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A Mathematical Analysis of Dolipore/Parenthesome Structure in Basidiomycetes

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Measurements were taken on the septal ultrastructure of 13 species of basidiomycete fungi from eight different orders. A continuum of dolipore size was found as opposed to the two size-types previously proposed. A cluster analysis was carried out on the measurements to suggest relationships between the species. Based on this and other published information on dolipores, possible evolutionary trends in the ultrastructure of the dolipore are discussed.

INTRODUCTION

The septal pore apparatus of the basidiomycetes was recognized by Buller (1933) as hemispherical pads on either side of the septal pore. Its complex structure was first elucidated by Girbardt (1958) and the structures were later termed dolipore and parenthesome by Moore & McAlear (1962). Since then, these structures have been found in a wide range of basidiomycetes and a comprehensive review of septal knowledge up to 1967 is given by Bracker (1967). Up to the present, the dolipore/parenthesome septum has been found in all basidiomycete groups with the exception of the Uredinales and Septobasidiales.

In most basidiomycetes the parenthesome takes the form of a dome-shaped cap showing qualitative differences between groups. It is perforate in members of the Agaricales, Aphyllophorales, Phallales, Melanogastrales and Lycoperdales (Thielke, 1972; Moore & Marchant, 1972; Eymé & Parriaud, 1970; Brooks, 1975; Marchant, 1969), non-perforate in some Tremellales (Wells, 1964; Moore, 1971), Tulasnellales (Moore, 1978), Dacrymycetales and Auriculariales (Moore & McAlear, 1962), and is modified into a series of cupulate units in some members of the Tremellales (Khan, 1976; Moore, 1978) and Ustilaginales (Filobasidiaceae) (Moore & Kreger-van Rij, 1972).

A few workers have taken measurements of dolipores or parenthesomes (Bracker & Butler, 1963; Wilsenach & Kessel, 1965; Setliff *et al.*, 1972; Ellis *et al.*, 1972) and, although incomplete, these suggest that there may also be quantitative differences between septa in different groups.

The purpose of this work was to take complete series of measurements on dolipore/parenthesome septa from a wide variety of basidiomycetes and compare them to see what quantitative differences exist between groups.

METHODS

The following strains were obtained from the Centraalbureau voor Schimmelcultures, Baarn, The Netherlands: *Amanita muscaria* (L. ex Fr.) Hooker (CBS 103.42); *Auricularia mesenterica* (Dicks.) Pers. (CBS 119.34); *Auricularia polytricha* (Mont.) Sacc. (CBS 439.67); *Boletus edulis* Bull. ex Fr. (CBS 563.70); *Calocera viscosa* Pers. (CBS 152.48); *Ceratobasidium cornigerum* (Bourd.) D. P. Rogers (CBS 148.54); *Exidia glandulosa* (Bull.) Fr. (CBS 176.38); *Exidia truncata* Fr. (CBS 216.63); *Hydnum septentrionale* Fr. (CBS 229.63); *Nidularia*

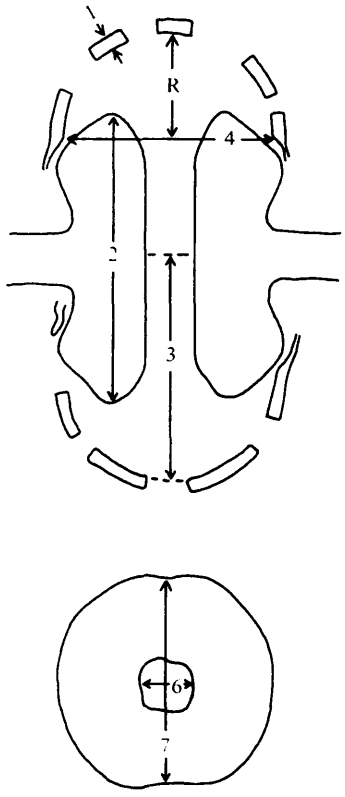


Fig. 1. Diagram showing methods of measurement of dolipore/parenthesome parameters. Parenthesome thickness (1) was measured at up to seven places on each parenthesome if both inner and outer delimiting membranes were clearly resolved. Septal pore length (2) was measured on both swellings and an average length noted. Parameters 3, 4 and 5 were measured for both parenthesomes. Septal pore diameter (6) and parenthesome hole diameter (8) were measured using an acetate sheet on which circles whose diameter increased in 1 mm steps had been drawn. This allowed the centre of each parenthesome hole to be marked with a pin for measurement 9. The pore body diameter (7) was measured at four orientations and an average measurement noted.

confluens Fr. (CBS 744.68); *Phallus impudicus* L. ex Fr. (CBS 178.57); *Polyporus biennis* (Bull. ex Fr.) Fr. (CBS 676.70). Many of these strains were clearly dikaryotic, as indicated by the presence of clamp connections; the remainder were also probably dikaryotic. A dikaryotic strain of *Schizophyllum commune* Fr. (699 × 845) was kindly provided by Professor J. G. H. Wessels, University of Groningen, The Netherlands. A dikaryotic strain of *Agaricus bisporus* (Lange) Singer, strain Sindon, was obtained from Dundarg Mushrooms Ltd, Coleraine, Co. Londonderry. A dikaryotic strain of *Corticium fuciforme* (Berk.) Wakefield was isolated from infected grass in the grounds of the New University of Ulster.

All strains were grown on cellophane laid over 2 % (w/v) malt agar, except *Hydnum septentrionale* which was grown directly on malt agar because cellophane reduced the growth rate and altered the growth pattern of this species. Small areas of mycelium from the edges of the colonies were fixed for 1 h in 3 % (v/v) acrolein in 0·1 M-sodium cacodylate buffer (pH 7·2), postfixed for 1 h in similarly buffered osmium tetroxide, and dehydrated in an acetone series interrupted by staining overnight in 1 % (w/v) uranyl nitrate at the 70 % acetone stage. *Polyporus biennis*, *Ceratobasidium cornigerum*, *Corticium fuciforme*, *Schizophyllum commune* and *Agaricus bisporus* were then embedded in Epon 812. Embedding proved a problem with the other 10 species, but was eventually found to be satisfactory after infiltration for 4 d with Spurr resin (Spurr, 1969). No difference was found in the cutting or staining properties of mycelia embedded in the different resins. Large sections were cut with a diamond knife on a Huxley Ultramicrotome Mark II and lifted routinely on uncoated 400 mesh copper grids, which gave maximum support without the staining problems and loss of resolution associated with support films. Sections were then poststained with lead citrate before examination at 80 kV in an AEI EM6G electron microscope.

