A Maximal Predictive Classification of Klebsiellae and of the Yeasts

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SUMMARY

The concepts of the numerical method of maximal predictive classification are illustrated with classifications of 13 species of enterobacteria and of 434 species of yeast. The method seeks to classify into a specified number of classes (k) such that more correct statements can be made about the constituent members than with any other classification. The best choice of k relates to the separation of the classes as measured by the average number of correct statements made for an individual assigned to a class to which it does not belong. The maximal predictive classifications are compared with previous classifications of the two groups, which seem to be poor predictively (in terms of the characters considered in this study). The results suggest that taxonomists may be more concerned with maximizing class separation rather than with prediction, but many more groups of organisms would need similar study before this view could be held with confidence.

INTRODUCTION

Without a fossil record, one can only conjecture about evolutionary history and, in these circumstances, no classification is likely to be 'phylogenetic'. Thus for micro-organisms, classification cannot be based on ancestral relationships, simply because these relationships are quite unknown. The development of numerical taxonomy (see Sneath & Sokal, 1973) has cleared the way for applying solely pragmatic concepts to the classification of micro-organisms and for rejecting obsessions with kinship (e.g. Kluver & van Niel, 1936; Kudriavzev, 1954; Marmur, Falkow & Mandel, 1963; Wickerham, 1969; van der Walt, 1970).

Of the principles that have been suggested for classification, Gilmour's (1937) dictum 'That a system of classification is the more general the more propositions that can be made about its constituent classes' seems to us most useful for practical taxonomy. Gower (1974) has constructed a maximal predictive criterion that expresses Gilmour's ideas mathematically. This criterion gives a set of predictions of the characteristics of an individual that can be made on being informed that this individual belongs to a specified one of k taxa. These k taxa are to be defined so that the number of correct predictions, W_k , when averaged over all n individuals, is greater than for any other choice of k taxa. W_k corresponds to Gilmour's 'number of propositions'.

Table 1. *Criteria values for Klebsiellae*

k	W_k	B_k	$W_k - B_k$
1	319	—	—
2	353	243.0	110.0
3	371	196.0	175.0
4	381	204.3	176.7
5	389	219.3	169.7
6	396	220.6	175.4
7	403	238.0	165.0
8	407	239.7	167.3
9	412	236.3	174.7
10	417	233.7	183.3
11	417	226.9	180.1
12	418	226.6	191.4
13	419	227.8	191.2

k , Number of classes; W_k , maximal predictive criterion; B_k , criterion of class-separation.

The results give the maximum values found for W_k ; B_k is calculated for the resulting classifications and is not itself minimized.

For a given number n of individuals the value of k may lie anywhere between 1 and n . Assuming that all taxa differ from each other, then as k increases the number of correct predictions W_k increases. However, as one of the aims of practical taxonomy is to reduce the number of groups, the ideal value of k lies between these two extremes. To determine k , a further criterion, B_k , which measures the gaps between the taxa was introduced. More precisely, B_k measures the average number of correct predictions of the characteristics of an individual belonging to one taxon when it has been incorrectly assigned to another taxon. W_k and B_k do not act independently. When $k = 1$, W_1 is least and B_1 is undefined; when $k = n$, W_n is maximum but B_n is also large. The best choice of k is related to a balance between having a large W_k and a small B_k ; a simple criterion, with some theoretical justification, is to maximize $W_k - B_k$ (Gower, 1974), or if too large a value of k is to be penalized, a slightly more complicated criterion can be used (Gower, 1973).

A simple example that fully illustrates how to compute class predictors W_k and B_k is given by Gower (1974), who also discusses how to deal with responses that are unknown, variable or at more than two levels.

No exact computational process is known for optimizing the criteria W_k , B_k , or $W_k - B_k$, but so-called transfer algorithms (see, for example, Gower, 1974) give acceptable, although possibly sub-optimal, results. As such algorithms may lead to local optima less than the best possible criterion value, it is usually recommended that the transfer algorithm should be used with several initial configurations. The algorithm tries to improve on the initial criterion value by moving an item from one class to another, or possibly by exchanging items between classes, stopping when no further improvement is possible. In this way W_k has been optimized both for the information on *Klebsiellae* (Bascomb, Lapage, Willcox & Curtis, 1971), and on the yeasts (Barnett & Pankhurst, 1974). The results are described below.

