

Notes on the genus *Ficinia* (Cyperaceae): morphological variation within the section *Bracteosae*

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ABSTRACT

Generic limits of *Ficinia* are reviewed. Morphological variation within the section *Bracteosae* Pfeiff. of *Ficinia* Schrad. (Cyperaceae) is examined and discussed. Diagnostic characters previously in use in classification are reviewed together with a number of new characters. These have enabled the limits of many existing taxa to be refined, and have provided the basis for the establishment of a number of new taxa recently described. Characters examined include: underground organs, leaf sheaths and ligules, leaf blades, inflorescence structure, prophylls, styles, anthers, achenes, gynophores and inflorescence axes.

INTRODUCTION

This paper is the second in a series on *Ficinia*. In the first (Arnold & Gordon-Gray, 1978) nine new taxa belonging to the section *Bracteosae* are described. In this paper morphological variations within the section are discussed, and will be followed by part three of the series in which a detailed account of the taxonomy, nomenclature and distribution of taxa in the section *Bracteosae* will be presented.

The major genera of the tribe *Scirpeae*, with the exception of *Ficinia* and to a lesser extent *Eleocharis*, have come under close scrutiny in recent years. *Scirpus* L., long considered unnatural, has been studied by a succession of workers including Beetle (1940; 1944 & 1945), Koyama (1961), Schultze-Motel (1971), Schuyler (1971) and Oteng-Yeboah (1974) and is still receiving attention. *Fimbristylis* Vahl and *Bulbostylis* Kunth have likewise been the subject of some degree of investigation, especially the African species (Gordon-Gray, 1965, 1971; Lye, 1971, 1973). The South African species of *Fuirena* are at present under revision (Forbes, pers. comm.) Koyama (1961) would include *Fuirena* in *Scirpus*. *Eleocharis* has been the subject of studies particularly in America (Harms, 1968, 1972), (Strandhede, 1967), (Svenson, 1939, 1947), but its African, especially South African, species are not adequately known. *Ficinia* is also placed within *Scirpeae*. Apart from studies of this genus for inclusion in regional floras (Clarke, 1898; Levyns, 1950) the most recent comprehensive investigation into the genus has been that of Pfeiffer (1920) at a time when generic limits were not so much in question as they are now.

At least 132 species have been described within the genus *Ficinia*, but of these only 55 to 60 appear to be good species, the rest having been relegated to synonymy. The majority of these species are endemic to South Africa, more especially its southern and south-western regions. One south-

western species, *F. nigrescens* (= *F. bracteata*), extends to South West Africa / Namibia (Podlech, 1967). Of the remaining species that exceed the boundaries of South Africa, two reach Mount Kilimanjaro (Clarke, 1898) but are also South African, two are recorded from Abyssinia, one of which is endemic there, whereas the other occurs in South Africa. The Abyssinian endemic, *F. clandestina*, is considered by Arnold & Gordon-Gray (1978) not to belong to *Ficinia*: its correct generic status is uncertain. Five extra-African species of *Ficinia* have been recorded, three are from the Malagasy Republic (Chermezon, 1937) and two, *F. indica* Lam. and *F. foliacea-bracteata* Pfeiff. were reported from the East Indies (Java). Raynal (1958) has shown that the last-named entity is not a species of *Ficinia* but rather *Cyperus cephalotes* Vahl, and it will be shown in a paper to follow that Lamarck's type of *F. indica*, collected by Sonnerat, is almost certainly from the Cape of Good Hope rather than from the East Indies. This means that, apart from three species in Malagasy, the genus is exclusively African, being predominantly southern and temperate, but extending northwards along mountain ridges into the eastern Cape, Natal, the Transvaal, Zimbabwe and the mountains of Kenya and Abyssinia. There are certainly undescribed species of *Ficinia* in eastern South Africa and presumably others in the rest of South Africa and Zimbabwe. These, however, will not be dealt with here, for the present study covers only the section *Bracteosae* which is confined in natural distribution to the south-eastern, south-western and western Cape from East London to the border of South West Africa and inland as far as Grahamstown, Graaff Reinet, Montagu and Clanwilliam. This section, according to Pfeiffer's 1920 classification, belongs to the subgenus *Eu-Ficinia*, comprises three subsections. Of these *Sickmannia* and *Arboriculmes* are each monotypic, with the third subsection, *Seticulmes*, comprising ten species.

Within *Ficinia* there are a number of individual species, and species groups that, in the past, have been used as 'dumping grounds' for plants difficult to identify. The largest and perhaps the most problematic of these groups is the *F. indica*/*F. pallens* complex which forms the major part of the section *Bracteosae*. All who have studied this complex have treated it differently. At one extreme its component taxa have been regarded as varieties

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of a single species (Schonland, 1922), whereas at the other extreme five distinct species are recognized (Levyns, 1950). None of the work carried out so far has been entirely satisfactory and, if anything, has tended to compound rather than to clarify the confusion.

In the present investigation, morphological variation is examined in the hope that this will clarify some of the taxonomic, distributional and nomenclatural problems existing in the section *Bracteosae* with special attention being focused upon the *F. indica*/*F. pallens* complex.

GENERIC LIMITS OF *FICINIA*

Within the tribe *Scirpeae*, *Ficinia* is most closely allied to the genus *Scirpus* and more especially to the section *Isolepis* of this genus. Before *Ficinia* was established, many of the species now assigned to it were included in this section. Species of *Ficinia* may be distinguished from it, however, by their possession of a small, obconical, pedicellike structure or gynophore (also referred to as a discus) responsible for elevating the achene above the receptacle.

According to C.B. Clarke (1898) it is difficult to attribute very much importance to this structure, because it is difficult to draw the line between it and the expanded foot associated with the achene of many species of *Scirpus*, therefore *Ficinia pulchella* of Kunth is *Scirpus pulchella* Boeck. Furthermore, a small gynophore is also present in some species of *Fimbristylis*, and varies greatly in development in one of the species in this genus, namely, *F. ferruginea* (L.) Vahl.

Schonland (1922) draws attention to the fact that an obpyramidal small stalk which becomes detached with the nut, besides being present in species of *Scirpus* and *Fimbristylis* is also found in *Scleria* and *Diplacrum* of the tribe *Rhynchosporae*. The main difference, however, between these genera and *Ficinia* lies in there being a small lobed somewhat fleshy outgrowth surrounding the base of the ovary in *Ficinia* and that this structure is normally three-lobed or has three main lobes.

