UNIVERSITY OF QUEENSLAND PAPERS

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a Statistical Study

BY

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DEPARTMENT OF BOTANY

Volume IV 1965 Number 15

UNIVERSITY OF QUEENSLAND PRESS

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Price: Two Shillings
Twenty Cents

University of Queensland Papers
Department of Botany
Volume IV Number 15
THE UNIVERSITY OF QUEENSLAND PRESS
St. Lucia
26 August 1965

WHOLLY SET UP AND PRINTED IN AUSTRALIA BY
WATSON FERGUSON AND COMPANY, BRISBANE, QUEENSLAND
1965

THE CLASSIFICATION OF THE POACEAE: A STATISTICAL STUDY

Introduction

The grasses (Poaceae) have always been a difficult family to classify, and widely divergent schemes of classification have been proposed. These are admirably summarized by Prat (1960), who has tabulated the subfamilies and tribes proposed by various workers over the past century and a half in such manner as to indicate both their similarities and differences.

Most of the earlier workers recognized only two subfamilies and something less than twenty tribes in the family, but since 1950 several taxonomists (e.g. Pilger, 1954; Tateoka, 1957; and Prat, 1960) have proposed that additional subfamilies be recognized, though they do not agree as to their number. Such discrepancies arise in several ways of which the three following are probably the most important. Different workers not infrequently base their classifications upon different sets of characters or, alternatively, they may employ the same range of characters but regard some as more important than others. It also happens that when further structures are accepted as taxonomically significant the existing classifications require emending.

When making such emendments there is always a likelihood of according too much or too little significance to either the established or the new characteristics. The only way to avoid such personal bias is to grant all characters studied equal status, so that the relationships between the taxa considered may be expressed arithmetically. The advantages and limitations of this technique have been summarized by Sneath (1961) and Sneath & Sokal (1962), who have applied the method to such dissimilar organisms as bees and bacteria and have shown that in so doing they confirmed and in some places improved the existing classifications. Accordingly it was decided to investigate the classification of the Poaceae, taking into account a wide range of characters and accepting each of these to be of equal taxonomic importance.

Materials and method

The genera studied and the method of comparison employed are basically the same as those used previously for investigating the relationships of *Micraira* (Clifford, 1964), but here additional genera have been included in the study and extra characters have been taken into account.

For a single species of each of the seventy grass tribes known to the writer to have been recognized this century, data were sought about as many as possible of the thirty-three characters listed in Table 1. In order to be acceptable for this study each character had to possess three properties. Its taxonomic value had to be well established, information concerning it had to be available for most of the species studied, and finally the character had to be capable of resolution into two mutually exclusive attributes.

TABLE 1

CHARACTERS EMPLOYED FOR CONSTRUCTING THE INDICES OF SIMILARITY BETWEEN GENERA

ORGAN	CHARACTER	ATTRIBUTE
Spikelet	disarticulation	above—below glumes
	rhachilla	prolonged—otherwise
	compression	lateral—dorsal
	palea	present—absent
	palea nerves	2—>2
	lemma nerves	3 or less—>3
Leaf	ligule	present—absent
	ligule	membranous—ciliate
	chlorenchyma	radiate—otherwise
	bundle sheath	single—double
	micro-hairs	present—absent
	arm cells	present—absent
	auricles	present—absent
	transverse veins	present—absent
	phyllotaxis fraction	$\frac{1}{2}$—$\frac{3}{8}$
Seedling	first leaf	erect—otherwise
	first leaf	narrow—broad
	mesocotyl	well developed—otherwise
Fruit	pericarp	free—fused
	starch grains	simple—compound
	hilum	punctiform—otherwise
	embryo size	large—small
Flower	ovary	glabrous—hairy
	styles	free—fused
	lodicules	present—absent
	posterior lodicule	present—absent
	lodicule texture	fleshy—membranous
	stamens	1 whorl—2 whorls
Embryo	epiblast	present—absent
	scutellum and coleorrhiza	free—fused
	edges of first leaf	meeting—overlapping
Culm	internode	solid—hollow
Root	epidermal cells	alternately long and short—uniformly long

The acceptance as valid of all tribes known to the writer to have been proposed this century ensured that the range of variability within the family was widely sampled and further prevented personal bias affecting the selection of tribes. Wherever possible a representative species from each tribe was chosen from amongst the grasses growing in the vicinity of Brisbane; otherwise the characteristics of the representative species were sought from herbarium material or the literature.