RESULTS AND DISCUSSION

The Klebsiellae

The data for this analysis are from Table 6 of Bascomb *et al.* (1971), which gives the results of 39 tests on 13 species of enterobacteria. Table 1 gives the maximum values that could be found for W_k , for $k = 1$ to 13, and the corresponding values of B_k and $W_k - B_k$.

Table 2. Eight classifications of 13 species of enterobacteria

In each column, species represented by the same integer belong to the same class.

	Source								
	Previous		Bascomb <i>et al.</i> (1971)	Best W_5-B_5	Maximal predictive				
	...	5	6	5	5	3	4	5	6
Number of classes (k)	...	5	6	5	5	3	4	5	6
<i>Klebsiella aerogenes</i> / <i>oxytoca</i> / <i>edwardsii</i>		1	1	1	1	1	1	1	1
<i>K. pneumoniae</i>		1	1	1	1	1	1	1	1
<i>K.</i> 'unnamed' group		1	1	1	1	1	1	1	1
<i>K. ozaenae</i>		1	1	1	1	1	1	1	1
<i>K. rhinoscleromatis</i>		1	1	1	1	1	1	1	1
<i>Enterobacter aerogenes</i> (syn. <i>Klebsiella mobilis</i>)		2	2	1	1	1	1	1	1
<i>E. cloacae</i>		2	2	2	2	2	2	2	2
<i>E. liquefaciens</i>		2	2	3	3	2	2	2	3
<i>Serratia</i> biotype I		3	3	3	3	2	2	2	3
<i>Serratia</i> biotype II		3	3	3	3	2	2	3	4
<i>Hafnia alvei</i>		4	4	4	2	2	2	2	2
<i>Chromobacterium typhi-</i> <i>flavum</i> / <i>Enterobacter</i> 'pigmenté'		2	5	2	4	2	3	4	5
<i>Edwardsiella tarda</i>		5	6	5	5	3	4	5	6
W_k		383.0	391.0	386.0	387.0	371.0	381.0	389.0	396.0
B_k		218.8	219.2	209.0	205.3	196.0	204.3	219.3	220.6
W_k-B_k		164.2	171.8	177.0	181.7	175.0	176.7	169.7	175.4

Plotting $W_k - B_k$ against k makes it clear that $W_k - B_k$ does not improve much when k is greater than 3. However, traditional classification divides the group into 5 genera: *Edwardsiella*, *Enterobacter*, *Hafnia*, *Klebsiella* and *Serratia*. The classification of the strains of *Enterobacter* 'pigmenté'/*Chromobacterium typhiflavum* is more controversial. As the name suggests, Leclerc (1962) assigned the strains studied to the genus *Enterobacter* but refrained from giving species status. Graham & Hodgkiss (1967) have shown *C. typhiflavum* to be a synonym of *Erwinia herbicola* and Bascomb *et al.* (1971) and Bascomb, Lapage, Curtis & Willcox (1973) have shown that the strains of *C. typhiflavum* and *E.* 'pigmenté' are similar and belong to *Er. herbicola*. If these strains are removed from *Enterobacter* then the group includes 6 genera. We therefore compared W_k , B_k and $W_k - B_k$ for the eight different classifications of the group given in Table 2. Three of these are intuitive with $k = 5$ and 6, four are maximal predictive classifications for $k = 3, 4, 5$ and 6 and one gives the biggest value found for $W_k - B_k$ when $k = 5$. Each column of Table 2 refers to one of the eight classifications, and genera with the same integer value in a column are assigned to the same class for that classification. The values of W_k , B_k and $W_k - B_k$ given in Table 2 do not vary much between the different classifications. Hence for these genera many different classifications have a similar predictivity and this reflects the difficulty there has been in agreeing on a classification.