The present investigation has shown these observations to be accurate, for all the taxa studied possessed an out-growth or outgrowths from the apex of the gynophore which enveloped all or part of the lower portion of the nut. The form of the outgrowth is highly variable within the genus, ranging from a cup-like structure to 2-3 lobes generally joined near their bases.

The use of the gynophore as the solitary attribute characterizing the genus *Ficinia* has, for the greater part, been successful in uniting a large, relatively heterogeneous group of plants, which in the past were considered by some workers to comprise a number of distinct genera.

Ficinia includes a number of taxa with nuts that lack a gynophore. Among these are *F. tenuifolia* Kunth and *F. rigida* Levyns. Because of the 'ficinioid facies' of these plants, it has been generally accepted that they be included in *Ficinia*. *Scirpus falsus* C.B.

Cl. and *Scirpus ficinioides* Kunth, on the other hand (to be dealt with in some detail in a separate paper), despite their 'ficinioid' appearance, have been placed in *Scirpus*, but not without recognition of the uncertainty of this relationship, reflected as it is, in their specific epithets. The two major attributes which dictated their inclusion in *Scirpus* were, firstly, the lack of a gynophore, and, secondly, the presence of six bristles surrounding each flower, a feature unrepresented in *Ficinia*, but characteristic of certain members of *Scirpus*. Therefore it is evident that the boundary between *Scirpus* and *Ficinia* is by no means clearcut nor well defined.

The 'ficinioid' appearance already mentioned is the cumulative effect of a number of minor features exhibited by a large number of species, particularly those of the section *Bracteosae*. It is a means by which plants of the genus can usually be distinguished quite readily from species of allied genera, often on superficial inspection alone.

The characters which collectively give this 'ficinioid facies' are the erect, and sometimes rigid, leaf blades that are often almost cylindrical and stem-like rather than flattened and leaf-like; the membranous or scarious leaf sheaths that in many instances are prolonged upwards into definite ligules, the often (but not always) condensed and highly compacted obovate to elliptical inflorescences enveloped almost completely, or only partially, in an involucre formed by the dilated bases of the outer bracts, the longitudinally striated appearance and, often, the hard, brittle texture of these bracts and sometimes of the smaller glumes within them.

This 'ficinioid facies' is not commonly exhibited by members of the section *Isolepiformes*, which closely resemble *Scirpus*, and it is a typical of the subgenus *Hemichlaena* in which the glumes are distichously ranked and the spikelets compressed.

This strongly suggests that present generic limits, defined almost exclusively as they are by the presence of a gynophore beneath the achene, are artificial, unnatural and probably too wide. There is, therefore, an important need to re-examine all species with a view to determining critical, and especially new, criteria that will effectively delimit natural groups within the genus.

DIAGNOSTIC CHARACTERS EXHIBITED BY THE SECTION *BRACTEOSAE*

The characters selected by past workers to delineate the different taxa within *Ficinia* have not always been entirely successful in fulfilling this function. Many, with use, have proved to exhibit a considerable range in variation, extending beyond the limits originally intended for them, and are therefore considered to be unreliable.

Many taxa at their establishment were inadequately defined by too few characters. With time, and under the interpretation of numerous workers, these taxa have become heterogeneous, so that on more careful scrutiny and with the application of more critical diagnostic criteria they fell, during the present work, into relatively homogeneous sub-units

worthy of independent recognition sometimes at specific, sometimes at infraspecific levels.

New characters and others previously in use that require special consideration are dealt with in sequence beginning with vegetative organs and proceeding to reproductive structures.

Underground organs

Growth is sympodial in all the taxa studied. In this sense all plants possess a rhizome, for even in the compactly tufted plants, a very abbreviated rhizome links successive shoots together.

Previous workers have made reference to the presence of stolons in some taxa of the section *Bracteosae* and their absence in others. These 'stolons' are essentially rhizomes, for they are underground stems clothed in leaf scales, but they are markedly elongated in comparison with the rhizomes developed in the more or less compactly tufted plants. Each gives rise to a new plant at its tip and thus the term 'stolon' is correctly applied to them (Lawrence, 1951, Willis, 1973). Two main rhizome forms, which differ in degree of development rather than basic structure, are represented in the section *Bracteosae* (Fig. 1).

(i) Abbreviated rhizomes

Many of the taxa studied possessed abbreviated rhizomes but these, despite their short length, were not uniform. They fell into two subgroups. Little variation occurred within the first. Here the rhizome did not exceed 2–3 mm in length. It is inconspicuous except when innovations are developed, being concealed by persistent leaf basis.

The rhizomes of successive shoots are very closely packed resulting in the development of plants with compactly tufted growth forms (Fig. 1A) for example *F. capitella*.

The second subgroup comprises plants in which the rhizome structure is more variable in length. Here it ranges from 2–25 mm and is either uniform in width or swollen apically, as in *F. pallens* var. *pallens*, to form a tuberous base to the aerial shoot. (Fig. 1B).

The rhizomes are clothed in short, obtuse, striate scale bracts that are usually persistent, for example *F. levynsiae*. Plants falling within this second subgroup, because of their less abbreviated rhizomes, develop a loosely tufted growth form, that, in its most extreme expression, is distinct from the compactly tufted growth form illustrated in Fig. 1A. Gradation occurred between the two forms, however, depending upon the length of the rhizome and the number of shoots developed in proximity to one another.

(ii) Elongated rhizomes

Here rhizome structure is relatively uniform. Some variation in length occurs, but all rhizomes are clearly well developed and elongated up to 150 mm in length. They are more or less uniform in width and clothed in linear-acuminate, striate, pale brown to yellow scale bracts that are persistent for the most part, but which in some taxa are lost as the rhizome became shrunken and wiry with age (Fig. 1C). Plants with elongated rhizomes have been described in the present study as stoloniferous, for example, *F. dunensis*.

Rhizome structure and growth form are useful in distinguishing some taxa (especially in the field). In the herbarium compactly tufted plants can only be differentiated from stoloniferous plants if stolons are included in the specimen.