Initally problems of stretching or tearing were encountered with silver/grey sections, but section stability,

Table 1. *Mean values (nm) and standard deviations for nine septal measurements (see Fig. 1) on 13 species of basidiomycete*

Species	1 Parenthesome thickness	2 Septal pore length	3 Distance from parenthesome to septum	4 Parenthesome diameter	5 Deviation of parenthesome shape	6 Septal pore diameter	7 Pore body diameter	8 Parenthesome hole diameter	9 Distance between centres of parenthesome holes	
1. *Auricularia polytricha*	27·5	549	387	469	−92	138	505	67·2	110	Mean
	2·8	129	92	87	63	18	59	11	14	S.D.
2. *Calocera viscosa*	24·9	455	309	270	−85	89	419	0	329*	
	2·5	62	34	42	24	19	57			
3. *Ceratobasidium cornigerum*	45·5	1242	1073	923	+12	266	1126	332	412	
	4·8	131	104	175	83	41	141	39	59	
4. *Corticium fuciforme*	34·8	858	717	499	+48	140	597	143	211	
	2·5	96	59	75	56	32	108	8	33	
5. *Exidia glandulosa*	24·7	383	282	344	−70	94	382	0	457*	
	0·8	37	23	35	23	16	41			
6. *Nidularia confluens*	28·4	541	383	394	−64	114	441	51·0	95	
	2·2	78	48	42	47	28	48	8·0	13	
7. *Phallus impudicus*	28·3	630	463	575	−114	141	605	70·3	133	
	2·1	68	51	77	44	24	54	20	27	
8. *Polyporus biennis*	29·9	599	449	522	−90	174	589	72·0	118	
	2·3	84	62	75	60	32	53	6	20	
9. *Schizophyllum commune*	30·5	587	466	477	−28	107	469	89·4	135	
	2·8	84	54	77	58	13	48	13	15	
10. *Agaricus bisporus*	29·6	706	518	514	−45	113	655	80·1	133	
	1·6	47	63	65	32	22	135	10	16	
11. *Amanita muscaria*	29·3	591	460	478	−27	175	584	88·3	131	
	2·7	137	107	57	59	20	68	8	11	
12. *Boletus edulis*	29·7	587	457	530	−58	152	621	92·4	136	
	1·7	65	44	58	38	3	5	11	12	
13. *Hydnum septentrionale*	31·3	577	488	440	−20	147	459	78·8	134	
	1·5	14	35	46	24	14	43	7	18	

Each mean value for species 1 to 9 is based on at least 26 measurements, but for parameters 1, 8 and 9, for which each photograph yielded more than one measurement, the mean values are based on 30 to 196 measurements. For species 10 to 13, mean values of parameters 2, 3, 4, 5, 6 and 7 are based on 4 to 7 measurements and parameters 1, 8 and 9 are based on 8 to 32 measurements.

* Calculated values: assuming that the median longitudinal section through the parenthesome is the arc of a larger circle, the distance from one parenthesome edge to the other was calculated.

an important factor when measurements are to be taken, was greatly improved by routinely cutting thicker (gold/silver) sections. The effects of stretching or tearing were further minimized by scanning only those grid squares where the section had no holes and was supported on all sides. The effect of section compression was minimized by measuring a large sample of dolipores.

Three sets of photographs were taken for each of nine species (species 1 to 9 in Table 1). (1) Approx. 30 median longitudinal sections: these were taken because not only is the dolipore symmetrical around this median but, since most dolipores only have one true median in this plane, a sample of 30 different dolipores was ensured. (2) Approx. 30 transverse sections through the dolipore: these were necessary to measure pore diameter. (3) Approx. 30 tangential glancing sections through parenthesome holes (where holes were present).

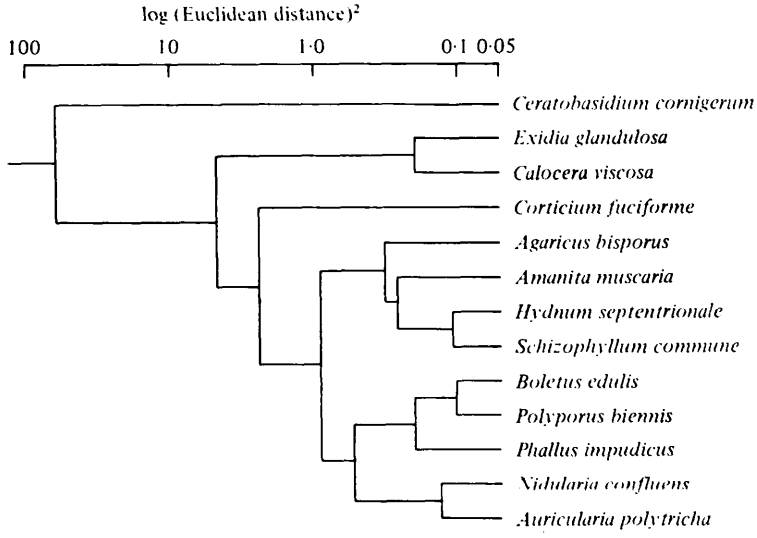


Fig. 2. Dendrogram showing the result of a cluster analysis using Ward's method.

A smaller number of photographs in each of these categories was taken for species 10 to 13 in Table 1. During the investigation the electron microscope was regularly calibrated using a diffraction grating, so that accurate measurements could be taken from each photograph. The data in Table 1 were standardized and a cluster analysis based on Ward's method (Ward, 1963) was carried out using the CLUSTAN 1A package (Wishart, 1969).

Sections of each species were also stained by the method of Thiéry (1967). Sections were lifted on uncoated, 200 mesh, stainless-steel grids and treated as follows: (i) 1 % (v/v) aqueous periodic acid for 30 min; (ii) four 5 min washes in water; (iii) 1 % (w/v) thiosemicarbazide in 10 % (v/v) acetic acid for 40 min; (iv) three 5 min washes in 10 % (v/v) acetic acid; (v) washed in a graded series from 10 % (v/v) acetic acid to water; and (vi) exposed to osmium tetroxide vapour at 67 °C for 1 h. The sections were examined without further staining.

