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Polyporaceae of Iowa: a taxonomic, numerical and electrophoretic study

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POLYPORACEAE OF IOWA: A TAXONOMIC, NUMERICAL AND ELECTROPHORETIC STUDY

Iowa State University PH.D. 1983

Polyporaceae of Iowa: A taxonomic, numerical and electrophoretic study

by

Robert John Pinette

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GENERAL INTRODUCTION

In its broadest interpretation, the Polyporaceae consists of wood-rotting basidiomycetes usually having a poroid hymenophore. In the classical Friesian system (Overholts, 1953), about 11 genera are delimited by macroscopic characters such as the shape of the pores and/or the texture of the basidiocarp. Despite the diverse assemblage of species grouped in these genera, the Friesian system has persisted, especially in the United States. European interpretations have emphasized microscopic features requiring hyphal analysis and critical examination of the hymenium. Such studies began in earnest with Patouillard's Essai Taxonomique (1900), and as a consequence of this difference in emphasis, the modern classification developed is radically different from the Friesian one. Until recently, many American mycologists have seemed reluctant to accept these changes, and as yet, no modern, comprehensive treatment of American polypores is available.

Since many polypores are cosmopolitan, European treatments, such as Domanski (1965), Domanski et al. (1967), and Ryvarden (1976, 1978), are applicable to our American flora. In reviewing these monographs, one soon realizes that the taxonomy of this family is very much in a state of flux. Although some genera such as Ganoderma and Phellinus are fairly well delimited, others such as Trametes and Coriolus are somewhat nebulous. Moreover, many small or monotypic genera have been split out of the large Friesian ones, such as Polyporus and Poria. A

good indication of taxonomic upheaval this family has undergone is given by Cooke (1959). His list of about 300 poroid taxa includes over 100 valid generic names. Delimiting many small genera is a trend prevalent throughout the Aphyllophorales, and in the opinion of Gilbertson (1980), "...the significance of the genus and its role in taxonomy of those families has seriously been weakened." Some of these new genera will probably withstand the test of time. However, in the case of the more controversial taxa, these differences are largely due to a casual attitude toward the definition of a genus and an overall absence of data analysis. Admittedly, subjective judgments must ultimately be made in taxonomic treatments; however, a need exists for some objective method of examining data as a basis for such decisions. Very frequently, only a few characters have been given taxonomic significance, and assuming such characters exist, this is not an entirely inappropriate method. Unfortunately, this approach is vexed by the fact that there often is a lack of agreement among mycologists as to which features are taxonomically important. Another problem is that polypore specialists have emphasized morphological evidence as the basis for classification, and only a few efforts to develop independent sources of evidence have been made. Studies of wood-rotting basidiomycetes in culture, such as Nobles (1958, 1965) and Stalpers (1978), are valuable contributions to the systematics of the Aphyllophorales; although these studies utilize physiological traits, other cultural features of these isolates cannot be considered as being independent from the morphological evidence. Chromatography is another potential source of taxonomic evidence that

has been widely used in higher plants. It is also used as a diagnostic aid in identifying lichens, but few studies have applied this technique to higher fungi. Most of these studies have been limited to the Agaricales. Fries (1958) investigated the use of chromatography in the Hymenomycetes. More recently, Parmasto and Parmasto (1979) examined the pigments of the Aphyllophorales using spectrophotometry. Generally speaking, studies such as these are rare, and their methodology is not commonly applied by students of free-living fungi. There is a similar dearth of cytological data, but this is largely due to technical difficulties, as well as to meiotic and mitotic irregularities found in many species fo fungi (Rogers, 1973). Contrary to these other sources of information, electrophoretic studies of fungi are gradually accumulating, but in this case, the sampling of natural populations and finding suitable means of data anlaysis may prove critical to successful applications.

This study has been primarily concerned with 1) investigating methods for establishing generic limits in the Polyporaceae, and 2) compiling a checklist of the polypores of Iowa utilizing modern nomenclature based on the examination of herbarium material and recent field collections.

PART I. ELECTROPHORESIS AND NUMERICAL ANALYSIS OF 20 POLYPORE SPECIES

Introduction

Numerous electrophoretic studies of fungi have been recorded since the 1960s. These studies have clearly shown the usefulness of this technique in taxonomic investigations of fungi. However, few of these studies attempted to quantify the genetic variability observed. Garber and Rippon (1968) and Garber (1973) reviewed the literature which applied electrophoresis as a taxonomic tool in microbial taxonomy. In these papers, intraspecific comparisons of banding patterns for a few enzymes were made by sight inspection. An examination of more recent electrophoretic studies of fungi indicates that statistical procedures still do not follow the methods applied in studies of higher plants as reviewed by Gottlieb (1977, 1981).

One exceptional study by Spieth (1975) did attempt to examine the population genetics of Neurospora intermedia (authority not cited); however, his population sample sizes were too small to determine traditional measures of genetic variability such as average heterozygosity and percent polymorphic loci. Lack of a suitable means for sampling natural populations is a problem that probably exists in studying many groups of fungi. Rayner and Todd (1982) reviewed the literature pertaining to the sampling and analyzing of natural populations of

wood-decaying fungi. Several sampling procedures have been described for a few common species, but the problem of dealing with rare taxa is not discussed. In spite of the fact that the vegetative mycelia may be perennial and omnipresent, unless the fruiting structures manifest themselves, there is no effective method for sampling populations of "rare" species.

In the absence of replication due to sampling problems, other statistical approaches have been proposed. Lawson et al. (1975) used hypergeometric distribution to obtain the probability of matches due to chance alone. In this analysis, low probability values indicate close relationships between individuals. This probability function was applied to electrophoretic data from a study of nine species of Polyporus (sensu Overholts, 1953) surveyed by Shannon et al. (1973). Harris et al. (1974) also applied this hypergeometric distribution on their Fomes data. In both instances, low probabilities were obtained between pairs of individuals belonging to closely related species. However, in the case of Polyporus, exceptions can be found where individuals of distantly related species also had low probabilities. Only one other study of polypores has attempted to demonstrate the usefulness of electrophoresis as a taxonomic tool in this group of fungi. Mazumder et al. (1980) compared the protein banding patterns obtained from reconstituted basidiocarps of Polyporus grammocephalus, Ganoderma lucidum, Hexagonia polygramma, and Daedalia flavida. However, this cursory investigation included only unrelated species, and its apparent lack of replication probably explains why they did not attempt to quantify their data.

Several studies of fungi have successfully employed numerical analysis to demonstrate taxonomic relationships based on electrophoretic evidence. Most of these authors (Landau et al., 1968; Shecter et al., 1972; Chesson et al., 1978; and Jones and Noble, 1982) investigated Deuteromycetous taxa. Lèger (1976) studied 22 species of Peniophora (Corticiaceae) and subjected the electrophoretic data to a type of ordination called factor analysis. These results were also compared to various classifications proposed for Peniophora as well as to an earlier numerical study of morphological data (Lèger and Poncet, 1976). These last two papers represent a novel approach in that both morphological and electrophoretic evidence are compared by means of numerical analysis. No reports of any numerical studies of polypore species have been found.

Methods and Materials

Species included in the following studies were initially selected on the basis of availability for electrophoresis. Because of enzyme extractions problems, brown hyphal species belonging to Phellinus, Inonotus and other genera were omitted. The final selection (Table 1) includes species from morphologically well-defined genera such as Ganoderma and Bjerkandera as well as some problematic taxa such as several Coriolus spp. and Trametes cervina.

Morphological analysis

Descriptions for the 20 operational taxonomic units (OTU's) studied here are taken from Domanski et al. (1967). Data from indigenous North American species (Ganoderma lobatum and Polyporus radicatus) not

described in this work and other missing data were obtained from original observations. The characters used in the phenetic analyses are listed in Table 2. Variables 1-8 are quantitative and consist of maximum and minimum values for each character. Variables of 9-20 are qualitative two-state or qualitative multistate characters scored in the two-state format (Sokal and Sneath, 1973).

Table 1. List of species studied and number of individuals sampled electrophoretically (n)

	Species	n
1.	Polyporus mori Pollini ex Fr.	5
2.	P. arcularius Batsch ex Fr.	5
3.	P. brumalis Pers. ex Fr.	1
4.	P. squamosus Huds. ex Fr.	3
5.	P. radicatus Schw.	4
6.	P. varius Pers. ex Fr.	3
7.	P. badius (Pers. ex S. F. Gray) Schw.	7
8.	Laetiporus sulphureus (Bull. ex Tr.) Murr.	7
9.	Meripilus giganteus (Pers. ex Fr.) P. Karst	4
10.	Grifola frondosa (Dicks. ex Fr.) S. F. Gray	4
11.	Bjerkandera fumosa (Pers. ex Fr.) P. Karst.	5
12.	B. adusta (Willd. ex Fr.) P. Karst.	6
13.	Trametes cervina (Schw.) Bres.	6
14.	Cerrena unicolor (Bull. ex Fr.) Murr.	3
15.	Coriolus versicolor (L. ex Fr.) Quel.	5
16.	Co. hirsutus (Wulf. ex Fr.) Quel.	5
17.	Co. pubescens (Schum. ex Fr.) Quel.	3
18.	Ganoderma applanatum (Pers. ex S. F. Gray) Pat.	5
19.	Ga. lobatum (Schw.) Atk.	2
20.	Ga. lucidus (Curt. ex Fr.) P. Karst.	4

Table 2. List of morphological characters

1.	Pileus thickness in cm
2.	Tube length in mm
3.	Pores per mm
4.	Basidium length in μm
5.	Basidium width in μm
6.	Spore length in μm
7.	Spore width in μm
8.	Generative hyphae diameter in μm
9.	Perennial or annual basidiocarp
10.	Attachment of pileus[a] (sessile, stipitate, or compound rosette)
11.	Pubescence on upper surface of pileus
12.	Squamules on upper surface of pileus
13.	Zonate patterns on upper surface of pileus
14.	Skeletal hyphae
15.	Binding hyphae
16.	Spore wall pigmentation
17.	Thickened spore wall
18.	Spore shape[a] (cylindric-ellipsoid or ellipsoid-ovate)
19.	Xanthochrous context
20.	Dark line between tubes and context

[a]Multistate character scored as a two-state variable.