TABLE 2

Indices of Similarity Between Twenty Species of Representative Grass Genera, Each Species Being Compared with the Remainder

Arundinaria japonica Sieb. et Lucc.	1.0																			
Bambusa vulgaris Schrad.	.86	1.0																		
Oryza sativa L.	.73	.86	1.0																	
Avena sativa L.	.73	.81	.89	1.0																
Triticum aestivum L.	.73	.83	.75	.96	1.0															
Phalaris canariensis L.	.67	.72	.74	.92	.86	1.0														
Poa annua L.	.67	.71	.71	.92	.85	.92	1.0													
Stipa ramosissima (Trin.) Trin.	.64	.70	.76	.93	.88	.92	.92	1.0												
Cynodon dactylon (L.) Pers.	.67	.67	.65	.76	.69	.75	.69	.74	1.0											
Aristida glumaris Henr.	.67	.69	.78	.69	.72	.69	.68	.77	.80	1.0										
Eragrostis tenuifolia (A.Rich.) Hochst. ex Steudal	.60	.62	.58	.71	.67	.77	.75	.72	.96	.82	1.0									
Sporobolus capensis (Willd.) Kunth.	.67	.62	.50	.68	.57	.74	.72	.72	.92	.76	.96	1.								
Phragmites vulgaris (Lamb.) Crep.	.60	.62	.52	.68	.67	.78	.79	.71	.96	.84	.81	.96	1.0							
Arundinella nepalensis Trin.	.50	.50	.63	.58	.47	.67	.68	.61	.84	.88	.89	.84	.78	1.0						
Isachne globosa (Thunb.) O.Ktze.	.62	.60	.60	.74	.65	.70	.70	.72	.79	.76	.76	.76	.67	.67	1.0					
Zoysia macrantha Desv.	.29	.43	.48	.42	.61	.70	.58	.65	.74	.68	.72	.72	.71	.78	.76	1 0				
Panicum maximum Jacq.	.33	.38	.46	.36	.42	.48	.48	.56	.69	.69	.77	.72	.75	.79	.86	.84	1.0			
Zea mays L.	.33	.41	.52	.44	.42	.48	.52	.60	.56	.67	.71	.64	.70	.79	.70	.75	.85	1 0		
Heteropogon contortus (L.) P. Beauv.	.27	.45	.39	.33	.38	.43	.46	.52	.62	.67	.69	.63	.67	.79	.76	.83	.92	.93	1.0	
Micraira subulifolia F.Muell.	.40	.57	.54	.45	.62	.59	.61	.65	.61	.72	.68	.58	.60	.59	.74	.72	.62	.62	.67	1.0

POOID ERAGROSTOID PANICOID

The information for each species was recorded on marginal punch cards, using for each a separate card. The species were then compared with each other using an Index of Similarity calculated as follows:

$$\text{Index of Similarity} = \frac{A}{A + B}$$

where A = number of matching attributes
B = number of non-matching attributes.

Since for a number of species pairs from each of several genera the Index of Similarity was equal to or close to unity, in this paper generic names only will be used instead of binomials, except in Tables 2 and 3 from which the species included in this study may be determined.

The Indices of Similarity between each possible pair of the seventy genera chosen for study were calculated, but since these data are unwieldy the results for twenty selected genera only are presented in full. These data are summarized in Table 2 in which the rows and columns have been arranged so that genera with similar Indices are placed near to one another.

