STUDIES IN THE ARUNDINELLEAE (GRAMINEAE) VIII.
THE PHYLOGENY — A HYPOTHESIS

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CONTENTS

ABSTRACT

This study considers the 163 species accepted as belonging to the tribe *Arundinelleae* (*Gramineae*) and arranges them into a putative cladogram. A discussion of the rationale is presented, 38 characters are studied for advanced versus primitive states, advancement indices calculated, and trends of variation discussed. The six major groups of Phipps (1966b) are maintained. The phylogeny conforms excellently with the geographical aspects of the continental drift hypothesis though it requires a greater age for the Angiosperms than is generally held to be the case.

1. INTRODUCTION

The present paper, the eighth in a series dealing with variation in the tribe *Arundinelleae* (*Gramineae*), is an attempt to derive a tentative phylogeny of a group quite intensively

studied morphologically (Hubbard 1936, Keng 1936, Bor 1955, Conert 1957, Phipps 1964, 1966a and b, 1967a, Correia, Lubke & Phipps, 1967) but lacking any known fossil record.

The classification of Phipps (1966b) can be considered to be the basis for this paper. In that study some taxonomic structure emerges, but not much, there being a lack of detailed hierarchisation and no numerical analysis. The rationale of that paper was mainly single linkage augmented by a proposed splitting of the tribe into six parts, though rigorous numerical techniques were not utilised in an attempt to justify conclusions. Phyletic considerations (the formation of groups A-F) were permitted to split *Loudetiopsis sensu* Conert even though phenetic evidence might have suggested the retention of *Diandrostachya* in *Loudetiopsis*.

This paper is a phyletic explanation of the classification of Phipps 1966b as that paper has been amended by Phipps 1967a and Correia, Lubke & Phipps, 1967. It includes a discussion of the rationale used, the characters used, the phylogeny derived, and an inference on the primitive Arundinellean or proto-Arundinellean.

2. THE NATURE AND INTERPRETATION OF PHYLOGENETIC EVIDENCE

(i) Phylogenies hypothetical

Phylogenies must inevitably be no more than hypotheses, so weak is the reliably interpretable evidence and, as a result, correspondingly strong the speculation, except in rare extremely well-documented cases. The evidence for a phylogeny is, of course, straightforward: it is the same data (characters) from which a phenetic taxonomy is drawn. The data will preferably be drawn from all members (i.e. fossil and extent) of the group under consideration and presumably the most reliable phylogenies are those based on a good fossil record. In such cases reliability depends on the number of fossilised individuals and on the number of characters which are preserved. In the ideal case the individuals form a (furcate) continuum in taxonomic (phenetic) hyperspace and geological time.

(ii) The interpretation of phylogenetic evidence

In these 'well-documented' situations, there need be little argument about the accuracy of the main lines of phylogeny produced. However, not infrequently there are gaps in the known fossil record and it is here that a combination of intuition and speculation (less kindly, 'guesswork') together with Simpson's 'aesthetic sense' (1961, p. 4) help us to extrapolate with our dotted phylogenetic line, through the gaps that are the empty regions of taxonomic hyperspace.

Are there any more reliable means of navigating the uncharted empty areas than those mentioned in the previous sentence? It seems that, subject to degrees of probability difficult to calculate, there may be. The fundamental problem to be solved since attempts at phylogenies have become fashionable involves defining the particular distinction between the more primitive (i.e. cladistically basal) and the more advanced (cladistically acropetal) states of a given character, and this is discussed further on. Meanwhile certain other factors must be discussed.

(iii) Conservative characters

In a sufficiently diverse group many significant (= obvious) characters vary. In the old days of phylogeny the more 'fundamental' (because 'conservative') characters (in our terms: conservative character 'states') would be used to indicate the main delineations

of the cladogram but it is now understood that as a premiss such an approach is unworkable for much parallelism exists in the phylogeny of any sufficiently diverse group (i.e. most sufficiently large groups) – an observation empirically attestable if one cares to juggle with cladistic re-arrangements to eliminate it. But though conservative characters are those displaying little or no parallelism and these characters may be known from the inspection of any adequately annotated cladogram, nonetheless, in a sufficiently complex situation (as is common) various alternative sets of character states could be made cladistically basal and consequently conservative. Accordingly, conservative characters. though they should emerge as a conclusion, have tended to be used as a premise, for unfortunately, in practice, there are rarely cogent reasons adduced for their choice which avoid circularity. It is therefore the point of view of the present writer that nothing whatsoever may be mentioned of conservative characters states except as conclusions.

(iv) Selection of advanced and primitive character states

There remains the problem of deciding on the particular advanced and primitive states of each character. Apparently there is no good or at least universal way of doing this. The principle criterion is the contention that more 'specialised' (i.e. more complex) character states are more advanced than less 'specialised' ones. However, this assumption may lead to apparently absurd (at least, unlikely) results. Consequently, it must be allowed that a complex state can sometimes proceed to a more simplified one, an escape fortunately justified by the example of certain well-documented phylogenies. Other criteria commonly used are that vestigial characters are advanced (really a special case of complex state proceeding to a more simplified one) and that embryonic or early ontogenetic character states tend to be 'conservative' (a criterion to be treated with great caution). In addition Sporne (1960) has demonstrated a fairly strong correlation among character state sets in Angiosperm families, the one set being primitive, the other advanced, though there is no criterion inherent in his statistical investigation for saying which is which. There has been very little follow up on Sporne's approach.

Wagner (condensed in Benson, 1962), using in-group—out-group comparisons, gives yet further criteria for probable primitiveness, this time based on the taxonomic distribution of character states, e.g.:

1) that which is most primitive exists in all taxa of the next lower rank and all nearly related taxa of the same rank;

8) that which is most advanced exists in the minority of the taxa of the next lower rank and in none of the taxa of the same rank. Wagner in his duplicated class-sheet lists 6 intermediate situations on a graded series.

Wagner's approach has been used by Iltis (1959), White (1963), and various other workers.

However, such criteria as Wagner's, when actually used for the likelihood of any given character state being primitive or advanced, may seem rather alarming, in principle, to use upon a new group. They have never been defended on a logical basis and seem to be intuitive. If they someday prove to be correct as generalisations they will be very important criteria. However, to be proved correct, they must be shown to be general in phylogenetic cases which have not used them as premises, and this investigation has yet to be made.

(v) The character states used

The literature indicates that the *Arundinelleae* are quite well described morphologically. Morphological data are available in the type descriptions and in very many floras and

nay be sought using the references given after each species in Phipps (1966b) and, for very recently described taxa, in Correia, Lubke and Phipps (1967). A general description of variations in Arundinellean characteristics may be found in the discussion in Phipps 1964 (pp. 88—92) and in the table (op. cit., opposite p. 120). However, we cannot utilise all known characteristics for deducing our phylogeny since for a number we have no opinion whatsoever as to which state might be advanced and which primitive. Table 1 illustrates the characters actually selected.

(vi) Number of characters used

Note that in order to produce a dichotomous cladogram in which no more than one O.T.U. occupies any terminal branch at least that number uf characters represented by the maximum number of furcations from any tip to the base of the cladogram must be utilised so long as evolutionary reversals are excluded. And in a perfectly symmetrical cladogram containing n ultimate entities, for each to be displayed separately, there must be x furcations (∴ use x characters) for this is the cladogram of minimal length. Since $2^x = n$ and $x = log_2 n$. But in a cladogram of maximum length there will be $n - 1$ furcations (greatest asymmetry) along the longest branch. This naturally corresponds exactly to the situation in dichotomous keys (Osborne, 1963). In order, therefore, to present a minimal (that is to say where the minimum number of furcations are used to separate all O.T.U.s) displayal of a given cladogram of n terminal entities a number of characters (y) lying between $log_2 n$ and $n - 1$ must be selected. However, where n is large the range between $log_2 n$ and n is also very great, consequently there is great uncertainty as to the appropriate value for y. In this paper it was hoped that when $y = 40$ adequate discrimination would result. This has proven to be so, there being not too great asymmetry in the resultant cladogram. [The *Arundinelleae* contains 163 species (Phipps, 1966b, Correia, Lubke & Phipps, 1967), consequently for the symmetrical cladogram $x = 7.5$ while for the most asymmetric situation $n - 1 = 162$]. We must operate in a range of characters for cladistic discrimination between 8 (i.e. immediately above 7.5) and 162, i.e. the 40 characters used. However, great asymmetry appeared unlikely and for a first investigation great discrimination is not required, therefore this number was not unsatisfactory on an *a priori* basis.

3. THE REPRESENTATION OF A PHYLOGENY

In principle there is no problem in the representation of a phylogeny. A dichotomous (or occasionally partly tri- to oligochotomous) tree drawn in two dimensions immediately displays the cladistic relationships deduced. However, the relationships in totality of the parts in taxonomic hyperspace cannot become part of the conventional cladogram without considerable distortion (for too many dimensions are being introduced for a visual representation to be satisfactory since this can at best attain three dimensions) unless a very high percentage of the total variation can be accounted for by two independent components.

In addition to cladistics what else might one wish to indicate in a phylogenetic diagram?
a) Chronology;
b) Advancement indices.
Both a) and b) are perfectly easy to incorporate where data are available.
In the ideal situation, that is to say where data are most nearly complete and speculation is minimal, the most appropriate procedure for displaying phylogenetic data is as follows:

a) a cladogram, which is necessarily an accurate representation of the branching sequence, plus the chronology and advancement indices;

b) devices which illuminate relationships of taxa in hyperspace (t × t tables, taxonomic dendrograms, ordinations).

The present paper concerns itself with a cladogram (broken down into figs. 1—17) in which many of the character states of table 1 are incorporated. No chronology is known for the *Arundinelleae* and hyperspace relationships are the subject of still unpublished work.

(i) Principles for arranging cladograms

Four useful principles for building phylogenies exist. They are:

a) the cladogram will be so arranged that the most similar terminal taxa come together (Wagner's method emphasises this aspect; see Benson, 1962, 414—416; Gupta 1962, 115);

b) parallelism in the cladogram shall be reduced to a minimum (Camin and Sokal's method — Camin and Sokal, 1965 — emphasises this aspect);

c) phyletic taxa formed shall be joined by their most primitive elements (Thorne, 1963);

d) reversal of evolutionary trends is rare (Camin and Sokal, 1965).

