related to the genera *Fimbristylis*, *Abildgaardia* and *Bulbostylis* respectively.

In 1805, MARTIN VAHL established the genus *Fimbristylis* to accommodate Cyperaceae with spirally imbricate glumes, each glume subtending a bisexual floret with a biconvex or trigonous achene carrying a basally expanded, usually fimbriate margined, two-or three- (since *F. miliacea* (L.) VAHL was included among the species listed) branched style. He also erected, at the same time, *Abildgaardia,* which he distinguished from *Fimbristylis* chiefly by the subdistichous basal glumes and the trigonous style base said to be persistent on the achene.

Within the next thirty years a number of other genera bearing close relationship to VAHL's taxa were also established. Among these were ROBERT BROWN's *Isolepis,* characterized in part by solitary spikelets; Lestiboudois' *Trichelostylis* with spirally imbricated glumes, trigonous achenes and three-branched styles, and BERTOLONI's *Pogonostylis* in which long hairs pendant from the style-bases overhung the achenes.

KUNTH, in 1837, recognized three sections within *Isolepis,* one of which be believed formed a link between this genus and *Fimbristylis.* For this section he suggested the name *Bulbostylis.* He did not form combinations under *Bulbostylis,* but despite this, the name was conserved from KUNTH (1837) in preference to the earlier *Stenophyllus* RAFIN. The authority and date for

the conserved name, *Bulbostylis*, should therefore be C. B. CLARKE (1893) as HOOPER (1968) has pointed out in her proposal to correct the entry for the conserved name in ICBN (1961: 236). KUNTH's section within *Isolepis* comprised sedges with styles that, basally, were bulbous thickened and, apically, developed two or three branches. The style base persisted as a tubercle on the achene. CLARKE (1893) in first describing *Bulbostylis* included therein annuals with slender stems leafy only at the base, the leaves very narrow with generally finely hairy sheaths: stamens 3—1, usually 2, the anthers without crests: style bases bulbiform and very small. Of these genera, only *Fimbristylis* and *Bulbostylis*, with a majority of *Isolepis* species incorporated in *Scirpus*, are maintained by many workers today.

Limits of *Fimbristylis* have been widened to include *Abildgaardia*, *Pogonostylis*, *Trichelostylis*, part of *Isolepis*, as well as other small genera, which now mostly form sections within the taxon. Limits of *Bulbostylis* have also been widened, but not as extensively as in *Fimbristylis*, so that there are now included here, perennials as well as annuals, stamens with and without crested anthers, two- or three-branched styles and lenticular as well as trigonous achenes. More than eighty species of *Isolepis* have been transferred here, as well as *Oncostylis* NEES.

As *Fimbristylis* and *Bulbostylis* are now understood, the main morphological distinction between them is the duration of the style base upon the achene. In the former, the style base does not generally form a close connection with the apex of the achene, and falls from it with the style (from which it is not differentiated by a clearly defined abscission zone) to leave the apex nude, before the achene is shed from the spikelet. In *Bulbostylis* the style base generally forms a close connection with the apex of the achene, persisting upon it until well after dispersal from the spikelet: the style is deciduous from a clearly defined point of abscission which develops immediately above the style base.

Correlated with this main difference are a plexus of minor features, mostly difficult to formulate individually, that result in a more or less distinctive facies for the majority of species within each genus. Despite a wider range of form in *Fimbristylis*, most members of this genus can usually be distinguished quite readily, often on superficial observation alone, from species of *Bulbostylis*. There exist, however, intermediates, which carry the name of one genus, the while exhibiting characteristics of the other *(F. hispidula : B. pilosa)*. It is not surprising, therefore, to find there are authorities (KOYAMA 1961) who do not distinguish between *Bulbostylis* and *Fimbristylis*, but sink the former in the latter. These authorities have mostly worked on a regional basis and thus limited the combinations made to species represented on a particular continent or within a particular country.

On the other hand, there are those who would maintain narrower generic limits, so that for example, *Abildgaardia*, as well as *Fimbristylis* and *Bulbostylis*, are upheld (ROBYNS and TOURNAY 1955). Again treatments ha-

ve mostly been on a narrow regional basis, so that at present, unfortunately, little uniformity exists for world species.

At its widest delimitation, that is including *Bulbostylis, Fimbristylis* comprises upwards of 350 species that are distributed in tropical and temperate regions of both hemispheres.

This is not the full compass of difficulties in relation to generic delimitation. We are not sure for example, that among these three hundred and fifty species there are not some, at least, that, despite their orthodox style bases, do not relate more closely in general form, to groups of species at present included within other genera of Scirpeae, *Scirpus* L. and *Eleocharis* R. Br. in particular, than they do to species within either *Fimbristylis* or *Bulbostylis. Bulbostylis schlechteri,* among South African species, is such an example, for it could be related to *Trichophorum* Pers., to *Scirpus,* or to *Eleocharis,* depending upon how the individual worker delimits these genera and which criteria he considers variable, which of particular importance.

In other words, there is at present no assurance that the relatively few morphological characters in use to distinguish genera within Scirpeae, even those genera most commonly included in this tribe, namely, *Scirpus, Eleocharis* and *Fimbristylis,* do indeed reflect phenetic similarity : similarity which today should underlie man-imposed generic limits, and which we expect to see expressed, to greater or lesser degree, by way of correlated character patterns, morphological, anatomical and cytological.

It is certainly necessary to question in how far the single character of the persistence, or not, of the style base on the achene reflects patterns of phenetic similarity within *Fimbristylis,* in its widest sense. The same may be said of most of the present generic limits applied within Scirpeae. Indeed, do we yet appreciate fully the diversity within Cyperaceae, do we yet know and understand sufficiently, all the patterns of reduction and specialization by which this diversity has come about, even to be in a position effectively to discuss generic limits?

Personally it is my opinion, that modification of the existing limits in Scirpeae in particular can be implemented competently only when there is available to the monographer, or better the team of workers undertaking monographic treatment, uniform and comprehensive information of world species — all known species that show a reasonable degree of alliance, even forgetting, perhaps, limits presently applied to distinguish Scirpeae from some tribes of Rhynchosporoideae. Thus I believe the best service a regional worker may render, at present, towards the accomplishment of this aim is a thorough study, from field as well as laboratory aspects, of relevant species in his area under their current generic names. Minor irregularities that such studies might reveal such as the inclusion of single species, or small complete groups of species, within one genus, when they are obviously better accommodated in other established genera, might be rectified, or better, pointed out, but to undertake transfer of arbitrary regional groups of taxa, without consideration of their world relatives, and on the basis of information deri-

ved from one, or few, aspects of investigation, is surely merely to accomplish little beyond increasing existing nomenclatural confusion.