Two species, *F. dunensis* and *F. pallens*, show variation in the development, or not, of stolons. *F. dunensis*, plants growing on sand dunes near the coast, regularly produce stolons that are usually represented on herbarium sheets. Plants from inland are compactly tufted with no evidence of elongated underground stolons. This difference may be attributed to the different habitat conditions under which the plants grow, as *F. dunensis* is a widely distributed species. In *F. pallens*, stolons are present only in var. *pallens*, distributed along the Cape Peninsula. In var. *lithosperma* from the Caledon area, no stolons have been recorded. This lack of stolons may be linked to the dry climatic conditions in this area as opposed to the wetter conditions that prevail along the Peninsula. Plants of var. *lithosperma* are compactly tufted, more rigid and have

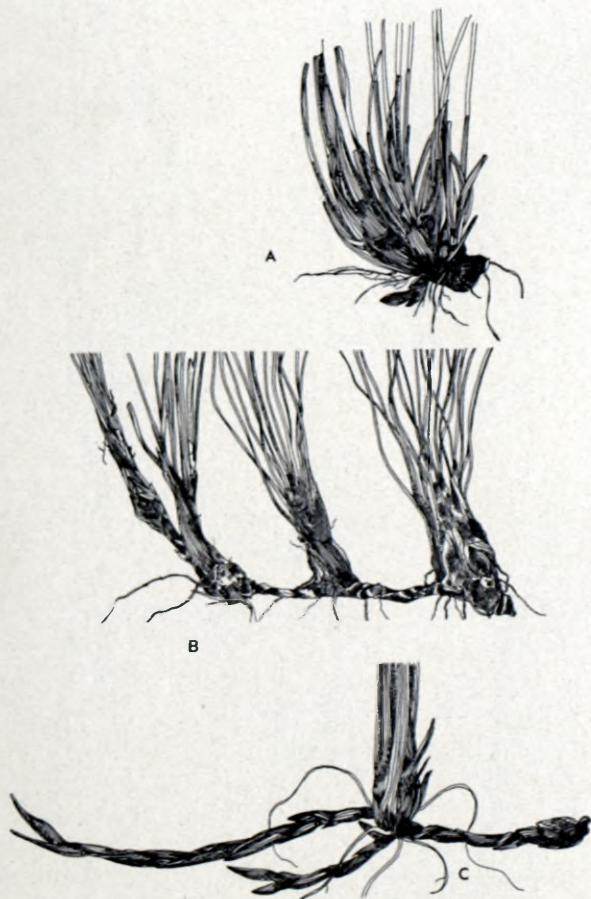


FIG. 1.—Rhizomes: A, rhizome very short, plants compactly tufted e.g. *F. capitella*; B, rhizome shortly elongate plants loosely tufted e.g. *F. pallens* var. *pallens*; C, rhizome elongate, plants stoloniferous e.g. *F. indica* (all natural size).

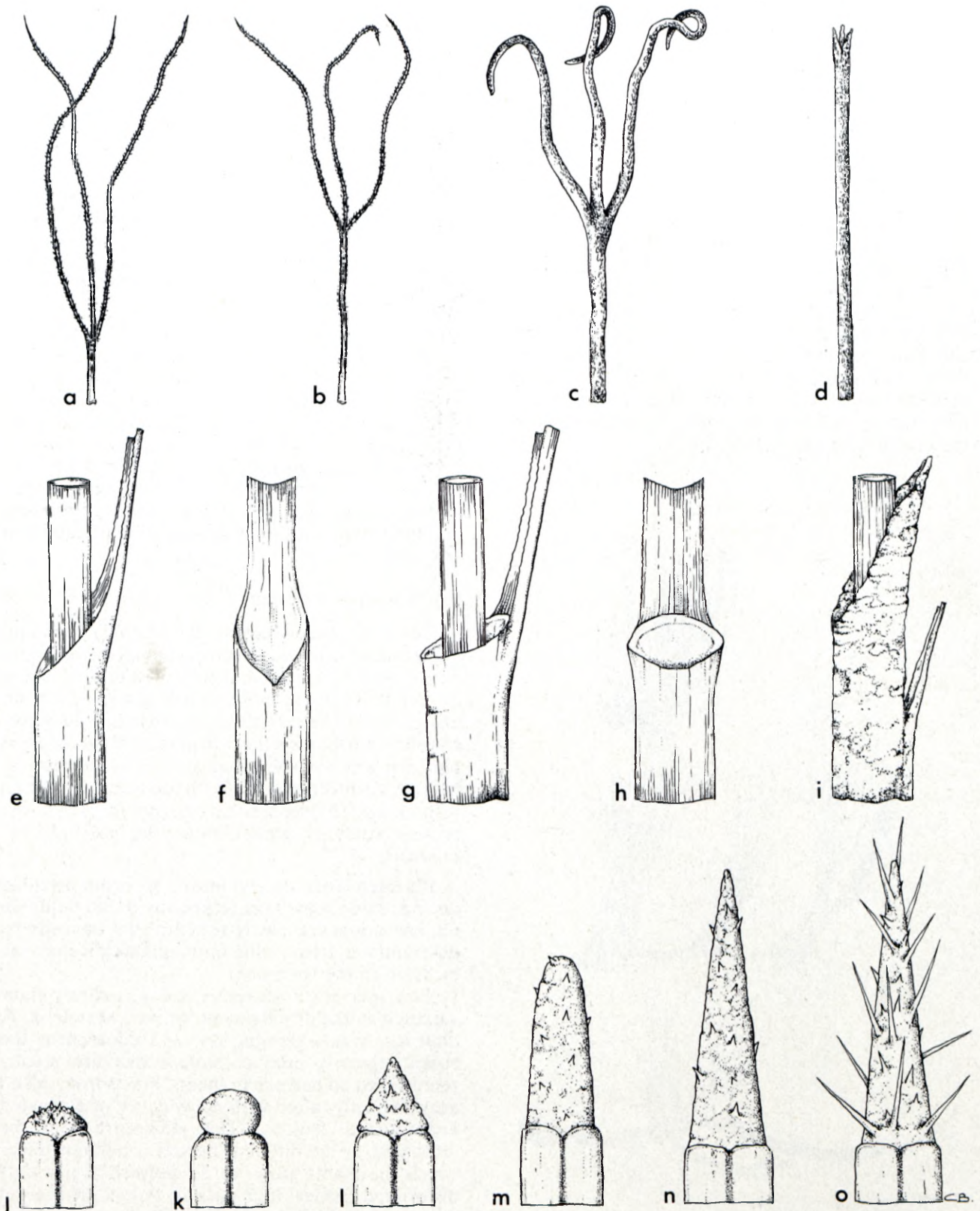


FIG. 2. — Styles and branches a-d ($\times 11$); leaf sheaths and ligules, e-i ($\times 7$); anther crests j-o ($\times 50$). a, *F. arenicola* var. *arenicola*; b, *F. ixioides*; c, *F. cedarbergensis*; d, *F. radiata*; e & f, *F. latifolia*; g & h, *F. nigrescens*; i, *deusta*; j, *F. petrophylla*; k, *F. grandiflora*; l, *F. levynsiae*; m, *F. arenicola*; n, *F. ixioides* subsp. *glabra*; o, *F. ixioides* subsp. *ixioides*.

distinctly harder inflorescence bracts than plants of var. *pallens*.