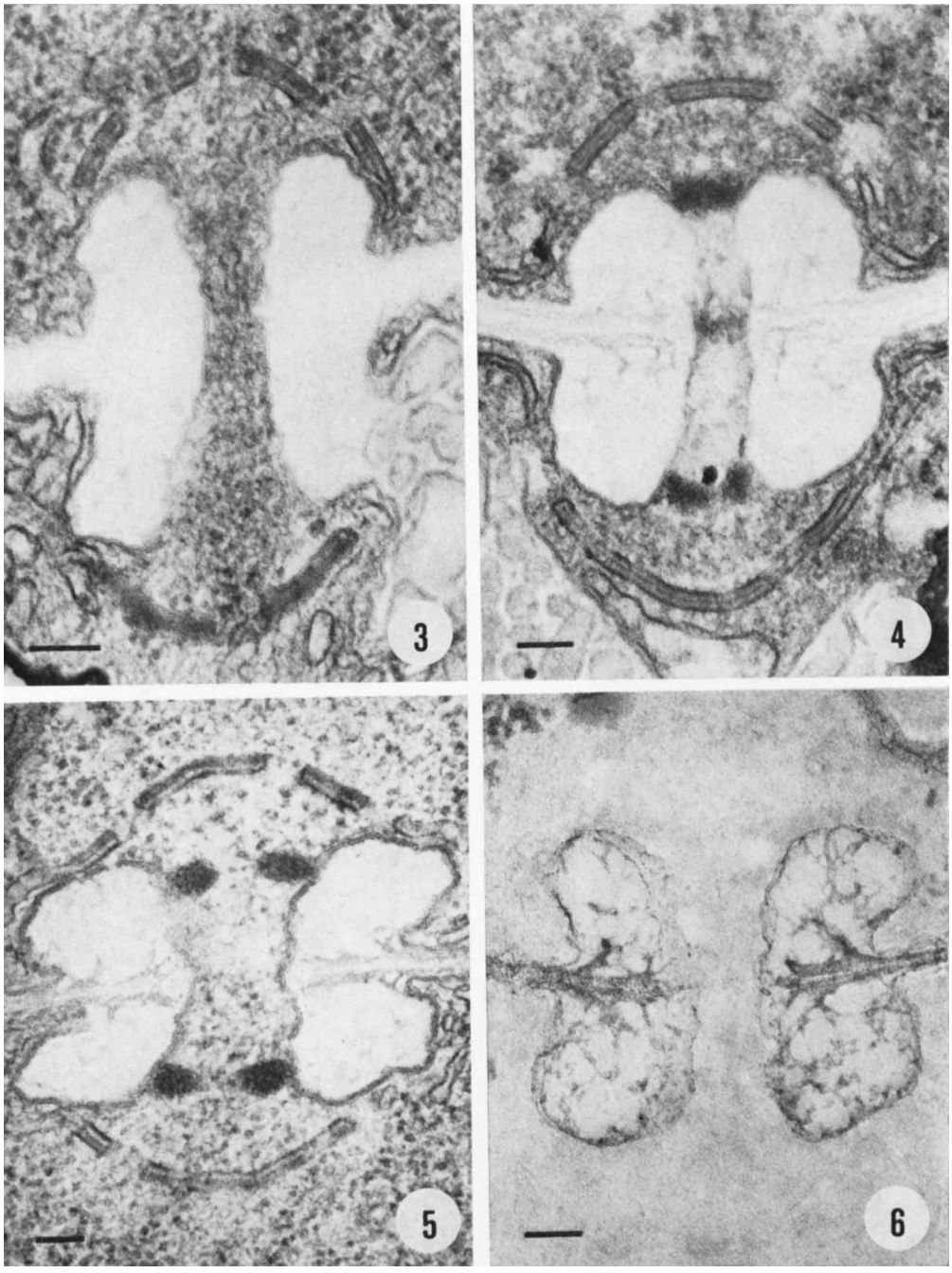
RESULTS

For each parameter in Fig. 1 a mean value and standard deviation were calculated for each species, producing the matrix shown in Table 1. Most of the standard deviations are falsely large because of the method of collection of the data, and reveal more about the degree of stretching and compression of the sections than about the inherent variability of the septal structure.

The wide variation in size of the septal pore apparatus can be clearly seen by comparing the micrographs of species such as *Calocera viscosa* (Fig. 9), a small species with non-perforate parenthesomes, with intermediate-sized species such as *Phallus impudicus* (Fig. 4) and *Schizophyllum commune* (Fig. 10), both of which have parenthesomes with numerous holes, and with large species such as *Ceratobasidium cornigerum* (Fig. 11), which have a few large holes in the parenthesome.

A cluster analysis was initially carried out on the mean measurements for the first nine species in Table 1, since the mean values for the remainder were based on fewer measurements. However, when the analysis was repeated on the complete matrix (13×9) the four extra species were added into the previous clustering pattern without basically altering it. The dendrogram produced by the larger cluster analysis is shown in Fig. 2.

It was the intention to enlarge the matrix yet again by the addition of some qualitative characters such as 'type of occlusion of pore channel' and 'degree of reticulation of dolipore



All bar markers represent 100 nm

Fig. 3. Median longitudinal section through a dolipore/parenthesome septum of *Auricularia polytricha*.

Fig. 4. Median longitudinal section through a dolipore/parenthesome septum of *Phallus impudicus*.

Fig. 5. Median longitudinal section through a dolipore/parenthesome septum of *Polyporus biennis*.

Fig. 6. Thiéry-stained median longitudinal section through a dolipore/parenthesome septum of *Polyporus biennis*. Note that the parenthesomes have not stained.