As a minute contribution to world knowledge of Scirpeae, this paper lists, as exhaustively as present knowledge permits, the species represented in Africa, south of the Zambesi and Kunene rivers, that may be included within *Fimbristylis* when the limits drawn by KOYAMA, (1961:71) are applied. The names used are those considered valid under *Fimbristylis* and *Bulbostylis,* since much information is still required before it is certain that the latter should be sunk in the former and the former remain intact without modification. The more important synonyms, which indicate, to some extent, the past generic history of certain species, are included.

This paper goes on to examine patterns of morphological and anatomical variation among these species in relation to habitat and distribution over the sub-continent. It then attempts to circumscribe into groups, species that exhibit phenetic similarity. Lastly such groups are considered to determine in how far they correlate with current generic limits within Scirpeae.

Fourteen species within *Fimbristylis* and seventeen species within *Bulbostylis* are listed (Tables 1 and 2). A number of these are not confined to southern Africa but are also widespread through west and east tropical Africa, so that it has been possible to study, by the kind permission of Curators of Herbaria who lent specimens, a wide range of dried material, as well as field populations in South Africa itself. Some species, especially among *Fimbristylis,* are pan-tropical in distribution, so that some extra-African specimens have been seen as well : also some related tropical African and extra-African taxa. The generalizations which follow concerning patterns of variation are derived from the study of African specimens (gross morphology) and southern African specimens (anatomy), respectively.

GROWTH FORMS AND HABITAT PREFERENCES

All species are herbs, the majority perennating by means of mostly compact, more or less swollen, sympodial rhizomes. Some are annuals. Many are grassland forbs that are able to survive dry conditions (particularly *Bulbostylis* spp.); others appear confined to swampy areas with restricted drainage *(F. hygrophila);* others are tolerant of saline conditions, either near the sea, in estuaries, or near hot springs *(F. obtusifolia : F. ferruginea : F. bisumbellata).* The annuals are mostly widespread, often weeds favouring a particular soil-type, especially sand *(F. hispidula),* or occurring ubiquitously where there is temporary moisture *(F. dichotoma).* All, except *F. aphylla* and possibly *F. longiculmis,* are heliophytes.

GROSS MORPHOLOGY

M a i n p a t t e r n s o f v a r i a t i o n a m o n g a n d w i t h i n s p e c i e s

Leaf blades. Associated to some extent with habitat preference is degree of leaf blade development. Some species always produce photosynthetic leaf

blades *(F. dichotoma : B. boeckeleriana);* others develop only small to minute projections from the apices of leaf sheaths *(F. hygrophila : B. parvinux);* yet others exhibit variation producing either well developed or markedly reduced blades *(F. complanata : B. orytrephes).* In some cases this variation is within the plant itself *(F. complanata),* the same root often, but not invariably, producing leaves with elongate blades in spring, others with reduced blades in autumn. More commonly the variation is regional and environmental, plants from tropical latitudes and hygrophilous habitats bearing reduced blades, those from further south and from drier grassland situations producing elongate blades *(B. orytrephes).* Presumably this is response to photoperiod in relation to seasonal change, as opposed to the more uniform conditions of tropical environments. Among some tropical species *(F. littoralis : F. miliacea)* the innermost leaf of a shoot produces a reduced blade, whereas all others carry fully developed blades. Leaf blade development thus exhibits variation in degree of expression in the plexus of species under consideration, being "fixed" in those species either always "leafy" or always bladeless, and showing plasticity in other species, either within plants, or within races (?).

CLARKE (1893:651) laid stress on the easy recognition of *Bulbostylis* species by their "fine leaves and needle-like hairs" (the hairs not only developed at the orifices of the leaf sheaths (BLAKE, 1969:5) although they are well developed there). At first sight this is correct, but field study of populations has revealed that in some species, at least, *(B. schoenoides)* there is variation, apparently in response to drier habitats accompanied by periodic firing, from fine leaves (in swamps in grassland) to considerably wider blades (grassveld away from swamps : a gradation in blade width from the one habitat extreme to the other can usually be detected). Similar variation in leaf width is represented in *F. ovata,* but in this species wide (robust) and narrow-leaved (more slender) plants often grow juxtaposed without environmental differences being readily detectable. In leaf width *B. pilosa* is obviously anomalous within the genus, but it possesses the needle-like hairs regarded as characteristic. However these are present, albeit in smaller amount, in a number of *Fimbristylis* species *(F. bis-umbellata : F. squarrosa :* other tropical African spp.).

Inflorescences. The inflorescence is extremely variable. In its most elaborate form it consists of a supradecompound "umbel" or "corymb" (the anthela of MEYER, 1819, according to RICKETT, 1944) (fig. 1). The largest "umbels" seen among South African plants did not exceed 15 cm in diameter and comprised not more than 250 spikelets. From these, to single, sessile spikelets, every possible intermediate may be represented — an undoubted example of reduction and condensation leading to apparent simplicity. Usually particular species produce predominantly either compound "umbels", "umbels" with clustered spikelets, single heads, or solitary spikelets (presumably the possible range in each species is controlled by the genotypes re-

Fig. 1. Supradecompound "umbel" (anthela) of *Fimbristylis dichotoma.*

presented), but in every taxon some range of variation occurs. Examples are:

Compound "umbel": *F. dichotoma: B. burchellii* (degree of branching and number, less often clustering, of spikelets often varies in each inflorescence, even on the same plant especially in different months of the year: limits of spikelet number recorded for *F. dichotoma* 73-3).

simple "umbels" with clustered spikelets: *(B. zeyheri)* = *B. contexta: F. obtusifolia* (compound "umbels" or single heads may occur)

single heads: *B. pilosa: B. filamentosa* (an occasional branch may be developed)

solitary spikelets: *F. ovata: B. macra: B. humilis* (branch(es), or heads of two
or more sessile spikelets, are often present.)