Combinations of these, working from phenetic data and evolutionary speculation, produce the final cladogram.

4. PHYLETIC CLASSIFICATIONS

Phyletic classifications are, perhaps, not particularly pointful. A good phenetic classification deals fairly adequately with the major variation trends and will inevitably show the stronger forms of clustering. Unless phyletically interpreted it may show grades, rather than clades. *Loudetiopsis sensu* Conert is here believed to be a grade.

Cladistic relationships are easy to illustrate (as used in this paper) and the cladogram can also readily incorporate other data such as advancement indices and evolutionary steps. However, to break down a cladogram into a hierarchy is not easy, there being no agreed set of rules to follow. Hennig's (1950) notion that the classification shall automatically follow the cladogram is not here considered satisfactory since cladistically close taxa may be phenetically very divergent and vice versa. A paper by Phipps (1966b) and the classification presented at the end of this paper are to some extent based on grades (e.g. inclusion of *Pleioneura* in *Loudetia*) but are also cladistic (for instance, in the separation of *Loudetiopsis* from *Loudetia*). The tendency here is to use the cladistic situation as definitive for the classification where there is strong parallelism and considerable branching separation (e.g. *Loudetiopsis sens. str.* and *Diandrostachya*) and also to use it as definitive where there is striking differentiation of certain characters but close cladistic relationship (e.g. *Loudetiopsis* is separated from *Loudetia*).

Genera are largely defined on the basis of sufficiently large or striking circumscribing discontinuities (the 'moats' of Wirth, Estabrook, and David Rogers, 1966).

5. CRITERIA ACCEPTED FOR THIS PAPER

This paper therefore takes the following stands:

i) Advanced versus primitive states are assigned on the bases of:

a) frequency in the tribe;

b) frequency in the *Gramineae*;

c) degree of complexity — the more 'specialised' state being the more advanced.

The specific decisions as to advanced and primitive character states are those given in table 1. Where the general arguments and their qualifications have been presented without inside evidence in the case of any given character (i.e. morphogenetic, embryological, etc.) Wagner's principles, speculation, or 'aesthetic judgement' become the arbiters. Table 1 includes some mention of the rationale.

ii) Closeness of phenetic relationship implies phyletic closeness. (It is assumed that sets of parallelism will not generally interfere with this stand so long as sufficient characters are utilised in the study. Where sufficient characters are employed, parallelistic developments, which might otherwise masquerade as monophyletic ones, should be recognisable). There is no reliable way, apparently, in the *Arundinelleae* of distinguishing between homoplastic and patristic homology (see definition in Sokal and Camin, 1965).

iii) Phyletic groups formed on the basis of close taxonomic resemblance will be united tentatively on the basis of their most primitive representatives. In the work for this paper the overall phylogeny has been built up by identifying small phenetic units (i.e. sets of very similar species such as genera, sections, etc.) and by successively uniting each group so identified.

iv) Parallelism shall be reduced to a minimum. This consideration is not treated rigorously in this paper due to the extremely numerous computations required for its solution.

v) Evolutionary reversals shall appear at minimal frequency.

Rigorous methods for evolving cladograms, using criteria i), iv), and v) have been developed by Camin and Sokal. They are consciously avoided in this paper which is a test-case of a subjective interpretation of stated criteria.

6. THE PHYLOGENY DEDUCED

Most of the remainder of this paper is concerned with the presentation of the cladograms (figs. 1—17) that have been inferred (partly with the use of the advancement indices mentioned earlier) and with a discussion of the individual cladograms. The discussion moves from the smaller groups (discussion of species within genera) to the overall group, in view of the fact that this was, for the most part, the method of approach.

(i) Individual genera

1) *Arundinella* (fig. 2)

This genus of 47 species is extremely homogeneous, and the characters used in tribal taxonomy give very little evidence for cladistic affinities within the genus. Nevertheless, an extremely tentative arrangement is given in figure 2. Many auxilliary characters would have to be studied in order to illuminate this situation.

2) *Jansenella*

This genus is monotypic.

3) *Loudetia* (figs. 3—7)

The 38 species of *Loudetia* fall into fairly clearly demarcated sections. However, the differences amongst these sections are, for the most part, quite small and difficult to put reliably into cladistic form. The result must be regarded as relatively tentative.

The small (2—3 spp.) section *Pleioneura* is well isolated on several characters and may be regarded as the beginning of a line to *Rattraya*. Trends to spiciformy (subsect. *Densispicae*), to annualism (some subsect. *Densispicae*, subsect. *Annuae*, sect. *Lophanthera*) and to a neuter lower floret and remarkable awn-column (sect. *Lophanthera*) may be regarded as particularly important. The genus *Loudetiopsis*, if *L. glabrata* be truly its

most primitive member, must needs originate within section *Loudetia*. The rationale used defines subsect. *Acuminatae* as the most primitive of existing *Loudetia*, largely on the basis of its possession of 3 stamens per floret.

Loudetia section *Loudetia* is characterised by its orange-buff-brown spikelet coloration, medium-sized (mostly 8—14 mm long) spikelets, lack of the varied characteristics of the upper floret so abundant in the Tristachyoid and Danthoniopoid groups (but also found in *Trichopteryx*, *Dilophotriche*, and *Jansenella*), and its generally paired spikelets. In general, lack of special characteristics is the feature, a situation shared by *Arundinella* and the more primitive Tristachyoids (especially *Tristachya*) that is notable in *Loudetia*. *Loudetia* section *Loudetia* are mainly plants of grassy to open-wooded savannas, some, though, occurring in wet grassy and other similar habitats.

Loudetia section *Pleioneura* approaches sub-gen. *Loudetia* closely but differs in its many nerves to lemma and glumes and in its pale-green, deep-purple variegated spikelets. This latter characteristic only appears elsewhere in the closely allied *Rattraya* and in many of the Danthoniopsoids. There appears to be a correlation with little burning, for most *Arundinelleae* possessing purple-variegated spikelets occur in regions which are relatively arid or at least where rocky habitats give considerable fire-protection.

4) *Rattraya* (see fig. 3)

This is a monotypic genus unique in the *Arundinelleae* for its remarkable pseudopetiole. The pseudopetiole, morphologically the lower part of the leaf-blade (if one is to judge by the situation of the ligule), is abscissile and the hypothesis is advanced that the resultant deciduous leaf and somewhat branched perennial stems have their origin in adaptation to ± fire-free environments.

Rattraya is obviously close to *Loudetia* section *Pleioneura*, particularly the Central African Republic *L. simulans*.

5) *Loudetiopsis* (fig. 8)

A genus difficult to characterise, ranging from the simple *L. glabrata* through to the much more advanced *Ll. falcipes* and *baldwinii*. Trends to lax triadism and a sigmoid hook with disarticulation just below the triad, as well as a trend to smaller spikelets, characterise the group. There is, in other words, a loss of characteristics typical to *Eu-Loudetia* and a replacement by Loudetiopsoid ones. *Loudetiopsis glabrata*, very clearly the most primitive *Loudetiopsis*, is close to *Loudetia* section *Loudetia*, particularly subsect. *Pungentes*. *L. glabrata* lacks the disarticulating sigmoid hook of the remainder of the genus and has the brightest orange spikelets.

The relationship of *Loudetiopsis* to *Diandrostachya* is certainly the most controversial problem at this level of Arundinellean classification. See under *Diandrostachya* for the discussion of the position of the latter.

6) *Tristachya* (fig. 10)

Few strong trends are very marked in this simple genus. Increasingly strong triadism and extra nerves to the lemma of the lower floret as well as the beginnings of bristles to the lobes of the lemma of the upper floret characterise the American species, *Tt. leiostachya*, *avenacea*, *angustifolia*, and *laxa*. Very open infloresences with only the barest indication of triadism characterise the Congo-Zambesi watershed species *Tt. hubbardiana* and *pseudoligulata*. The hardly interdistinguishable *Tt. lualabaensis* and *hitchcockii* have adapted to swamp and flood plain habitats. These last two species have much smaller spikelets than other *Tristachyas* and show a striking change to purple-variegation.

Tristachya is, on the whole, characterised by very large (30—40 mm) spikelets in color orangish to brownish, lacking tubercle-based setae to the glumes and lower lemma. It is mainly savannoid in ecological distribution.

7) *Apochaete*

This small genus, characterised by dense triadism, very large spikelets, enormous awns, and hairy ovary appears to be near the base of the Isaloid line. *Aa. thollonii* and *hispida* which are very similar to one another are somewhat removed from the glabrous-glumed *A. auronitens*.

8) *Dolichochaete* (fig. 11)

The only easily definable trends in this coherent group are those to tubercle-based setae on the glumes and to smaller spikelets. Spikelets tend to be a dull, not very dark, somewhat shiny brown to purplish brown. *D. bicrinita*, though extremely close to *D. bequaertii*, has evolved a pair of tufts of hair to the lemma of the upper floret — an interesting piece of parallelism, being found in other quite unrelated taxa (e.g. *Gilgiochloa*, *Dilophotriche*, *Trichopteryx*).

9. *Muantijamvella*

Monotypic.

10. *Isalus*

This very advanced genus consists of 2 or 3 rupicolous Malagasian endems. *I. betsileensis* is not very close to the bushy, perennial *Ii. humbertii-isalensis* complex.

11. *Diandrostachya* (figs. 12 and 13)

A genus with two clearly marked subdivisions: firstly, the perennials with sigmoid hook below the triad, and secondly the annuals (with one perennial) lacking this feature.

Common to most of the group are the medium-large spikelets, heavily built awn, rather narrow glumes, and bristly yellow-setose-tuberculate spikelets. These Tristachyoid characteristics fit this genus much more happily as a branch off the Veseyochloid line of the Tristachyoid group than as a near relative to *Loudetiopsis*. It is true that *Loudetiopsis* and *Diandrostachya* share lax triadism and that neither is very highly specialised but there is not one typically Arundinellean specialisation common to the two groups. Even where the sigmoid hook of the inflorescence branches is concerned, this branch attains great delicacy in *Loudetiopsis* but is heavy and crude by comparison in *Diandrostachya*.