For each of the remaining fifty genera there has been tabulated in Table 3 the genus that each most closely resembled from amongst those listed in Table 2, along with the appropriate Index of Similarity and the number of comparisons involved in its estimate. The latter number gives an indication of the reliability of the Index value.

TABLE 3

THE RELATIONSHIPS OF GENERA OTHER THAN THOSE LISTED IN TABLE 2 EXPRESSED IN TERMS OF THE MAXIMUM INDEX OF SIMILARITY SHARED WITH ANY GENUS IN THAT TABLE

Selected Genera	Most Similar Genus from Table 1	Index of Similarity	Number of Characters
Agrostis avenacea J. F. Gonel	*Poa*	.966	29
Anomochloa marantoidea Brongn.	*Arundinaria*	.910	11
Anthephora elegans Schreb.	*Zea*	.900	20
Arthrostylidium capillifolium Griseb.	*Arundinaria*	.942	18
Arthropogon villosus Nees	*Heteropogon*	.938	16
Ampelodesmos mauritanica (Poir.) Dur. et Schinz	*Avena*	.960	25
Boivinella comorensis A. Camus	*Stipa*	.866	15
Brachyelytrum erectum (Schreb.) Beauv.	*Stipa*	.888	18
Brachypodium sylvaticum (Huds.) Beauv.	*Triticum*	.960	25
Bromus catharticus Vahl	*Avena*	.930	29
Buergersiochloa bambusoides Pilger	*Stipa*	.865	22
Centotheca lappacea (Linn.) Desv.	*Eragrostis*	.800	25
Chusquea tenella Nees	*Bambusa*	.843	19
Coleanthus subtilis (Tratt.) Seidel	*Poa*	.822	17
Cortaderia selloana (Schult.) Ascher. et Graebn.	*Phragmites*	.942	18
Danthonia longifolia R. Br.	*Cynodon*	.914	23
Diarrhena americana Beauv.	*Poa*	.950	19
Elytrophorus spicatus (Willd.) A. Camus	*Eragrostis*	.833	12
Ehrharta longiflora Sm.	*Aristida*	.834	30
Enneapogon nigricans (R.Br.) Beauv.	*Eragrostis*	.885	26
Garnotia courtallensis Thwaites	*Zea*	.900	19
Glyceria fluitans (L.) R.Br.	*Poa*	.964	28
Hubbardia heptaneuron Bor	*Oryza*	.814	16
Jouvea pilosa Scribner	*Zoysia*	.855	21

TABLE 3—*Continued*

Selected Genera	Most Similar Genus from Table 1	Index of Similarity	Number of Characters
Lecomtella madagasceriensis A. Camus	*Panicum*	.917	12
Lepturus repens (G. Forst.) R.Br.	*Panicum*	.814	16
Lygeum sparteum L.	*Oryza*	.779	18
Melica uniflora Retz	*Poa*	.965	29
Melinis minutiflora Beauv.	*Panicum*	.917	24
Melocanna bambusoides Trin.	*Bambusa*	.815	16
Milium effusum L.	*Stipa*	.923	26
Molinia caerulea (L.) Moench	*Phragmites*	.920	25
Monerma cylindrica (Willd.) Coss. et Dur.	*Poa*	.895	19
Nardus stricta L.	*Stipa*	.774	22
Olyra latifolia L.	*Arundinaria*	.864	22
Pappophorum alopecuroideum Vahl	*Eragrostis*	.889	18
Pariana campestris Aubl.	*Oryza*	.792	24
Perotis rara R.Br.	*Eragrostis*	.880	25
Phaenosperma globosum Munro	*Stipa*	.880	25
Pharus latifolius L.	*Oryza*	.704	27
Phyllorachis sagittata Trimen	*Bambusa*	.736	19
Pommereulla cornucopiae Linn. f.	*Eragrostis*	.938	17
Sesleria caerulea (L.) Ard.	*Avena*	.866	15
Spartina townsendii H. & J. Groves	*Zoysia*	.833	24
Streptochaeta spicata Schrad.	*Arundinaria*	.750	24
Streptogyna crinita Beauv.	*Arundinaria*	.942	17
Thysanolaena maxima (Roxb.) Kuntze	*Oryza*	.812	16
Trachys muricata (L.) Pers. ex Trim.	*Panicum*	.847	13
Uniola latifolia Michx.	*Arundinaria*	.846	21
Zizania latifolia (Griseb.) Turcz.	*Oryza*	.910	22