Cluster analysis (CA) and principal component analysis (PCA) are two computerized analyses generally used in phenetic studies. FORTRAN was used in the cluster analysis program, and clustering was accomplished by the unweighted pair group centroid method (Sokal and Sneath, 1973). Zeta Plotting Software was used to generate the dendrograph.

Statistical Analysis System programming was used in the PCA. Although the number of principal components is equal to the number of variables, only the first three components are generally recovered because they usually account for most of the variability (Sokal and Sneath, 1973). Typically, these first three components are used to construct two- or three-dimensional plots of the OTUs.

Electrophoresis

Basidiocarps, gathered from various sites in Iowa, were collected over a period of several years for electrophoresis. Only fresh basidiocarps were selected in the case of annual species. Perennial specimens were collected in late summer and autumn, but in most instances, evidence of new growth was not ascertained. On extended trips, specimens were kept in Styrofoam containers with ice. After returning to the laboratory, specimens were stored in an ultrafreezer at about -25°C. When extractions were made, shavings from a medial longitudinal section of the basidiocarp (about 1 cm^3) were pulverized with a mortar and pestle in liquid N_2. Enough 0.2 M KH_2POH_4 pH 7.0 buffer (containing 10% 10T polyvinylpyrrolidone) was added to give the tissue a paste-like consistency. Whatman no. 1 filter paper, cut into 9 x 5 mm wicks, was used to absorb the crude enzyme extractions.

Horizontal starch gel electrophoresis was carried out following the procedures outline by Schaal and Anderson (1974). Twelve percent gels were prepared by adding 333 ml of gel buffer to 40 g of Sigma potato starch. A summary of gel buffers, amperage and enzyme stains used is given in Table 3. Buffers II and IV were used as continuous systems; borate electrode buffers pH 8.6 and 8.2 were used with gel buffers I and III, respectively. Electrophoresis was conducted at 5°C, and the voltage adjusted as needed to maintain a constant amperage indicated in Table 3. Bromophenol blue was used to mark the progress of the front which was allowed to migrate 5 cm in all four systems. All gels were stained at room temperature for approximately one hour, except for CAT which developed in about 10 minutes.

Table 3. Summary of gel buffers, amperage and stains used for electrophoresis

	Gel Buffer	pH	mA	Enzyme Assayed
I.	tris-citric acid[a]	8.0	40	acid phosphatase (ACP)[b]
II.	tris-glycine[c]	8.7	50	catalase (CAT)[d]
III.	Poulik[d]	8.7	40	esterase (EST)[b]
				leucine aminopeptidase (LAP)[b]
				peptidase (PEP)[b]
IV.	dehydrogenase[d]	9.0	40	hexokinase (HEX)[b]
				malate dehydrogenase (MDH)[e]
				tetrazolium oxidase (TO)[e]

[a]Mitton et al. (1977).

[b]Shaw and Prasad (1970).

[c]Prepared by dissolving 6 g tris with 28.8 g glycine in 2 l water.

[d]Schaal and Anderson (1974).

[e]Siciliano and Shaw (1960).

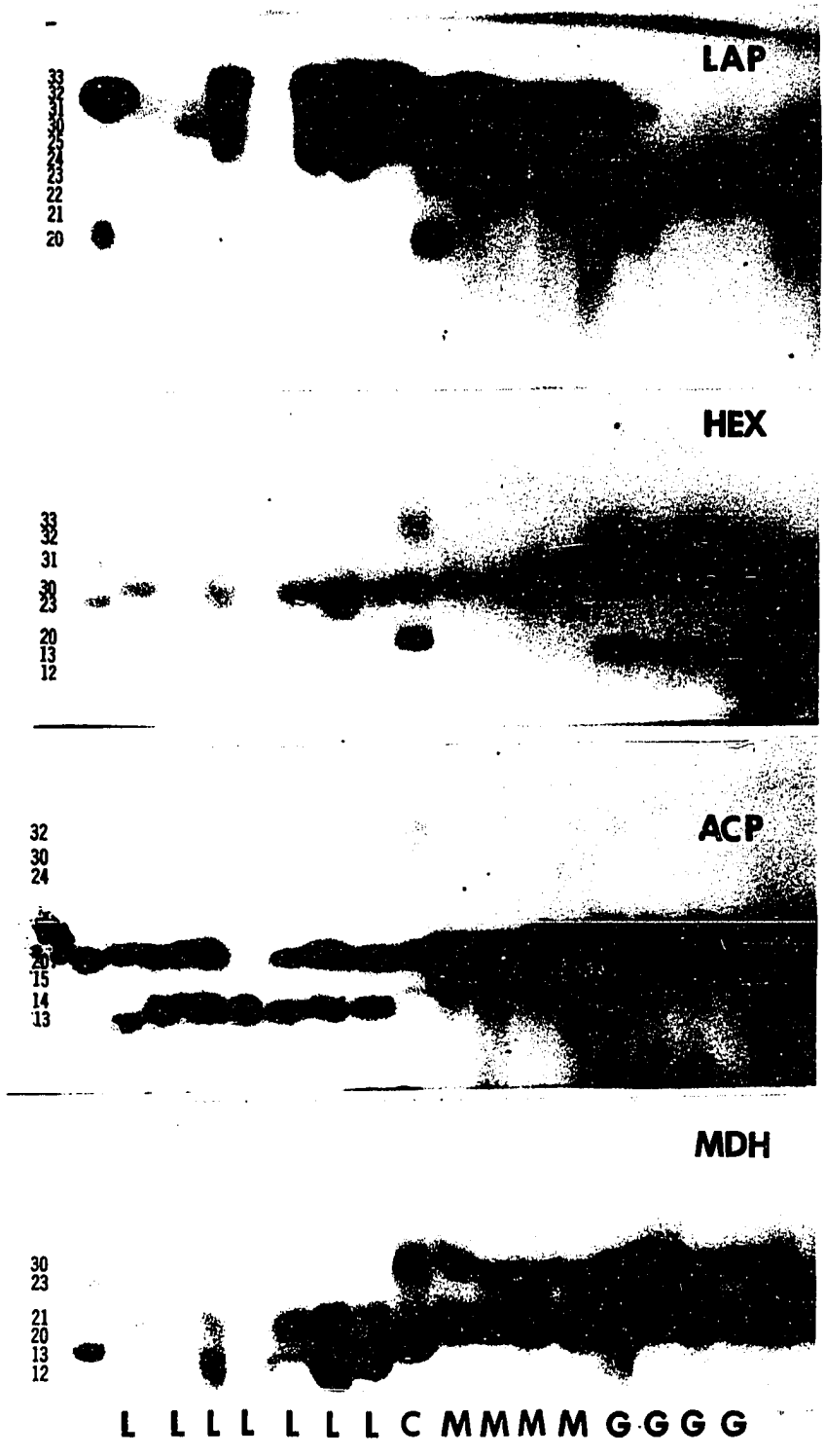
With nine genera included in this survey, the variation encountered among these taxa made consistent scoring between different gels difficult. To overcome this problem, extractions from a single individual of Coriolus hirsutus (2452) were used as a standard on all gels. This individual conveniently manifested combinations of slow-medium, slow-fast, or medium-fast allele pairs for most enzymes assayed. Using the isozyme patterns of this individual as a standard, several regions of the gel could be reliably delimited. Figure 1 illustrates how gels for four enzymes were scored. For example, in the case of MDH, two bands of Coriolus hirsutus (2452) were labeled as 20 and 30. Bands with different mobilities belong to other individuals on this gel are thereby delimited into three migratory zones. In the second zone between the markers, 20 and 30, bands can be more specifically labeled as 21, 22 or 23. Patterns in the first and third zones were recorded in a similar fashion.

Activity for all but two enzymes were scored in this manner. Because CAT bands were often unresolved, the range of activity in mm on the gel was recorded in this case. TO was scored on the basis of maximum migration of bands in mm. In both TO and CAT, fluctuations between gels were adjusted according to differences in the migration of the standard bands before scoring.

Electrophoretic analysis

As in the phenetic study, electrophoretic data were subjected to both cluster analysis and ordination. Because sample sizes used in this

Figure 1. Scoring of four enzymes is demonstrated for L. suplhureus (L), M. giganteus (M) and Gr. frondosa (G). Marker bands of Co. hirsutus (C) are designated as 20 and 30 in each case


LAP
33
32
31
30
23
22
21
20
HEX
33
32
31
30
23
20
13
12
ACP
32
30
24
20
15
14
13
MDH
30
23
21
20
13
12
L L L L L L L C M M M M G G G G

study are small (usually three to five individuals per species), banding patterns for each species were pooled for analysis. Pooled data also simplified the treatment of individuals that added to the variability of banding patterns, but had poor activity for one or two enzymes.

The cluster analysis program used in this case is identical to the one used in the phenetic study except that Sorensen's index of similarity (Mueller-Dombois and Ellenberg, 1974) was substituted for the correlation coefficient. An ordination technique devised by Bray and Curtis (1957) was substituted for principal component analysis because it uses Sorensen's index of similarity which is more amenable to qualitative data. Two Cornell Ecology Programs were used to calculate the resemblance or distance matrix and for ordination.