This is suggestive of adaptation to drier conditions. It is also possible that the presence or absence of stolons is to some extent genetically controlled, as the two varieties are, for the most part, allopatric in distribution, and could therefore represent independent gene pools.

Leaf sheaths and ligules

Two distinct types of leaf sheath are represented among the taxa studied. The first of these is membranous, usually transparent or pale brown to red, glabrous and splitting longitudinally with age. Such leaf sheaths are eligulate, or carry very short inconspicuous ligules that seldom exceeded 3 mm in length. In the eligulate forms the membranous sheath-tissue is joined to the two margins of the thicker sheath tissue that, when extended, formed the leaf blade. Therefore the membranous tissue does not extend across the inner surface of the leaf blade, for example, *F. radiata* and *F. latifolia* (Fig. 2e & f). In the ligulate forms this membranous portion of the sheath extends across the inner surface of the blade to form a complete cylinder, for example *F. arenicola* and *F. nigrescens* (Fig. 2g & h). The sheath apices of the eligulate forms are oblique, whereas those of the ligulate forms are more often truncate.

The second type of leaf sheath is markedly scarious or papery, wrinkled, fragile and white or greyish, and generally flecked with brown markings, for example, *F. deusta* (Fig. 2i). In this sheath type the ligule is always well developed and up to 3 cm in length in some taxa. The ligule apices, although commonly oblique, are sometimes suboblique two-lobed, or occasionally truncate. This variation occurs not only among taxa, but within them, so that as a diagnostic character the shape of the sheath apex of this second type is unreliable. It is often difficult to distinguish the original form of the stem apex because the scarious tissue, being very delicate, tears and splits easily, giving rise to a ragged, conspicuous, but uninterpretable mass of tissue near the apex of the shoot. Despite this, the two clearly different types of sheath are useful in the separation of some taxa.

Leaf blades

Most of the taxa in *Ficinia* exhibit well developed leaf blades. Only in a few taxa are elongate leaf blades absent, in the section *Bracteosae* this condition is exhibited only by *F. gynomontana*.

Leaf blade length, although not a completely reliable character in most species, is useful in distinguishing *F. petraphylla* and *F. arenicola* from other species of the section. In these two taxa the blades are characteristically longer than the culms.

Considerable variation exists in the presence and degree of development of the leaf margins. In some taxa the blades are flat, with well defined margins: in others the margins are scarcely or not represented since the blades are cylindrical. Between these extremes a complete range occurs.

Metcalf (1970) correlated the degree of infolding of the leaf margins with environmental conditions, regarding infolding as a response to dry conditions as it effectively reduces the leaf area over which transpiration can take place.

This is exhibited by plants of *F. ixioides* and *F. arenicola* var. *erecta*. In *F. ixioides* subsp. whereas distributed in the wetter south-western Cape the leaf blades are lax and broad and flattened, whereas in subsp. *glabra* distributed in the drier north-western Cape, the blades are rigid, subcylindrical and stem-like.

In many species the leaf blades exhibit a considerable range of form. Nevertheless, if used judiciously, this character is useful as an easily observable means of distinguishing those taxa in which blade form is reasonably constant and distinct. This applies especially to taxa with blades that represent extremes in the range of form.

Anatomical studies of leaf blades by Arnold (unpublished) suggest that internal structure will provide more valuable diagnostic features on which to distinguish taxa and on which to base relationships, than the gross morphology of the leaves.

Inflorescences

Inflorescences in the majority of species within the section *Bracteosae* are characteristically compact and are surrounded by an involucre of bracts. The bases of these bracts are conspicuously dilated and envelope the lower third or more of an inflorescence. The apices of the lowest 2–7 of these bracts are conspicuously attenuate into linear, photosynthetic blades that closely resemble leaf laminae.

Despite this superficial uniformity in external appearance, considerable variation is found on dissection of the inflorescence. The structural differences found, appear to be the result of different degrees of reduction within the inflorescence.

An explanation of inflorescence structure within the section *Bracteosae* is given as an aid to understanding the process of reduction that is evident.

In its most complex form the inflorescence comprises a central axis (axis 1, Fig. 3A*) that bears up to 12 or more, spirally imbricate bracts (b). These bracts are alike structurally but decrease progressively in size from base to apex. Developed in the axil of each bract is a partial inflorescence, the size and complexity of which also decrease progressively towards the axis apex.

Each partial inflorescence comprises an axis of the second order, axis 2. At the base of this axis two distichous appendages (p), are situated, one slightly

* The diagrams in (Fig. 3) are schematic representations of steps in the sequence of reduction represented within inflorescences of taxa of the section *Bracteosae*. They have been simplified for ease of drawing. No attempt has been made in this study to undertake accurate comparative morphological interpretation of the different structures represented within the inflorescences, as it was felt this was a study in itself. For taxonomic identification comparisons between structural types are considered sufficient.

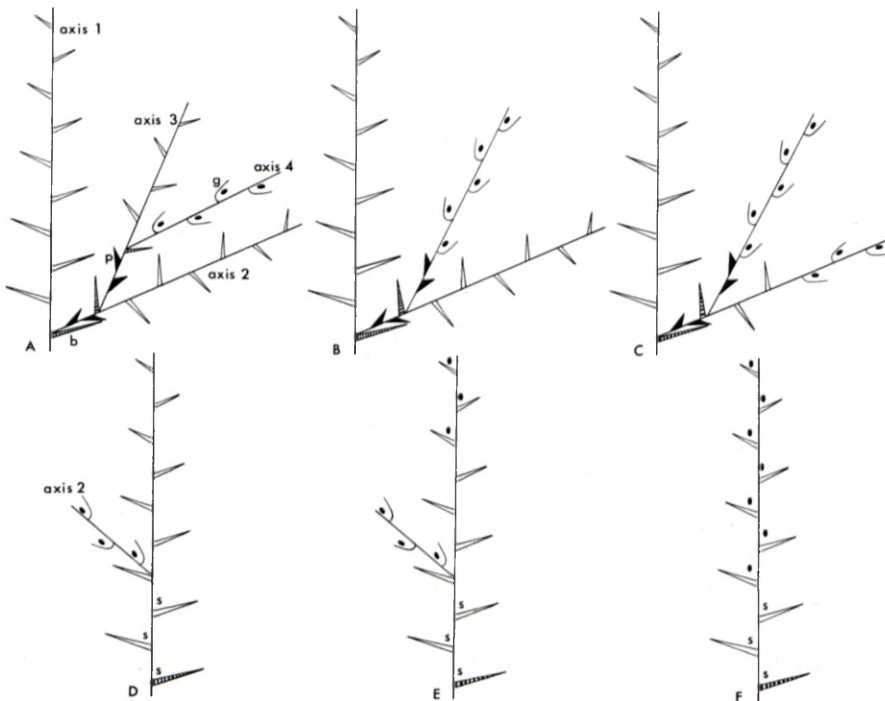


FIG. 3.—Inflorescence forms: diagnostic representation of the reduction series in *Ficina* section *Bracteosae*. A, most complex form; B–E, intermediate forms; F, most reduced form; b, bract subtending partial inflorescence or floret (partial inflorescence comprising axes 2–4); p, prophyll; g, glume; s, empty bract.