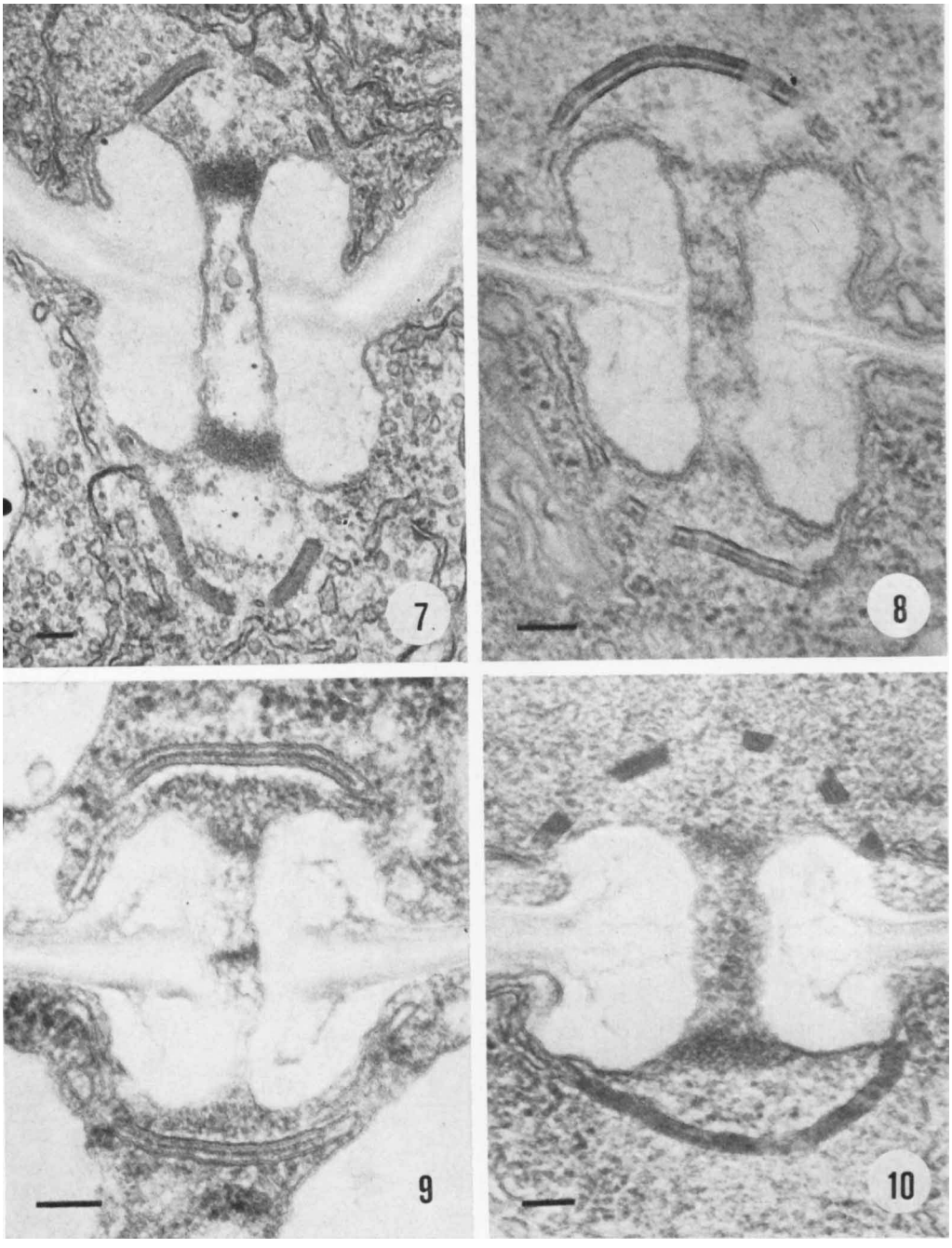


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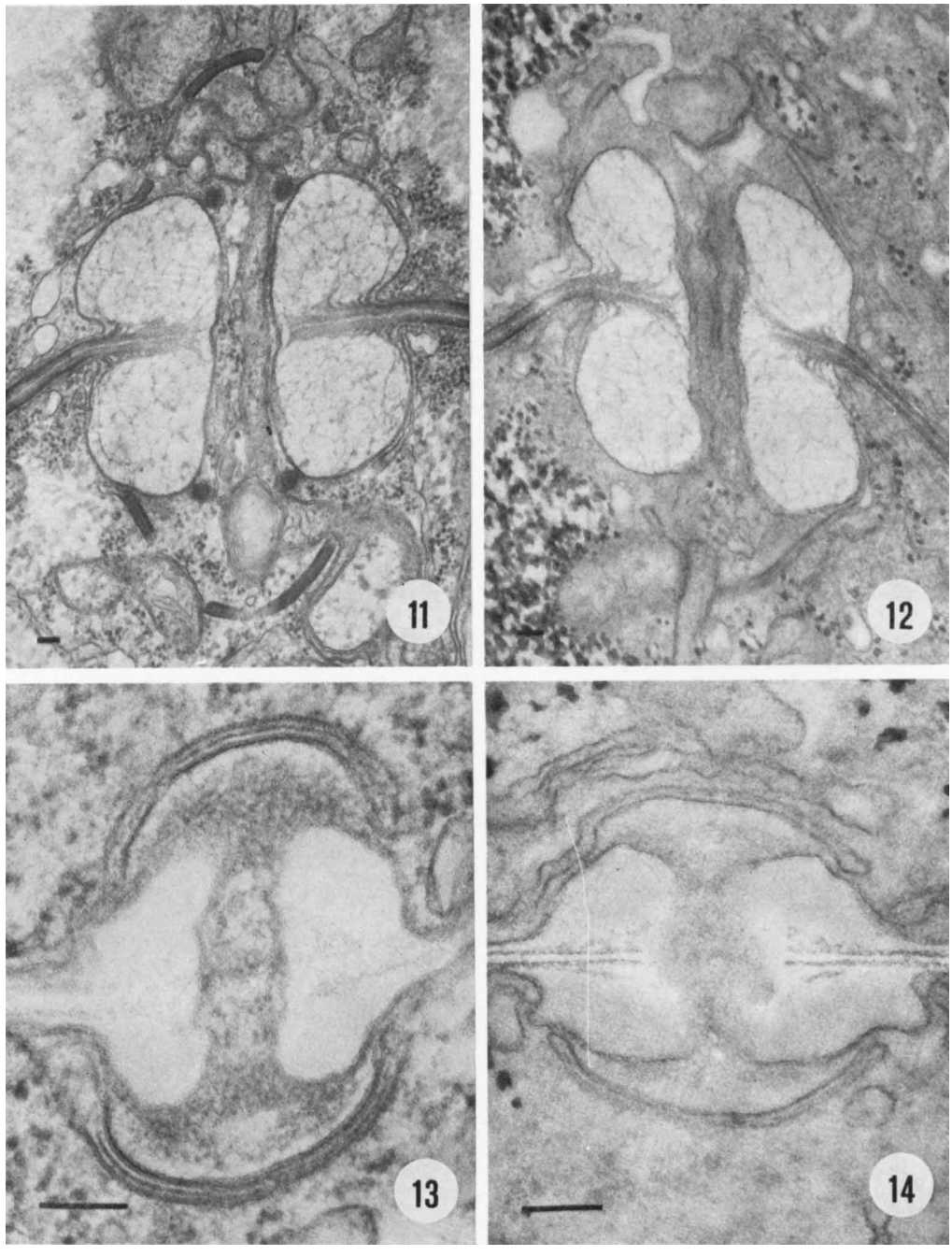
Fig. 7. Median longitudinal section through a dolipore/parenthesome septum of *Corticium fuciforme*.

Fig. 8. Median longitudinal section through a dolipore/parenthesome septum of *Nidularia confluens*.

Fig. 9. Median longitudinal section through a dolipore/parenthesome septum of *Calocera viscosa*.

Fig. 10. Median longitudinal section through a dolipore/parenthesome septum of *Schizophyllum commune*.



All bar markers represent 100 nm

Fig. 11. Median longitudinal section through a dolipore/parenthesome septum of *Ceratobasidium cornigerum*. Note the presence of mitochondria in the pore channel and in areas under the parenthesomes.

Fig. 12. Thiéry-stained median longitudinal section through a dolipore/parenthesome septum of *Ceratobasidium cornigerum*.

Fig. 13. Median longitudinal section through a dolipore/parenthesome septum of *Exidia glandulosa*. Note the granular occlusions which extend from the pore channel into the region enclosed by the parenthesome.

Fig. 14. Thiéry-stained median longitudinal section through a dolipore/parenthesome septum of *Exidia glandulosa*. In this species the parenthesomes have stained.