Some species (for example *B. contexta : B. orytrephes*) show exceptional
plasticity in this respect.   Several inflorescence types may sometimes be re-
presented on a single plant at one time (fig. 2); frequently a range of types
may occur on juxtaposed plants under field conditions.   Study of these "pla-
stic" species over a wide distributional range has revealed that least reduced
inflorescences are commonest in the tropics, reduction being roughly correla-
ted with increasing southern latitude, until, approaching southernmost di-
stributional limits, branching is almost absent.   [*B. kirkii]* (simple umbels
with spikelets solitary on the rays) = *[B. zeyheri]* (simple umbels with spi-
kelets clustered on the rays) = *[B. collina]* = *B. contexta* (single heads)
are names that have been applied within one such series (fig. 3).

Branching within the inflorescence takes place under especially favour-
able environments, so that disruption of this broad latitudinal gradient is
frequent wherever particularly favourable micro-environments exist.   In
spring, too, plants that for the remainder of the year produce sparsely bran-
ched, or unbranched, inflorescences, often develop unusually lax, branching
examples at this season, which contrast with the reduced forms developed la-
ter. BLAKE (1969:3) has also referred to inflorescence variation in *Fimbristy-
lis*.

CLARKE (1902) and BODARD (1963) both used the degree of pubescence of
the flowering stem below the inflorescence in distinguishing sections within
Bulbostylis, but from field study it is obvious that pubescent and glabrous

Fig. 2. Four inflorescences borne on a plant of *Bulbostylis orytrephes* at the same
time showing variation in form.

stems may occasionally be borne on an individual plant, commonly on plants juxtaposed in the same population.

Spikelets. Spikelets are usually cylindric, because the glumes are spirally arranged upon the rachilla. KOYAMA (1961:99) stated that he found angular, rather loosely-flowered spikelets correlated with true trigynous pistils; terete, densely flowered spikelets where true digynous pistils were developed. In my opinion both *F. bis-umbellata* and *F. squarrosa* are exceptions to this since they possess spikelets clearly angled by the projecting glume keels, which feature further emphasizes their relationship to one another and the affinity of the former with section Pogonostylis rather than with section Fimbristylis (GORDON-GRAY 1968:394).

In *F. ovata*, *F. triflora*, *F. hygrophila* and *F. variegata* the bases of the spikelets are flattened (most clearly observed in young spikelets) due to the lowermost glumes being two-ranked. KOYAMA (1.c.:100) placed little importance in this. It perhaps reflects a transition to *B. pilosa* and *B. parvinux* in which the spikelets are flattened throughout.

Glumes are either glabrous abaxially *(F. dichotoma* and many other *Fimbristylis* spp.), or finely pubescent *(F. hispidula* and many other *Bulbostylis* spp.) or pubescent only in the distal half *(B. pilosa : B. parvinux).*

Styles. In the literature much has already been written concerning variation in style form, number of branches and achene shape in Scirpeae. It is

Fig. 3. Four inflorescences of *Bulbostylis contexta* borne on plants growing side by side under field conditions.

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sufficient to state here that, apart from the possible exception of *B. humilis,* (if this is not treated as distinct from *B. striatella* : the many intermediates perhaps represent hybrid swarms), no southern African species of either *Fimbristylis* or *Bulbostylis* has been found to exhibit regular variation in style branch number and achene shape, but this is not so with tropical African species, some of which parallel in range of variation, some tropical Asian taxa.

Persistence, or not, of the style base on the achene until after its dispersal from the spikelet, is not as clear cut as its use as a means of generic distinction might imply. In *F. hispidula* the style may, or may not, fall with the style base : if the base persists it may do so temporarily, or until after dispersal of the fruit. In *B. pilosa* the style usually falls first, but the base often persists only briefly. Achenes and style bases, too, sometimes show different dispersal patterns in the field, from those taking place after artifical drying for herbarium purposes.

ANATOMY

The conclusions given are drawn from the study of preparations made according to the recommendations of METCALFE (1960:1963). The terminology used in description is, as far as possible, that suggested by METCALFE and GREGORY (1964). Whenever material permitted, at least three plants from different localities and, if possible, different environments, were considered.

General Structure

The anatomy of the organs investigated (leaf blade, flowering stem and the epidermal layers of these organs), has shown uniformity that suggests, in my opinion, the possibility of a common origin for both genera. In other words, no marked differences in structural organization indicate fundamentally different relationships for *Fimbristylis* as distinct from *Bulbostylis.* A number of variation patterns can certainly be detected among the range of species studied. These, I suggest, represent response of a particular set of structural characters to different environments, many of these environments differing only slightly one from another, and thus some gradational sequence in anatomy can be detected in response to them.

Fig. 4. Leaf blades in transverse section showing anatomical structure as seen in plan:
A Fimbristylis ovata
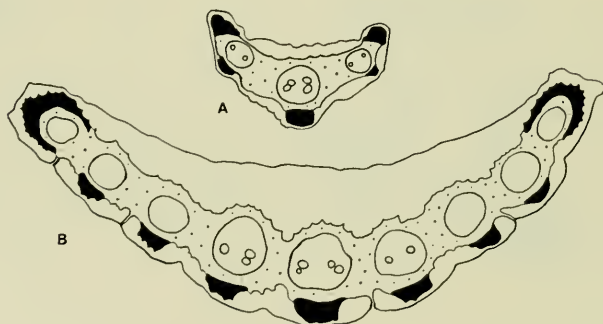B Fimbristylis obtusifolia
C Fimbristylis dichotoma

Fig. 5. Leaf blades of *Bulbostylis schoenoides* in transverse section showing anatomical structure as seen in plan:
A: narrow leaf from plant growing under vlei conditions (such a leaf with 3 vascular strands is typical of leaf structure in most *Bulbostylis species*).
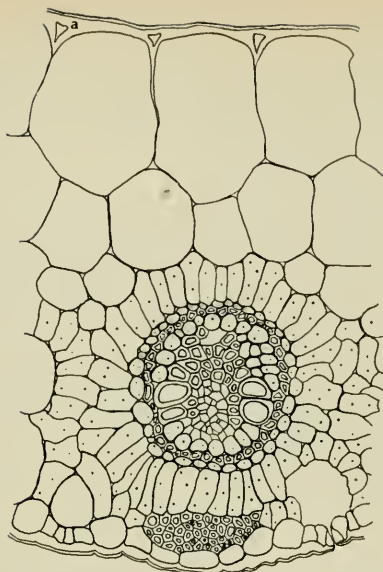B: wider leaf from plant of the same population but growing under drier grassland conditions.