Results

The results reported here represent a preliminary effort in the application of numerical taxonomy to the classification of the polypores. Following Donk's generic interpretation (1974), the 20 species selected for this study are distributed among 9 genera (Table 1). Three genera, Ganoderma, Bjerkandera and Polyporus, are ostensibly well-defined and these homogeneous taxa are probably good indicators of a successful numerical analysis. A CA based on morphological data is shown in Figure 2. Correlation values in this phenogram vary between slightly less than 0.0 and over 0.9. If a 0.5 phenon line is arbitrarily selected, seven clusters are recognizable. As expected Ganoderma and Bjerkandera (Clusters V and VI) form two homogeneous phenons. However, the genus

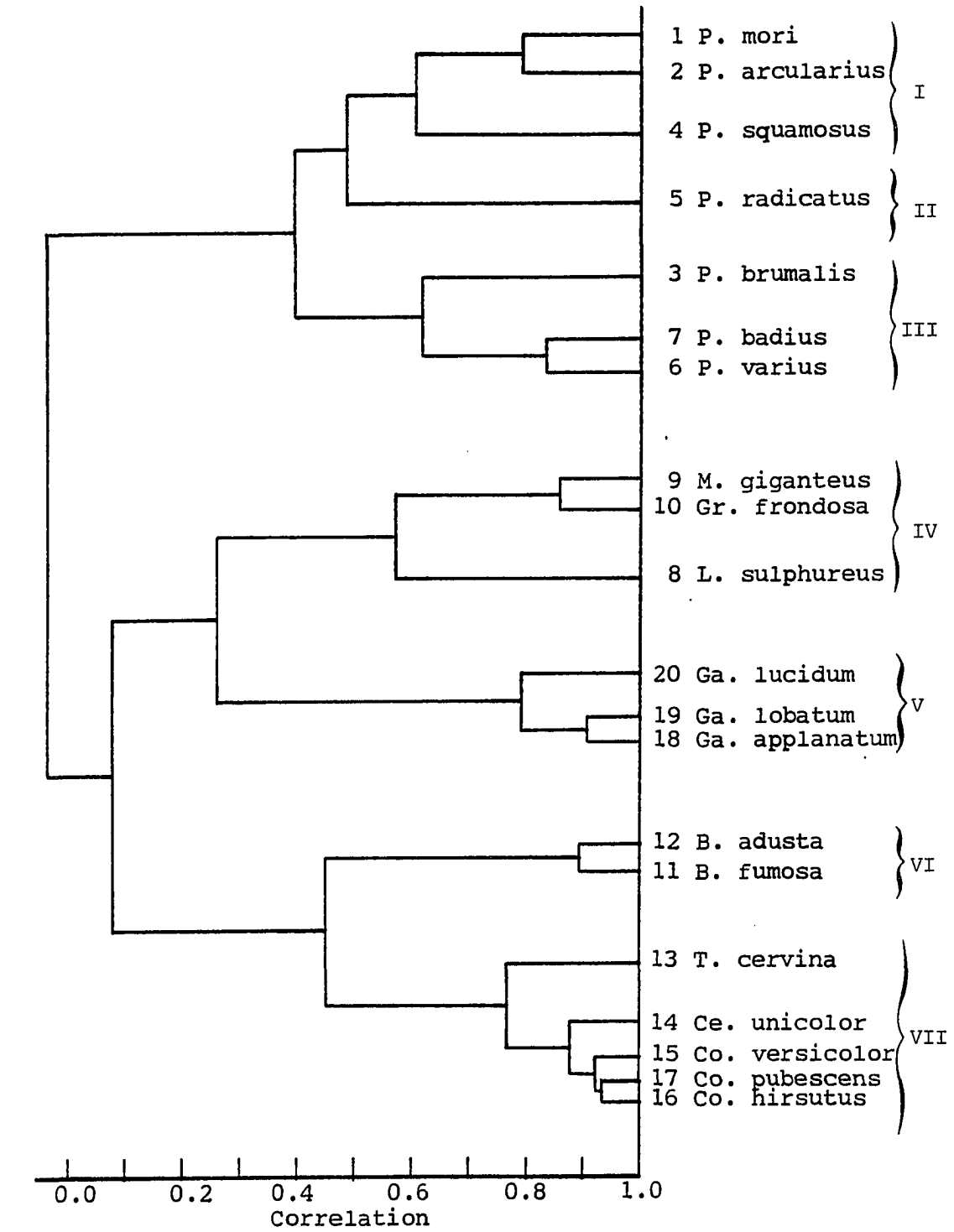


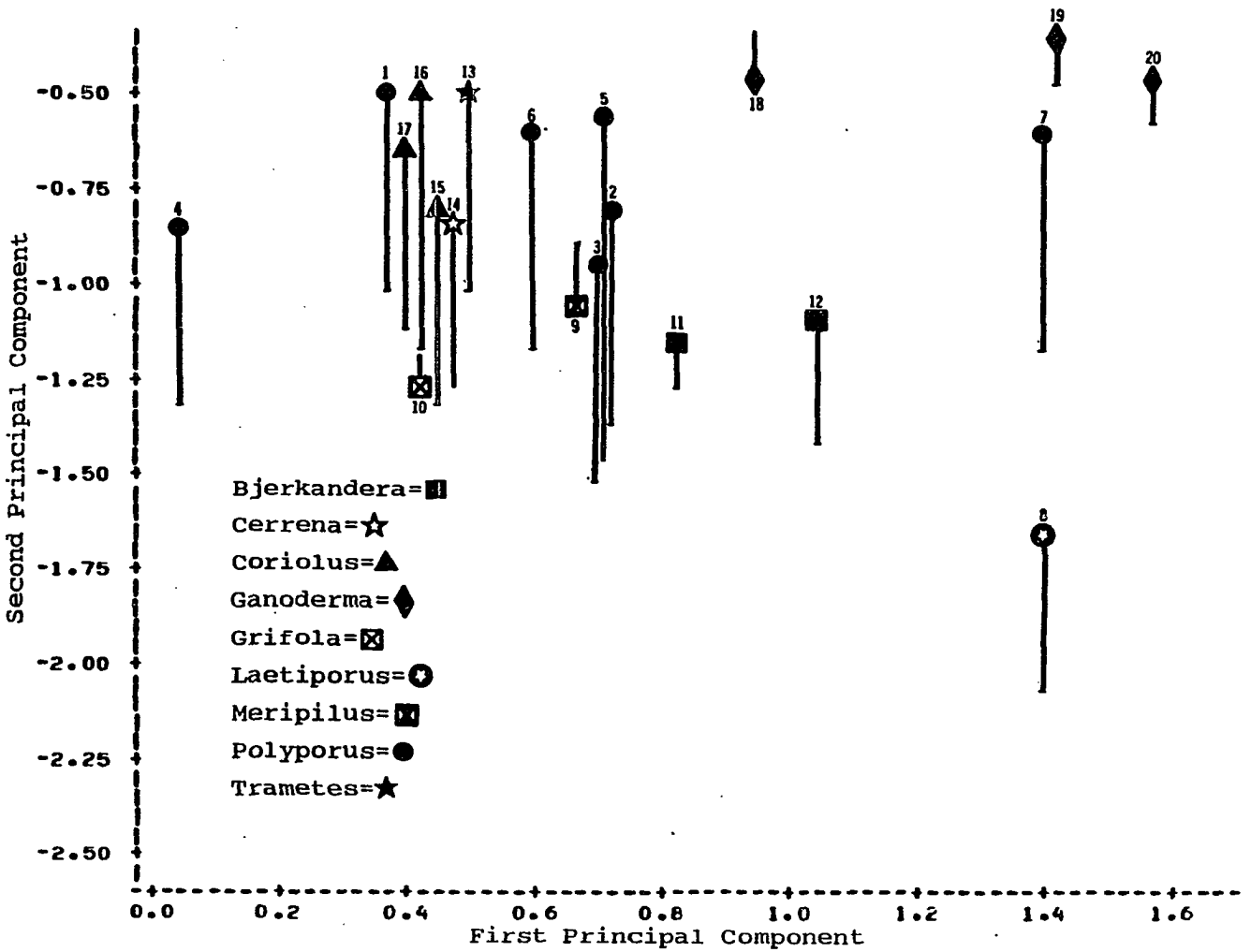
Figure 2. Dendrograph showing the results of a CA based on morphological data

Polyporus is delimited into three groups. Cluster I consists of OTUs 1, 2 and 4; while OTUs 3, 6 and 7 form Cluster III. Cluster II consists of only OTU 5. In Cluster IV, the strong morphological resemblance between M. giganteus and Gr. frondosa is clearly evident, and although L. sulphureus is clustered with these two taxa, resemblance to them is much lower (about 5.5 versus 8.5). Cluster VII consists of T. cervina, Ce. unicolor and all three Coriolus spp.

A PCA of the morphological data (Figure 3) confirms several aspects of the CA. For example, all Coriolus spp., T. cervina, and Ce. unicolor form a tight grouping in the PCA reflecting the strong resemblance (above 0.6) among them that was seen in the dendrograph. This is also true for Bjerkandera and Ganoderma. On the other hand, the fact that several Polyporus spp. (OTUs 1, 4 and 7) do not group with the other species of this genus corresponds with the low resemblance (less than 0.5) shown in the dendrograph. Another point where the PCA differs from the CA is that L. sulphureus does not cluster with M. giganteus and Gr. frondosa; instead, it is an outlier distinctly separate from all the other OTUs.

Electrophoresis of the 20 species listed in Table 1 and assayed for eight enzymes resulted in 108 banding sites (Figures 4 and 5). These data were used in a CA to generate a dendrograph (Figure 6) that is similar, in many respects, to the phenetic analysis based on the morphological evidence (Figure 2). Despite the fact that Sorensen's index of similarity resulted in a more narrow range of resemblance (about 0.5 to 0.8), an arbitrary value of 0.5 is again used to distinguish the following

Figure 3. PCA of 20 polypores based on the morphological evidence. Note that the third principal component is represented by the vertical lines which are projected from the surface of the plane formed by the first and second principal components


Second Principal Component
-0.50
-0.75
-1.00
-1.25
-1.50
-1.75
-2.00
-2.25
-2.50
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
First Principal Component
Bjerkandera=
Cerrena=
Coriolus=
Ganoderma=
Grifola=
Laetiporus=
Meripilus=
Polyporus=
Trametes=
1
16
13
17
15
14
10
6
5
4
2
3
9
11
18
12
19
20
7
8