Choice of k on the basis of $W_k - B_k$ leads to four taxa, where all the *Klebsiella* species including *K. mobilis* (Bascomb *et al.* 1971) are put into one class, *Edwardsiella tarda* and *C. typhiflavum*/*E.* 'pigmenté' into two separate classes, and the rest of the species form a fourth heterogeneous class (Table 2). However, when $k = 3$ then $W_k - B_k$ is nearly the same, though *C. typhiflavum*/*E.* 'pigmenté' is now included in the heterogeneous class.

Fig. 1. Natural hierarchical classification found for the maximal predictive classifications of Klebsiellae for $k = 2, 3, \dots, 6$.

Table 3. *Criteria values for yeast taxa*

k	W_k	B_k	$W_k - B_k$
2	14 794	11 601	3193
10	15 816	12 365	3451
20	16 343	12 116	4227
41	15 106	10 901	4205

For $k = 2, 10, 20$ the results give the maximum values found for W_k ; B_k is calculated for the resulting classifications and is not itself minimized. When $k = 41$, values are given for the unaltered classification into 41 genera given by Barnett & Pankhurst (1974).

The traditional classifications into five or six genera have smaller values of W_k than, and very similar values of B_k to, those of the corresponding maximal predictive classifications. The values of $W_k - B_k$ are necessarily smaller. Bascomb *et al.* (1971) improved on the traditional classifications (for $k = 5$), both by increasing W_5 and by appreciably decreasing B_5 . However, their values of $W_5 - B_5$ can be bettered, as shown in Table 2, column 4. This gives an even lower value of B_5 together with a higher value of W_5 which is only slightly less than the maximal predictive value ($W_5 = 389$, see Table 2, column 7).

Edwardsiella tarda, which is known to be quite different from the other species in this study, appears separately in all classifications. The maximal predictive classifications include *Enterobacter aerogenes* with the *Klebsiella* species, thus endorsing Bascomb *et al.* (1971) who renamed the species as *Klebsiella mobilis*. All members of the genus *Klebsiella* are grouped together in every classification, reflecting the homogeneity of the genus. The grouping of the three remaining species of *Enterobacter* (*Enterobacter cloacae*, *E. liquefaciens* and *E. 'pigmenté'*/*C. typhiflavum*), the two *Serratia* biotypes and *Hafnia alvei* varies in different classifications, reflecting the controversy about the division within the tribe. The best $W_k - B_k$ classification groups *E. liquefaciens* with the two *Serratia* biotypes, *E. cloacae*

with *H. alvei*, and places both *Er. herbicola* and *Ed. tarda* in separate groups. The transfer by Bascomb *et al.* (1971) of *E. liquefaciens* as *Serratia liquefaciens* is thus endorsed by this criterion.

Gower (1974) discusses how, in principle, maximal predictive hierarchical classifications can be formed. Normally the classes found for $k = 1, 2, \dots, n$ will not be nested, but if they are, the taxa may be said to have a natural hierarchical classification. It is remarkable that the maximal predictive classifications for $k = 1, 2, \dots, 6$ form the hierarchy shown in Fig. 1.

The yeasts

The values found by maximizing W_k , with corresponding values of B_k and $W_k - B_k$ are shown in Table 3, which was derived from the results of 62 physiological tests on 434 species of yeast (Barnett & Pankhurst, 1974). The time required to compute each line of this Table was so great that each calculation was done for only one starting configuration. Further calculations with different starting configurations would probably yield better local optima than those given in the Table. No attempt was made to find an optimum classification for $k > 20$ and the last line of Table 3, where $k = 41$, corresponds to the 41 genera listed by Barnett & Pankhurst (1974).

The value of W_k for the 41 actual yeast genera is less than the best value found for $k = 20$, and hence must be much lower than the best value for $k = 41$. $W_k - B_k$ for the 41 yeast genera is similar to, but less than, the best value (that for $k = 20$), mainly because the value for B_k is strikingly small for the 41 genera.