Discussion of results

The twenty genera listed in Table 2 were chosen for detailed study, as they are widely representative of the family. Furthermore, the Indices of Similarity calculated for these genera are mostly more reliable than those calculated for the remainder, being in no instance based upon less than twenty comparisons.

It may be seen from Table 2 that, except for *Micraira*, each genus considered shares an Index of Similarity equal to or exceeding .80 with at least one other genus, and that at this level of similarity the nineteen remaining genera are associated into three groups or pleista (Sneath, 1957). Within each of these three pleista there is reasonable homogeneity, and between them there is no overlap. For convenience the grasses belonging to these three pleista are hereinafter referred to as pooid, eragrostoid, and panicoid, the names being derived from well-known, widespread genera in each. The neutral term pleiston has been used instead of group so as to prevent any confusion with formal taxonomic categories.

The pleista established have been based upon Indices of Similarity of .80 rather than any other value, because at higher values there was an almost linear relationship between the values of the Indices of Similarity and the number of pleista to be recognized, and at lower values all genera belonged to one pleiston. This is shown in Figure 1 in which the results of Table 2 have been summarized to show the number of pleista that result from accepting as members of the same pleiston those genera with Indices of Similarity equal to or exceeding particular values. It is clear from Figure 1 that the point of inflexion on the curve corresponds to Index values of about .80, and so this value is a convenient level at which to establish pleista.

Further it may also be seen from Table 2 that, although the three pleista recognized are quite discrete at this level of discrimination, they become linked to one another at Indices of Similarity of .75 or less. At this lower level the pooid and eragrostoid grasses are linked and also the panicoid and eragrostoid, but there are no genera linking either the pooid and eragrostoid or the pooid and panicoid grasses.

Of the genera listed in Table 3, the majority have an Index of Similarity of at least .80 with one or more of the genera listed in Table 2, but nevertheless not all at this level of discrimination belong solely to one only of the three pleista recognized