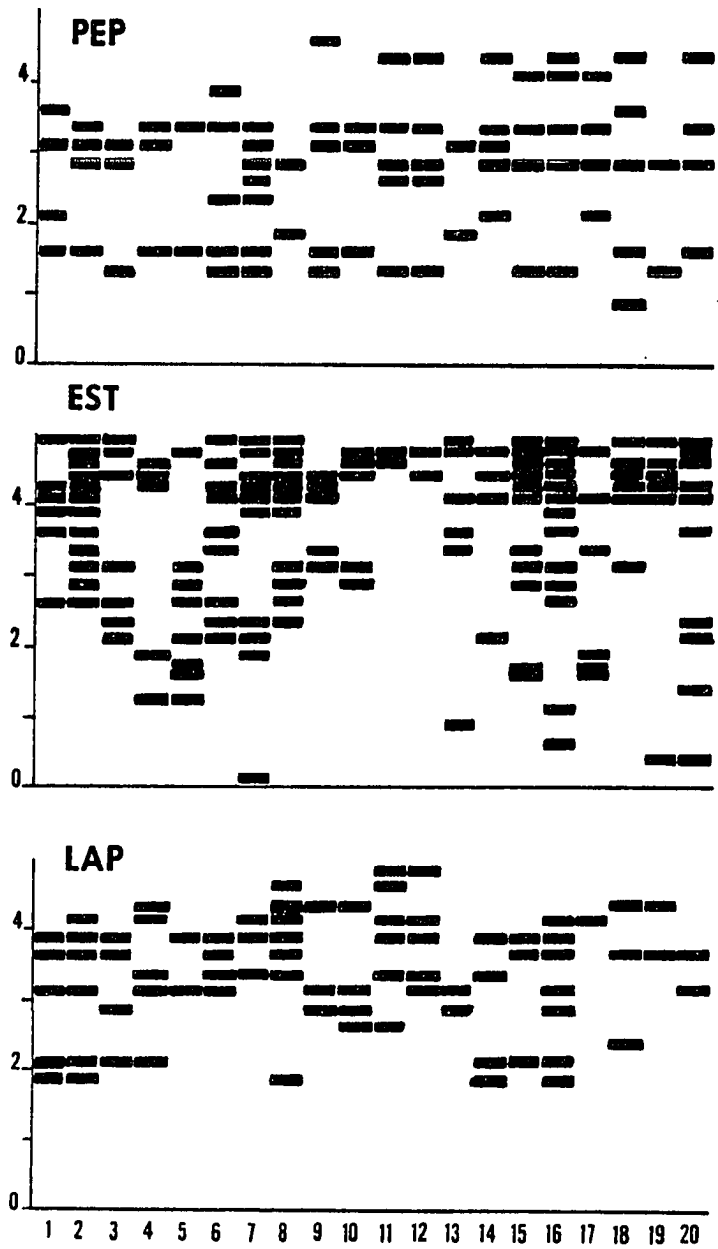


Figure 4. Zymograms of three enzymes showing the pooled variability of 20 polypore species. The numbers on the lowermost abscissa correspond to the OTUs listed in Table 1, and the anodal migration of bands is indicated in cm on each ordinate

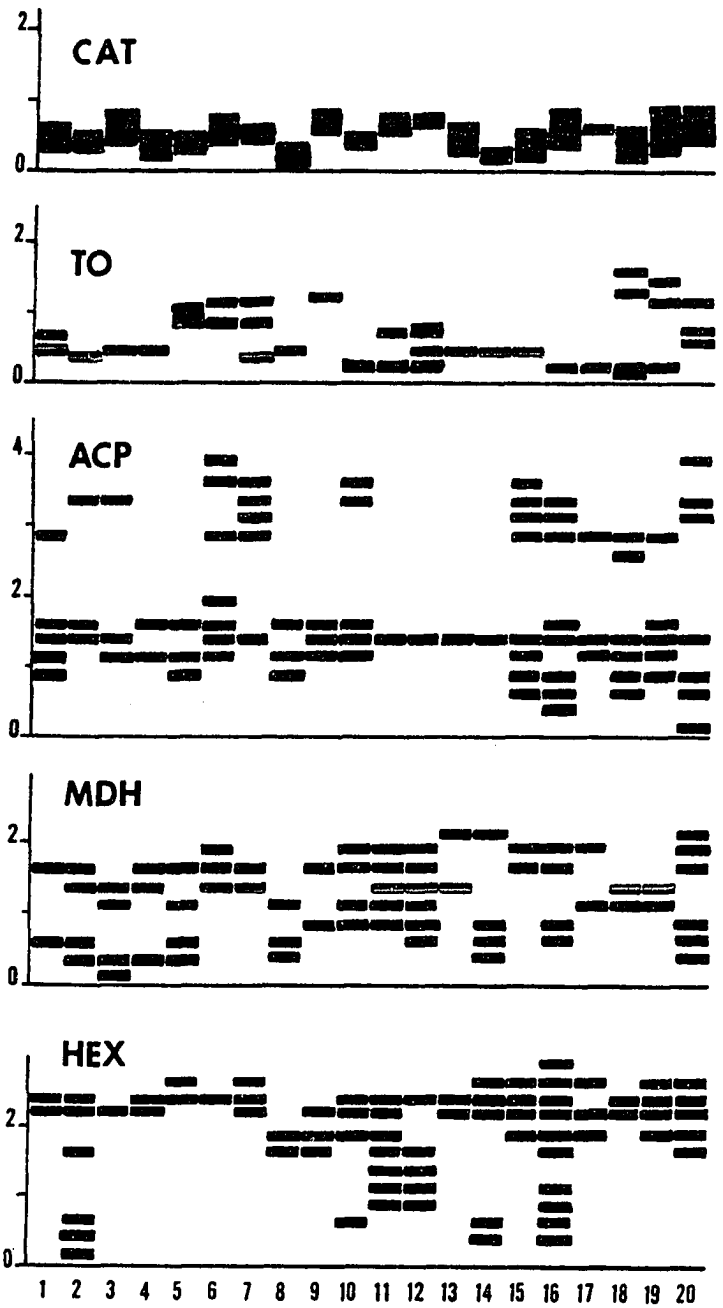


Figure 5. Zymograms of five enzymes showing the pooled variability of 20 polypore species. The numbers on the lowermost abscissa correspond to the OTU's listed in Table 1, and the anodal migration of bands is indicated in cm on each ordinate