However, the clinching argument comes when one tries to put the two groups together. What is superficially the most similar *Diandrostachya* to *Loudetiopsis* is *D. glabrinodis*, a species which, however, appears terminal on the annual Diandrostachyan line. Lacking a sigmoid hook, it would have to be placed near *L. glabrata*. Not only would this require evolutionary reversal of the normal perennial → annual trend but it would place the Afro-American *D. chrysothrix* near terminally, a difficult situation, chronologically.

Still, it has to be admitted that a *Diandrostachya* - *Loudetiopsis* relationship cannot be entirely ruled out and that considerably more phenetic information is required in an attempt to resolve this argument. Conert's anatomical data (1957) on this point do indeed favor the *Loudetiopsis* - *Diandrostachya* relationship.

12) *Piptostachya*

Monotypic.

13) *Veseyochloa*

Monotypic.

14) *Zonotriche*

Monotypic.

15) *Mitwabachloa*

Monotypic.

16) *Petrina*

Petrina parva and *P. pruinosa* must be considered extremely closely allied. Both are

rupicolous species not very close to the Angolan *P. lignosa* which is riparian and the only 'reed' in the tribe.

17) *Gazachloa*

Two species.

18) *Xerodanthia*

Two species.

19) *Danthoniopsis* (fig. 15)

A considerable (*D. viridis, catangensis, intermedia, acutigluma, westii,* and *minor*) group of species of extremely close inter-alliance constitutes the 'core' of the genus. None of these species is really common, except *D. viridis*. This group is characterised by a special wing ('door-like flap') to the palea of the upper floret, by purple-variegation of the spikelets, and rupicoly. Undoubtedly nearest the ancestral position is the Congolese *D. wasaensis*, with orange spikelets and poorly developed wings.

D. chevalieri from Guinea has purple-variegated spikelets but is not rupicolous, lacks wings, and possesses papillae to the sulcus of the palea of the upper floret. *D. chevalieri* is the most isolated member of the genus and requires much further phenetic study.

20) *Jacquesfelixia*

One species.

21) *Gilgiochloa*

One or two species.

22) *Dilophotriche* (fig. 16)

The six described species of this genus fall into two groups. The first, characterised by *D. occidentalis*, not only lacks triads and a sigmoid hook, but has different-shaped spikelets, these being longer and narrower than in the other *Dilophotriche* species as well as being glabrous-glumed. *D. occidentalis* is at best distantly related to the main group of *Dilophotriche*.

The number of species in the main group of *Dilophotriche* is open to question but at least two, the perennial *D. tristachyoides* and the annual *D. pobeguinii*, stand out. *D. pobeguinii* is a much larger species than *D. tristachyoides* and bears prop-roots from the lower nodes after the manner of many fairly robust tropical annual grasses. It may be presumed to be the more advanced species. Other names in the genus have been treated as synonyms of *D. tristachyoides* and *D. pobeguinii*. Their taxonomy is elucidated by Clayton (in press).

23) *Trichopteryx* (fig. 17)

This genus of eight species splits into two groups. The first is perennial and bears hairs at the tips of its pedicels. The second, annual, group lacks the above-mentioned hairs and has a neuter lower floret. The annual group may be considered the more advanced.

(ii) Discussion of genera within groups

A. The Arundinelloid group (fig. 1).

Characterised by much smaller spikelets than any other except the Trichopterygoid group, the Arundinelloid group also generally possesses purple (though non-variegated) spikelets and a membranous or membranous-ciliate ligule. The scabrous lemma of the upper floret of *Arundinella* is another decisive feature. *Arundinella* itself is extremely homogeneous and none of its species is at all closely related to the highly specialised *Jansenella*. *Arundinella*, unlike other *Arundinelleae*, is pan-tropical and must be an ancient genus. It is mainly found in regions of medium-high rainfall or in marshy habitats.

Its phyletic relationship to *Jansenella* is predicated to a very large extent upon the common ligule and small spikelets as well as the Asian distribution of the two genera. It must be admitted, however, that *Jansenella* is an extremely isolated and specialised genus.

B. The Loudetioid group (fig. 3).

That the Loudetioid group is a 'natural' assemblage can hardly be doubted. No major difference exists between any taxon in this group and that most similar to it. As a whole the Loudetioid group is rather unspecialised and it has three main branches: firstly, *Loudetia* section *Loudetia* with primitive subsect. *Acuminatae* ranging to more advanced sect. *Lophanthera*; secondly, the *Loudetiopsis* line which is probably an offshoot of lower *Loudetia* section *Loudetia*; and, thirdly, the line through *Loudetia* section *Pleioneura* to *Rattraya*. Trends to annualism are evident in *Loudetia* section *Loudetia*, to triadism and a sigmoid hook in *Loudetiopsis*, to many nerves and variegated spikelets in the *Pleioneura - Rattraya* line. Stamen loss (3 → 2) appears as an early characteristic, but is reversed in the more specialised *Loudetiopsis* species.

The Loudetioid group is dominantly African savannoid though it possesses 1 species in the New World, 3 or 4 in Madagascar, and 1 in Asia. All the non-African taxa are the same as, or extremely closely related to, others found in Africa.

C. The Tristachyoid group (fig. 9).

The most general trends in this group are from weak triadism to strong triadism, from gigantism (tall plants, spikelets 25—44 mm long) to more average size plants (with spikelets 15—25 mm long), from glabrous glumes to glumes strongly beset with tubercle-based hairs, from a sharp to a blunt callus, from a glabrous to a hairy ovary, and from a non-disarticulating to a disarticulating peduncle.

Tristachya, at the base of the Tristachyoid genera, is extremely unspecialised and, but for its gigantism, very similar to elements in *Loudetia* section *Loudetia*. It is topologically close in the cladogram to *Dolichochaete* and *Apochaete*.

Three main evolutionary lines are postulated, in which there is considerable parallelism. Firstly, there is the Mitwabachloid line, characterized by white setae from black bases and 6—8 tufts of hair across the lemma of the upper floret; secondly there is the Veseyochloid line which lacks the latter feature and has yellow-golden setae from black tubercles; while finally there is a line leading to the very advanced *Isalus*. Parallelism is particularly evident in the very striking feature of the disarticulating sigmoid hook to the inflorescence branches, found in such different genera as *Zonotriche*, *Mitwabachloa*, part of *Diandrostachya*, *Piptostachya*, and *Veseyochloa*. This feature is only associated with triadism in the *Arundinelleae* and some functional connection might be postulated, probably in connection with distribution.

The Tristachyoids, though showing great diversification and very strong evolution from primitive *Tristachya* to such advanced genera as *Mitwabachloa* or *Isalus* are nevertheless a fairly natural group without great differences between any given taxon and that most similar. Nearly all species, except some recently described by the present writer, have been included under *Tristachya* at some time or other.

Controversially placed genera are *Isalus*, regarded as *Danthoniopsis* by Conert, and *Diandrostachya*, regarded as *Loudetiopsis* by Conert and Clayton. It is true that the leaf-anatomy of *Isalus* is rather Danthoniopsioid, but *Isalus humbertii* (the species considered by Conert) is so xeromorphic that leaves atypical from a Tristachyoid standpoint might be expected. Its spikelet morphology is, moreover, essentially Tristachyoid. The real problem with the present cladistic placement of *Isalus* is that it is a Malagasian endem

and must most suitably arise at a low point in the cladogram, rather than as a near ally of *Mitwabachloa*, which would be convenient phenetically but is rejected in this treatment.

The problem of *Diandrostachya* has been discussed under that genus. *Diandrostachya* will easily fit as a side-branch to the Veseyochloid line, without any forcing. Stamen loss is all that is necessary for this purpose.

Tristachyoids are essentially African savanna plants, with only 2 or 3 species (*Isalus*) in Madagascar, and 5 species (4 *Tristachya* and 1 *Diandrostachya*) in the New World. They demonstrate considerable evolutionary specialisation and diversification.

D. The Danthoniopsoid group (fig. 14).

Characterised by medium-sized spikelets with tufts of hairs across the lemma of the upper floret and rupicolous habitat, this group possesses a number of marked trends. The colour change from orange-brown (*Petrina*) to purple-variegated (most of the remainder) is very striking as is the development of the asymmetric leaf margin (in *Danthoniopsis, Jacquesfelixia,* and *Gilgiochloa*). Xeromorphy and lax triadism characterise *Xerodanthia,* minor hygrophylly with soft stems *Gazachloa,* annualism *Jacquesfelixia* and *Gilgiochloa,* and appendages to the palea of the upper floret *Danthoniopsis, Jacquesfelixia,* and *Gilgiochloa. Gilgiochloa,* with aristate glumes and neuter lower floret in addition to some of the characters above, is the most advanced and isolated genus.

The Danthoniopsoid group is natural, with most genera too small to appear very well-defined. The group as a whole is African, though *Xerodanthia* extends into SW. Asia from Yemen to Sind. The group is almost entirely rupicolous except for the riparian *Petrina lignosa* and *Gilgiochloa,* an annual. It may be assumed to be a fire-intolerant line.

E. The Dilophotrichoid group.

See under *Dilophotriche.*

F. The Trichopterygoid group.

See under *Trichopteryx.*

(iii) The tribe as a whole (fig. 1)

Assuming the naturalness of each of the groups A—F, how do they fit together? In the first place, the Loudetioid, Tristachyoid and Danthoniopsoid groups are quite close among their basal members. Considerable similarities exist between the most primitive *Tristachyas* (e.g. the African *superba, pedicellata,* and *augusta*) and the simpler *Loudetias* (e.g. subsect. *Acuminatae*). The main difference is the gigantism of the former and it may be assumed that these groups are cladistically as well as phenetically close. As for the Danthoniopsoids, working from the primitive *Petrina,* these are readily derivable from pre-*Pleioneura* stock.

Trichopteryx is so isolated and constant that its precise affinities are difficult to detect. Its bright orange spikelets suggest an origin near Loudetioid stock but its very specialised vegetative morphology (many nodes, short, broad, assymetric leaf blades) and constant spikelets (lobes and tufts to lemma 2) make it hard to place precisely.

As for *Dilophotriche,* this, too, is hard to place and it may be diphyletic. The origin near the Danthoniopsoid base is entirely speculative.

Arundinella, though primitive like the lower Tristachyoids and Loudetioids, does not seem to be too closely related to that group in view of its different ligule, very small spikelets, and scabrous lemma of the lower floret. Clayton (personal communication)

concurs that it is probably well separated phyletically from the main group of the tribe. Investigation of still further characters should aid in elucidating this problem.