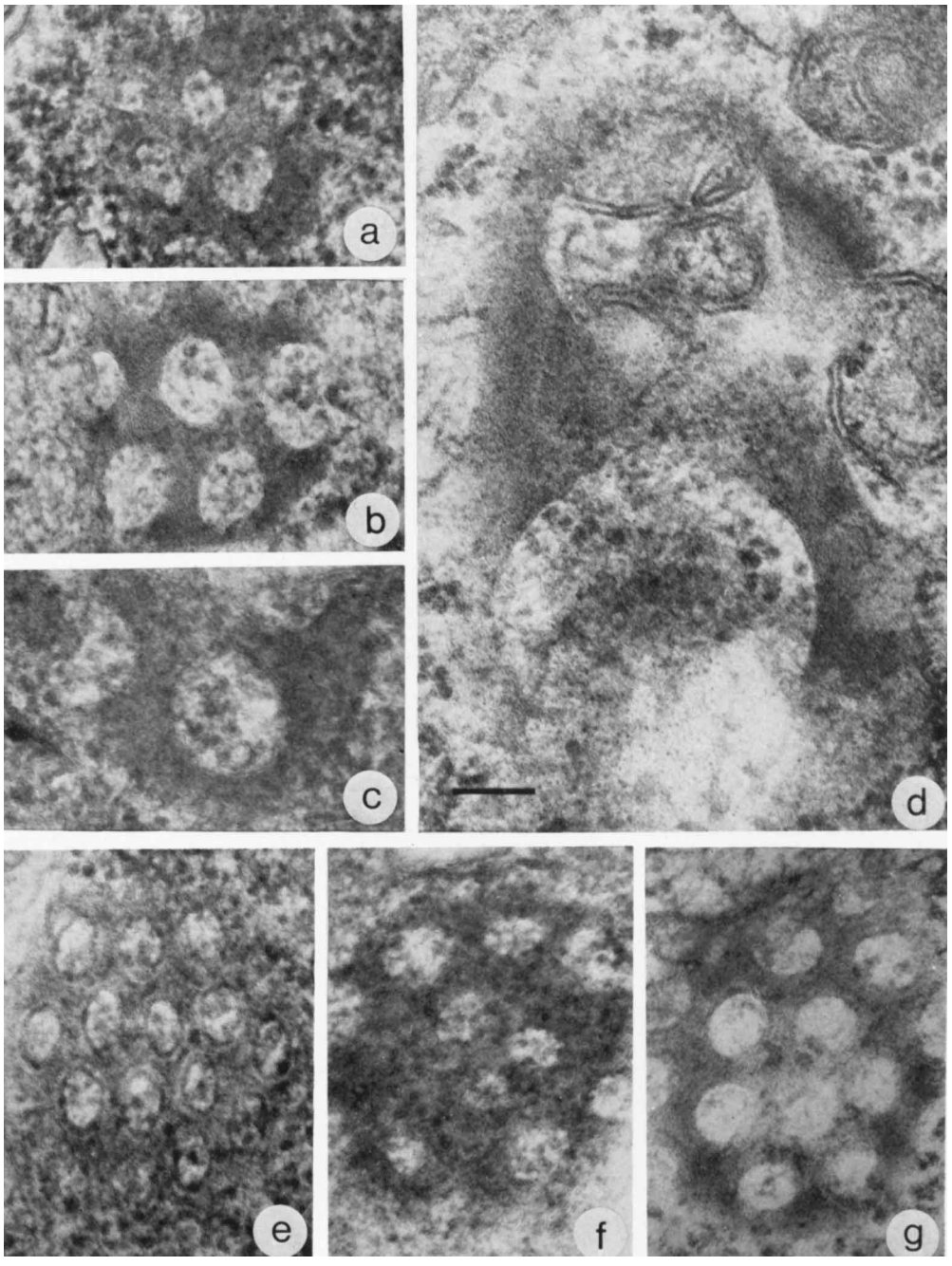


Fig. 15. Tangential glancing sections through the parenthesomes of (*a*) *Auricularia polytricha*, (*b*) *Schizophyllum commune*, (*c*) *Corticium fuciforme*, (*d*) *Ceratobasidium cornigerum*, (*e*) *Nidularia confluens*, (*f*) *Phallus impudicus*, (*g*) *Polyporus biennis*. Bar marker represents 100 nm.

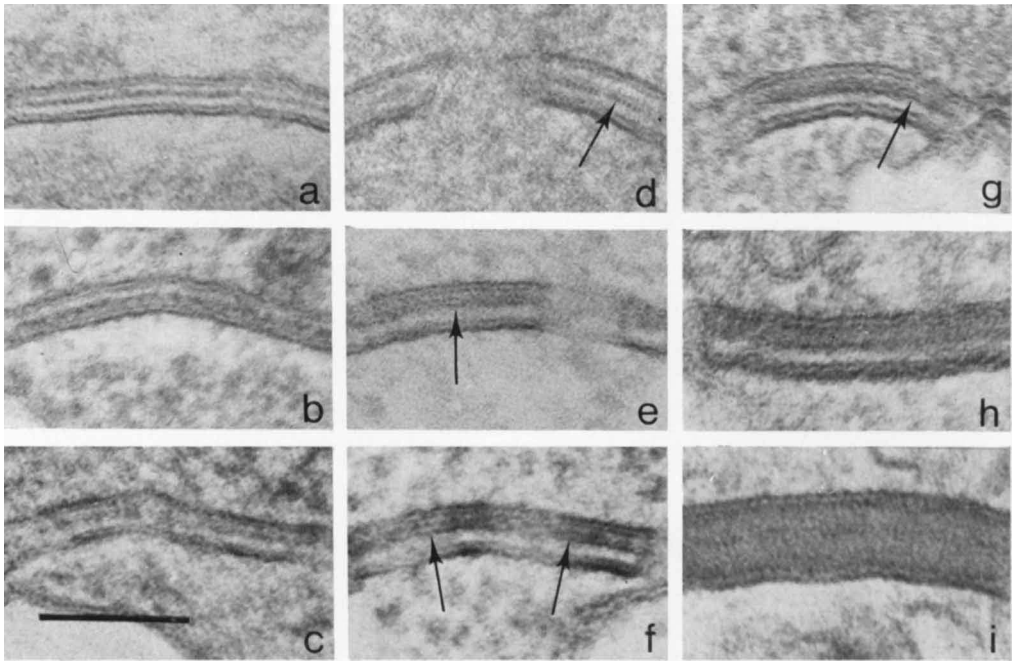


Fig. 16. Sections through parenthesomes, arranged in order of increasing thickness: (*a*) *Exidia glandulosa*, (*b*) *Calocera viscosa*, (*c*) *Auricularia polytricha*, (*d*) *Phallus impudicus*, (*e*) *Nidularia confluens*, (*f*) *Polyporus biennis*, (*g*) *Schizophyllum commune*, (*h*) *Corticium fuciforme*, (*i*) *Ceratobasidium cornigerum*. Arrows indicate central unit membrane. Bar marker represents 100 nm.

swellings'. However, examination of the photographs for each species showed that these characters were very variable. In some of the slow-growing species, for example *Auricularia polytricha* and *Nidularia confluens*, most of the cells were dead, except at the growing edge of the mycelium. Sections were therefore cut close to the hyphal tips and none of the dolipores had occluded pore channels (see, for example, Figs 3 and 8); but it was not considered valid to score these species thus since occlusions may have been present a little further back from the edge of the mycelium, if, as Bracker & Butler (1963) suggest, 'plugging' only occurs in the dolipores of older hyphae. This may indeed be the case since in *Ceratobasidium cornigerum* some of the pore channels had no occlusions, some had open-ring shaped occlusions (Fig. 11) and others were almost completely occluded.

As regards reticulation of the swellings, some species clearly had a network of material which stained heavily with lead or Thiéry stain, for example *Polyporus biennis* (Figs 5 and 6), *Corticium fuciforme* (Fig. 7) and *Ceratobasidium cornigerum* (Figs 11 and 12), while others clearly did not, for example *Exidia glandulosa* (Figs 13 and 14) and *Auricularia polytricha* (Fig. 3). However, in *Nidularia confluens* the swellings appeared reticulate in some cases (Fig. 8), non-reticulate in others, and some dolipores were found with the half of the dolipore on one side of the septum reticulate, and the half on the other side non-reticulate. Also, although in the strain of *Agaricus bisporus* examined the dolipore swellings (from an ageing part of the mycelium) were not reticulate, those in a strain of the same species studied by Thielke (1972) were reticulate.

Thus occlusion of the pore channel and reticulation of the dolipore swellings appeared to be characters which may undergo changes during differentiation of fungal hyphae and so were not suitable for use as characters in the present study.