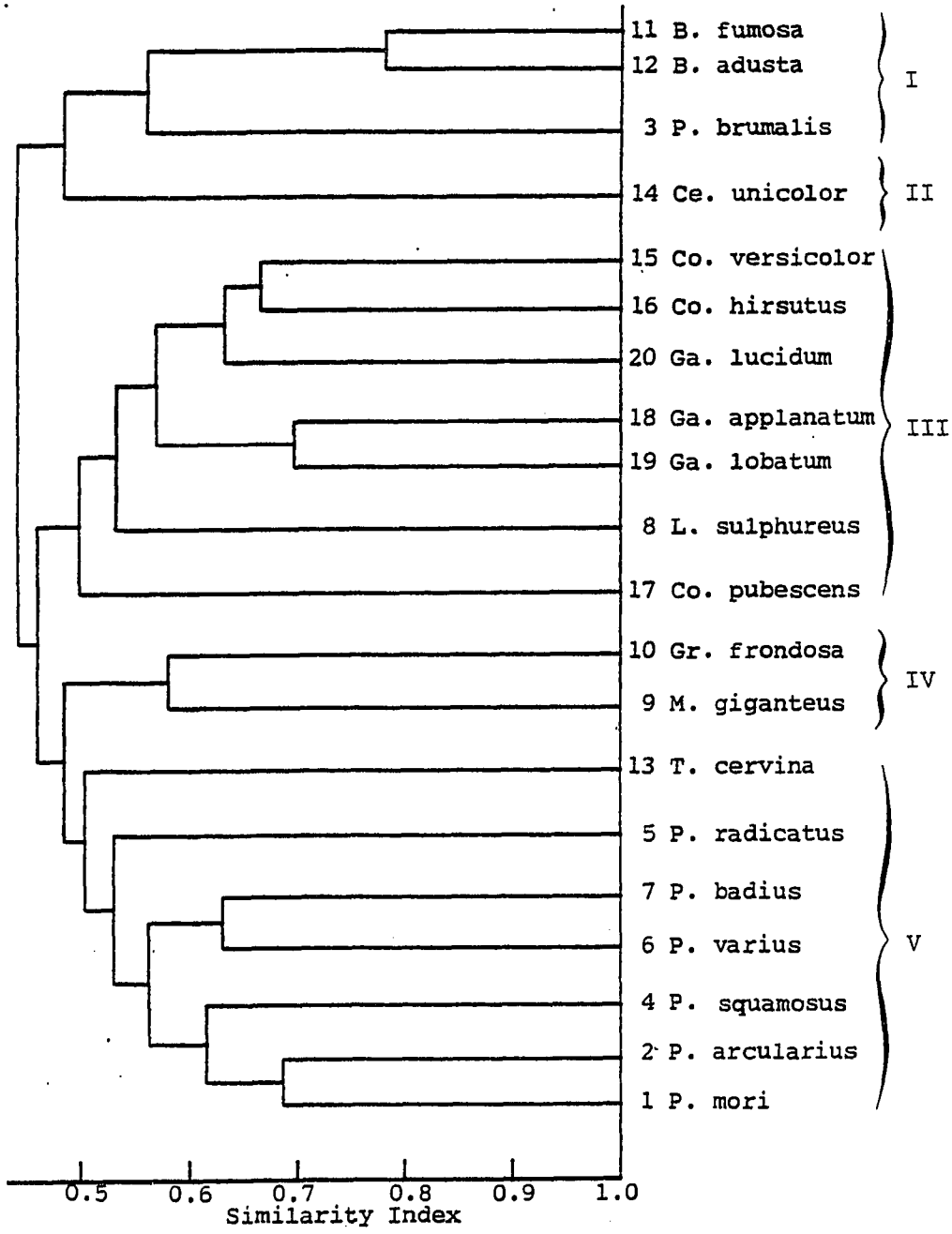


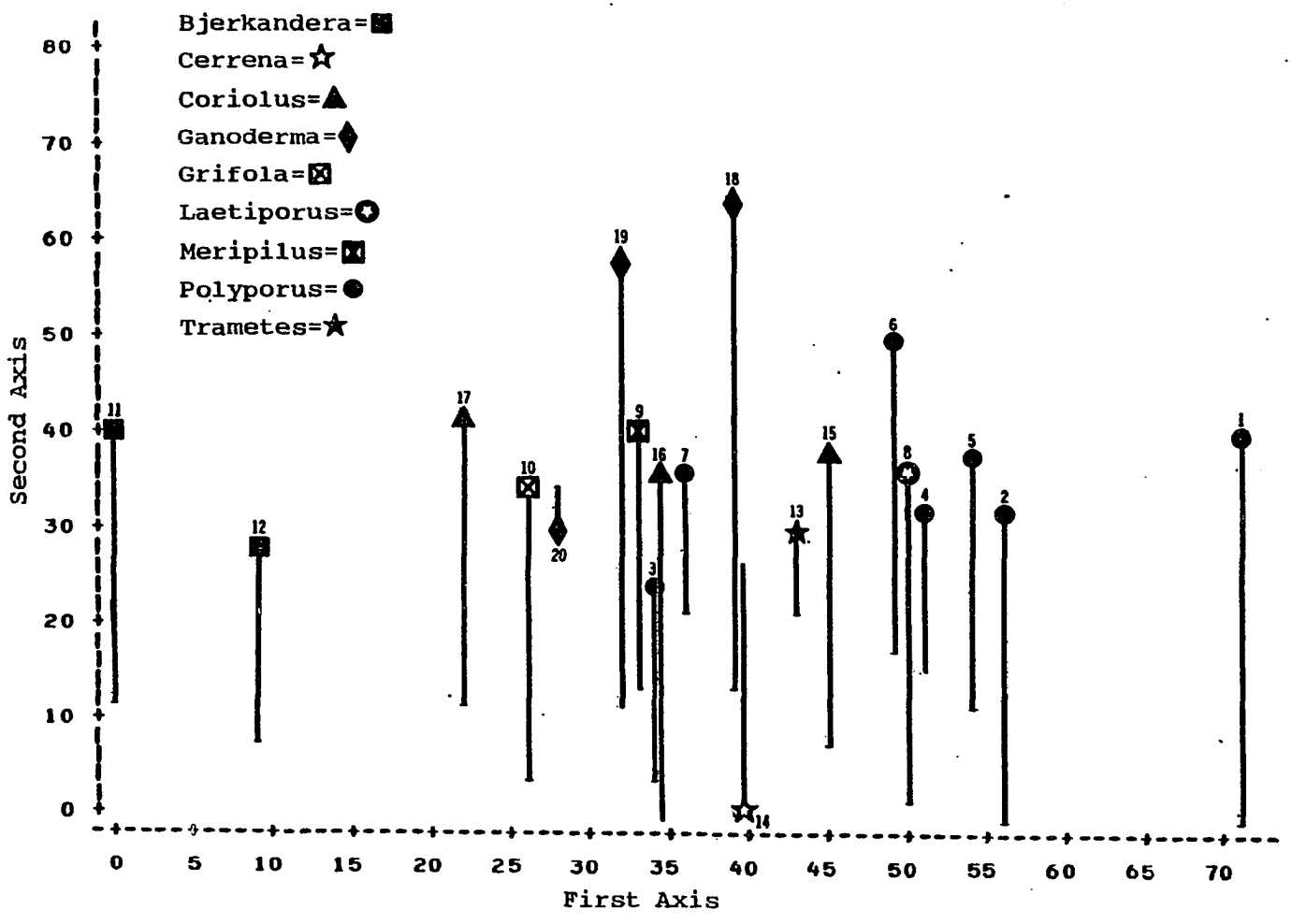
Figure 6. Dendrograph from CA based on electrophoretic data

clusters. Cluster I consists of the genus Bjerkandera and one misplaced OTU (P. brumalis). Cluster II consists solely of Ce. unicolor. With the exception of L. sulphureus, Cluster III is basically comprised of two genera, namely, Coriolus and Ganoderma. Although two OTUs (17 and 20) are misplaced with respect to each of these genera, at least they are still within their main cluster.

In Cluster IV, Gr. frondosa and M. giganteus once again pair together, and Cluster V represents the genus Polyporus except for one misplaced OTU (T. cervina). Note that the subclusters (consisting of OTUs 1, 2 and 4; 6 and 7; and 5) are identical to those observed in the phenogram shown in Figure 2 except that P. brumalis, as already indicated, is misplaced in Cluster I. Two main differences from the morphological phenogram should be noted. One is that neither T. cervina nor Ce. unicolor cluster with Coriolus, and second, L. sulphureus is, once again, not grouped with Gr. frondosa and M. giganteus.

Ordination of the 20 OTUs, using electrophoretic data, produced few discrete groupings (Figure 7). The genus Bjerkandera consists of outliers (OTUs 11 and 12) to one side of this three-way ordination. Another group consisting of Ga. applanatum and Ga. lobatum (OTUs 18 and 19) cluster together, but Ga. lucidum (OTU 20) is somewhat distant from the latter two with respect to the third axis. Despite the fact that most of the OTUs do not form discrete taxonomic groupings, some patterns of association remain consistent with previous analyses. M. giganteus and Gr. frondosa (OTUs 9 and 10) do cluster near each other, but remain distant from L. sulphureus (OTU 8). Coriolus spp. (OTUs 15-17) are

Figure 7. Bray-Curtis ordination of 20 polypore species based on electrophoretic data. Note that the vertical lines represent the third ordination from the surface of the plane formed by the axes of the first and second ordinations. The numbers near each symbol correspond to the OTUs listed in Table 1


Bjerkandera=
Cerrena=
Coriolus=
Ganoderma=
Grifola=
Laetiporus=
Meripilus=
Polyporus=
Trametes=
Second Axis
First Axis
0
10
20
30
40
50
60
70
80
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70

distinctly separated by the first ordination, but exhibit little variability with respect to the second and third ordinations. OTUs 13 and 14 (T. cervina and Ce. unicolor) appear distinct from the other OTU's belonging to Polyporus (1-7), only 2, 4, 5, and 6 are grouped together.

Discussion and Conclusions

In his remarks on the genus Tyromyces, Ryvarden (1978) commented,

> If one wants to separate one or several of these species, it is difficult to avoid a score of smaller genera based on characters like cystidia or not, simple septate generative hyphae, broadly ellipsoid spores versus allantoid-cylindric ones, etc. It is hard to find reliable and convincing arguments that one of these characters should have stronger generic impact than another. Basically it is, as in all taxonomy, a matter of personal taste whether to prefer small genera. No one, of course, can claim to be 'right' or 'wrong' in these matters.

This casual attitude expressed by Ryvarden is too whimsical, and certainly does not conform to any traditional definition of a genus. With regard to generic limits, it would be more appropriate to ask, "Do these species resemble each other?"

Classification based on one-several characters has too often formed the mainstay of orthodox taxonomy. This is not always an unsuccessful approach depending on the group of organisms at hand. But, in the case of polypores, one-character taxonomy has produced clearly artificial systems such as the Friesian classification. Although many more polypore genera are recognized in recent treatments, some of these modern taxa are equally artificial. For example, the separation of Daedaleopsis from Daedalea is based primarily on the presence of catahymenium in the latter species. Moreover, diagnostic characters are not always present,

especially in the case of large genera. For example, the genus Phellinus can be characterized as having perennial sporocarps with setae in the hymenium, and spores with pigmented walls. The hyphal system is dimitic with brown, thick-walled skeletal hyphae. All parts of the basidiocarp are xanthochrous. None of these characters are diagnostic, and except for the hyphae and xanthochrous reaction, these attributes are not present in all species of the genus. Phellinus is ostensibly a natural taxon, but it is the overall attributes of the genus which give the species an unmistakable resemblance. Although the genus Phellinus is a tribute to orthodox taxonomy, it also exemplifies a type of complexity where numerical analysis could be an advantageous technique. Our human capacity is limited to assessing a few characters for a few species at one time, but the utilization of high-speed computers in numerical analysis has made feasible the simultaneous assessment of numerous attributes for large numbers of taxa. It is no coincidence that advancements in numerical taxonomy have closely followed the development in these machines.

With respect to the species included in this study, numerical analyses of both morphological and electrophoretic data of those OTUs belonging to Ganoderma, Bjerkandera and Coriolus are generally correctly grouped. The consistent grouping of M. giganteus and Gr. frondosa strongly suggests that these two species are congeneric. The former species was split out of Grifola simply because its generative hyphae lack clamp connections. This is in spite of the fact that these two taxa resemble each other in just about every other aspect except size.

L. sulphureus, however, is neither related to these two species nor any of the other species in this analysis.

In many respects, Ce. unicolor is very similar to the genus Coriolus except for the dark line between the upper surface tomentum and context. This feature is considered diagnostic for the taxon. The similarity between Cerenna and Coriolus is manifested in the numerical analysis of the morphological data, but this is not supported by the analyses of the electrophoretic information.

Trametes cervina was included in this study because several treatments of the Polyporaceae (Domanski, 1967 and Ryvarden, 1976) combined Coriolus under Trametes along with several other taxa, including T. suaveolens (Fr.) Fr. Unfortunately, the latter species is uncommon in Iowa and material was not available for electrophoretic comparisons. The resemblance between Coriolus and T. cervina is weak and superficial, and examination of both morphological and electrophoretic data by numerical analysis does not appear to support the combination of these species into the same genus.

The species of Polyporus included in this numerical study are representative of the genus as recognized in modern treatments. The low morphological resemblance observed among the species was somewhat unexpected, and the consistent groupings of certain species (P. mori with P. squamosus and P. arcularis; P. brumalis with P. varius and P. badius; and P. radicatus by itself) suggest that this genus may be more heterogeneous than expected.

Numerical analyses of both morphological and electrophoretic data provide a stronger basis of evidence than would either type of information alone. It is essential that numerical analysis of the morphological data is corroborated by another source of evidence because the selection of characters used or not used in an analysis can be a source of bias which may have a profound effect on the final results. Gottlieb (1977) has discussed the advantages and disadvantages of electrophoresis over other sources of evidence. Electrophoresis is free of bias to the extent that the buffer systems and enzyme stains are selected on the basis of what works, although this does not necessarily constitute a random sample (Gottlieb, 1981).

Analysis of electrophoretic data in this study, unfortunately, shows very few discrete groupings, but the gradations which have been observed do correspond with the morphological clusters. Whether the lack of discreteness exhibited in the analyses of electrophoretic data is due to the different ordination techniques or different algorithms or simply because of the nature of the electrophoretic data is not known at this point. However, the special significance of this study is that there is some degree of correspondence between the morphological and electrophoretic evidence. One classification based on one set of characters reflecting a classification obtained by a separate class of characters is what Sokal and Sneath (1973) call congruence. In connection with the concept of congruence, Sokal and Sneath have postulated the hypothesis of nonspecificity which presumes that separate classes of genes governing independent sources of characters do not exist. Farris (1981) has

pointed out that this hypothesis is unnecessary because in any given group the organisms share a common ancestry.