7. PHYLETIC CONCLUSIONS

(i) Geographical considerations

The tribe *Arundinelleae* is possibly diphyletic — there then being an Arundinelloid line, consisting certainly of *Arundinella* and possibly *Jansenella*, and a Loudetioid-Tristachyoid-Danthoniopsoid line to which *Trichopteryx* and *Dilophotriche* would somehow be attached. This is the situation as illustrated in fig. 1. Based on their present distributions, the latter line is most likely African in origin, while the Arundinelloid line is then African if the tribe is monophyletic or alternatively Indo-SE. Asian if the tribe is diphyletic.

The present distribution of the *Arundinelleae* easily conforms to the hypothesis of continental drift, except that this hypothesis would require a very great age for the tribe-extending back to the Jurassic, if not to the Trias or Permian, which would place the origin of the *Gramineae* very much earlier than any known fossil record could substantiate. Darrah (1960, p. 223) gives the most ancient fossil grasses, poorly preserved, as upper Cretaceous in time, but the family must certainly be earlier than this. It is clear that the entire thesis developed in this paper requires not only that the *Gramineae*, but that the Angiosperms as a whole, are an older group than fossil evidence indicates[*]. As a hypothesis we will admit the most developed views on the specific happenings of continental drift, such as those put forward by S. W. Carey (1958) and others. Even so, the many detailed alternative events within the general drift theory are of little consequence to our data. Thus, Arundinellean evolution can have reached its present state whether or not Pangaea existed as a unitary block largely split by the Tethys Sea or whether, alternatively, there were two macro-continents — Laurasia and Gondwanaland. Neither is it of great significance, again within the context of Arundinellean knowledge, whether peninsular India only later joined the present Central Asia nor, in like vein, is it significant by precisely which route Australia and New Guinea arrived in their present position. All of these regions have had warm-latitude components since the Cretaceous.

What does appear to be significant, however, is the apparent inability, except in quite abnormal circumstances, for Arundinellean diaspores to cross any significant marine interval and this is used as a premise in this interpretation.

Readers with sufficient doubt or disbelief in the main points of continental drift as conventionally outlined, are referred to the erudite, but more 'conservative' palaeobiogeographical papers of Florin (1963) and Van Steenis (1962) for alternative explanations.

Creer (1965), a proponent of continental drift, is a student of palaeomagnetism. He indicates (p. 33 op. cit.) magnetic polar positions for Africa and South America beginning to converge in the Jurassic and reaching their present relative positions in the Cretaceous. This would indicate that overland dispersal of *Arundinella*, *Tristachya*, and *Loudetia flammida / phragmitoides* must have been completed by about this time, i.e. before the Mid and South Atlantic intervals had widened to any extent (fig. 18).

So far as Malagasy is concerned, our taxonomic and cenogeographical data require

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[*] A similar conclusion is found in J. G. HAWKES and P. SMITH (1965). Continental drift and the age of Angiosperm genera. Nature 207: 48—50.

us to postulate a later date for the Mozambique Channel interval than for the Atlantic one. The main reason for this is the presence of *Trichopteryx* (advancement index 26 %) in Malagasy but not in South America. The existence of the very advanced Tristachyoid genus *Isalus* in Malagasy, however, has to be predicated on accident, or, more likely, on the evolution of that genus wholly within Malagasy from primitive Tristachyoid ancestors which in that case arrived more or less simultaneously with the entire original Malagasian Arundinellean flora. Recent evidence (Nairn, 1965) places Malagasy and Tanzania in their present relative positions by the mid-Cretaceous.

The Red Sea–Gulf of Aden interval, being very narrow, poses few distribution problems. It is in any case as late as Middle Tertiary (Irving, 1964, p. 251). *Xerodanthian* migration could well have been late with *X. stocksii* evolving in Asia. There is no problem either in accepting *Loudetia flavida* as relatively primitive, yet the only Asian taxon of this genus. Migration across the Red Sea could have taken place recently either over sea or by a land connection near Djibouti where the sea is now very shallow (max. depth 500′), possibly even in Pleistocene times.

(ii) Parallelism

Examples of parallism are manifold in the *Arundinelleae*. The most striking is the trend to triadism. It is essentially universal in the Tristachyoid genera commencing with very lax groups of three in *Tristachya* and reaching dense triads in all other genera of this group except *Diandrostachya*. Weak triadism also occurs in *Loudetiopsis*, *Loudetia* sect. *Lophanthera* (Group B), *Dilophotriche* (Group E), and *Xerodanthia* (Group C), thus evolving in five separate lines. Associated with triadism in certain cases is the remarkable sigmoid hook or the inflorescence branches and which is associated with disarticulation. This last situation occurs in *Loudetiopsis* (most spp.); in *Diandrostachya* (some spp.); in *Piptostachya* and *Veseyochloa*; in *Zonotriche* and *Mitwabachloa*; and in *Dilophotriche*, thus appearing five times.

Where spikelets are not arranged in threes they are most usually paired — one on a longer, the other on a shorter pedicel. Whether or not the spikelets are truly paired is usually fairly easily evident except in some very congested (e.g. *Loudetia* subsect. *Densispicae*) and in other especially lax inflorescences. This paired arrangement is characteristic of *Arundinella*, *Trichopteryx*, and most Loudetioids.

Tufts of hair to the lemma of the upper floret are common in the *Arundinelleae*, two tufts being found in *Trichopteryx*, *Dolichochaete bicrinita*, *Dilophotriche*, and *Jansenella* — a quartet that on no cladistic or phenetic grounds can be at all close. Six to eight tufts appears to be a separate line of development and is common in the Tristachyoids and characteristic of the Danthoniopsoids. In the former group *Zonotriche*, *Mitwabachloa*, and *Isalus* are examples, while in the latter group all but *Gilgiochloa* and one *Xerodanthia* possess this condition. Three phyletic lines are thus involved for this character.

The neuter lower floret exemplifies another specialized and parallelistic situation. It occurs in the unrelated *Loudetia togoensis*, the annual *Trichopteryxes*, *Diandrostachya glabrinodis*, and *Gilgiochloa*, four different phyletic lines. As an anomaly this characteristic occurs in individuals of certain species of *Arundinella* and perennial *Trichopteryx*.

The character of tubercle-based setae on the spikelet (usually the glumes and lemma of the lower floret), and also often on the pedicels, is rather widespread in the *Arundinelleae* (rather weaker tubercle-based hairs are widespread in vegetative parts of *Arundinelleae*). This characteristic is common in *Arundinella*, scattered through *Loudetia* section *Loudetia*, usual in *Loudetiopsis*, characteristic of the Tristachyoids, though absent from

the more primitive ones (e.g. *Tristachya*, some *Dolichochaete*, and a few other species), and usual in *Dilophotriche*. Due to the re-appearance of this characteristic in many parts of *Loudetia* section *Loudetia* the total number of its beginning appearances is at least twelve. The character of tubercle-based setae to the spikelet and pedicels is the most striking one considered in this paper which may be present or absent in a single species. Excellent examples are to be found in *Loudetia simplex* and *Dolichochaete nodiglumis*.

As for vegetative characters, annualism is probably the most striking example of parallelism, being frequent in *Arundinella* (12 species in 9 series), in *Loudetia* (6 species in 3 sections), and occurring in the Tristachyoid genera *Diandrostachya* and *Veseyochloa*, the Danthoniopsoid *Jacquesfelixia* and *Gilgiochloa*, and in *Dilophotriche* and *Trichopteryx*. This involves 17 lines.

Xeromorphy (not necessarily strong) is found in *Loudetia migiurtina*, *Isalus humbertii*, and *Xerodanthia*.

Many further examples of parallelism might be noted and these can easily be found by the reader using table 1 and the cladograms. Parallelism clearly abounds in the *Arundinelleae* and since it is so common in many striking features of the spikelet the reason becomes clear why generic delimitations (see Phipps 1964, 1966b, 1967b) have often been at odds in different classifications. Thus is explained why *Loudetiopsis* (*sensu* Conert) has been divided into three different genera and lines by Jacques-Félix (1960) and in papers by the present author. It is interesting to note, however, that though the phyletic situation determines how many genera comprise *Loudetiopsis sensu* Conert this is arrived at by phenetic data.

The other actual result of strong parallelism in the *Arundinelleae* with respect to the generic classification of the tribe, is the problem of how to treat the extremely diverse Tristachyoid groups and the diverse Danthoniopsoid group. The present author's solution (Phipps, 1966b) of using many small genera in each case is argued there and in Phipps (1964). The only other satisfactory alternative is to use two genera, respectively *Tristachya sens. lat.* for all the Tristachyoids and *Danthoniopsis sens. lat.* for all the Danthoniopsoids except *Gilgiochloa*.

(iii) Evolutionary reversals

Evolutionary reversals are believed to be relatively uncommon but their lack of frequency in phylogenies may well be a partial result of the use of this position as an intuitive premise. In the *Arundinelleae* there appear to be only a few striking evolutionary reversals.

Perhaps the most striking is the gigantism of the primitive Tristachyoid spikelet which in all major lines (even within the genus *Tristachya* itself) is reversed. Other reversals are the regaining of a third stamen in advanced *Loudetia* and *Loudetiopsis*, the reversal of the primitively sharp callus to a blunt one in several *Loudetia* species and Tristachyoid genera, and the loss of orange spikelet color in most Danthoniopsoids and Tristachyoids as well as in a few Loudetioids.

(iv) Postulation of a primitive or proto-Arundinellean

Using Wagner's typological ground-plan device one can construct a primitive or proto-Arundinellean by simply summing all the primitive character-states shown in table 1 into a composite description or illustration. It is, however, superfluous to construct such a description at this point, fitting though it might appear for the end part of the paper, for reference to table 1 suffices.

However, beyond superfluity a far more serious objection emerges, namely that there is no guarantee that any taxon has ever existed simultaneously possessing all the character-states mentioned, even if each one, taken separately, has indeed been correctly interpreted as primitive. The reason for this is that designated primitive states are not necessarily monophyletic at the point of conjunction of all Arundinelloid lines. On the other hand, however, if each such state is primitively patristic then all must necessarily exist simultaneously at least at the top of the common stem.