above the other. These differ in form from the bracts and are empty. They represent prophylls and will be referred to as such in the remainder of the text. Above the prophylls a number of spirally imbricate bracts are situated, also designated (b), since they resemble in structure the bracts on axis 1 and, like them, decrease in size towards the axis apex.

Each of the bracts along axis 2 subtend an axis of the third order, axis 3. Two distichous prophylls (p) similar in structure to those on axis 2 are situated at the base of this axis. Above these prophylls are a number of spirally imbricate bracts (b) resembling again the bracts on the first and second order axes.

The bracts on axis 3 each subtend an axis of the fourth order, axis 4. This axis carries a number of fertile bracts which, since each subtends a single bisexual flower and differs in form from the bracts (b), are considered to represent glumes (g). Axis 4 therefore represents what, in species within *Scirpeae* (which presumably have undergone much reduction) is usually interpreted as a spikelet. This form of inflorescence was found in *F. pallens* and *F. arenicola*.

In the remaining species varying degrees of reduction of this inflorescence form are represented. The principal effect of reduction is to decrease the number of axes comprising each partial inflorescence (see Fig. 2B & C); to decrease the number of partial inflorescences per main axis (see Fig. 2D) and to reduce the number of prophylls or to eliminate these (see Fig. 3D–F, in which prophylls are entirely lacking.)

With the loss of a single axis within the partial inflorescence, axis 4, a condition represented in (Fig. 3B) resulted. Here, each of the bracts on axis 3

subtends a single bisexual flower. These bracts have the form and function of glumes, (they resemble the glumes on axis 4 in Fig. 3A and therefore are designated — g).

In most taxa, reduction of the partial inflorescence is not uniform, being more pronounced at the apex of the different taxa than at their bases. This results in the condition (Fig. 3C) in which the upper bracts of axis 2 each subtend a single bisexual flower, while the lower bracts subtend a complete axis, axis 3. This state is found in *F. elatior* and *F. ixiioides*.

In some species the partial inflorescence is reduced to a single axis, axis 2 (Fig. 3D). The bracts on this axis resemble glumes and each subtends a single bisexual flower. In such taxa it is common for bracts on the upper portion of axis 1 to subtend single bisexual florets, while bracts on the lower portion of the same axis subtend a complete axis, axis 2 (see Fig. 3E). Characteristic of this inflorescence form are the empty 2–8 lowest bracts on axis 1, which have lost their axillary partial inflorescences.

The ultimate stage in reduction is an inflorescence comprising a single axis, axis 1 (Fig. 3F). The lowest 2–10 bracts on this axis are always empty, the remaining bracts each subtend a single bisexual flower. In this unispicate inflorescence form and the type shown in Fig. 3D & E, the bracts that subtend single bisexual flowers have maintained their bracteaceous nature, this is, however, not the case with the bracts of axis 2 and 3 of Fig. 3A–C, which also subtend single flowers but which are glumaceous, being thinner, softer, smaller, more membranous and pallid and less obviously longitudinally striate.

Accompanying the reduction of the branching axes is a reduction in the number of prophylls (p) at the base of each axis of the partial inflorescence. The inflorescence forms exhibited in Fig. 3A–C, all have a pair of distichous prophylls at the base of axes 2, 3 and 4?. In the inflorescences of *F. compasbergensis* Drège, *F. fascicularis* Nees, *F. monticola* Kunth, *F. pinguior* C.B.Cl. and *F. anceps* Nees, also included in the section *Bracteosae* by Pfeiffer (1920), only a single prophyll is situated adaxially at the base of each of these axes. Apart from exhibiting a single prophyll the first three taxa above also have branching inflorescences, considered to be a typical of the section *Bracteosae* in which the majority of taxa have, compact capitate inflorescences enveloped to a lesser or greater degree by an involucre of dilated inflorescence bracts. These three taxa are therefore, on the grounds of inflorescence form, tentatively excluded from the section *Bracteosae* pending revision of all the sections in the genus.

Although the single prophyll conditions suggests a more reduced condition from paired prophylls, this may not be the case in *Ficinia*. In this genus the progression in prophyll number is considered to have been from 1→2→0. This sequence is suggested firstly by the fact that taxa with a single prophyll include those with branching inflorescences, generally regarded as representing a condition of limited reduction in the Cyperaceae. Secondly those taxa exhibiting the most inflorescence reduction are all wanting in prophylls. In all these taxa, except one, *F. nigrescens* (Schr.) J. Rayn., reduction of the branching system is complete, producing a unispicate inflorescence. In *F. nigrescens* reduction is not always maximal so that, together with plant bearing unispicate inflorescences, there are also plants in which all or few of the lateral branching systems (partial inflorescences) constitute single spikelets. In

both these conditions prophylls were found to be wanting.

The three prophyll states in *Ficinia* are considered to be related to the degree of reduction in number and size of branching axes comprising each partial inflorescence. With compaction there is a comparable increase in pressure on the internal structure of the inflorescence, this being greatest in the axil of each branch in the region of the lowest adaxially situated bract (Fig. 4A). The result being to alter its size and structure transforming it into what is commonly referred to as a prophyll. This situation represented by the single prophyll condition is found in the majority of taxa in *Ficinia*.

In the section *Bracteosae*, compaction of the inflorescence has been accompanied by a change in the nature of the inflorescence bracts. The base of each bract has to a lesser or greater degree become dilated, expanding around the partial inflorescences in the form of an involucre. The dilated portions have also become thickened, hard and rigid. The result has been to further increase the internal pressure within the inflorescence, this time concentrated in the region of the second lowermost bract of each axis (Fig. 4B), reducing it to a further prophyll.