A somewhat analogous debate exists in evolutionary biology where it has been demonstrated in several groups of animals, including man, that electrophoretic data and morphological evidence do not always coincide. Kornfield and Koehn (1975) have shown that Cichlids, a group of freshwater fish, are electrophoretically monomorphic, but morphologically polymorphic. Similar circumstances have been documented in the California minnow (Avise et al., 1975) and between man and chimpanzees (King and Wilson, 1975).

The reverse situation is also known to occur. In the Drosophila willistoni group, Ayala (1973) used electrophoretic evidence to separate subspecies among morphologically indistinguishable conspecific populations. Similarly, in freshwater flatworms, Nixon and Taylor (1977) have shown that biochemical divergence does not correspond with the absence of morphological differentiation in certain species of Planaria. Kimura (1968) originally proposed that different rates of evolution exist at the molecular level to explain this phenomenon. Under his selective neutrality hypothesis, allelic variation is assumed to be nonadaptive; and in small populations, random genetic drift may result in what appears to be enzyme polymorphism.

Despite this theoretical controversy, this preliminary effort has demonstrated that electrophoresis is a worthwhile approach for gathering information for the purpose of delimiting polypore genera. Small

samples of about five individuals have yielded reasonable results when evaluated by means of numerical analysis, and slightly larger samples may improve the accuracy of the analyses.

As might be expected from an exploratory study, many more questions are encountered than answered. From the standpoint of electrophoresis, it would be desirable to know what effect the age of basidiocarps have on the banding patterns. Moore and Jirjis (1981) have shown electrophoretic differences in developmental stages of the basidiocarps of Coprinus cinereus (Schaeff. ex Fr.) S. F. Gray. Schanel et al. (1971) electrophoresed three- and ten-day old cultures of Co. hirsutus and Co. versicolor. They not only found differences due to age, but between the intra- and extra-cellular enzymes as well. Abbott and Hallard (1975) have shown that the composition of culture media affects the protein patterns obtained by electrophoresis of Gaeumannomyces graminis (Sacc.) Arx & Olivier. Because of such nutritional effects, the comparison of isolates grown in a standard medium with naturally occurring basidiocarps might detect some variation due to different host-substrates. Population genetics studies of polypores might also be possible by accumulating isolates from populations over time.

With respect to numerical analysis, a common algorithm suitable for both morphological and electrophoretic data would be desirable. Gower (1971) has proposed a coefficient which is suitable for both quantitative and qualitative data. However, in the case of strictly two-state characters, such as used in the numerical analysis of the electrophoretic data of this study, this algorithm becomes equivalent to Jaccard's

index of similarity. Unfortunately, alternative procedures are used to accommodate quantitative characters, and consequently, the potential effects of different algorithms may still exist; however, Gower's coefficient may at least eliminate the need for different ordination techniques for different types of data.

PART II. CHECKLIST OF THE POLYPORES OF IOWA

Introduction

The Polyporaceae of Iowa has been monographed by Wolf (1931). This text is largely based on Overholts' treatment of the midwestern species (1915). However, Wolf also includes what now constitutes the Boletaceae (Agaricales) as well as Merulius, Fistulina and Poria. Most of the species reported by Wolf are documented by voucher specimens in the University of Iowa Herbarium (SUI). In a checklist of the homobasidiomycetes of Iowa, Gardner (1947) reported 136 species in the Polyporaceae. This latter work is based on a review of the literature up to that time. As a consequence, many errors have been introduced as well as perpetuated, but it is a good bibliographical source of floristic works on the Iowa polypores. Wolf's checklist has also served as a starting point for the updated version presented here. Twenty polypore species have been added to this list (Appendix I). Seventeen of these are based on recent collections while three others are based on SUI specimens annotated by Josiah Lowe, but heretofore unreported. Seventeen species reported by Gardner have been excluded from the present list due to synonymy, misidentified specimens, or lack of voucher material (Appendix II).

Because the Polyporaceae of the Friesian classification has recently been subdivided into five or more families, the informal term "polypore"

has been substituted. Although the familial disposition of the polypore species is not treated here, it should be noted that certain genera included in this checklist are no longer classified with the polypores proper, but have been relegated to other families of the Aphyllophorales (Donk, 1964). This includes Merulius, Meruliopsis, Serpula, and Lindternia. (Also see accompanying citations in the checklist.) On the other hand, Cerrenella farinacea and Hirschioporus fuscoviolaceus, both previously placed in the Hydnaceae, are now accepted as polypore species.

The purpose of this checklist is to update the inventory of polypores which are known to occur in Iowa, and to bridge the gap between American literature, based on the Friesian classification, and more recent classifications proposed principally by European mycologists. Overholts (1953) represents the most comprehensive treatment of pileate polypores for North America north of Mexico. Lowe (1966) complemented this earlier publication with a monograph of Poria. Altogether, Overholts and Lowe recognized 11 genera, but both of these works are taxonomically out of date. Presently, nearly 90 genera of American polypores are represented in Pegler's key to the world genera (1973). Because 80% of the species found in Europe also occur on this continent (Gilbertson, 1980), careful attention must be given to European literature. However, numerous points of disagreement exist among recent monographs and selection of any modern interpretation over another at this time would seem to be arbitrary.

Because Donk (1974) provides a comprehensive listing of European species, as well as an extensive synonymy for each taxon, his generic interpretation is used in the checklist presented here. This Iowa list is primarily designed to assist in finding the modern equivalents of names used by Overholts (1953), Lowe (1966) and Gardner (1947). Many synonyms as well as basionyms have been omitted for the sake of brevity.

To assist locating names in the checklist, an index of epithets has been provided at the end. Citations and their corresponding abbreviations used in this checklist are listed below.

Special Problems

At least six species included in this checklist have no modern generic designations. Two new species for Iowa, Polyporus robiniophilus and P. compactus are included here. Fomes fraxinophilus should probably be transferred to the genus Perenniporia (R. L. Gilbertson, Department of Plant Pathology, University of Arizona). Several species obviously belong to certain existing, modern genera, but formal name changes have not yet been proposed. Among these, Daedalea ambigua, Polyporus graveolens, and Poria nigra should probably be relegated to Daedaleopsis, Inonotus and Phellinus, respectively. The above six species have been maintained under the old Friesian names in this checklist to avoid nomenclatural confusion that might otherwise occur until these relationships and synonymies have been carefully examined.

Pileate and resupinate forms of the same species is a frequent taxonomic problem in the polypores. Mating studies have been commonly

used to resolve these problems. Tyromyces semisupiniformis and T. transmutans are two instances where rare pileate forms may have been described for Junghuhnia nitida and Parmastomyces kravtzevianus, respectively (R. L. Gilbertson, 1980). But this requires further study before this statement can be confirmed.

Abbreviated Citations Used in the Checklist

BM 63 Lindsey, J. P. and R. L. Gilbertson. 1978. Basidiomycetes that decay aspen in North America. J. Cramer, Lehre, Germany. (Bibliotheca Mycologica 63). 406 pp.

CJB 54 Ginns, J. H. 1975. Merulius: s.s. and s.l, taxonomic disposition and identification of species. Can. J. Bot. 54:100-167.

FPG 2 Domanski, S. 1965. Basidiomycetes: Aphyllophorales: Polyporaceae I, Mucronoporaceae I. In Flora Polska (Grzyby) 2. Foreign Scientific Publications, Warsaw, Poland. 234 pp. Translated from Polish by A. Radziwill.

FPG 3 Domanski, S., H. Orlos and A. Skirgiello. 1967. Basidiomycetes: Aphyllophorales: Polyporaceae II, Mucronoporaceae II, Ganodermataceae, Bondarzewiaceae, Boletopsidaceae, Fistulinaceae. In Flora Polska (Grzyby) 3. Foreign Scientific Publications, Warsaw, Poland. 330 pp. Translated from Polish by A. Radziwill.

FPP Gilbertson, R. L. 1974. Fungi that decay Ponderosa Pine. The University of Arizona Press, Tucson, Arizona. 197 pp.

FTP 80 Lowe, J. L. 1957. Polyporaceae of North America. The genus Fomes. State Univ. New York Coll. For. Tech. Publ. 80:1-97.

FTP 90 Lowe, J. L. 1966. Polyporaceae of North America. The genus Poria. State Univ. New York Coll. For. Tech. Publ. 90:1-183.

MNY 28 Gilbertson, R. L. 1976. The genus Inonotus (Aphyllophorales: Hymenochaetaceae) in Arizona. Mem. New York Bot. Gard. 28:67-85.

MTN 2 Lowe, J. L. 1975. Polyporaceae of North America. The genus Tyromyces. Mycotaxon 2:1-82.

MTN 6 Martin, K. J. and R. L. Gilbertson. 1977. Synopsis of wood-rotting fungi on spruce in North America: I. Mycotaxon 6:43-77.

MTN 7 Martin, K. J. and R. L. Gilbertson. 1978. Synopsis of wood-rotting fungi on spruce in North America: II. Mycotaxon 7:337-356.

MNT 9 Gilbertson, R. L. 1979. The genus Phellinus (Aphyllophorales: Hymenochaetaceae) in Western North America. Mycotaxon 9:51-89.

MYC 60 Ginns, J. H. 1968. The genus Merulius I. Species proposed by Burt. Mycologia 60:1211-1231.

PNE 1 Ryvarden, L. 1976. The Polyporaceae of North Europe. Fungiflora 1:1-214.

PNE 2 Ryvarden, L. 1978. The Polyporaceae of North Europe. Fungiflora 2:219-507.

TBMS 47 Pegler, D. N. 1964. A survey of the genus Inonotus (Polyporaceae). Trans. Br. Mycol. Soc. 47:175-195.

USAC Overholts, L. O. 1953. Polyporaceae of the United States, Alaska and Canada. Univ. Michigan Press, Ann Arbor. 468 pp.