Consequently a typologically-derived common ancestor must be used with considerable caution in attempting identification with a fossil putative common ancestor unless an excellent phenetic range of fossil intermediates is also known.

(v) A phyletic classification

In this representation the cladograms of figs. 1 to 17 are formalised into a hierarchy.
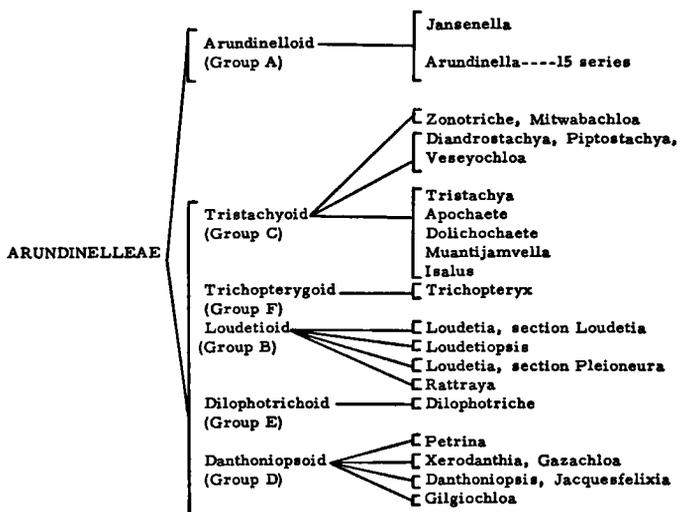
The above table is presented as an end-product in order to satisfy demands that a phylogeny be presented in hierarchic form. In actuality it is no more than a formalised cladogram. Diagrams such as the above, though conventionally offered, have little value. The ordinary cladogram much more adequately shows cladistic relationships (which have to be greatly simplified in the classification) while the delimitation of taxa (such as the un-named groups of genera to the right) is at the utmost limits of arbitrariness, neither being phenetic, nor being based on any consistant cladistic criterion, for cladistics has no scale.

8. SUMMARY

This essay presents an attempt to set up a phylogeny, utilising a fairly large number of characters, and the following general rules:

a) the simple form of a character shall usually be considered primitive;

b) the evolutionary advancement of a taxon is a function of the number of advanced character states it possesses;

c) phenetic similarity shall determine cladistic affinity;

d) parallelism shall be minimised;

e) evolutionary reversals are rare.

The resultant phylogeny displays the tribe in two major stems — the Arundinelloid and the non-Arundinelloid, the latter breaking into 3 major (the Loudetioid, Tristachyoid, and Danthoniopsoid) and two minor (the Trichopterygoid and Dilophotrichoid) lines.

The Tristachyoid line is the most diverse and the Loudetioid and Danthoniopioid lines next so.

Evolutionary heights are reached in *Jansenella* — Arundinelloid group (advancement index 34 %), *Isalus* — Tristachyoid (advancement index 32 %), *Veseyochloa* — Tristachyoid (advancement index 30 %), and *Gilgiochloa* — Danthoniopsoid (advancement index 34 %), and others.

The isolated *Jansenella*, *Trichopteryx*, and *Dilophotriche* are the most difficult genera to which to attach a cladistic position.

There is no fossil evidence for Arundinellean evolution and the phylogeny must be regarded as tentative. This phylogeny, though based on objective data, is subjectively derived according to a set of specified principles. It may be used as a hypothesis to be checked against rigorous numerical methods.

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Table 1. Characters used in the phylogeny

char. no.	character	primitive state	advanced state	comments
* 1.	ecology	mesomorphic	xeromorphic or hydromorphic	latter types more 'specialised'
* 2.	coldest season	warmer	cooler	most Arundinelleae are tropical
3.	longevity	perennial	annual	most Arundinelleae are perennial; also believed to be a frequent trend
4.	habit	caespitose	rhizomatous or stoloniferous	-------------
5.	culms	not flexuous	flexuous	left-hand column more usual
6.	culms	not brittle	brittle	left-hand column more usual
7.	culms	not woody	woody	left-hand column more usual
8.	culms	not branched	branched	left-hand column more usual
9.	node number (average)	2 - 8	1 or 9 and 9+	right hand column includes extremes
10.	pseudopetiole	absent	present	right-hand column 'specialised'
11.	section of leaf	flat	convolute-setaceous	right-hand column 'specialised'
12.	plan of leaf	narrow	broad	right-hand column 'specialised'
13.	tip of leaf	not pungent	pungent	right-hand column 'specialised'
14.	margin of leaf	symmetric	asymmetric	right-hand column 'specialised'
15.	inflorescence	elongate axis	umbellate	left-hand column more 'generalised'
16.	inflorescence	paniculate	spicate or racemose	left-hand column more 'generalised'
17.	spikelet arrangement	1, 1-2, 2	3, (3)	triadism rare in Gramineae
18.	inflorescence branches below triad	sigmoid hook absent	sigmoid hook present	right-hand column involves new dispersal mechanism

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19.	pedicel indumentum	lacking tubercle-based setae	having tubercle-based setae	tubercle-based setae specially characteristic of Arundinelleae
20.	spikelet colour	uniform	variegated	right-hand column more 'specialised'
21.	sex of lower floret	not neuter	neuter	right-hand column more 'specialised'
22.	upper floret stamen no.	3	2 or 1	3 stamens in more simple Arundinelleae
23.	disarticulation between upper glume and lower floret	yes	no	disarticulation probably vestigial to when lower floret hermaphrodite
24.	ratio: spikelet length/lower glume length	low	high	probable primitive similarity of glume and lemma lengths
25.	lower glume nervation number	1 - 4	5 - 9	right-hand column correlated with other 'advanced' features
26.	lower glume indumentum	lacking tubercle-based setae	possessing tubercle-based setae	tubercle-based setae specially characteristic of Arundinelleae
27.	upper glume nervation number	1 - 4	5 - 9	right-hand column correlated with other 'advanced' features
28.	lemma of lower floret nervation number	1 - 4	5 - 9	right-hand column correlated with other 'advanced' features
29.	palea of lower floret	present	absent	latter state 'obviously' vestigial
30.	palea of lower floret induration	not strongly indurated	strongly indurated	right-hand column rare in Arundinelleae, Gramineae
31.	anthers tip	glabrous	penicillate	right-hand column rare in Arundinelleae, Gramineae
32.	callus of upper floret tip	obtuse or acute	bipointed or truncate	right-hand correlated with other 'advanced' features

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33.	lemma of upper floret nervation number	1 - 5	6 - 11	right-hand correlated with other 'advanced' features
34.	bristles to lobes of lemma of upper floret	absent	present	left-hand column more 'generalised'
35.	special indumentum of lemma of upper floret	characteristics of right-hand column lacking	2, 4, 6 or 8 tufts of hair, a horizontal row of hairs or 6 vertical rows of hair	right-hand column a very specialised feature in Gramineae.
36.	palea of upper floret keel wings	absent	present	left-hand column more 'generalised'
37.	palea of upper floret "door-like flaps" in lower half	absent	present	right-hand column rare in Arundinelleae, Gramineae
38.	palea of upper floret - other appendages	absent	present	right-hand column rare in Arundinelleae, Gramineae
39.	palea of upper floret indumentum of sulcus	none	papillose or pubescent	left-hand column more 'generalised'
40.	ovary indumentum	glabrous	hairy	left-hand column more 'generalised'

* these two characters not utilised in calculating advancement indices.

Table 2. Advancement Indices

Notes:
(a) In matrix zeros (0) represent more primitive state of character and ones (1) represent more advanced state. See text and table 1 for fuller explanation.
(b) Rows represent species and columns the characters numbered as in table 2.
(c) Right-hand column show calculation of advancement indices.

	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Advancement Index (actual)	Advancement Index (per cent)
Arundinella nepalensis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	6	15.8
Arundinella deppeana	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	7	18.4
Arundinella hookeri	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	6	15.8
Arundinella mesophylla	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	10	26.3
Arundinella metzii	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	10.5
Arundinella pumila	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	5	13.15
Arundinella spicata	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	15.8
Jansenella griffithiana	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	13	34.21
Loudetia simplex	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	5	13.15

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Species		
Loudetia lanata	5.25	2
Loudetia acuminata	10.5	4
Loudetia gossweileri	15.8	6
Loudetia echinulata	13.15	5
Loudetia annua	13.15	5
Loudetia phragmitoides	13.15	5
Loudetia togoensis	23.68	9
Loudetia simulans	21.05	8
Rattraya petiolata	29.95	11
Loudetiopsis glabrata	18.4	7
Loudetiopsis thoroldii	13.15	5
Loudetiopsis baldwinii	26.3	10

-3-

Taxon			%
Tristachya superba	1	3	7,89
	2		
Tristachya angustifolia	1	6	15,8
	5		
Tristachya hitchcockii	6	9	23,68
	3		
Apochaete hispida	4	8	21,05
	4		
Dolichochaete rehmannii	1	8	21,05
	7		
Dolichochaete bequaertii	2	8	21,05
	6		
Dolichochaete bicrinita	2	9	23,68
	7		
Muantijamvella huillensis	4	7	18,4
	3		
Isalus betsileensis	5	12	31,58
	7		
Isalus humbertii	4	12	31,58
	8		
Zonotriche decora	3	8	21,05
	5		
Mitwabachloa brunnea	3	10	26,3
	7		

-4-

Species			Total	%
Diandrostachya chrysothrix	4	3	7	18.4
Diandrostachya kerstingii	5	4	9	23.68
Diandrostachya glabrinodis	5	5	10	26.3
Piptostachya inamoena	3	6	9	23.68
Vesseyochloa viridearistata	4	7	11	29.95
Petrina pruinosa	5	6	11	29.95
Gazachloa chimanimaniensis	4	8	12	31.58
Xerodanthia barbata	5	8	13	34.21
Danthoniopsis chevalieri	2	7	9	23.68
Danthoniopsis wasaensis	2	5	7	18.4
Danthoniopsis viridis	3	6	9	23.68
Jacquesfelixia dinteri	4	8	12	31.58

-5-

Species			
Gilgiochloa indurata	4 / 9	13	34.21
Dilophotriche tristachyoides	5 / 3	8	21.05
Dilophotriche occidentalis	2 / 5	7	18.4
Trichopteryx fruticulosa	5 / 5	10	26.3
Trichopteryx elegantula	5 / 5	10	26.3
Trichopteryx delicatissima	5 / 5	10	26.3