So on both the W_k and the $W_k - B_k$ criteria, the accepted classification of the yeasts (Lodder, 1970; Barnett & Pankhurst, 1974) is poor. However, this may be because the analysis considers genera and not species, and accepted yeast genera are defined chiefly in terms of microscopical appearance and life cycles. The information used here for calculations is based entirely on responses to physiological tests which bear little relation to the classification of yeasts into the traditional genera.

Table 4 defines the characteristics of each of the twenty predictive-taxa, and Table 5 shows how the species of each of 41 accepted genera are distributed amongst those taxa. The salient features of this distribution are as follows: (i) genera, such as *Candida*, *Torulopsis* and *Endomycopsis*, each recognized as particularly heterogeneous, are indeed spread widely amongst the predictive taxa; (ii) *Pichia* and *Hansenula* are also spread widely; (iii) for *Saccharomyces*, on the other hand, which is a fairly uniform genus nutritionally, 84 % of the species are included in the three predictive taxa, XIV, XV and XVI; (iv) 64 % of the pink yeasts, *Sporobolomyces*, *Rhodotorula*, *Rhodospiridium* and *Sporidiobolus*, are in taxa XVII and XIX; (v) all the species of *Hanseniaspora* and *Kloeckera* are in taxon IX; (vi) 67 % of *Brettanomyces* species are in I; (vii) 58 % of *Cryptococcus* species are in VI; (viii) 50 % of *Debaryomyces* are in VII; (ix) 48 % of *Kluyveromyces* are in X.

CONCLUSION

The classifications offered are not intended to be definitive, but they give the results of a simple method for comparing different classifications, and show how the new criteria have been used to construct classifications which are, in certain respects, better than accepted ones.

Although the aim has been to maximize W_k and select k by examining $W_k - B_k$, other approaches of the same general kind are open. For example B_k could be minimized or $W_k - B_k$ maximized. Minimizing B_k amounts to choosing the classes so that they have maximum separation, and this is not equivalent to forming classes with the greatest homogeneity although the two properties are related. There is some suggestion that the intuitive

Table 4 (cont.)

Test code no	Test name	Predictive taxa																			
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX
39	Methyl α -D-glucoside	+	+	+	+	+	-	+	-	-	-	+	-	+	-	-	-	+	-	-	-
41	Lactate	+	-	-	-	-	-	-	+	+	+	+	+	+	-	+	-	-	-	+	+
42	Succinate	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	+	-	-	-
43	Citrate	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	+	-	-	-
44	Inositol	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
46	Nitrate	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
47	Ethylamine	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	+	-	-	-
48	No vitamins	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
49	10% NaCl + 5% glucose	+	-	+	+	+	+	-	+	+	-	+	+	-	+	+	+	+	+	+	+
50	50% Glucose	-	+	+	-	+	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-
51	60% Glucose	-	-	+	-	+	-	-	-	-	+	-	-	-	+	-	-	-	+	-	-
52	37 °C	+	+	+	-	+	-	-	+	+	+	+	+	+	-	+	-	-	-	-	-
53	Ester production	+	+	+	+	-	+	+	-	+	+	+	+	+	+	+	+	+	-	-	-
54	Acid production	+	-	-	-	-	-	-	-	+	+	-	-	-	+	+	-	-	+	-	-
55	Cycloheximide resistance	+	±	-	±	+	-	±	±	±	±	±	+	±	-	-	-	+	-	±	±
56	Glucono- δ -lactone	-	±	-	-	+	+	+	+	+	+	+	-	+	+	±	-	+	+	+	+
57	2-Keto-gluconate	+	±	+	+	-	+	+	-	+	+	+	-	+	+	±	+	-	-	+	+
58	5-Keto-gluconate	-	±	-	-	-	+	+	-	-	-	-	-	+	-	±	-	-	-	-	-
59	Nitrite	-	-	-	-	-	+	+	-	-	-	-	-	+	-	±	+	-	+	+	+
60	Gelatin liquefaction	-	±	-	-	-	-	-	-	-	-	-	-	+	-	±	+	-	+	-	-
61	Urea hydrolysis	±	-	-	-	-	+	+	-	-	±	-	-	-	+	±	+	+	±	+	+
62	Starch production	-	-	-	-	-	+	+	-	-	-	-	-	-	-	±	-	-	-	-	-

+, Positive test; -, negative test; ±, either positive or negative test.