The micrographs of glancing sections through parenthesome holes from different species at the same magnification (Fig. 15) show that there is a wide range of sizes of parenthesome

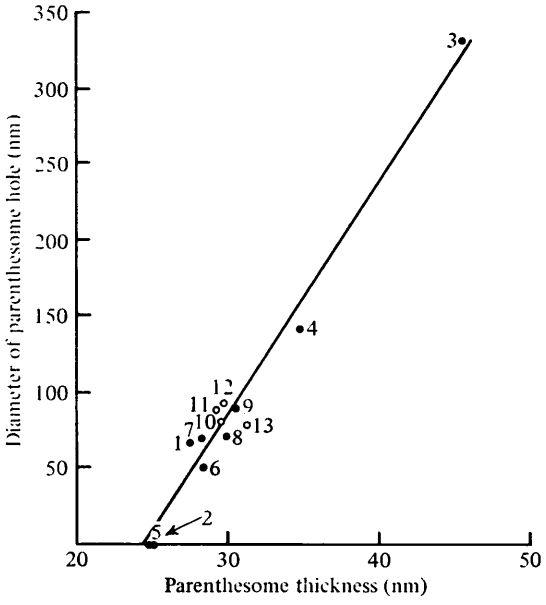


Fig. 17. Relationship between the thickness of the parenthesome and the diameter of the parenthesome holes. Numbers refer to species as in Table 1.

Table 2. *Correlation matrix, showing the correlation coefficient (r) for each pair of parameters (see Fig. 1)*

	1	2	3	4	5	6	7	8
1								
2	0·968							
3	0·986	0·992						
4	0·895	0·905	0·895					
5	0·695	0·640	0·697	0·379				
6	0·847	0·809	0·819	0·892	0·380			
7	0·893	0·934	0·914	0·958	0·415	0·883		
8	0·986	0·972	0·980	0·937	0·632	0·877	0·935	
9	0·238	0·232	0·266	0·137	0·190	0·130	0·254	0·228

holes; parenthesome thickness is also very variable (Fig. 16). A linear relationship exists between these two parameters (Fig. 17); regression analysis showed a significant correlation (at 0·1 % level) with a coefficient $r = 0{\cdot}986$.

A matrix was obtained (Table 2) giving the correlation coefficient for every possible combination of pairs of parameters. There was a high degree of correlation ($r = 0{\cdot}809$ to 0·992) between all pairs except those involving parameters 5 or 9. This suggests that, in general, as one parameter increases so do the others, i.e. as the pore body diameter increases (a size range of comparable pore bodies is shown in Fig. 18), so does the septal pore diameter and the length of the dolipore (i.e. septal pore length). Also, as the dolipore increases in size so do most of the parenthesome parameters, i.e. the diameter and thickness of the parenthesome and the size of its holes. Parameter 5 is an index of parenthesome shape and as such is not affected by size, but parameter 9 is the distance between parenthesome hole centres and so might be expected to increase with increasing parenthesome diameter and hole size. If we picture the distance between holes as the width of the parenthesome bridge between adjacent holes (i.e. the distance between adjacent hole centres *minus* 1 hole diameter), it is clear from Fig. 19 that the width of the bridge does not increase in step with the hole size but fluctuates about a mean of 53 nm. Thus the large holes in the *Ceratobasidium*

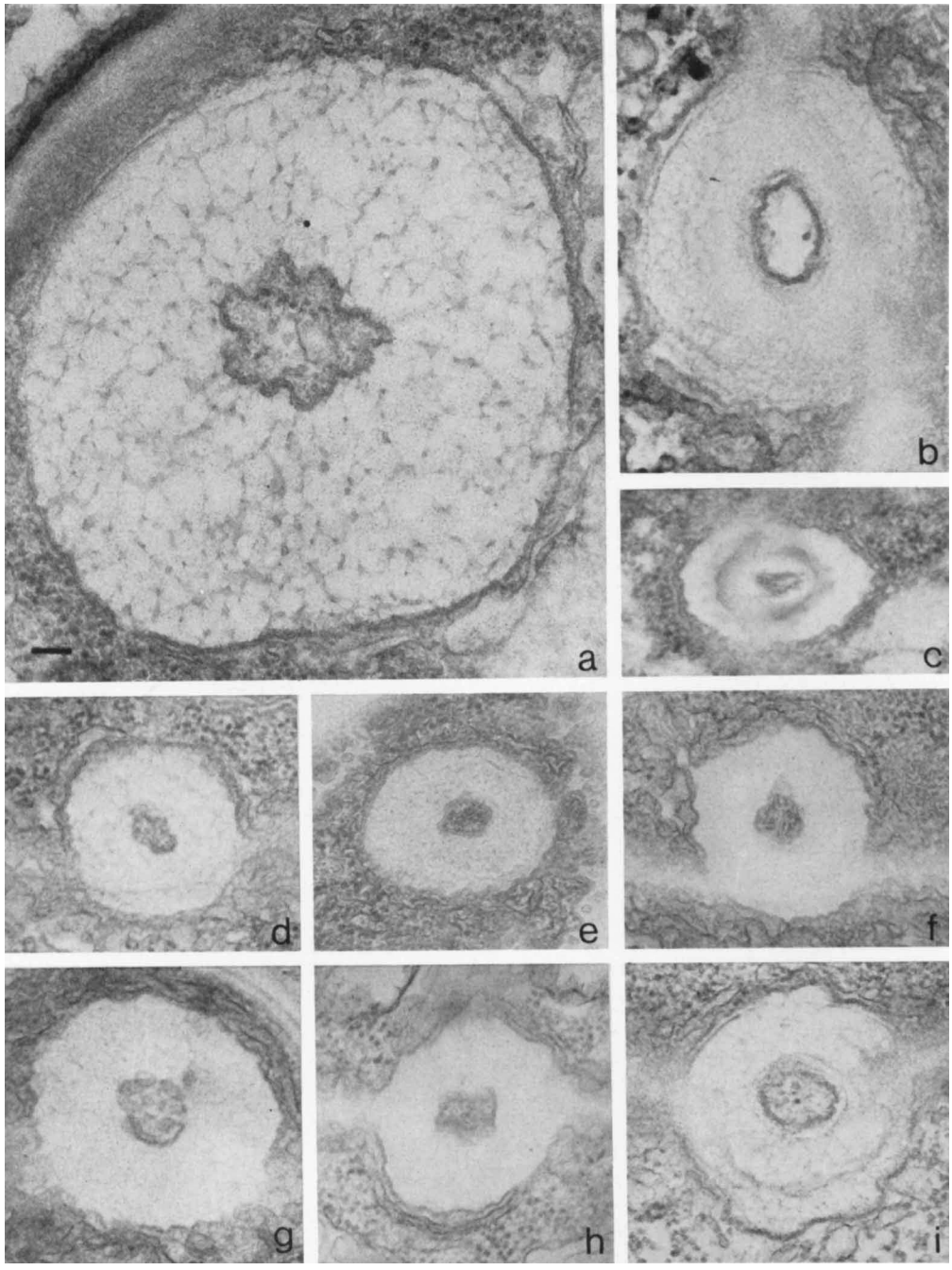


Fig. 18. Transverse sections through the dolipore swellings of (*a*) *Ceratobasidium cornigerum*, (*b*) *Corticium fuciforme*, (*c*) *Calocera viscosa*, (*d*) *Nidularia confluens*, (*e*) *Schizophyllum commune*, (*f*) *Auricularia polytricha*, (*g*) *Phallus impudicus*, (*h*) *Exidia glandulosa*, (*i*) *Polyporus biennis*. Bar marker represents 100 nm.