The degree of dilation, thickening and hardening of the inflorescence bracts decreases progressively towards the centre (apex) of the inflorescence. Because of this the extent to which the two lowermost bracts/glumes on axes 3 and 4 (Fig. 3 A–D) have been modified is generally less than in axes 1 and 2, so that they are not always distinguishable as prophylls. At the other extreme, the 1–2 lowermost bracts of axis 1 exhibiting the greatest degree of dilation and hardening, and therefore the greatest pressure, are in many taxa sterile.

In those taxa, in which prophylls were wanting, the number of sterile bracts at the base of axis 1 ranged between 2 and 6. This increase over taxa with 1–2 sterile bracts (plants with double prophylls) is probably due to the overall increase in dilation and hardening of bracts along axis 1. In these taxa the increased pressure along axis 1 has not only caused the loss of the double prophyll condition but has also reduced each partial inflorescence to a single floret. Therefore, whereas in most Cyperaceae the absence of prophylls represents a less specialized condition of limited reduction, in the section *Bracteosae* of *Ficinia* this condition is synonymous with maximum reduction and specialization.

In *F. pinguior* C.B.Cl., placed by Pfeiffer in the section *Bracteosae* although the inflorescence bracts have undergone dilation they have not become thickened or hardened. As this taxon exhibits a single prophyll condition, hardening of the bracts is seen as an essential factor responsible for the production of the second prophyll. Another taxon in which this may be observed is *F. paradoxa* (Schr.) Nees, placed by Pfeiffer in the subsection *Capitulae* of the section *Isolepiformes*. *F. pinguior* is considered here to be more closely related to this taxon than any of the taxa included in the section *Bracteosae*. It is not known at this stage whether *F.*

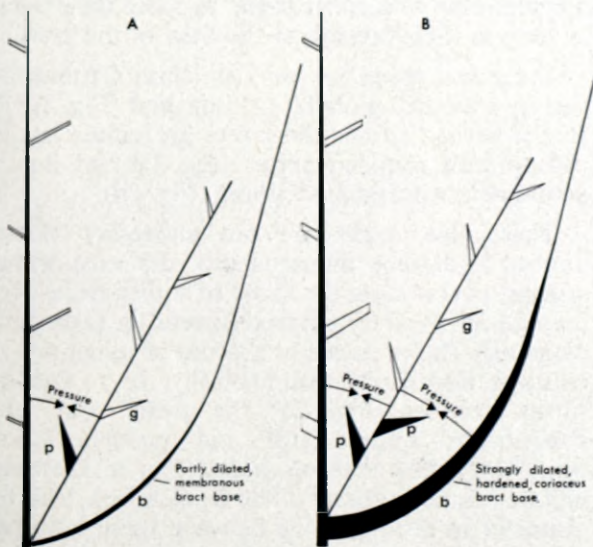


FIG. 4.—Prophyll states: A, single prophyll state characteristic of all sections other than section *Bracteosae*; B, double prophyll state represented by the majority of taxa in the section *Bracteosae*.

pinguior with *F. paradoxa* should be included within the section *Bracteosae* or not. The evidence so far gathered suggests not, and *F. pinguior* is therefore tentatively excluded from the section pending revision of the genus.

Also included by Pfeiffer in the subsection *Capitulae* of the section *Isolepiformes* are *F. argyropa* Nees (= *F. paradoxa* (Schrad.) Nees var. *argyropa* (Nees) C.B.Cl. and *F. laevis* Nees. Not only do these two taxa have hardened, dilated bases to the inflorescence bracts, but they also exhibit the double prophyll condition. Their closest ally within the genus is considered to be *F. indica* (Lam.) Pfeiff. On the basis of this they are included here in the section *Bracteosae*.

Another species warranting special consideration is *F. anceps* Nees, also considered by Pfeiffer to belong to the section *Bracteosae*. This taxon has only a single prophyll per inflorescence axis. Although its bracts have undergone dilation and hardening this is not so marked as in other taxa in the section. The lowest bract and partial inflorescence in many plants is up to 1.5 cm distant below the partly compacted upper section of the inflorescence. It therefore probably represents an intermediate stage towards the development of section *Bracteosae*. *F. anceps* is most closely allied to *F. fastigiata* Nees. This latter species also exhibits a single prophyll condition and is included by Pfeiffer in subsection *Capitulae* of the section *Isolepiformes*. *F. anceps* has therefore also been omitted from this treatment of the section *Bracteosae* until its relationship with the rest of the genus is better understood.

It should perhaps be noted at this point that prophylls are associated only with the axes that comprise partial inflorescences. It is probable that these appendages, despite their different appearance, are morphologically equivalent to the bracts of ancestral less reduced inflorescences. This has been accepted by Blaser (1944) and Koyama (1961) but, perhaps, needs further confirmation from anatomical and vascular investigation. The recording of the presence of prophylls in inflorescences within the section *Bracteosae* is an important step forward in appreciating the heterogeneity of *Ficinia* as it is at present delimited. Prophylls have not been recorded previously for the genus and they are certainly absent from those of its species with 'simpler' more reduced spikelets that are of the *Scirpus* type.

The degree of reduction of the inflorescence is not completely constant within each species. Many taxa exhibit two or occasionally three (for example *F. nigrescens*) inflorescence forms. Despite this the degree of reduction of the inflorescence, together with the number of prophylls present, are extremely important characters by which to distinguish different taxa within this section.

Style and style branches

Three main types of style are represented in the taxa studied. The differences between these types depend mainly upon robustness, slenderness and on relative lengths of style and style branches. In the commonest type, the style and its branches are

slender and relatively elongate, pale brown and flecked with darker markings, with the style branches obviously papillate. The lengths of the fused lower portion of the styles relative to those of their branches varied considerably within the section and proved to be a useful means by which to distinguish many species. In some taxa the fused section is short (1–2) mm in length with very long branches 6–10 times the length of the fused section, for example *F. capitella* and *F. arenicola* var. *arenicola* (Fig. 2a). In other taxa the fused section and branches are approximately equal in length, for example *F. ixioides* (Fig. 2b).

The second type comprises styles that are notably broad and stout, red or pale brown with brown flecks and with the style branches granular rather than obviously papillate. The difference in appearance of the style branches depends upon the reduced length of the papillae. Examples of this type are *F. cedarbergensis* and *F. levynsiae* (Fig. 2c).

The styles of *F. radiata*, which also belongs to the second type (Fig. 2d), are characteristic of this species alone. They are broad, stout and granular and either lacked branches entirely or possessed three minute notches at the style apex that represented branches. On these features, together with a few other individual characters, this taxon was at one time placed in *Sickmannia*, a monotype genus distinct from *Ficinia*. (Such a treatment is not upheld by Arnold, 1979.)