Figure 1 Postulated interrelationships of major groups of Tribe
(vertical axis corresponds very roughly to degree of
advancement)
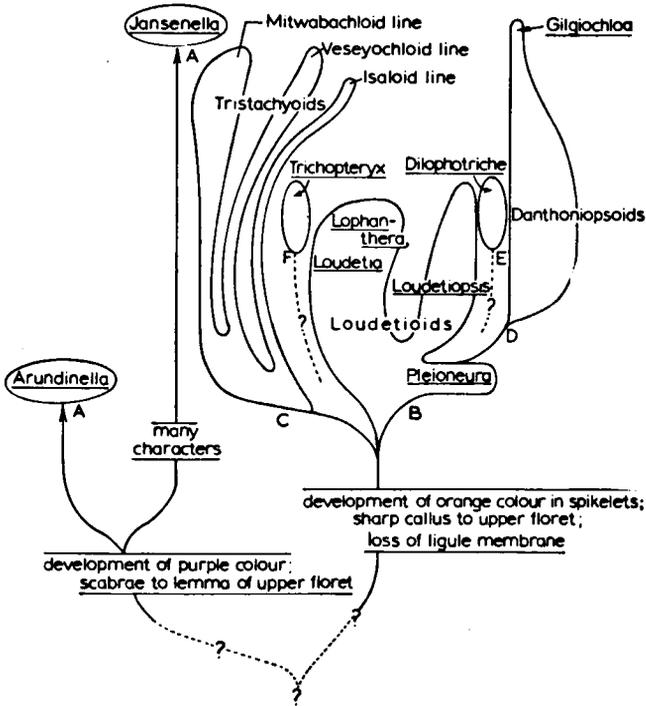
Legend. Letters A–F indicate major groups of Phipps (1966).
Notes across stems indicate cladistic position of new character states

Figure 2 GroupA. ARUNDINELLA SERIES
numbered as in Phipps 1967a
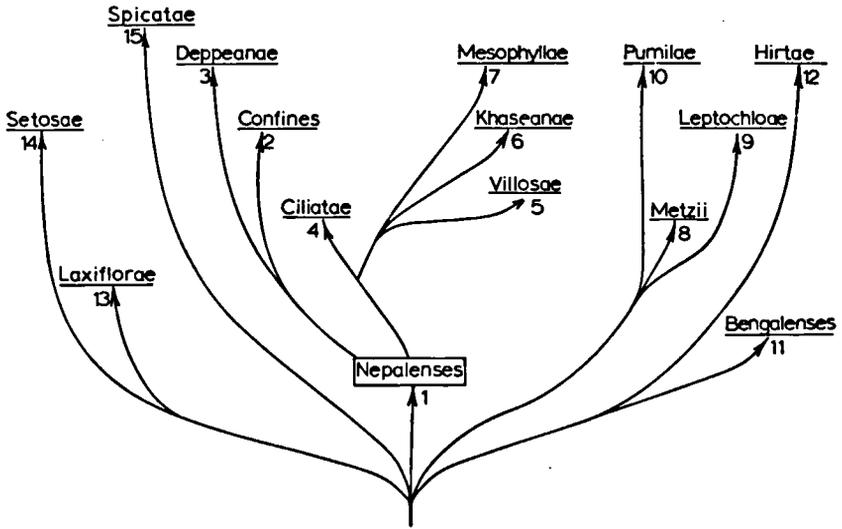
Figure 3 LOUDETIA, etc.
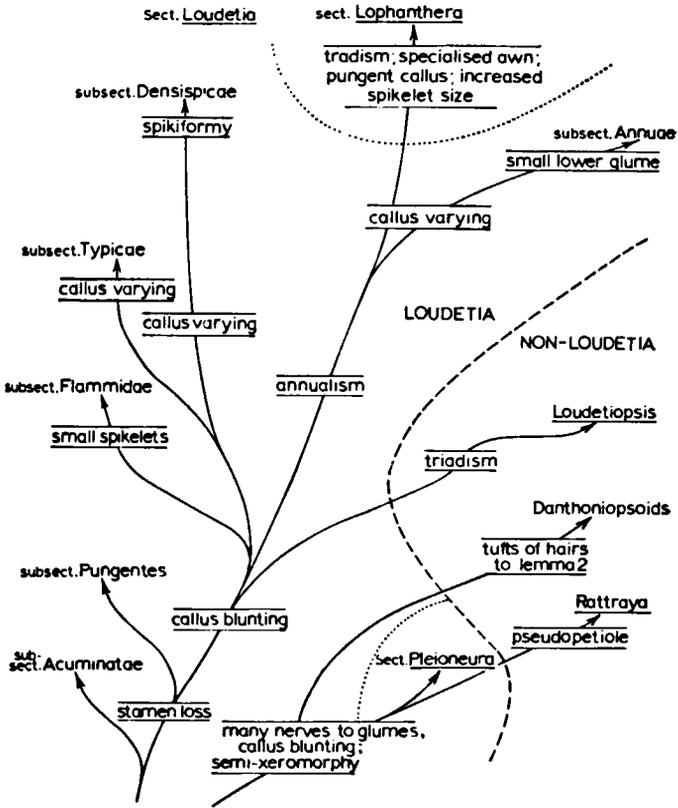
Figure 4 Loudetia subsect. Acuminatae

pennata   cuanzensis   migiurtina

more hairy

filifolia,
two subspecies

some
xeromorphy

acuminata

flavida

plants becoming
smaller
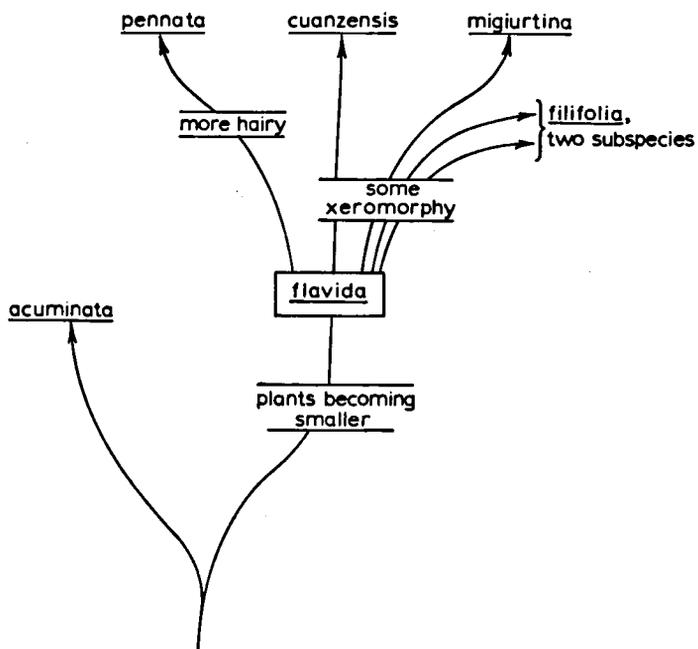
Figure 5 Loudetia subsect.Pungentes
(very tentative)

lanata

longipes

increase in relative size
of inflorescence;
increase in hairiness

crassipes

demeusei

vegetative
gigantism
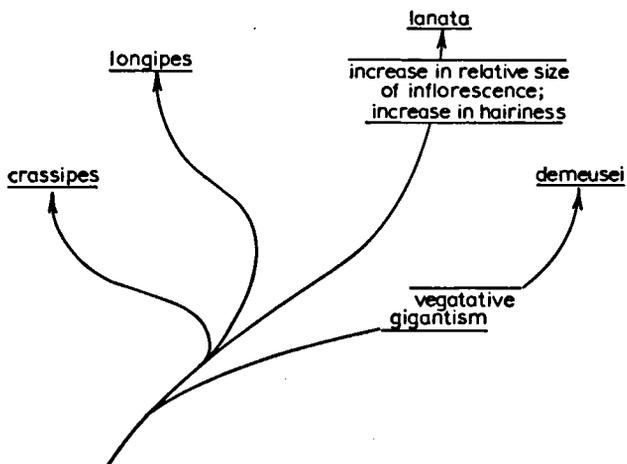
Figure 6 Loudetia subsect.Typicae

madagascariensis

stipoides and
perrieri

eriopoda   camerunensis

kagerensis

simplex

arundinacea

callus bi-pointed

thomasii   vegetative
                            gigantism

angolensis   smaller
              spikelets
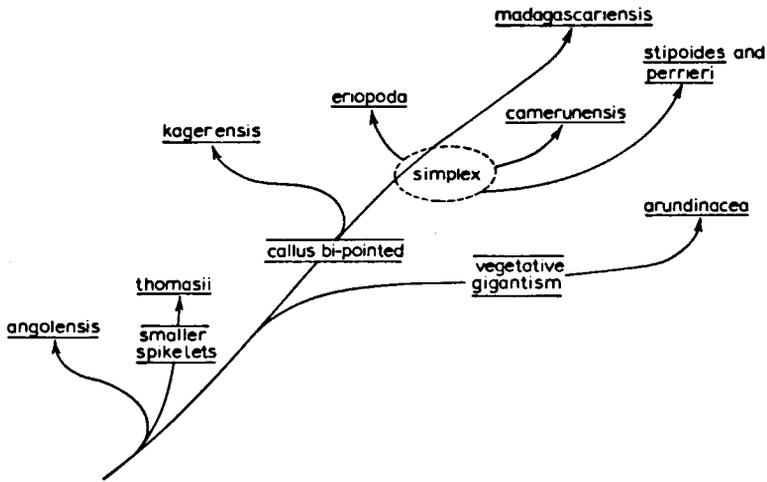
Figure 7 Loudetia subsect. Densispicae

echinulata

very large   tisserantii
  spikelets

gossweileri

glabrous glumes;
  acute callus;
larger spikelets

                            annualism;
                            callus oblique-
                              truncate