FIGURE I

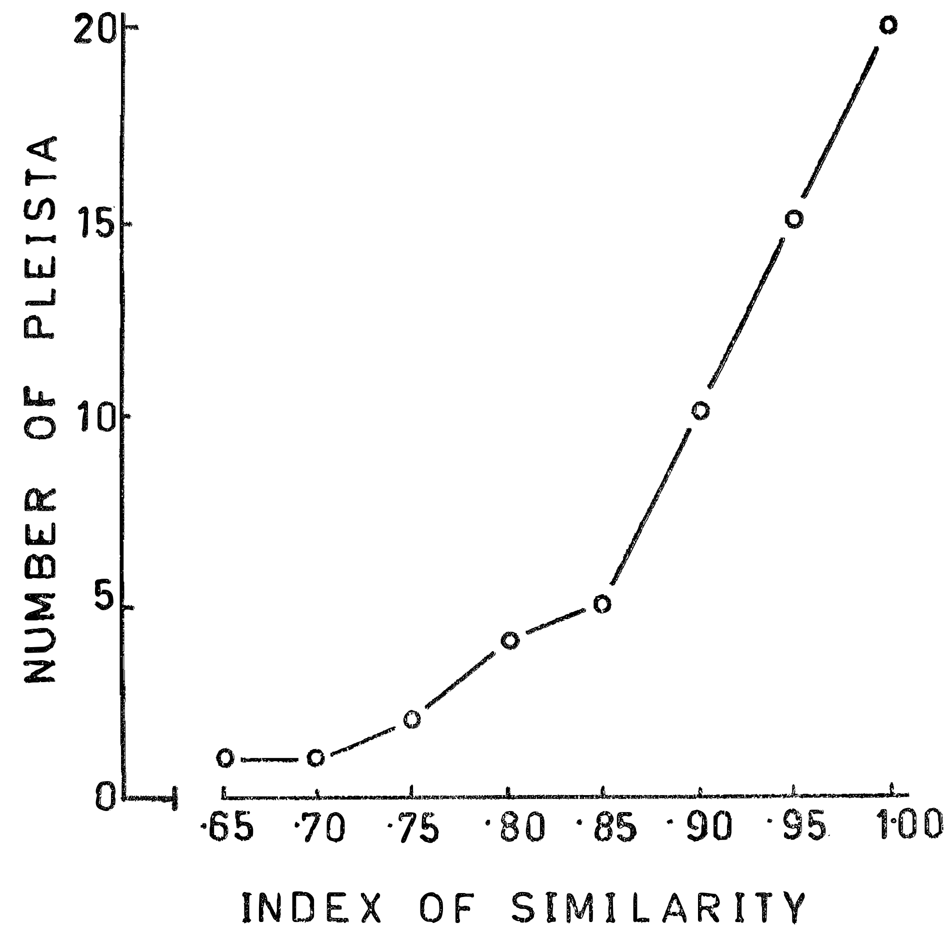

FIG. 1.—The numbers of pleista resulting from basing the requirements for their formation upon Indices of Similarity of different values. (Data from Table 2.)

from Table 2. This is shown in Table 4 in which the genera of Table 3 have been arranged to show their relationships with the three pleista—pooid, eragrostoid, and panicoid. Each genus has been accepted as belonging to a pleiston if its Index of Similarity is equal to or exceeds .80 when compared with any genus in any of the three pleista defined in Table 2.

It therefore follows that amongst the additional genera being considered it is possible that some may be regarded as belonging to more than one of the pleista recognized because of their close similarity with genera in different pleista.

TABLE 4

THE GENERA OF TABLE 3 ARRANGED ACCORDING TO THEIR DEGREE OF SIMILARITY WITH THE PLEISTA DEFINED IN TABLE 2

PLEISTON	GENERA LISTED IN TABLE 3
Pooid	*Agrostis, Ampelodesmos, Anomochloa, Arthrostylidium, Brachyelytrum, Bromus, Buergersiochloa, Coleanthus, Chusquea, Diarrhena, Glyceria, Melica, Melocanna, Milium, Monerma, Olyra, Phaenosperma, Sesleria, Streptogyna, Thysanolaena, Uniola, Zizania*
Eragrostoid	*Centotheca, Cortaderia, Ehrharta, Elytrophorus, Enneapogon, Pappophorum*
Panicoid	*Anthephora, Garnotia, Lepturus, Spartina, Trachys*
Pooid-eragrostoid	*Boivinella, Danthonia, Hubbardia, Molinia*
Eragrostoid-panicoid	*Arthropogon, Jouvea, Lecomtella, Melinis, Perotis, Pommereulla*
Pooid-panicoid	—
Pooid-eragrostoid-panicoid	—
None of the above	*Lygeum, Nardus, Pariana, Pharus, Phyllorachis, Streptochaeta*

Reference to Table 4 shows that this expectation was realized and that the genera presented in Table 3 assumed six of the eight relationships that are possible with the three pleista.

It is interesting to consider the numerical distribution of genera in the eight classes listed in Table 4. About 70 per cent of the genera may be classified as belonging to one only of the three pleista being recognized from Table 2, a further 20 per cent of the genera can be regarded as intermediate between pleista or as belonging to more than one pleiston, with the remaining 10 per cent belonging to none of them.

The relatively small proportion of genera that may be classified as belonging to two of the pleista, and the failure of any to belong to all three of them, confirm the reality of the three major pleista resulting from the analysis of Table 2.