Fig. 6. Portion of transverse section of leaf of *Fimbristylis ovata* in detail showing vascular bundle with three leaf sheaths, of which the outer and innermost are chlorenchymatous, the middle sclerenchymatous:
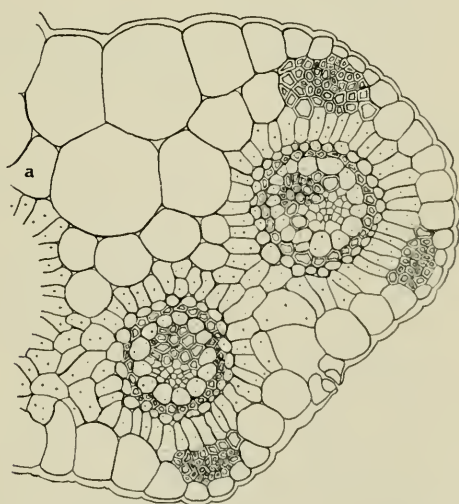(a — silica in convolutions of ripple walls of epidermal cells)

Fig. 7. Portion of transverse section of leaf of *Fimbristylis contexta* in detail.
(a — cell of hypodermis)

Leaf Blades

The main pattern of leaf blade structure as seen in transverse section is shown in plan in figs. 4 & 5, in detail in figs 6 & 7. This will not be commented on except to point out the general uniformity which may be summarized as follows:

shape: all species are variants of the thickly crescentiform leaf (flat, thickly crescentiform or sub-triangular, adaxially concave).

epidermis: adaxial — large clear cells (no stomata, no bulliform cells) abaxial — large clear cells, smaller than adaxial, interrupted by stomata, alternating with small, silica-containing cells over sclerenchyma strands.

sclerenchyma strands: usually small, of small elements: strands pulviniform, rectangular ,inversely securiform or triangular in shape.

vascular bundles: uniform, in 1 row mostly of 2 sizes: sheaths 3, outer and inner parenchymatous, middle sclerenchymatous.

cells containing phenolic constituents: always scattered in mesophyll especially near stomata (not in every plant, but in every species).

The features that exhibit variation may be summarized as follows:

hypodermis: consisting of large, clear, presumably water storing cells between adaxial epidermis and abaxial mesophyll: either absent (plants near or in fresh water), or 1-3 layers in width (plants under saline conditions), in same sp. *(F. ferruginea: F. dichotoma)* or varying among spp. (many *Bulbostylis* spp.)

chlorenchyma: radiate round bundles, with larger cells (not radiate) between bundles *(F. ovata:* many grassland *Bulbostylis* spp.), or not always clearly radiate *(F. dichotoma: F. bis-umbellata: B. pilosa).*

sclerenchyma strands: the number and size of the sclerenchyma strands developed adaxially in individual species seems correlated with the degree of development of the hypodermis and the leaf width and thickness.

F. obtusifolia (fig. 4), with thickest leaves of all species studied, is the only one in which sclerenchyma strands are developed between the adaxial epidermal cells and the hypodermis; small strands sometimes occur among the hypodermal cells also (in all other species, when a hypodermis is present, the sclerenchyma strands lie between this and the mesophyll.

number of vascular bundles: this is correlated with leaf width: most *Bulbostylis* spp. with narrow leaves contain 3 bundles only, but there is variation from 3, 4, 5, 7, 9, 11 in wider leaves, either on a single plant (only part of the range), or on plants within a population under differing environmental conditions *(B. schoenoides),* or on plants growing side by side under apparently uniform environmental conditions *(F. ovata).*
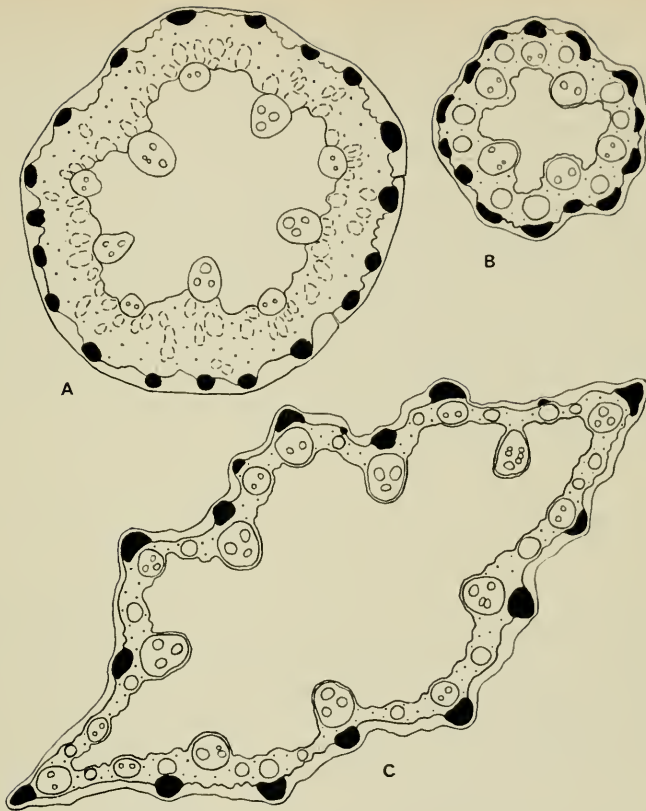
Fig. 8. Flowering stems in transverse section showing anatomical structure as seen in plan:

A: *Fimbristylis variegata* (note that all vascular bundles project into the central parenchymatous zone: dark coloured cells containing phenolic compounds have been indicated by broken lines in this species: they are present in all species but have been omitted from illustrations for clarity).

B: *Fimbristylis ovata.*

C: *Fimbristylis tenera.*

Flowering Stems

Transverse sections of representative flowering culms are shown in fig 8. These vary in outline, especially within *Fimbristylis,* but no particular shape sets these species (as a group) apart from *Bulbostylis* spp. The main point of difference among all species (apart from variation in development of air

chambers which feature is undoubtedly environmentally influenced), is the position of the vascular bundles. These are in two rows with the largest bundles innermost. These larger bundles occasionally lie completely within the mesophyll, more often they only contact its inner margin: the outer smaller bundles all lie within the assimilatory zone. In *F. variegata*, however, even the smaller bundles of the outer ring lie, not within the mesophyll, but merely in contact with its inner margin: the bundles thus all project into the central large-celled, water-storing pith. The mesophyll in this species is especially well organized, the cells being palisade-like.