densispica   vanderystii

                            reduction in
                            spikelet size

coarctata   juncoid
             stems
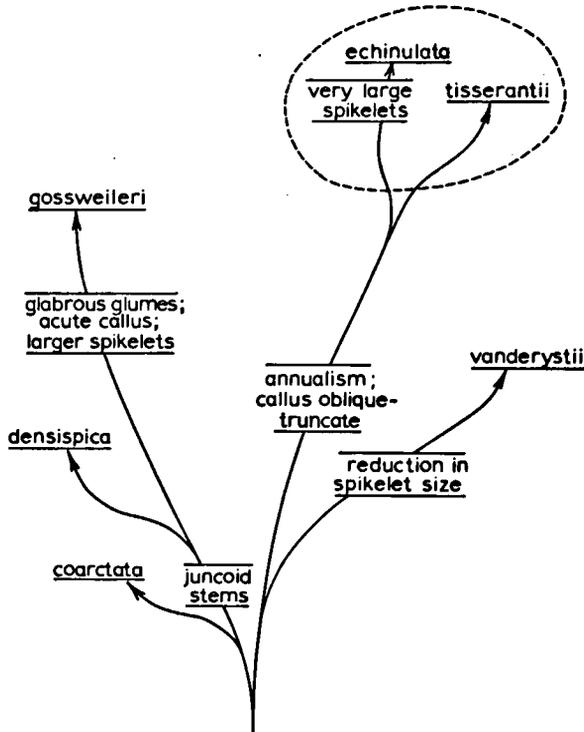
Figure 8 LOUDETIOPSIS
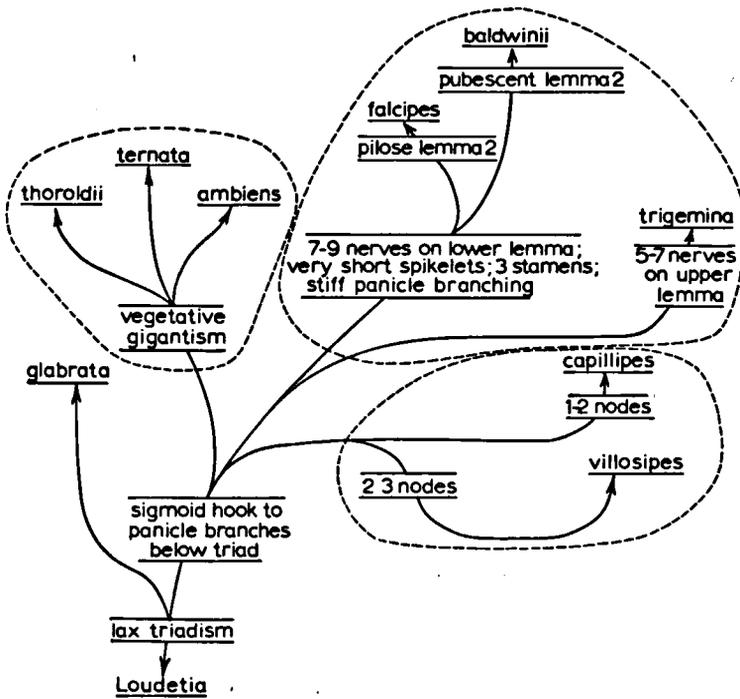
Figure 9 TRISTACHYOID GROUP(C)
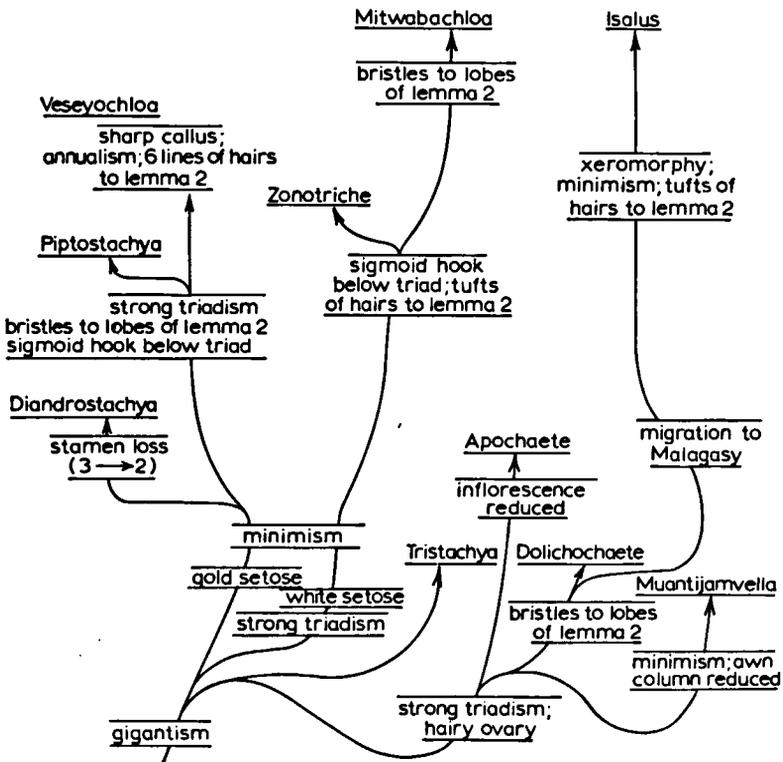
Figure 10 TRISTACHYA
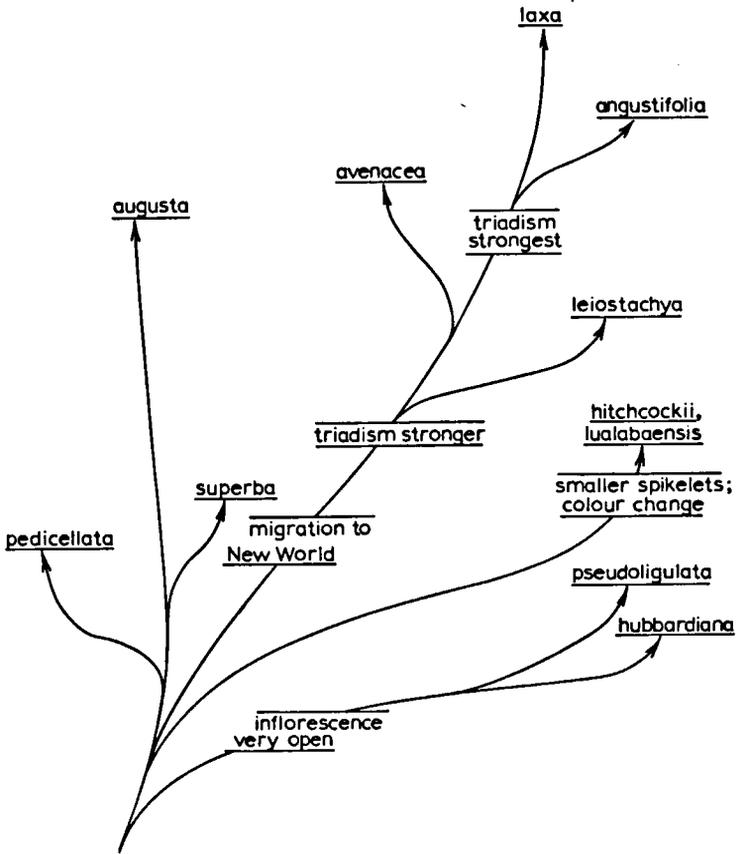
Figure 11   DOLICHOCHAETE
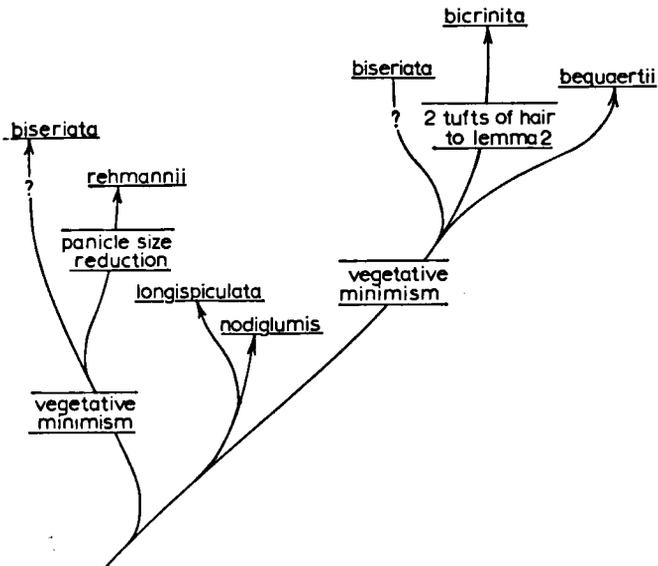
Figure 12 DIANDROSTACHYA
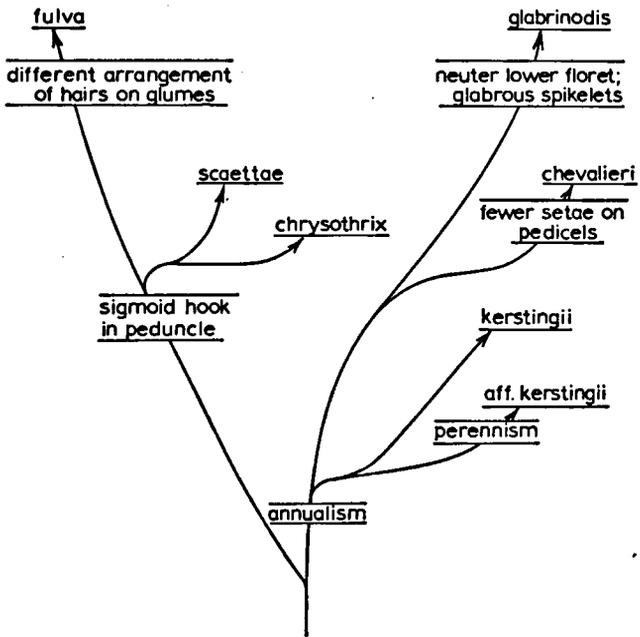
Figure 13 Diandrostachya, if close to
             Loudetiopsis