The genera from Table 4 which have high Indices of Similarity with members of two pleista may be regarded as link genera. Nevertheless, though these link genera have many characteristics in common with the two pleista they link, in all instances they closely resemble a given genus in one of the pleista, as has been shown in Table 3, and could be classified as belonging to that pleiston. This stresses the fact that the relationships between the pleista are complex, with the pleista themselves being centres of density of similar genera in a multidimensional continuum.

The genera which fail to attain Indices of Similarity as great as .80 with any of the genera of Table 2 are further removed than the remainder from these centres of density or pleista and so occupy an isolated position in the classification of the family. This has been generally accepted, and each belongs to a small tribe in most modern classifications of the Poaceae. The genera concerned are *Lygeum*, *Nardus*, *Pariana*, *Micraira*, *Pharus*, *Streptochaeta*, and *Phyllorachis*.

It would seem therefore from the above analyses that, at levels of Indices of Similarity equal to or exceeding .80, the genera of Poaceae considered in this study may be arranged into ten pleista. Of these, three are large pleista containing several genera each, whilst the remaining seven comprise single genera only. If it were required that group formation be dependent upon Indices of Similarity greater than .80, it would be necessary to recognize more major pleista than the three generated by Indices of that magnitude.

General discussion

The method of classification developed above has been derived almost entirely by objective methods, and so it is of interest to compare the results obtained with two recent classifications of the Poaceae put forward by Pilger (1954) and Prat (1960). These have been chosen as the basis of comparison both because they are recent and because they reflect the mature thoughts on this subject of two agrostologists of long standing repute. The classification proposed by Tateoka (1957) will not be considered since it has been published only in outline.

Pilger arranged the genera of the Poaceae into nine subfamilies, of which six are represented by the nineteen genera recorded in Figure 2 in which his scheme of classification is superimposed upon the grouping of these genera based upon Indices of Similarity equal to or exceeding .80 in value.

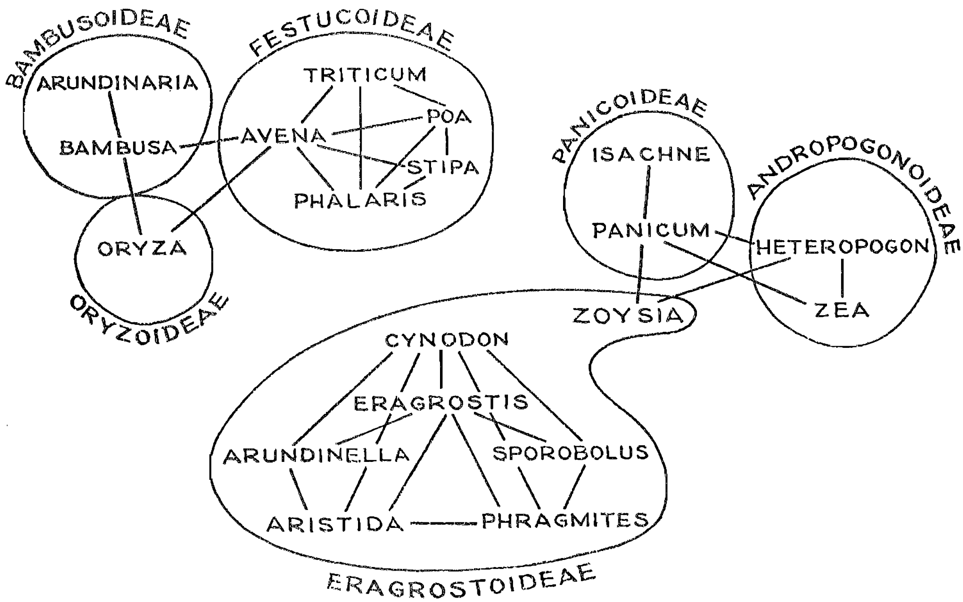

FIG. 2.—Genera with Indices of Similarity equal to or exceeding .80 are connected with a solid line. Superimposed upon this arrangement are the subfamilies of Pilger (1954).