Anthers

Anthers in *Ficinia* are crested. In the section *Bracteosae* the shape and degree of development of the crests provided a useful additional character by which to delineate many of the taxa.

Five basic forms are recognized (Fig. 2j–o). These fall into two broad groups. The first group includes those with crests as long as, or shorter than, their breadth at the base of the crests, group two includes taxa with crests twice, or more than twice, as long as their breadth at the base of the crest.

In the first group the crests are either flattened or slightly rounded, globular or triangular (Fig. 2j–l). In the second group the crests are either linear-oblong with rounded apices (Fig. 2m) or linear-acuminate with pointed apices (Fig. 2n).

These five forms are not altogether clearly defined and some intermediates, did exist within species, nevertheless the shape of anther crests does provide an ancillary character useful in taxonomic diagnosis. The presence or absence of spines on the crests is also useful taxonomically. In *F. ixioides* subsp. *ixioides* (Fig. 2o) the crests bear long conspicuous spines (stiff and possibly silica-containing) while in subsp. *glabra* (Fig. 2n) these are minute (virtually absent). This is, therefore, a useful character in distinguishing between these infraspecies.

Achenes

Achenes of the different taxa differed in size, shape, colour and surface texture.

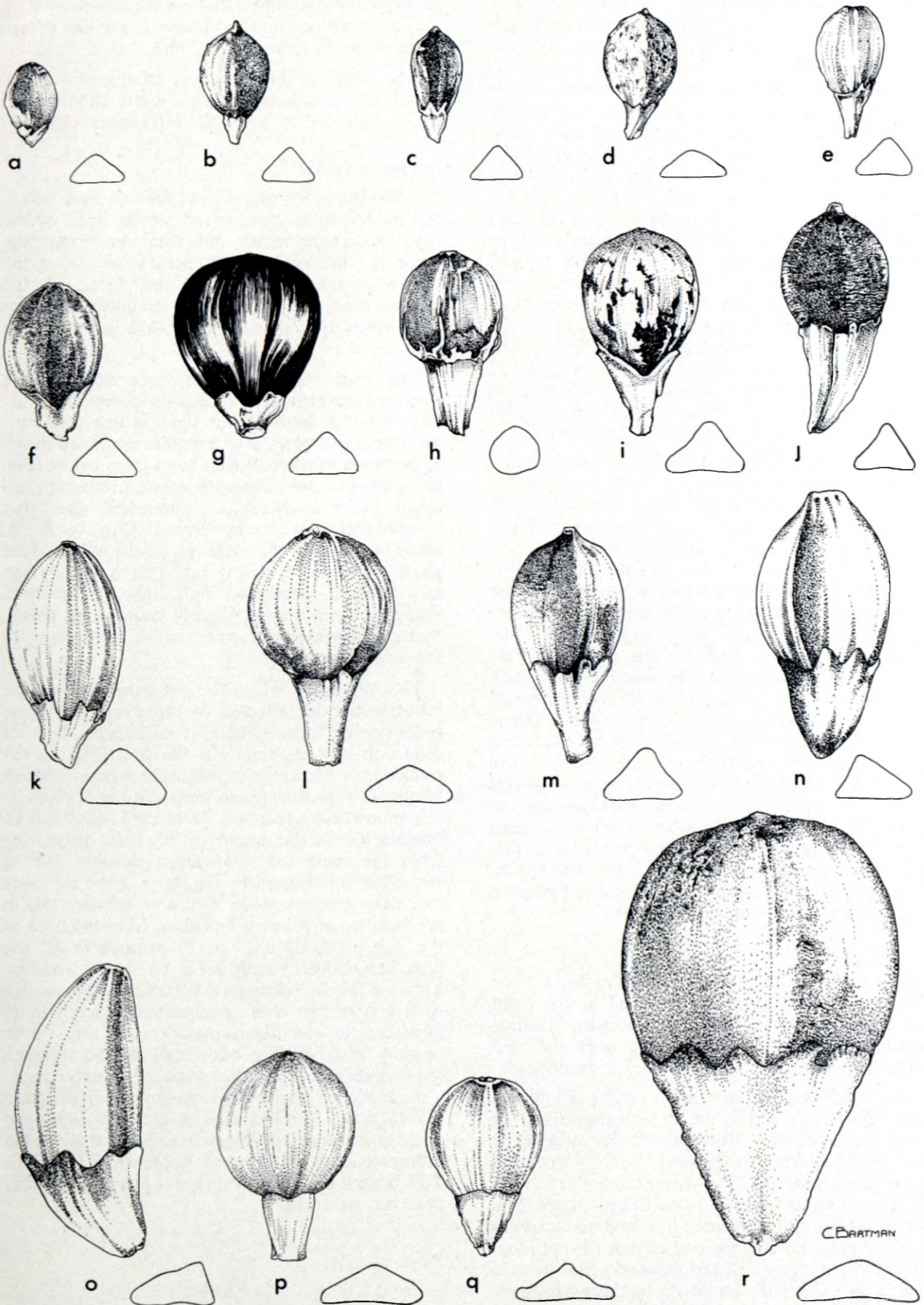


FIG. 5.—Achenes and gynophores; a, *F. pusilla*; b, *F. indica* taxon *indica*; c, *F. capitella*; d, *F. arenicola* var. *erecta*; e, *F. pygmaea*; f, *F. nigrescens*; g, *F. ixioides* subsp. *glabra*; h, *F. latifolia*; i, *F. arenicola* var. *arenila*; j, *F. dunensis*; k, *F. pallens* var. *lithosperma*; l, *F. petrophylla*; m, *F. pallens* var. *pallens*; n, *F. cedarbergensis*; o, *F. levynsiae*; p, *F. gydomontana*; q, *F. grandiflora*; r, *F. deusta* (all $\times 10$). Insets represent shape, in transverse section, at widest part (not drawn to scale).

Achene size ranged from 1.5–2 mm in length by 1 mm wide (*F. pusilla* Fig. 5a) to ± 6 mm in length by ± 4 mm in width (*F. deusta*, Fig. 5r). On individual plants and within taxa there is generally little size variation despite the fact that, especially in herbarium material, it is sometimes difficult to establish whether the achenes are fully mature and fertile or not. Achenes are usually three-angled or trigonous but often the ridges are not very sharp; mostly the faces equal each other in width (*F. ixiooides* Fig. 5g), but in *F. cedarbergensis* (Fig. 5n) and *F. levynsiae* (Fig. 5p) they are unequal resulting in asymmetrical achenes. In *F. deusta* (Fig. 5r) and *F. grandiflora* (Fig. 5q) achenes are planoconvex, whereas in *F. latifolia* they are spherical (Fig. 5h). Achene apices also differ in some taxa. Most apices are obtuse or rounded; a few are acute often with a distinct but small beak for example *F. capitella* (Fig. 5c) and *F. dunensis* (Fig. 5j), whereas others are broad and flattened or retuse as in *F. cedarbergensis* and *F. levynsiae* (Fig. 5n & o).