Checklist

Abortiporus biennis (Bull. ex Fr.) Sing. FPG 3:35
Polyporus biennis Bull. ex Fr. USAC:224
Heteroporus biennis (Fr.) Laz. PNE 1:199

Albatrellus cristatus (Schaeff. ex Fr.) Kotl. & P. FPG 2:41; PNE 1:51
Polyporus cristatus Pers. ex Fr. USAC:221

Antrodia malicola (B. & C.) Donk
Trametes malicola B. & C. USAC:150
Coriolellus malicola (B. & C.) Murr. FPG 2:107

Antrodia sepium Berk.
Trametes sepium Berk. USAC:136
Coriolellus albidus Fr. ex Fr. FPG 2:98
Antrodia albida (Fr.) Donk. PNE 1:68

Antrodia serialis (Fr.) Donk. PNE 1:90
Trametes serialis (Fr.) Fr. USAC:138
Coriolellus serialis (Fr.) Murr. FPG 2:100

Bjerkandera adusta (Willd. ex Fr.) P. Karst. FPG 3:51; PNE 1:98
Polyporus adustus Willd. ex Fr. USAC:364

Bjerkandera fumosa (Pers. ex Fr.) P. Karst. FPG 3:54; PNE 1:101
Polyporus fumosus Pers. ex Fr. USAC:366

Ceraceomyces serpens (Fr.) Ginns. CJB 54:147
Merulius ceracellus B. & C.

Cerrena unicolor (Bull. ex Fr.) Murr. FPG 3:167; PNE 1:119
Daedalea unicolor Bull. ex Fr. USAC:125

Cerrenella farinacea (Fr.) Murr.
Irpex farinaceus Fr.
Daedalea farinacea (Fr.) Overh. USAC:128

Ceriporia purpurea (Fr.) Donk. PNE 1:113
Poria purpurea (Fr.) Cooke
Ceriporia bresadolae (Bourd. & G.) Donk. FPG 2:61

Ceriporia viridans (B. & Br.) Donk. FPG 2:56; PNE 1:116
Poria griseoalba (Fr.) Sacc.
Poria rhodella (Fr.) Cooke. FTP 90:30

Chaetoporellus latitans (Bourd. & G.) Sing. FPG 2:35
Poria latitans Bourd. & G. FTP 90:72; FPP 131

Climacocystis borealis (Fr.) Kotl. & P. FPG 3:58; PNE 1:121
Polyporus borealis Fr. USAC:312
Tyromyces borealis (Fr.) Imaz. MTN 2:48

Coltricia cinnamomea (Jacq. ex Pers.) Murr. FPT 3:292; PNE 1:124
Polyporus cinnamomeus Jacq. ex Pers. USAC:386
Polystictus cinnamomeus Jacq. ex Pers. Sacc.

Coltricia montagnei (Fr. ex Mont.) Murr. PNE 1:121
Cyclomyces greenei Berk. USAC:116
Polyporus montagnei Fr. USAC:393

Coltricia perennis (L. ex Fr.) Murr. FPT 3:290; PNE 1:127
Polyporus perennis L. ex Fr. USAC:387
Polystictus perennis (L. ex Fr.) P. Karst.

Coriolellus variiformis (Peck) Sarkar. MTN 7:343
Trametes variiformis Peck. USAC:140

Coriolus hirsutus (Wulf. ex Fr.) Quel.
Polyporus hirsutus Wulf. ex Fr. USAC:345
Trametes hirsuta (Wulf. ex Fr.) Pilat. FPT 3:233; PNE 2:425

Coriolus pubescens (Schum. ex Fr.) Quel.
Polyporus pubescens Schum. ex Fr. USAC:346
Trametes pubescens (Schum. ex Fr.) Pilat. FPG 3:230; PNE 2:429

Coriolus versicolor (L. ex Fr.) Quel.
Polyporus versicolor L. ex Fr. USAC:342
Trametes versicolor (L. ex Fr.) Pilat. FPG 3:238; PNE 2:435

Coriolus zonatus (Nees ex Fr.) Quel.
Polyporus zonatus Nees ex Fr. USAC:344
Polystictus zonatus (Nees ex Fr.) Fr.
Trametes zonatus (Nees ex Fr.) Pilat. FPG 3:236
T. zonatella Ryv. PNE 2:426

Daedalea ambigua Berk. USAC:126

Daedalea quercina L. ex Fr. FPG 3:170; PNE 1:134; USAC:122

Daedaleopsis confragosa (Bolt. ex Fr.) J. Schroet. FPG 3:173; PNE 1:138
Daedalea confragosa Bolt. ex Fr. USAC:120

Datronia epilobii (P. Karst.) Donk
Datronia stereoides (Fr.) Fyv. FPG 2:112
Polyporus planellus (Murr.) Overh. USAC:377

Datronia mollis (Sommerf.) Donk. FPG 2:111; PNE 1:141
Trametes mollis (Sommerf.) Fr. USAC:146

Fistulina hepatica Schaeff. ex Fr. FPG 3:306

Fomes fomentarius (L. ex Fr.) Fr. FPG 3:176; PNE 1:153; USAC:91

Fomes fraxinophilus (Peck) Sacc. USAC:46

Fomitopsis cajanderi (P. Karst.) Kotl. & P. FPG 3:184
Fomes subroseus (Weir) Overh. USAC:57

Fomitopsis rosea (A. & C. ex Fr.) P. Karst. FPG 3:183; PNE 1:159
Fomes roseus (A. & C. ex Fr.) Cooke. USAC:56

Fomitopsis scutellata (Schw.) Bond. & S.
Fomes scutellatus (Schw.) Cooke. USAC:51

Funalia gallica (Fr.) Bond. & S.
Trametes hispida Bagl. USAC:147
Trametella extenuata (Dur. & Mont.) Dom. FPG 3:217
Coriolopsis gallica (Fr.) Ryv. PNE 1:131

Funalia trogii (Berk.) Bond. & S.
Trametes trogii Berk. PNE 2:433; USAC:142
Trametella trogii (Berk.) Dom. FPG 3:220

Ganoderma applanatum (Pers. ex S. F. Gray) Pat. FPG 3:298; PNE 1:163
Fomes applanatus (Pers. ex Wallr.) Gillet. USAC:98

Ganoderma curtisii Murr.
Polyporus curtisii Berk. USAC:213

Ganoderma lobatum (Schw.) Atk.
Fomes lobatus (Sch.) Cooke. USAC:102

Ganoderma lucidum (Curt. ex Fr.) P. Karst. FPG 3:295; PNE 1:166
Polyporus lucidus (Fr.) Cooke. USAC:208

Gloeophyllum protractum (Fr.) Imaz.
Trametes americana Overh. USAC:151
Gloeophyllum odoratum (Wulf. ex Fr.) Imaz. FPG 3:196
Osmoporus protractus (Fr.) Bond. PNE 2:289

Gloeophyllum sepiarium (Wulf. ex Fr.) P. Karst. FPG 3:189; PNE 1:178
Lenzites saepiaria (Wulf. ex Fr.) Fr. UASC:111

Gloeophyllum trabeum (Pers. ex Fr.) Murr. FPG 3:194; PNE 1:180
Lenzites trabea Pers. ex Fr. USAC:110

Gloeoporus dichrous (Fr. ex Fr.) Bres. FPG 3:64
Polyporus dichrous Fr. USAC:361
Caloporus dichrous (Fr.) Ryv. PNE 1:109

Gloeoporus pannocinctus (Romell) Jo. Erikss. FPG 2:44; PNE 1:183
Poria pannocincta (Romell) Lowe. FTP 90:71
Poria zameriensis (Pilat) Overh.

Grifola berkeleyi (fr.) Murr.
Polyporus berkeleyi Fr. USAC:238

Grifola frondosa (Dicks ex Fr.) S. F. Gray. FPG 3:67; PNE 1:187
Polyporus frondosa Dick. ex Fr. USAC:246

Grifola umbellata (Pers. ex Fr.) Pilat
Polyporus umbellatus Pers. ex Fr. USAC:249; FPG 3:149; PNE 2:389

Hapalopilus rutilans (Pers. ex Fr.) P. Karst.
Polyporus nidulans Pers. ex Fr. USAC:398
Hapalopilus nidulans (Fr.) P. Karst. FPG 3:70; PNE 1:190

Heterobasidion annosum (Fr.) Bref. FPG 3:158; PNE 1:195
Fomes annosus (Fr.) Cooke. USAC:40

Hirschioporus abietinus (Pers. ex Fr.) Donk. FPG 3:112
Polyporus abietinus Dicks. ex Fr. USAC:333
Trichaptum abietinus (Fr.) Ryv. PNE 2:441

Hirschioporus fusco-violaceus (Ehrenb. ex Fr.) Donk. FPG 3:113
Irpex fusco-violaceus (Ehrenb. ex Fr.) Fr.
Trichaptum fusco-violaceus (Fr.) Ryv. PNE 2:445

Hirschioporus laricinus (P. Karst.) Teramoto. FPG 3:114
Polyporus abietinus var. abietis (Lloyd) Overh. USAC:334
Trichaptum laricinus (P. Karst.) Ryv. PNE 2:447

Hirschioporus pargamenus (Fr.) Bond. & S. FPG 3:116; BM 63:270
Polyporus pargamenus Fr. USAC:336
Trichaptum biformis (Fr. ex Kl.) Ryv. PNE 2:443

Hirschioporus subchartaceous (Murr.) Bond. & S. BM 63:270
Polyporus subchartaceous (Murr.) Overh. USAC:338

Incrustoporia semipileata (Peck) Donk
Polyporus semipileatus Peck. USAC:295
Leptotrimitus semipileatus (Peck) Pouz. FPG 3:221
Incrustoporia nivea (Jungh.) Ryv. PNE 1:208

Incrustoporia subincarnata (Peck) Dom. FPG 2:133; PNE 1:213
Poria subincarnata Peck. FTP 90:92

Inonotus cuticularis (Bull. ex Fr.) P. Karst. TBMS 47:185; FPG 3:280; PNE 2:227
Polyporus cuticularis Bull. ex Fr. USAC:412

Inonotus dryophilus (Berk.) Murr. TBMS 47:187; FPG 3:279; PNE 2:231
Polyporus dryophilus Berk. USAC:417

Inonotus glomeratus (Peck) Murr. TBMS 47:183
Polyporus glomeratus Peck. USAC:422
Poria setigera Peck. FTP 90:165

Inonotus rheades (Pers.) Bond. & S. TBMS 47:188; FPG 3:278; PNE 2:245
Polyporus dryophilus var. vulpinus (Fr.) Overh. USAC:418

Irpex lacteus (Fr.) Fr. FPG 2:137; PNE 2:249
Polyporus tulipiferae (Schw.) Overh. USAC:329

Ischnoderma benzoinum (Wahl.) P. Karst. PNE 2:253
Polyporus resinosus Schrad. ex Fr. USAC:301
Ischnoderma resinosum (Fr.) P. Karst. FPG 3:120

Junghuhnia nitida (Pers. ex Fr.) Ryv. PNE 2:261
Poria europa (P. Karst.) Cooke. FTP 91:122
Poria attenuata (Peck) Cooke
Chaetoporus nitidus (Pers. ex Fr.) Donk. FPG 2:89

Laetiporus sulphureus (Bull. ex Fr.) Murr. FPG 3:161; PNE 2:267
Polyporus sulphureus Bull. ex Fr. USAC:343

Lenzites betulina (L. ex Fr.) Fr. USAC:109; FPG 3:207; PNE 2:271

Lindtneria trachyspora (Bourd. & G.) Pilat. FTP 90:46
Poria trachyspora Bourd. & G.
Sistotrema sulphureum var. retigera Bourd. & G.