It would seem such organization is in response to the bladeless nature of the species and the environmental conditions under which it grows, but other bladeless species *(F. aphylla* and *F. longiculmis* — both hygrophilous and more tropically distributed than the species in question) do not exhibit the same organization, however. Even *B. parvinux,* a taxon of dryland, bladeless plants does not agree in this respect with *F. variegata. B. schlechteri* was not studied due to lack of material.

Epidermal Layers, including Stomata,
Silica Bodies and Trichomes

General organization of the epidermal layers was similar in all the species studied. Variation was in degree rather than in basic structural form or arrangement of components. Stomata were all paracytic. Macroscopic trichomes of the needle-like type said to characterize *Bulbostylis* were well represented on fine-leaved plants usually referred to this genus. Trichomes of the same type were also present on plants of *Fimbristylis* (sensu stricto), *F. bis-umbellata* and *F. squarrosa* in particular. Some of these trichomes were direct extensions of epidermal cells and thus were one-celled, others were two-celled (proximal cell short, distal elongate), both types often being present together. Prickle-hairs were ubiquitous, but varied in number and situation from plant to plant and species to species.

Silica bodies were deposited in the epidermal cells of narrow diameter overlying sclerenchyma strands in flowering stems, leaf sheaths and blades: they were also present in the flowering glumes, in the long cells overlying the nerves and often also in the broader, shorter ripple-walled cells of the membranous lateral tissues. The silica bodies were conical, without, or with one, or more, rows of satellites. Bodies without satellites were found only in some of the fine leaved *Bulbostylis* species. Where these occurred near the apices of leaf blades, very often bodies with satellites were represented towards the base of the blade or in the sheath, so that the type was not constant for individual plants and certainly not for all plants of a species. In the same way, bodies with one, or more, rows of satellites were present in different parts of individual plants and there was variation among plants of the same species. The number of bodies to a cell varied also. Where cells were com-

paratively short and wide (most *Fimbristylis* spp. s. s.) the number of bodies was generally low (1—3), large and small bodies often occurring in the same cell, with extremes of variation frequently being represented in a single microscopic field. Where cells were longer and narrower (many *Bulbostylis* spp.) 2—9 bodies could be found in individual cells, but great variation occurred from one part of a plant to another, and often even within adjacent cells.

METCALFE and GREGORY (1964) not only differentiated between cones with and without satellites, but distinguished both of these from nodular bodies (cones with very many satellites?). They also regarded as significant the number and size (relative to one another) of the bodies within a cell.

After studying preparations from different parts of several plants of each species under consideration in the present paper, I was left with a strong impression that METCALFE and GREGORY's different illustrations might represent stages in a progressional series in the deposition of silica within epidermal cells, and felt I should begin afresh in an attempt to obtain evidence supporting this. Firstly a cone could be laid down : as its diameter increased with the deposition of additional layers, so one, then a second row of satellites could become evident, leading, with further additions, to the formation of a nodal body. These changes probably take time and may reach fullest expression only in environments where a reasonable level of silicon is in solution for uptake by the plant.

I also gained two other impressions, both of which need experimental confirmation, if possible. Firstly, plants of *Fimbristylis* (sensu stricto), in general more water-loving than those of *Bulbostylis,* contained, when considered collectively, larger and more numerous silica bodies, and thus more opaline silica, than did plants of *Bulbostylis.* This is, perhaps, only to be expected when the environment favoured by each genus is taken into account. The second impression was that the number of bodies in each cell was correlated with cell length, for in the generally longer cells of flowering stems in comparison with those of leaf blades, and in the longer cells of *Bulbostylis* in comparison with those of *Fimbristylis* species, more bodies were present.

Minute silica bodies were also often deposited in the folds of the ripples of the exposed surfaces of the inter-costal epidermal cells.

To summarize, it must be stressed that no special form nor arrangement of the silica bodies suggested a basis on which the species studied might be segregated into two clearly defined groups.

CHROMOSOMES

The only work so far carried out on chromosome complements of the southern African species under consideration is that of FRANKISH (1960 : unpublished thesis) in which three Natal populations of *F. complanata* each ga-

ve counts of 2n = 10, which differed from 2n = 16 recorded by TANAKA (1939) for tropical plants of the same taxon.

Counts recorded for plants from other parts of the world (not only representative of the southern African species under consideration) are 2n = 10, 16, 20, 24, 44 for *Fimbristylis;* 2n = 10, 84 for *Bulbostylis* (DARLINGTON and WYLIE 1955).

KOYAMA (1961 : 71) stated in support of his sinking of the former genus in the latter, that " ... *Bulbostylis* and *Fimbristylis* are cytologically the same, having (the) same basic number and similar size of chromosomes, ... "

I must agree with VAN DER VEKEN (1965:323) that far too little work has been done for chromosome morphology and number to provide any reliable guide to the recognition of generic limits.

OTHER ASPECTS OF STUDY

VAN DER VEKEN (1965) has given valuable evidence of embryo structure within many species of *Fimbristylis* and *Bulbostylis* as well as within some of their associates in Scirpeae. This line of study must be completed for all southern African species.

Other aspects of achene wall structure as well as stages in germination also await investigation. The shape and arrangement of the epidermal pericarp cells is known for each species, and no distinctive patterns distinguish *Bulbostylis* from *Fimbristylis* species. More detailed work on reproductive organs, now we have electron scanning microscopes to assist, may yet provide further clues that will guide generic delimitation.

The chemical components of these plants also await study. That phenolic constituents are frequent in all southern African species is certain from the presence in the vegetative organs of cells with dark reddish brown coloration to the cell sap. Most species also possess reddish glumes. Fats are frequent in the endosperm.

DISTRIBUTION AND EVIRONMENT

The species under consideration follow a rather uniform distributional pattern in southern Africa. Wide-spread across the continent in the tropics, the majority of taxa show a south-eastern extension of their range which narrows with increasing latitude until, at or before 34°S, all but the annual, *B. humilis,* which continues to the Cape Peninsula, have fallen away. Some extend intermittently, from Angola down the west coast as far as Clanwilliam.

Refinement of this general pattern reveals some differences between the more moisture-loving entities and those which possess greater tolerance of drier environments. The former, mostly *Fimbristylis* spp. s. s., have follo-

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wed a "tropical" route southwards, for they require warm moist situations and thus are found mainly on the low-lying coastal plain of Moçambique and northern Natal. *F. longiculmis, F. bis-umbellata* and *F. squarrosa* fall away about 27°S. Others of this group persist further, but reductions in species number continue progressively, until *F. complanata* reaches its southernmost limit near George.