The surface texture of the achenes is smooth and often polished, for example *F. ixiooides* subsp. *glabra* (Fig. 5g), finely dotted (muricate), for example *F. indica* taxon *indica* (Fig. 5b), or transversely ridged as in *F. capitella* (Fig. 5c) and *F. dunensis* (Fig. 5j). Surface patterning of the achenes differs only negligibly within taxa therefore achene size, shape and surface markings are useful criteria in identifying taxa. Achene colour is not so satisfactory. All immature nuts are more or less uniformly pale yellow to brown in colour. This colour changes with maturity to black, grey, brown or red. Although there is a difference in achene colour between species at maturity, the possibility always exists that there is a colour range as the achenes develop to full size on the plant after fertilization so that no one colour is specific for a taxon. There is also no guarantee that unfertilized achenes follow the same colour sequence during development nor that achene colour does not alter in the herbarium. Consequently not much reliance should be placed on this character in taxonomic diagnosis.

Gynophore

The presence of a gynophore below the achene was (and still is) generally accepted as the main character that distinguishes *Ficinia* from its allied genera. Despite this, there have been included within *Ficinia* several taxa that lack a gynophore.

As mentioned earlier Clarke (1898) felt that it was difficult to attach much importance to the gynophore in *Ficinia*. Although this may certainly be true in the diagnosis of generic limits it does not apply infragenerically. The present investigation has shown there to be little variation in gynophore form within species and subspecies but from one taxon to another gynophore shape and degree of specialization of the margins differed markedly thus being a satisfactory character on which to recognize many species and sometimes infraspecific sub-units.

In the section *Bracteosae* the gynophore envelops the lower portion of the achene. It shows a considerable range in variation from two or three lobed as in *F. nigrescens* (Fig. 5f), to cup-shaped

with the upper margin crenate as in *F. levynsiae* (Fig. 5o) or developed into prominent finger-like projections as in *F. latifolia* (Fig. 5h).

The length of the gynophore relative to the total length of the achene is also a useful character. It ranges from 1/6 to 2/3 of the total achene length.

Inflorescence axis

After the bracts glumes and achenes have fallen, the inflorescence axis persists at the apex of the culm, remaining intact until the culm breaks up. Since the old culms often persist until after the following flowering season the form of the inflorescence axis is a readily available character with which to distinguish many taxa in the section *Bracteosae*.

The least reduced inflorescence axis shows a structure in which the branches associated with bract scars occur at intervals through the axis (Fig. 6a). More reduced types have branches restricted to the upper third of the axis with bract scars below (Fig. 6h). Inflorescences where the greatest reduction had taken place resulted in unbranched axes that resemble elongate empty strobili (Fig. 6n & p). Some breakage of these axes especially falling of the small branchlets probably takes place as they age and become weathered but, apart from these changes (which may be slightly misleading), persistent axes provide a convenient and reliable character for identifying taxa.

The sequence of reduction exhibited in the inflorescence is reflected in the structure of the inflorescence axis. A number of possible lines of reduction are apparent. In the first (Fig. 6a–e) reduction is concentrated within the main axis which becomes progressively shortened until in *F. capitella* it is almost receptacle-like. Associated with this is an obvious loss in the number of branches originating from the main axis. A second possible line of reduction is indicated by Fig. 6f–j. Here the main axis has become swollen with a progressive loss in the number of primary branches, from the base of the axis upwards until in *F. petraphylla* all the branches are lost. Finally in Fig. 6k–p, the tendency has been for the main axis to become elongate with a total loss of branches in these taxa, except in *F. nigrescens* in which some members still retain their primary branches (Fig. 6m). In *F. ixiooides* although the branches have been lost some individuals possess a single branch originating from the base of the main axis (Fig. 6k). This branch is often as well developed as the main axis, equalling it in length and giving the inflorescence axis a forked appearance (Fig. 6l). This branch if present is however generally smaller than the main axis.

CONCLUSION

Most previous workers tended to rely mainly on easily observed morphological features such as the presence or absence of leaf blades the nature of the leaf sheath together with the presence or absence of a ligule, and the gross structural form of the

inflorescence. Only when these characters failed was there any searching for less obvious differences such as the structural features of glumes, style and achene. Consequently, many highly suitable characters that could have been used to define the different taxa clearly and which would have provided a better understanding of the interrelationships within the genus, were not considered.

This investigation has revealed a number of characters within the inflorescence previously unused in classification. These include: the structure of the inflorescence, the presence, absence and number of prophylls, the style and style-branches, anther

crests, achenes, gynophores and inflorescence axis. These have provided a valuable means by which the limits of many existing taxa have been refined. They have also provided the basis on which a number of new taxa have been established (Arnold & Gordon-Gray, 1978). Therefore their use has clarified, or partially clarified, some of the taxonomic confusion that existed within the genus, and by this has improved understanding of relationships within it.

UITTREKSEL

Die grense van die genus Ficinia word hersien. Morfologiese variasie binne die afdeling Bracteosae



FIG. 6.—Inflorescence axes after floral parts have fallen: a, *F. pallens*; b, *F. latifolia*; c, *F. indica*; d, *F. capitella*; e, *F. dunensis*; f, *F. elatior*; g, *F. radiata*; h, *F. cedarbergensis*; i, *F. levynsiae*; j, *F. petrophylla*; k & l, *F. ixiodides*; m, *F. nigrescens*; n, *F. nigrescens* and *F. gydomontana*; o, *F. grandiflora*; p, *F. deusta*. (all $\times 3$).

Pfeiff van Ficinia Schrad. (Cyperaceae) word bestudeer en bespreek. Kenmerkende eienskappe wat voorheen in klassifikasies gebruik is, word saam met 'n aantal nuwe eienskappe hersien. Hulle het dit moontlik gemaak dat die grense van baie bestaande taksa duideliker vasgestel kan word en het die grondslag verskaf waarop 'n aantal nuwe taksa wat onlangs beskryf is, vasgestel kon word. Eienskappe wat bestudeer is, sluit in: ondergrondse organe, blaarskedes, ligule, blaarskywe, strukture van bloeiwyses, skutblaartjies, style, helmknoppe, dogvrugte, stamperstele en die asse van bloeiwyses.

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