Meripilus giganteus (Pers. ex Fr.) P. Karst. FPG 3:104; PNE 2:273
Grifola giganteus Pers. ex Fr.
Polyporus giganteus Pers. ex Fr. USAC:242

Meruliopsis ambiguus (Berk.) Ginns. CJB 54:117
Merulius ambiguus Berk.
Byssomerulius ambiguus (Berk.) Gilb. & Bud.

Meruliopsis corium (Fr.) Ginns. CJB 54:126
Merulius corium Fr.
M. confluens Schw.
Byssomerulius corium (Fr.) Parm. FPP:45

Merulius tremellosus Fr. CJB 54:153

Onnia triqueter (Fr.) Imaz.
Polyporus tomentosus var. circinatus (Fr.) Sart. & M. USAC:392
Mucronoporus circinatus (Fr.) Ell. & Ev. FPG 3:287
Onnia circinata (Fr.) P. Karst. PNE 2:279

Osteina obducta (Berk.) Donk. FPG 3:73; PNE 2:291
Polyporus osseus Kalchbr. USAC:226

Oxyporus corticola (Fr.) Dom. FPG 2:68; PNE 2:295
Poria corticola (Fr.) Cooke. FTP 90:19

Oxyporus late-marginatus (Dur. & Mont.) Donk. FPG 2:69
Poria late-marginatus (Dur. & Mont.) Cooke. FTP 90:17

Oxyporus populinus (Schum. ex Fr.) Donk. FPG 3:106; PNE 2:297
Fomes connatus (Weinm.) Gillet. USAC:52

Parmastomyces kravtzevianus (Bond. & Parm. ap. Parm) Kotl. & P.
FPG 2:49; PNE 2:303
Polyporus subcartilagineus Overh. USAC:358
Tyromyces subcartilagineus (Overh.) Dom. MTN 2:28

Perenniporia medulla-panus (Jacq. ex Fr.) Donk. FPG 2:149; PNE 2:309
Poria medulla-panis (Jacq. sensu Pers.) Bres. FTP 90:107

Perenniporia pulchella (Schw.) Cooke
Poria tenuis (Schw.) Cooke. FTP 90:110
Perenniporia medulla-panis var. pulchella Lowe. FTP 90:110

Perenniporia subacida (Peck) Donk. FPG 2:151; PNE 2:311
Poria subacida (Peck) Sacc. FTP 90:109

Phaeolus schweinitzii (Fr.) Pat. FPG 3:165; PNE 2:315
Polyporus schweinitzii Fr. USAC:395

Phellinus chrysoloma (Fr. Donk. FPG 2: 204; PNE 2:323; MTN 9:57
Fomes pini var. abietinus. USAC:79

Phellinus conchatus (Pers. ex Fr.) Quel. FPG 3:261; PNE 2:327; MTN 9:58
Fomes conchatus (Pers. ex Fr.) Gillet. USAC:69
F. johnsonianus (Murr.) Lowe. FTP 90:157

Phellinus everhartii (Ell. & Gall.) Ames. MTN 9:60
Fomes everhartii (Ell. & Gall.) Schrenk & Spauld. USAC:82

Phellinus ferruginosus (Schrad. ex Fr.) Pat. FPG 2:200; PNE 2:337;
MTN 9:63
Poria ferruginosa (Schrad. ex Fr.) P. Karst. FTP 90:160

Phellinus gilvus (Schw.) Pat. FPG 2:270; MTN 9:65
Polyporus gilvus Schw. USAC:401

Phellinus ignarius (L. ex Fr.) Quel. FPG 3:249; PNE 2:341; MTN 9:67
Fomes ignarius (L. ex Fr.) Kickx. USAC:60

Phellinus laevigatus (Fr.) Bourd. & G. FPG 2L201; PNE 2:343; MTN 9:47
Fomes ignarius var. laevigatus (Fr.) Overh. USAC:63
Poria laevigata (Fr.) P. Karst. FTP 90:156

Phellinus pini (Brot. ex Fr.) A. Ames. FPG 3:260; PNE 2:353; MTN 9:70
Fomes pini (Thore ex Fr.) P. Karst. USAC:76; FTP 90:162

Phellinus pomaceus (Pers. ex S. F. Gray) Maire. FPG 3:254; PNE 2:356; MTN 9:72
Fomes pomaceus (Pers.) Lloyd. USAC:64

Phellinus punctatus (Fr.) Pilat. FPG 2:198; PNE 2:360; MTN 9:73
Poria punctata (Fr.) P. Karst. FTP 90:163

Phellinus ribis (Schum. ex Fr.) P. Karst. FPTG 3:264; MTN 9:74
Fomes ribis Schum. ex Fr. USAC:95
Phylloporia ribis (Fr.) Ryv. PNE 2:371

Phellinus robiniae (Murr.) A. Ames. MTN 9:76
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GENERAL SUMMARY

Twenty species of polypores were assayed for eight enzymes by means of horizontal starch gel electrophoresis. A total of 108 bands were obtained and analyzed by means of numerical taxonomy. Morphological data based on 20 characters were also analyzed by similar methods for these same species. Clusters of OTUs in the morphological and electrophoretic dendrographs consisted of similar groups of species except for several misplaced OTUs in the latter dendrograph. Ordination of both types of evidence produced more discrete groups with morphological data than with the electrophoretic information. Taxonomic congruence was observed among species of Coriolus, Ganoderma and Bjerkandera. These analyses also suggest that M. giganteus and Gr. frondosa are congeneric. Laetiporus sulphureus did not cluster with any of the species in this study. The seven species of Polyporus examined here appear to cluster into three subgroups. The fact that there are low resemblance values among these subgroups suggests that this genus, as presently recognized, is probably heterogeneous. Trametes cervina and Ce. unicolor were compared to three species of Coriolus. Cerrena unicolor had a strong morphological resemblance to Coriolus, but this was not supported by the electrophoretic evidence. Neither the morphological nor the electrophoretic evidence supported a generic affiliation between Coriolus and T. cervina.

A revised checklist of Iowa polypores based on SUI Herbarium material and recent collections is presented here. An updated nomenclature for 151 species distributed in 59 genera is included in this inventory.

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APPENDIX I. NEW POLYPORE SPECIES FOR IOWA

Chaetoporellus latitans (Bourd. & G.) Sing.

Gloeoporus pannocinctus (Romell) Jo. Erikss.

Hirschioporus subchartaceous (Murr.) Bond. & S.

Incrustorporia subincarnata (Peck) Dom.[1]

Lindtneria trachyspora (Bourd. & G.) Pilat

Oxyporus late-marginatus (Dr. & Mont.) Donk

Parmastomyces kravtzevianus (Bond. & Pam. ap. Parm.) Kotl. & P.

Poria cocos (Schw.) Wolf

Poria gilvescens Bres.

P. oleagina Overh.

P. overholtsii Pilat[1]

P. vaillantii (DC. ex Fr.) Cooke[1]

Polyporus compactus Overh.[2]

P. robiniophilus (Murr.) Lloyd[2]

Tyromyces fissilis (B. & C.) Donk

T. fragilis (Fr.) Donk

T. semisupiniformis Murr.[2]

T. transmutans (Overh.) Lowe[2]

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[1]University of Iowa Herbarium specimens annotated by Josia Lowe.

[2]See section on Special Problems for comments.

APPENDIX II. EXCLUDED OR SYNONYMIZED SPECIES

Favolus rhipidium Berk. All Iowa material labeled with this name in the SUI Herbarium are misidentified specimens of Polyporus mori.

Fomes fraxineus (Bull. ex Fr.) Cooke. This species is not represented in Iowa herbaria, and reports of its occurrence in state can be traced to Wilson (1909). It is probably based on a specimen of F. fraxinophilous.

Ganoderma sessile Murr. = G. lucidum

Merulius confluens Schw. = Meruliopsis corium

M. incarnatus Schw. Based on misidentified collection of M. tremellosus.

Polyporus arcticus Fr. A doubtful species according to Murrill (1909).

P. crispus Fr. = Bjerkandera adusta

P. elegans Fr. = P. varius

P. epileucus Fr. Based on a report by Macbride (1895), but it is not represented in the SUI Herbarium.

P. heteroclitus Fr. = Laetiporus sulphureus

P. hispidus Bull. ex Fr. Based on a misidentified specimen of Coriolus hirsutus.

P. iowensis Lloyd = Tyromyces galactinus

P. licnoides Mont. According to Overholts (1953), this species is more southern in distribution. Martin (1925) reported a single collection from Iowa, but no voucher has been found in the SUI Herbarium.

Poria setigera Peck = Inonotus glomeratus

P. taxicola (Pers.) Bres. Based on a misidentified specimen of Ceriporia collected in Iowa City by MacBride.

P. terrestris (DC. ex Fr.) Sacc. Based on misidentified specimen of P. vaillantii.

P. obliqua Fr. Based on a misidentified specimen of Phellinus laevigatus.