Bulbostylis spp. s. s. have tended to follow higher land in their migration southwards as befits their greater tolerance of drier environments. They are thus often to be found in the shallow soil of rock outcrops, or in grassveld situations. It is the annuals which are most ubiquitous and most widespread.

In origin the whole plexus of species must surely have been tropical and water loving, *Fimbristylis* representing the more closely equatorial, older ancestral element; *Bulbostylis* the more recent, derived, no doubt, under the stimulus of more extreme habitats in more temperate latitudes.

DISCUSSION

It is obvious that knowledge of the southern African species of *Fimbristylis* sensu lato, is still far from complete. Nevertheless, it is essential to summarize available information and to look for phenetic patterns that may, or may not, be repeated in regional groups of species from other parts of the world.

Firstly, it seems apparent that the species under consideration represent a reasonably homogeneous assemblage. Certainly the main character patterns, morphological, anatomical, embryological, and perhaps cytological, are sufficiently uniform and have been well enough studied to discount the presence of any markedly discordant element, or elements, directly suggestive of origin from an unrelated stock, or stocks. In this *B. schlechteri* must remain excepted, for its morphological form, apart from achene and style base which fit reasonably well with *Bulbostylis*, is somewhat aberrant in the plexus. Vegetatively there is some similarity with *B. parvinux,* but the spikelets are quite different. From other aspects, *B. schlechteri* is inadequately known and so must be held apart until further material becomes available for study. On the basis of spikelet form, there is, perhaps, affinity with the tropical *F. polytrichodes* R. Br. which is included in the section Eleocharoides of *Fimbristylis.*

If *B. schlechteri* is excepted (at least temporarily), there is, in the light of evidence provided, no hindrance to the acceptance of Koyama's (1961) arrangement whereby generic limits for *Fimbristylis* are drawn sufficiently widely to include *Bulbostylis,* as well as *Abildgaardia, Pogonostylis* and the rest. This is the broad view. In this perspective *Fimbristylis* comprises a gradient of adaptive forms : at one extreme, the tropical, more or less waterloving, morphologically diverse representatives, closest, no doubt, to the im-

mediately ancestral generic stock, or stocks : at the other, the more temperate, "dryland", morphologically more uniform species, derived, it would seem, in response to the stresses of more demanding environments : between, a zone of intermediates linking the extremes. Under such an interpretation the fundamentally uniform anatomy and morphology, each with what appears to be an adaptive range of diversification, is explicable : even the range in style base form and persistence is perhaps more clearly understandable against such a background.

ROBINSON (1962) suggested from results derived from simple experimentation that the corky hypogynium developed under the achene in some species of *Scleria* served as a float for fruit dispersal by water along channels that would later provide ideal habitat conditions for the germinating seedlings. Does not the soft, spongy, expanded style base in *Eleocharis* that fits the achene apex so snugly, serve similar purpose? If so, is the smaller, drier harder style base of *Bulbostylis* not part of a reductional sequence? Is not the less closely fitting, readily falling style base of *Fimbristylis* section *Fimbristylis* perhaps an offshoot from the main line of adaptation that resulted in derivation of the fine-leaved *Bulbostylis* species, through intermediate *Abildgaardia*-like forms, from tropical, trigonous-achened, *Trichelostylis*-like stock?

VAN DER VEKEN (1965:327) found the embryos of *F. cioniana* SAVI, [*F. exilis* R. & S.] = *F. hispidula* VAHL and *F. hensii* C. B. CL. to be not of the *Fimbristylis* type, but rather variants of the *Bulbostylis* type. *B. pilosa* had an embryo similar to that found in species previously referred to *Abildgaardia*, for which genus van der Veken found no distinct embryo type recognizable.

B. pilosa possesses, in plenty, the needle-like hairs of *Bulbostylis* and a persistent (but only temporarily so) style base. Anatomically and in general morphology it fits much more closely with *Fimbristylis* (in the vicinity of *F. ovata* and *F. hygrophila)* than with *Bulbostylis*. CLARKE (1902: 425 and 436) described *Fimbristylis africana* and *Bulbostylis aphyllanthoides* respectively : both are *B. pilosa*. He thus also perceived the relationship of this species with both genera! Anatomically and morphologically *F. hispidula,* despite its readily falling style base, is much more closely allied with *Bulbostylis* than with *Fimbristylis*.

If these anomalies are corrected the southern African species can be arranged in adaptive sequence (Table 3). In such a sequence the embryological irregularities encountered by VAN DER VEKEN are smoothed out, for *B. pilosa* becomes associated with *F. ovata* and its allies, with which group it agrees best according to every aspect of structure so far studied, even to a style base that is only temporarily persistent on the achene. *F. hispidula* comes to be placed with *Bulbostylis,* but near the *Abildgaardia* group.

In Table 3, continuous horizontal lines separate the extremes from the central intermediate group : dotted horizontal lines distinguish less well-mar-

ked groups within the main groups (in *Bulbostylis* such minor groups appear lacking) : perennials are to the left, annuals set slightly to the right.

Suppose these species do not represent an adaptive sequence as has been suggested. If other interpretations are sought for, the cytological information available does not indicate whether the extremes might be parental forms, or relatives of these, the intermediates hybrid progeny. We need not only more cytological information, but knowledge of breeding patterns and isolating mechanisms within the plexus. No matter how the plexus is interpreted, it seems possible to recognize within it three main groups that relate to *Fimbristylis, Abildgaardia* and *Bulbostylis,* respectively.

Generically the broad view of KOYAMA, while indicative of the overall relationship of the species, is too coarse a classification to delimit finer, yet well-marked, phenetic similarities among them. If, at the other extreme, generic limits are drawn to emphasize the smallest phenetic groups recognizable, then the genera will be many and mostly far too uniform and narrow for recognition of sections or series within them.

Present evidence thus seems to support most strongly a middle course under which three genera would be maintained (a course already followed by some workers). These would be defined as follows:

1. the diverse, tropical, water-loving, predominantly perennial species with spirally imbricate glumes, often glabrous or almost so, 3 or 2-angled achenes, expanded deciduous style base and a "*Fimbristylis*-type" embryo (*Fimbristylis* VAHL).
2. the more uniform intermediate, water-loving to dry-land perennial species, with spikelets flattened basally only or throughout, glumes glabrous or pubescent, achenes 3-angled, sometimes narrowing into a basal claw, and a "*Bulbostylis*-like" embryo (*Abildgaardia* VAHL).
3. the fine-leaved, dry-land perennial and annual species, with spirally imbricate spikelets, finely pubescent glumes, 3- or 2-angled achenes, persistent style base and a "*Bulbostylis*-type" embryo. (*Bulbostylis* C. B. CL.)