D. fulva

different arrangement   D. scaettae
   of hairs on
     glumes   D. chrysothrix

sigmoid hook in peduncle

                          D. aff. kerstingii

D. kerstingii

D. chevalieri   perennism

some setae on   many setae on
   peduncles   peduncles

D. glabrinodis

                         increasing yellow
                         setose-tuberculation   other
                            to glumes   Loudetiopsis

neuter lower floret

L. glabrata
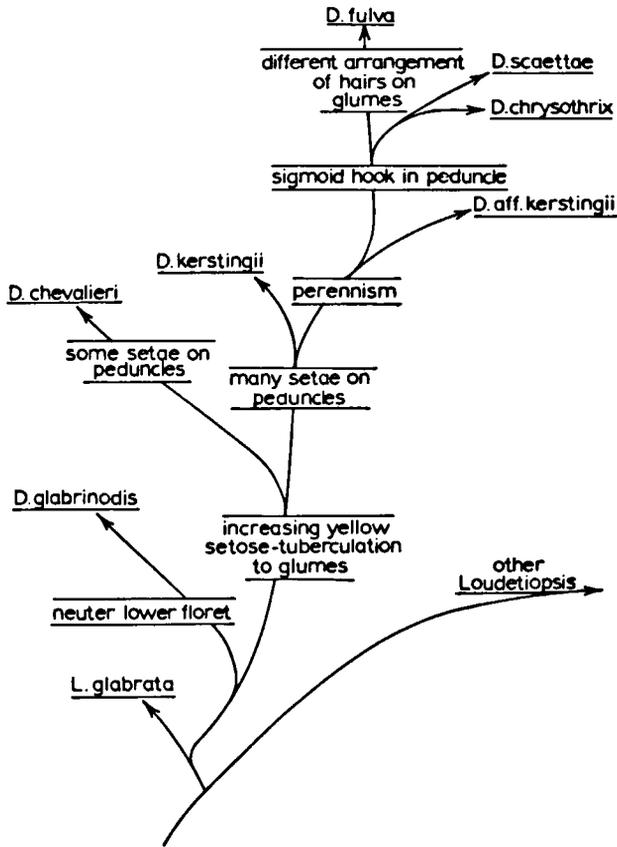
Figure 14 DANTHONIOPSOID GROUP(D)
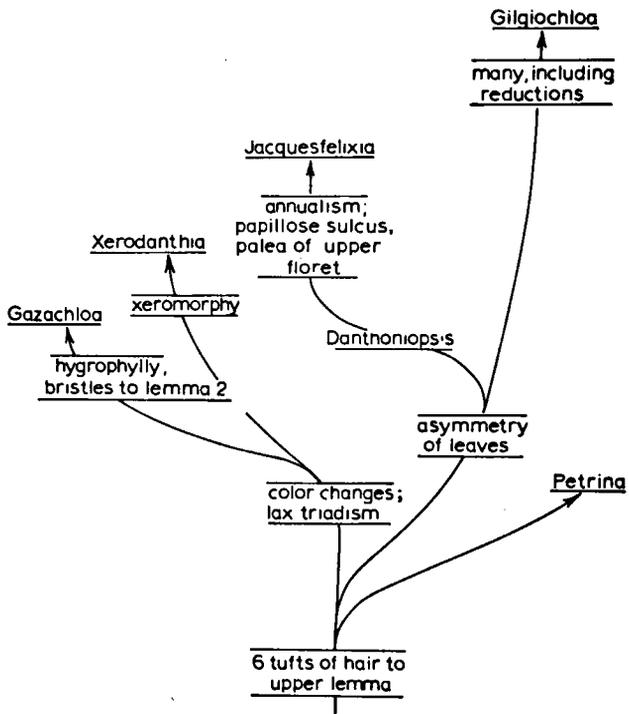
Figure 15 DANTHONIOPSIS

acutigluma
catangensis
intermedia
minor
viridis
westii

undescribed species

conspicuous wings to
palea of upper floret

wasaensis

chevalieri

papillose sulcus
to palea 2

color change
(purple-variegation)
in spikelets

orange-golden spikelets;
6 tufts of hair to upper lemma
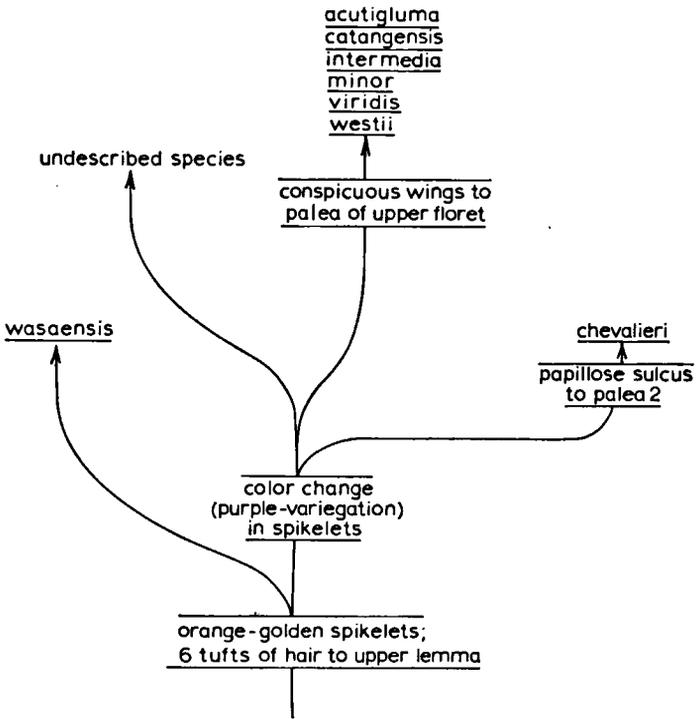
Figure 16 DILOPHOTRICHE

pobeguinii (?multinodis)

annualism

purpurea
tuberculata
tristachyoides
?multinodis

occidentalis

sigmoid hook to
peduncle; triads lax

two tufts of hair and
bristles to lobes of
upper lemma

Figure 17   TRICHOPTERYX

dregeana

perlaxa

delicatissima

fruticulosa

glanvillei

elegantula

marungensis

gracillima

annualism ;
neuter lower floret

hairs at tips
of the pedicels

very small, orange brown spikelets;
two tufts of hair and bristles to lobes of
upper lemma

Figure 18. TAXONOMY OF ARUNDINELLEAE RELATED TO CONTINENTAL DRIFT

(Advancement indices below generic names are those from Table 2; arrows show postulated direction of migration)

Americas | Africa | Malagasy | Arabia | rest of Asia | New Guinea - Australia

Arundinella (mainly 0 - 16%)
5 spp. v. little evol. — by Jurassic → 3 spp. little evol. — by mid Cretaceous → 1 sp. v. little evol. Tertiary to Pleistocene — late Gondwana times or, via Arabia, during Tertiary → 40 spp. little evol. — Tertiary → 6 spp. v. little evol.

Loudetia (mainly 5 - 16%) and **Rattraya** (30%)
1 sp. almost ident. with African sp. — by Jurassic → 33 spp. little to moderate evolution — by mid Cretaceous → 3 or 4 spp. almost ident. w. African spp. → 1 sp. ident. w. African sp.
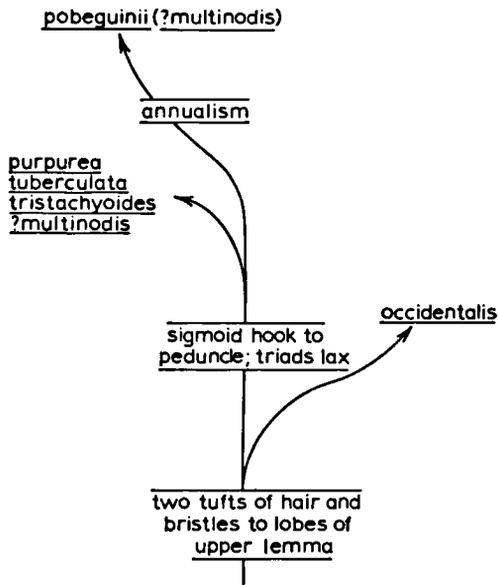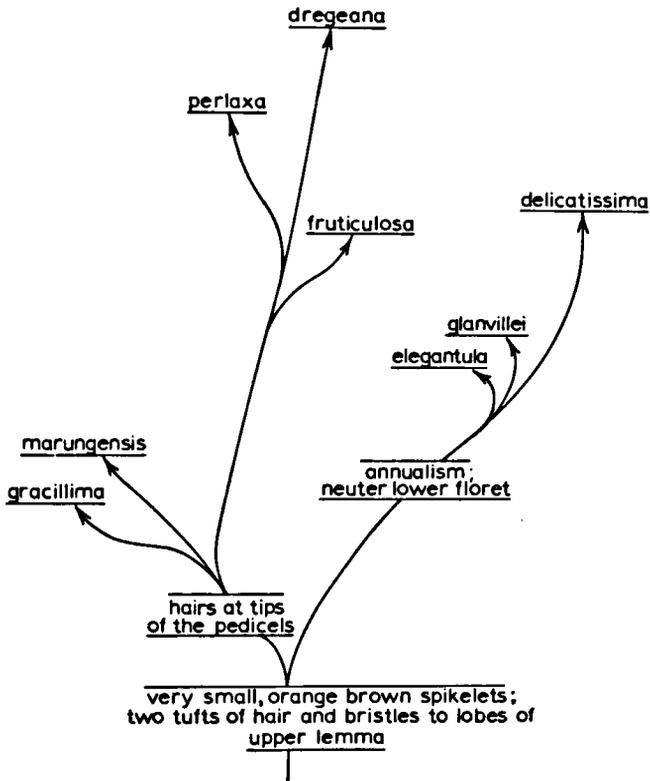
Loudetiopsis (18-26%)
9 spp. moder. evol.

Diandrostachya (18-26%)
1 sp. ident. w. Afr. sp. — by Jurassic → 7 spp. mod. evol.

Tristachya (8-24%)
4 spp. little evolution — by Jurassic → 8 spp. little evol.

other Tristachyoids (23-32%)
15 spp. mod. to great evol. — by mid Cretaceous → 3 spp. great evol.

Trichopteryx (26%)
8 spp. mod. evol. — by mid Cretaceous → 1 sp. ident. w. African sp.

Dilophotriche (18-21%)
3-5 spp. mod. evol.

Danthoniopsoids (18-34%)
17 spp. mod. to great evol. — ?Tertiary → 1 sp. same as an African sp. — ?Tertiary → 1 or 2 spp. sim. to Arabian sp.

Jansenella (34%)
1 sp. great evol. since Arundinella

Mesozoic and Tertiary

Abbreviations: Afr. = African, evol. = evolution, ident. = identical, mod. = moderate, sim. = similar, w. = with, v. = very