From the figure it is clear that there is a close similarity between the two arrangements of genera. The three subfamilies not represented in the figure each contain one or a few genera only. His Olyroideae and Anomochloideae belong, according to the writer, amongst the pooid grasses. The third subfamily, the Micrairoideae, contains a single genus only and was one of the six genera which were shown by the above statistical analysis to occupy an isolated position in the family.

Likewise there is a reasonably close agreement between the classification of the grasses suggested by Prat (1960) and that derived statistically above. He has arranged the grass genera into six subfamilies and a seventh group of "genres à position discutée". Within three of his subfamilies he has further groups of isolated genera. A comparison of his scheme and that presented above is given in Table 5 and Figure 3.

TABLE 5

A Comparison of the Supra-tribal Groupings Within the Poaceae According to Clifford and Prat (1960)

Clifford Pleista	Prat Subfamilies
Pooid	Festucoidée Bambusoidée Pharoidée
Eragrostoid	Chloridoidée Phragmitiformes
Panicoid	Panicoidée
Genera not included above	Genres à position discutée

From Table 5 it may be seen that two of the three major pleista proposed by the writer embrace more than one of Prat's subfamilies. This discord is however more apparent than real for two reasons, one concerning the statistical method of analysis, the other resulting from the manner in which Prat has defined his subfamilies.

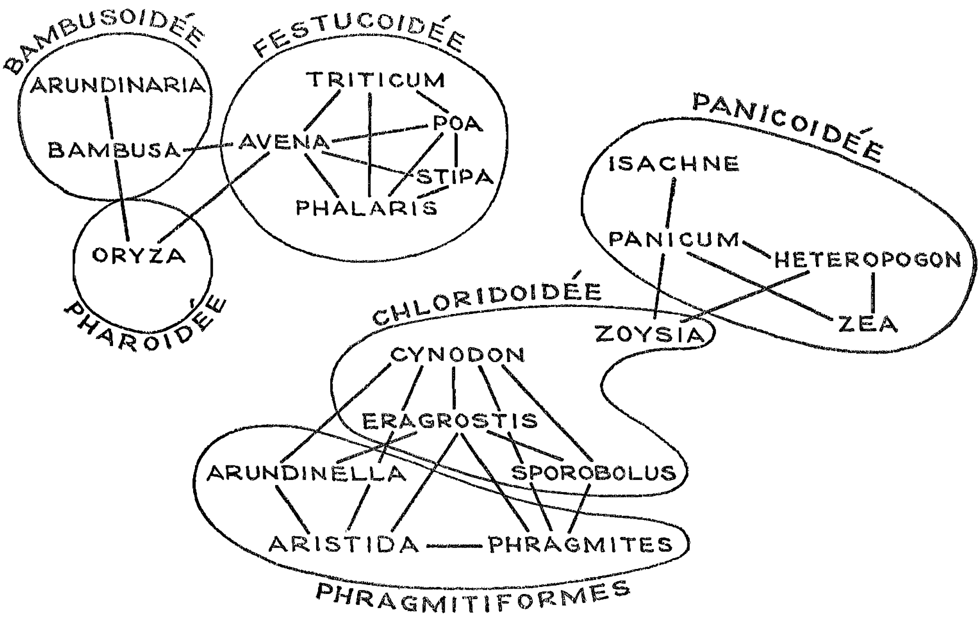

Fig. 3.—Genera with Indices of Similarity equal to or exceeding .80 are connected with a solid line. Superimposed upon this arrangement are the subfamilies of Prat (1960).

With the method of analysis employed above, the number of pleista recognized depends upon the value of the Index of Similarity chosen as the basis for pleiston definition. This may be conveniently illustrated for the pooid grasses by considering the effects of advancing the requirements for group formation from an Index of Similarity amongst members from .80 to .90.

In these circumstances the pooid grasses may be subdivided into three sub-pleista which correspond almost exactly to the Festucoidée, Bambusoidée, and Pharoidée of Prat. Similarly, the eragrostoid grasses may be subdivided into further sub-pleista, but those obtained do not match the subfamilies proposed by Prat, and so the correspondence between the two schemes of classification being discussed is, as far as the eragrostoid grasses are concerned, less close than with the pooid grasses discussed above.