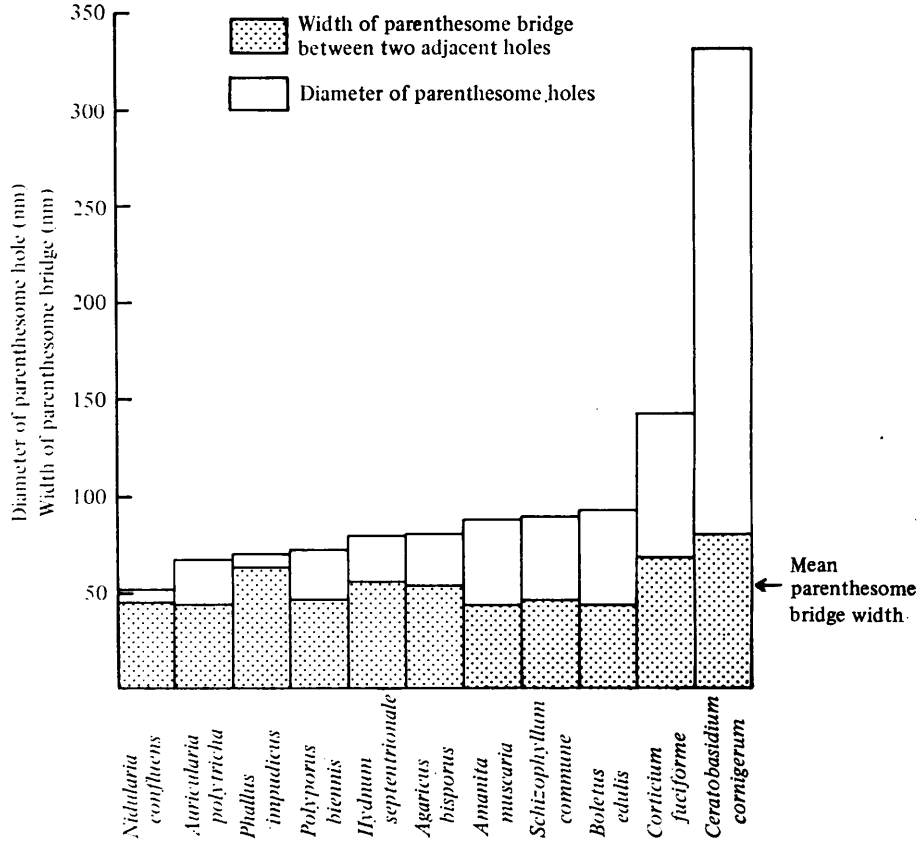


Fig. 19. Histogram showing the parenthesome hole diameter and the corresponding width of the parenthesome bridge between two adjacent holes. Species are arranged in order of increasing parenthesome hole diameter.

cornigerum parenthesome are relatively much closer together than the smaller holes of the other species. This is substantiated by calculation of the percentage of hole in the parenthesome area (based on a hexagonal arrangement of holes), which was 59% in *Ceratobasidium cornigerum*, 40 to 42% in *Corticium fuciforme*, *Boletus edulis*, *Amanita muscaria* and *Schizophyllum commune*, 31 to 34% in *Hydnum septentrionale*, *Agaricus bisporus*, *Polyporus biennis* and *Auricularia polytricha*, and only 26% in *Phallus impudicus* and *Nidularia confluens*.

DISCUSSION

There are obvious quantitative differences between the dolipore/parenthesome septa in basidiomycetes of different groups. Those with non-perforate parenthesomes are considerably smaller than the two main clusters of species containing members of the Agaricales and Aphyllophorales. The two species at the other end of the size scale are *Ceratobasidium cornigerum* and *Corticium fuciforme*. The Ceratobasidiaceae, previously in the Tulasnellales, have been reclassified as members of the Corticiaceae (Shaffer, 1975). This is fortunate in the present context since the Tulasnella species studied by Moore (1978) has a dolipore with non-perforate parenthesomes and is similar in size to *Exidia glandulosa*. *Corticium* (*Rhizoctonia*) *solani* has dolipores in the same size range as *Ceratobasidium cornigerum*, while those of *Corticium fuciforme* are much smaller. That *Ceratobasidium cornigerum* and *Corticium solani* have, based on other characters, both been placed in the genus *Pellicularia* Cooke, a

segregate from the genus *Corticium*, would suggest that the separation of *Corticium fuciforme* from *Ceratobasidium cornigerum* in the cluster analysis (Fig. 2) is a true distinction.

The *Auricularia* species examined in the present study, *Auricularia polytricha* and *Auricularia mesenterica*, both have perforate parenthesomes, while the species previously considered as *Auricularia auricularis* (= *Auricularia auricula-judae*), which was examined by Moore & McAlear (1962) and has since been transferred to the genus *Hirneola* and re-examined by Moore (1978), has non-perforate parenthesomes. Again this discrepancy underlines an area of uncertainty in classification. Donk (1958) segregated the genus *Hirneola* Fr. from *Auricularia* on growth form, *Auricularia auricula-judae* being placed in the genus *Hirneola* as *Hirneola auricula-judae* while *Auricularia polytricha* and *Auricularia mesenterica* remained in the genus *Auricularia*.

Exidia glandulosa and *Calocera viscosa*, which have non-perforate parenthesomes, are also separated off together on the basis of quantitative parameters. Measurements made on published micrographs of other septa with non-perforate parenthesomes, i.e. *Exidia nucleata* (Wells, 1964), *Dacrymyces deliquescens* and *Auricularia auricularis* (= *Hirneola auricula-judae* sensu Donk) (Moore & McAlear, 1962), suggest that they are all in the same size range as *Exidia glandulosa* and *Calocera viscosa*. [The only major anomalous observations are those of Setliff *et al.* (1972) and Traquair & McKeen (1978) who have reported non-perforate parenthesomes in two field-collected members of the Polyporaceae.] It is also interesting to note that *Filobasidium capsuligenum* (Moore & Kreger-van Rij, 1972) has a septal pore length and parenthesome thickness almost identical to that of *Exidia glandulosa*, and the structure in *Filobasidium capsuligenum* may represent a multiple non-perforate parenthesome situation. The evidence supports the suggestion of Wilsenach & Kessel (1965) that modifications of septal pore structure within the basidiomycetes may have phylogenetic significance, particularly as the septal complex is likely to be a conserved structure not subject to rapid evolutionary changes. Shaffer (1975) points out that the division of the basidiomycetes into Hemibasidiomycetes, Heterobasidiomycetes and Homobasidiomycetes is in accord with many taxonomists' evolutionary ideas, but the Heterobasidiomycetes lack a significant unifying diagnostic feature. Perhaps the possession of a small dolipore with a non-perforate parenthesome is such a feature. If this were the case, *Hirneola* (with non-perforate parenthesomes) would remain in the Heterobasidiomycetes while *Auricularia* would be removed. In the cluster analysis, the septum most similar to that of *Auricularia polytricha* is *Nidularia confluens*, so perhaps the Auriculariales and Nidulariales are closely linked phylogenetically.