It remains to determine whether, when world species are fully known, division into only three genera, as favoured here, will be adequate to reflect the more important phenetic patterns then evident. The final decision as to whether a broad and coarse, or narrow and fine, interpretation of genera will more truly reflect patterns of relationship as they have been developed in nature, will only be possible when we are vastly more knowledgeable about all taxa that today are delimited within the tribe Scirpeae.

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Table 1. List of *Fimbristylis* species recorded for Africa south of the Zambesi and Kunene Rivers, August, 1970, including basionyms, more important synonyms, known world distribution and habitat preferences.

Name and Synonyms	Known World Distribution	Habitat Preferences in southern Africa
1. *F. ovata* (BURM. F.) KERN = *Carex ovata* BURM F. = *Fimbristylis monostachyos* (L.) HASSK. = *Abildgaardia monostachya* VAHL	pantropical	moist to dry grassland
2. *F. triflora* (L.) K. SCHUM. = *Cyperus triflorus* L. = *Abildgaardia tristachya* VAHL	tropical and southern Africa India	marsh to moist grassland
3. *F. hygrophila* GORDON-GRAY	tropical and southern Africa	marsh: restricted drainage

Name and Synonyms	Known World Distribution	Habitat Preferences in southern Africa
4. *F. variegata* GORDON-GRAY	southern Africa	damp sandy soil among rocks: drainage good
5. *F. ferruginea* (L.) VAHL = *Scirpus ferrugineus* L. (including *F. sieberana* KUNTH)	pantropical	damp sand, or sandy clay: some tolerance to saline conditions
6. *F. longiculmis* STEUD.	tropical and eastern southern Africa, Malagasy	damp sand or sandy clay: marsh or moist grassland
7. *F. dichotoma* (L.) VAHL = *Scirpus dichotomus* L. = *F. diphylla* (RETZ.) VAHL	pantropical	marsh or riverine areas: often a weed of damp, disturbed situations
8. *F. bis-umbellata* (FORSK.) BUB. = *Scirpus bis-umbellatus* FORSK. = *Fimbristylis dichotoma* (L.) VAHL	tropics, except America	damp sand or loam-clay: marsh or marginal to rivers and hot-springs: often a weed
9. *F. squarrosa* VAHL = *Pogonostylis squarrosa* (VAHL) BERTOL.	pantropical	as for *F. bis-umbellata:* sometimes an early colonizer of mudflats
10. *F. complanata* (RETZ.) LINK = *Scirpus complanatus* RETZ. =*Trichelostylis complanata* NEES = *Fimbristylis consanguinea* KUNTH = *F. kraussiana* HOCHST. ex KRAUSS	pantropical	marsh to moist grassland: some tolerance to saline conditions
11. *F. tenera* R. & S. = *F. microcarya* F. v. MUELL. = *F. complanata* (RETZ.) LINK var. *microcarya* (errore "*microcarpa*") (F. v. MUELL.) C. B. CL. = *F. autumnalis* (L.) R. & S. var. *microcarya* (F. v. MUELL.) KÜK. = *F. thonningiana* BOECK.	pantropical, except America	damp sandy areas or earth pockets among rocks: annual

Name and Synonyms	Known World Distribution	Habitat Preferences in southern Africa

12. *F. obtusifolia*[1] (LAM.) KUNTH
    = *Scirpus obtusifolius* LAM.
    = *Trichelostylis obtusifolia* NEES
    = *Fimbristylis rigidula* RIDL.
	tropical and southern Africa, America	damp sand near sea or in estuaries

13. *F. aphylla* STEUD.
    = *F. globulosa* (RETZ.) KUNTH var. *aphylla* (STEUD.) MIQ.
    = *F. quinquangularis* C. B. CL. p. p.
    = *F. quinquangularis* (VAHL) KUNTH var. *crassa* C. B. CL.
	tropical and southern Africa, Java, Sumatra, India	permanently wet, often shaded marsh situations, sometimes with impeded drainage

14. *F. hispidula*[2] (VAHL) KUNTH
    = *Scirpus hispidulus* VAHL
    = *Isolepis exilis* KUNTH
    = *Fimbristylis exilis* (KUNTH) R. & S.
    = *Fimbristylis rhodesiana* (RENDLE)
	pantropical	sandy disturbed areas in particular: annual weed

Table 2. List of *Bulbostylis* species recorded for Africa, south of the Zambesi and Kunene Rivers, August, 1970, including basionyms, more important synonyms, known world distribution and habitat preferences.

1. *B. filamentosa* (VAHL) C. B. CL.
    = *Scirpus filamentosa* VAHL
    = *Isolepis filamentosa* KUNTH
    = *Fimbristylis cardiocarpa* RIDL.
    = *Bulbostylis cardiocarpa* (RIDL.) C. B. CL. p. p.
    = *B. rehmanii* C. B. CL. (nomen nudum)
	tropical and southern Africa, Malagasy	sandy *Brachystegia* woodland or dampish grassland

1   It is probable that the African and American *F. obtusifolia* should be sunk with the Malaysian *F. cymosa* (LAM.) R. BR. and the Indian *F. spathacea* ROTH. under *F. glomerata* (RETZ.) NEES.

2   In accepting as the valid name, *F. hispidula* (VAHL) KUNTH, I follow KERN (Reinwardtia 4: 95, 1956).
Species numbered 2, 3, 4, 6, 8, 13 have not been investigated with regard to embryo structure.