Nevertheless, this does not necessarily raise any serious difficulties, for, as Prat has indicated (p. 69), both his Phragmitiformes and Pharoidée are provisional subfamilies only and are less homogeneous than the other three subfamilies.

Furthermore, both Prat and the writer accept that a number of genera fail to fit into any of the major pleista or subfamilies established, and here too there is close correspondence between the two schemes of classification being considered. Four of the seven genera listed above by the writer as failing to fit into one of the three pleista—pooid, eragrostoid, and panicoid—have been accepted by Prat as "genres à position discutée" and so have not been placed in any of his six subfamilies. These are the genera *Micraira*, *Nardus*, *Lygeum*, and *Phyllorachis*.

Of the remaining three genera, two—*Pariana* and *Streptochaeta*—have been placed in the subfamily Pharoidée, but attention is drawn to the fact that they occupy an isolated position in that subfamily.

The sixth of the genera that failed to fit into one of the three pleista proposed by the writer was *Pharus*, and this Prat has placed without comment in the subfamily Pharoidée. Yet even so this does not indicate any serious disagreement between the two schemes of classification being considered, for although *Pharus* is excluded from any one of the three pleista by reason of its low Indices of Similarity with other genera, it has more in common with *Oryza* than any other genus of Table 2, and *Oryza* is placed by Prat in the Pharoidée.

There is therefore reasonable agreement between the scheme of classification derived statistically and the schemes derived otherwise by Prat and Pilger. This agreement applies not only to the overall classification, but may also be demonstrated by considering the relationships of several generic pairs which, though formerly regarded as related, have in recent years been separated into different subfamilies. For example, the statistical analyses support the view that *Poa* and *Eragrostis* belong to different subfamilies, likewise that *Stipa* and *Aristida* are also to be widely separated, and that *Phalaris* is well separated from *Ehrharta*.

From Figures 2 and 3 it might appear that the statistical approach to the classification of grasses has failed to place satisfactorily the genus *Zoysia*, since both Prat and Pilger place it in a subfamily included in the pleiston of eragrostoid grasses, whereas the statistical analysis places it amongst the panicoid grasses. The existence of this discrepancy is interesting, for both Bentham (1883) and Hackel (1887) placed this genus near to the tribe Andropogoneae amongst the panicoid grasses.

In the absence of objective means for determining the relative merits of the different schemes of classification, it is impossible to determine which of the three considered above has the most merit. But should the viewpoint of Adanson (1763) be accepted that, if a classification is to be based upon similarities between individuals, as many characters as possible should be taken into account, there is considerable merit in the statistically derived classification for in no other way is it possible to consider large numbers of characters simultaneously. It is sometimes objected that such schemes accord all the characters equal taxonomic status unless there is direct evidence to the contrary, but this would seem to be more realistic than to weight characters arbitrarily.

The dangers attendant upon stressing some rather than other characters when classifying the grasses have previously been stressed by both Bews (1929) and Hubbard (1934), whose opinions were aptly summarized by Hubbard when he wrote: "In such a natural family as the Gramineae it would seem unwise to place absolute reliance on external morphological resemblances, for it frequently happens that species with similar facies differ considerably in their anatomy and cytology, (e.g. species of *Poa* and *Eragrostis*)".

If absolute reliance is not to be placed on external morphological resemblances, there is no reason why it ought to be placed on either anatomical or cytological resemblances. Instead, all characters must be considered, which means employing some method of statistical analysis such as that employed above.

Acknowledgments

The writer acknowledges with pleasure numerous discussions on the subject of quantitative taxonomy with Drs. J. E. C. Aberdeen and S. T. Blake during the preparation of this paper. Professor D. A. Herbert and Dr. R. F. Langdon kindly read and commented upon the manuscript. Figures 2 and 3 were prepared by Mr. E. E. Savage, Department of Geography, University of Queensland.

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