The majority of the species studied in this work belonged to the Agaricales and Aphyllophorales and, with the exception of *Corticium fuciforme* and *Ceratobasidium cornigerum*, all these species have similar dolipores in the middle size range. The gasteromycetes *Phallus impudicus* and *Nidularia confluens* occupy the same cluster, which also contains the two representatives of the pore-bearing fungi *Boletus edulis* and *Polyporus biennis*. The remaining major cluster comprises *Agaricus bisporus*, *Amanita muscaria*, *Hydnum septentrionale* and *Schizophyllum commune*. The analysis has thus separated these toothed and gilled fungi from the pore-bearing species.

The increase in parenthesome thickness as the holes in its structure get larger may have some structural significance, as an increase in thickness may be necessary to support the larger holes which are also relatively closer together. However, since neither the composition nor the mechanical properties of the material comprising the parenthesomes is known, the reason for this relationship remains obscure. Also the increase in thickness of the parenthesome is not a proportional one; all the parenthesomes are bound top and bottom by similar unit membranes (Fig. 16) but the position and configuration of material between these membranes varies. *Ceratobasidium cornigerum* has widely spaced delimiting membranes and the area between is filled with a dense even matrix. At the other extreme, *Exidia glandulosa* and *Calocera viscosa* have only a thin layer of densely staining matrix midway

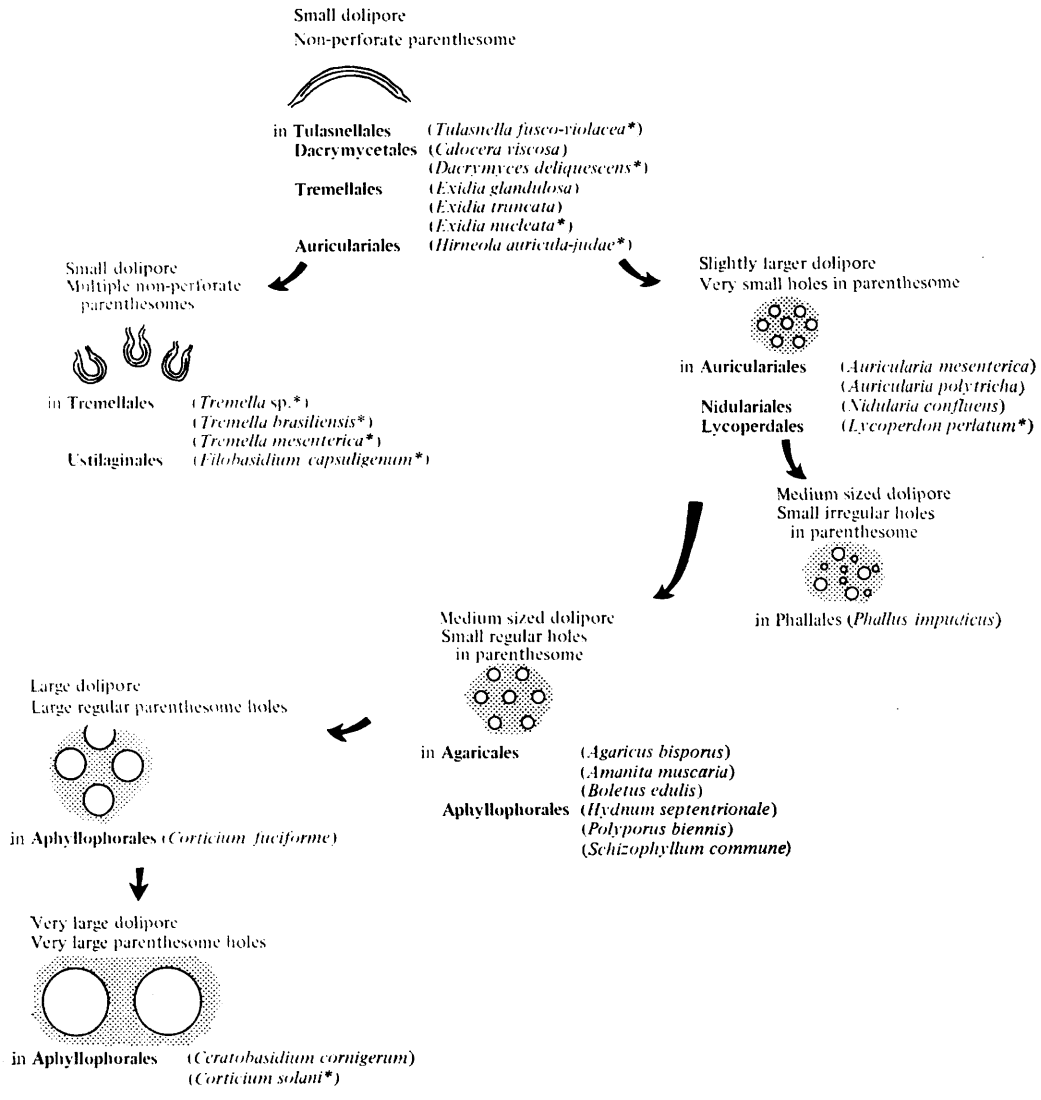


Fig. 20. Diagram illustrating a possible phylogeny of the dolipore/parenthesome septum of the basidiomycetes. (* Structural types in these species were derived from published literature.)

between the membranes, while in slightly thicker parenthesomes this layer appears to be resolved into a third unit membrane (arrowed in Fig. 16) as described by Moore & Patton (1975).

The function of the dolipore/parenthesome may be to maintain the strict segregation of nuclei found in many basidiomycetes, whilst still allowing cytoplasmic continuity where necessary. For instance, Trinci (1971) suggested that a number of hyphal compartments contribute material for the extension of the hyphal apex. In basidiomycetes the unplugged dolipore apparatus may allow transport of material from a supporting region behind the growing hyphal tips. If this were the case, the factors determining the size of particles which can move through the septum are (i) the diameter of the parenthesome holes and (ii) the diameter of the pore channel. In all species except *Ceratobasidium cornigerum* and *Corticium fuciforme* the parenthesome hole diameter is the limiting dimension; in *Corticium fuciforme* both dimensions are equal, while in *Ceratobasidium cornigerum* the limiting aperture is the

septal pore. Thus in all species except *Ceratobasidium cornigerum* the parenthesome may function to grade particles before they reach the pore channel.

Wilsenach & Kessel (1965) suggested, from the evidence available at that time, that there were two types of dolipore, a small Polyporus-type with a large number of small parenthesome holes and a large Rhizoctonia-type with a small number of large parenthesome holes. The results of the present study suggest that the range of structure is continuous in nature, and it is possible to construct a simple phylogeny of the dolipore (Fig. 20).

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