Name and Synonyms	Known World Distribution	Habitat Preferences in southern Africa
2. *B. scabricaulis* H. CHERM. = *B. cardiocarpa* (RIDL.) C. B. CL. p. p. (HOLUB only) = *B. cardiocarpa* (RIDL.) C. B. CL. var. *holubii* C. B. CL. = *F. collina* RIDL. = *B. filamentosa* (VAHL) C. B. CL. p. p.	tropical and southern Africa, Malagasy	grassland
3. *B. schoenoides* (KUNTH) C. B. CL. = *Isolepis schoenoides* KUNTH = *Scirpus schoenoides* BOECK. = *Bulbostylis scleropus* = *B. megastachys* (RIDL.) C. B. CL. = *B. stricta* TURRILL	tropical and southern Africa, Malagasy	grassland: damp vlei or dry areas
4. *B. oritrephes* (RIDL.) C. B. CL. = *Fimbristylis oritrephes* RIDL. = *F. oritrephes* K. SCHUM. = *F. koniankensis* A. CHEV. = *Bulbostylis trichobasis* (BAK.) C. B. CL. (exl. descr.) = *B. caespitosa* PETER = *B. trichobasis* (BAK.) C. B. CL. var. *caespitosa* (PETER) KÜK.	tropical and southern Africa	grassland, often where there is poor grass cover
5. *B. trichobasis*[1] (BAK.) C. B. CL. = *Scirpus trichobasis* BAKER = *Fimbristylis cinerea* RIDL.	tropical and southern Africa, Malagasy	grassland
6. *B. burchellii* (FIC. & HIERN.) C. B. CL. = *Fimbristylis burchellii* FIC. & HIERN. = *F. huillensis* RIDL. = *F. hispidula* BOECK. p. p.	tropical and southern Africa	semi-marsh conditions in granite sand, or among rocks where water is available for part of year
7. *B. contexta* (NEES) BODARD = *Trichelostylis contexta* NEES = *Fimbristylis contexta*	tropical and southern Africa	sandy grassveld, or among rocks, often where grass cover is poor: occasionally a weed

1 It may prove eventually that *B. trichobasis* and *B. oritrephes* are variants of a single species.

Name and Synonyms	Known World Distribution	Habitat Preferences in southern Africa
KUNTH = *Ficinia contexta* NEES (nomen nudum) = *Scirpus collinus* BOECK. = *Isolepis collina* KUNTH = *Bulbostylis collina* (KUNTH) C. B. CL. = *B. burkei* C. B. CL. = *B. zeyheri* (BOECK.) C. B. CL. p. p. = *B. kirkii* C. B. CL.		
8. *B. boeckeleriana* (SCHWEINF.) BEETLE = *Scirpus boeckelerianus* SCHWEINF. = *Bulbostylis collina* (KUNTH) C. B. CL. = *S. collinus* (KUNTH) BOECK. var. *boeckeleriana* SCHWEINF. = *B. zeyheri* (BOECK.) C. B. CL. p. p. = *B. transiens* (K. SCHUM.) C. B. CL.	tropical and southern Africa	grassland — dry areas with poor grass cover, or on rock outcrops
9. *B. densa*[1] (WALL.) HANDEL-MAZZ. = *Scirpus densus* WALLICH = *Isolepis densa* (WALL.) SCHULTES = *Isolepis trifida* NEES ex WIGHT = *Bulbostylis trifida* (NEES) NELMES = *B. capillaris* (L.) C. B. CL. var. *trifida* (NEES) C. B. CL. = *Fimbristylis capillacea* HOCHST. = *F. parva* RIDL. = *Bulbostylis parva* (RIDL.) C. B. CL.	world-wide, if the American *B. capillaris* is included (see footnote 2)	sparse soil of rock outcrops, either in shade or full sun: moist, or drier conditions where only temporary water available: delicate annual

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1   I agree with KOYAMA 1961: 103 that *B. densa* is not distinct from the American *B. capillaris* (L.) C. B. CL., but I have not compared types.

Name and Synonyms	Known World Distribution	Habitat Preferences in southern Africa
10. *B. melanocephala*[1] (RIDL.) C. B. CL. = *Fimbristylis melanocephala* RIDL. = *Bulbostylis moggii* SCHONL. & TURRILL	tropical and southern Africa	damp margins of marshes and rivers where soil periodically inundated: annual
11. *B. trabeculata* C. B. CL. = *Fimbristylis barbata* (ROTTB.) Benth. var. *subtristachya* RIDL.	tropical and southern Africa	margins of marsh or river: periodic moisture available: annual
12. *B. humilis* (KUNTH) C. B. CL. = *Isolepis humilis* KUNTH = *Fimbristylis arenaria* NEES = *Scirpus arenarius* BOECK. = *Bulbostylis breviculmis* (KUNTH) C. B. CL. (including *B. striatella* C. B. CL.)	southern Africa: more mountainous areas of tropical Africa	soil of rock outcrops, or in moss mats on rock outcrops, or a weed of exposed dry soils: annual
13. *B. macra* (RIDL.) C. B. CL. = *Fimbristylis macra* RIDL. = *Bulbostylis zambesica* C. B. CL. = *Fimbristylis zambesica* K. SCHUM.	tropical Africa and Rhodesia (not further south)	arid, often stony areas in open woodland
14. *B. parvinux* C. B. CL.	eastern southern Africa	on white and pale red sand in *Terminalia* and *Acacia burkei* woodland
15. *B. schlechteri* C. B. CL.	southern Africa	damp sandy riverine areas
16. *B. buchanani* C. B. CL.	tropical Africa, Rhodesia (not further south)	soil of rock outcrops
17. *B. pilosa* (WILLD.) CHERM. = *Schoenus pilosus* WILLD. = *Abildgaardia pilosa* NEES = *Fimbristylis pilosa* BENTH. (non VAHL) = *F. aphyllanthoides* RIDL. = *F. africana* C. B. CL. = *Bulbostylis aphyllanthoides* (RIDL.) C. B. CL.	tropical Africa, Rhodesia (not further south)	on sandy soils in woodland

1   Perhaps no more than a variant of *B. densa:* the type is young.

Table 3. List of *Fimbristylis* and *Bulbostylis* species recorded for Africa, south of the Zambesi and Kunene Rivers, placed in sequence to show phenetic relationships and proposed generic limits: perennials left, annuals right.

	F. longiculmis
	F. ferruginea (short-lived perennial or annual)
	F. dichotoma (sometimes perennial)
	F. bis-umbellata
	F. squarrosa
Fimbristylis	
	F. aphylla
	F. obtusifolia
	F. complanata
	F. tenera

	F. variegata
	F. hygrophila
Abildgaardia	*F. triflora*
	F. ovata
	B. pilosa
	B. parvinux

	F. hispidula
	B. contexta
	B. boeckeleriana
	B. schoenoides
	B. macra
	B. trichobasis
	B. orytrephes
Bulbostylis	*B. burchellii* (sometimes annual)
	B. scabricaulis
	B. filamentosa
	B. melanocephala
	B. densa
	B. buchanani
	B. trabeculata
	B. humilis

B. schlechteri (?)