Table 5. *Distribution of the 41 accepted genera of the yeasts amongst the 20 predictive taxa*

Entries in this Table are numbers of species.

	Accepted genera	Predictive taxa																				Totals
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	
1	<i>Ambrosiozyma</i>	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2
2	<i>Brettanomyces</i>	6	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.	9
3	<i>Bullera</i>	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3
4	<i>Candida</i>	2	14	8	5	9	.	9	.	2	2	7	12	6	2	2	2	8	10	4	.	104
5	<i>Citeromyces</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1
6	<i>Cryptococcus</i>	.	.	.	1	.	11	1	.	.	.	2	1	.	.	.	1	.	.	2	.	19
7	<i>Debaryomyces</i>	.	.	2	.	.	.	5	.	.	1	1	.	.	.	.	.	.	.	1	.	10
8	<i>Dekkera</i>	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
9	<i>Endomycopsis</i>	.	1	1	2	.	.	.	.	.	.	.	3	2	.	.	.	.	1	.	.	10
10	<i>Filobasidium</i>	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
11	<i>Hanseniaspora</i>	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	3
12	<i>Hansenula</i>	2	2	3	.	1	.	.	5	1	2	.	.	6	.	.	.	.	3	3	.	28
13	<i>Kloeckera</i>	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	4
14	<i>Kluyveromyces</i>	3	.	.	1	.	2	1	.	.	9	.	1	.	2	.	4	.	.	.	.	19
15	<i>Leucosporidium</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	7
16	<i>Lipomyces</i>	.	.	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	3
17	<i>Lodderomyces</i>	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
18	<i>Metschnikowia</i>	.	.	.	1	1	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	5
19	<i>Nadsonia</i>	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2
20	<i>Nematospora</i>	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1
21	<i>Oosporidium</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
22	<i>Pachysolen</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
23	<i>Pichia</i>	1	4	2	2	4	.	3	5	.	.	1	6	6	.	.	.	1	6	4	.	45
24	<i>Rhodospiridium</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
25	<i>Rhodotorula</i>	.	.	.	.	.	.	.	.	.	.	3	.	1	.	.	.	2	.	2	.	10
26	<i>Saccharomyces</i>	1	.	.	.	.	.	.	.	.	1	.	2	.	13	14	10	.	3	.	.	44
27	<i>Saccharomycodes</i>	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	1
28	<i>Saccharomycopsis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
29	<i>Schizoblastosporion</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1

approach of taxonomists might be to minimize B_k rather than maximize W_k (see, for example, B_5 and B_6 in the first two columns of Table 2, and B_{41} in Table 3). It would be worth studying how the values of W_k , B_k and $W_k - B_k$ actually achieved in traditional taxonomic classifications relate to their optimum values.

Identification and classification are two concepts whose differences rather than similarities have been emphasized in recent years. Perhaps this tendency has been taken too far, as it is often advantageous for classification and identification to go hand-in-hand. Gower (1973) has shown that many classification algorithms produce classes with optimum identification properties, and in particular this is true of maximal predictive classes. To assign an individual to one of k maximal predictive classes it is sufficient to count the number of matches m_i ($i = 1, 2, \dots, k$) the individual has with the test results predicted by each of the k class predictors. The individual must belong to the class i for which m_i is greatest. Complete identification is achieved in the usual hierarchical manner of a dichotomous diagnostic key when the members of each class are themselves classified into nested sets of classes, each with its own predictor. The practical disadvantage of this approach is that at each step of the identification process all test results are required rather than the single test of a traditional key. The possibility that fewer tests might suffice has yet to be investigated.

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