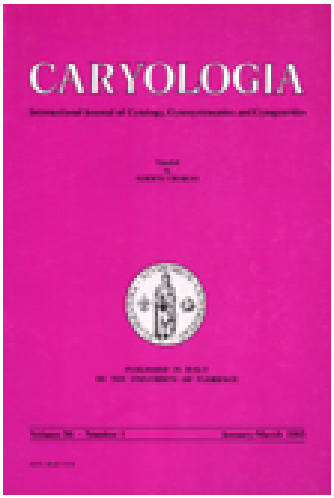

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SEPTAL PORE APPARATUS ULTRASTRUCTURE IN *TREMELLA FOLIACEA* PERS. EX FR. AND *TREMELLODON GELATINOSUM* (SCOP.) PERS.

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SUMMARY — Most Basidiomycetes are characterized by dolipores with parenthesomes that are multiperforate, imperforate or pauciperforate. Electron micrographs of *Tremellae*, however, show dolipore septa with banded material in the orifices and vesiculate parenthesomes. We have studied the fine structure of *Tremella foliacea* Pers. ex Fr. and *Tremellodon gelatinosum* (Scop.) Pers. In these two species we describe several considerable differences which question the phylogeny suggested by some authors, within the Basidiomycetes. Ultrastructural similarities found in the dolipore of *Tremella foliacea* and in the pore of a few Ascomycetes could suggest that the most primitive dolipore is the *Tremella*-type.

INTRODUCTION

The septal pore apparatus of Basidiomycetes, except the Uredinales and Septobasidiales, is a complicated structure which MOORE and MARCHANT (1972) called a dolipore/parenthesome. Its structure is not the same in all Basidiomycetes. The parenthesome is perforate in some Agaricales, Aphyllophorales, Phallales, Melanogastrales and Lycoperdales (MARCHANT 1969; MOORE and MARCHANT 1972; THIELKE 1972; BROOKS 1975), imperforate in some Tremellales (WELLS 1964; MOORE 1971; KHAN and KIMBROUGH 1980) Tulasnellales (MOORE 1978), Dacrymycetales and Auriculariales (MOORE and MC ALEAR 1962) and formed by a cluster of cupulate units in other species of Tremellales (KHAN 1976; MOORE 1978) and some Ustilaginales (MOORE and KREGER VAN RIJ 1972). These different pore structure arrangements, according to some authors, are of great phylogenetic and taxonomic importance.

Our researches were aimed at species whose phylogenetic position is debatable. Amongst these, *Tremella foliacea* and *Tremellodon gelatinosum* seemed particularly interesting, in relation to the disputed taxonomic position of Tremellales. This work describes the ultrastructure of the septal pore apparatus of these two species, with particular attention to the septal pore cap.

MATERIALS AND METHODS

Fully developed basidiocarps of *Tremella foliacea* Pers. ex Fr. and *Tremellodon gelatinosum* (Scop.) Pers. were collected by Mycological Society Bresadola of Trento (Italy).

Small blocks of fresh fruiting bodies (1 mm^3) were fixed in 3% glutaraldehyde, postfixed in 2% osmium tetroxide, dehydrated and embedded in Epon-Araldite.

Sections, cut with an ultratome, doubled stained in uranyl acetate and lead citrate (REYNOLDS 1963), were examined with a Siemens Elmiskop 1A electron microscope.

RESULTS

The structure of the *Tremella foliacea* basidiocarp is illustrated in a l|µ-thin section in Fig. 1. Subhymenial dikaryotic hyphae form a little compact mycelium. A regular hymenium, with characteristic basidia of *Tremella* sp., is clearly visible: young and mature basidia are septate and each bears four basidiospores on very long sterigmata (Figs. 1 and 2).

Septa of subhymenial hyphae, seen in ultrathin section, have dolipores. The parenthesome or pore cap appears as a three-dimensional, radiating array of closely packed tubular-like structures. In section, however, the pore cap appears to be constituted of two different parts. The first, close to the pore opening, apparently comprises a small number of radiating elements whose ends are closed and which lie in a lens-shaped area of undifferentiated cytoplasm without ribosomes, the distal one is of more closely packed parallel elements and homogeneus (Fig. 3). In transverse section, the diameter of the elements that constitute the pore cap differ, being 250 Å in the distal region, and about 500 Å in the proximal region near the pore opening (Fig. 3, insets).

A band of electron dense material crosses the pore channel and two electron dense bands are often visible at each end of the pore channel (Fig. 3). The electron dense material of each dolipore orifice presents a barred appearance which appears to be due to, as scarcely obvious, elements parallel to the pore walls and whose diameter is almost the same as the external tubules (Fig. 3). Each opening of the pore shows, depending on the plane of different sections, a limiting membrane which appears variously broken or continuous.

The septal pore between the basidium and the lower hypha is ultrastructurally similar but not identical (Fig. 4 and inset). In fact, tubular like-structures are absent even though radiating array of microfibrils can be identified.

The dolipore structure of *Tremellodon gelatinosum* is different. The dolipore opening is occluded by granular electron dense material. The pore cap is imperforate (Fig. 5). An electron dense lamella is present in the lumen

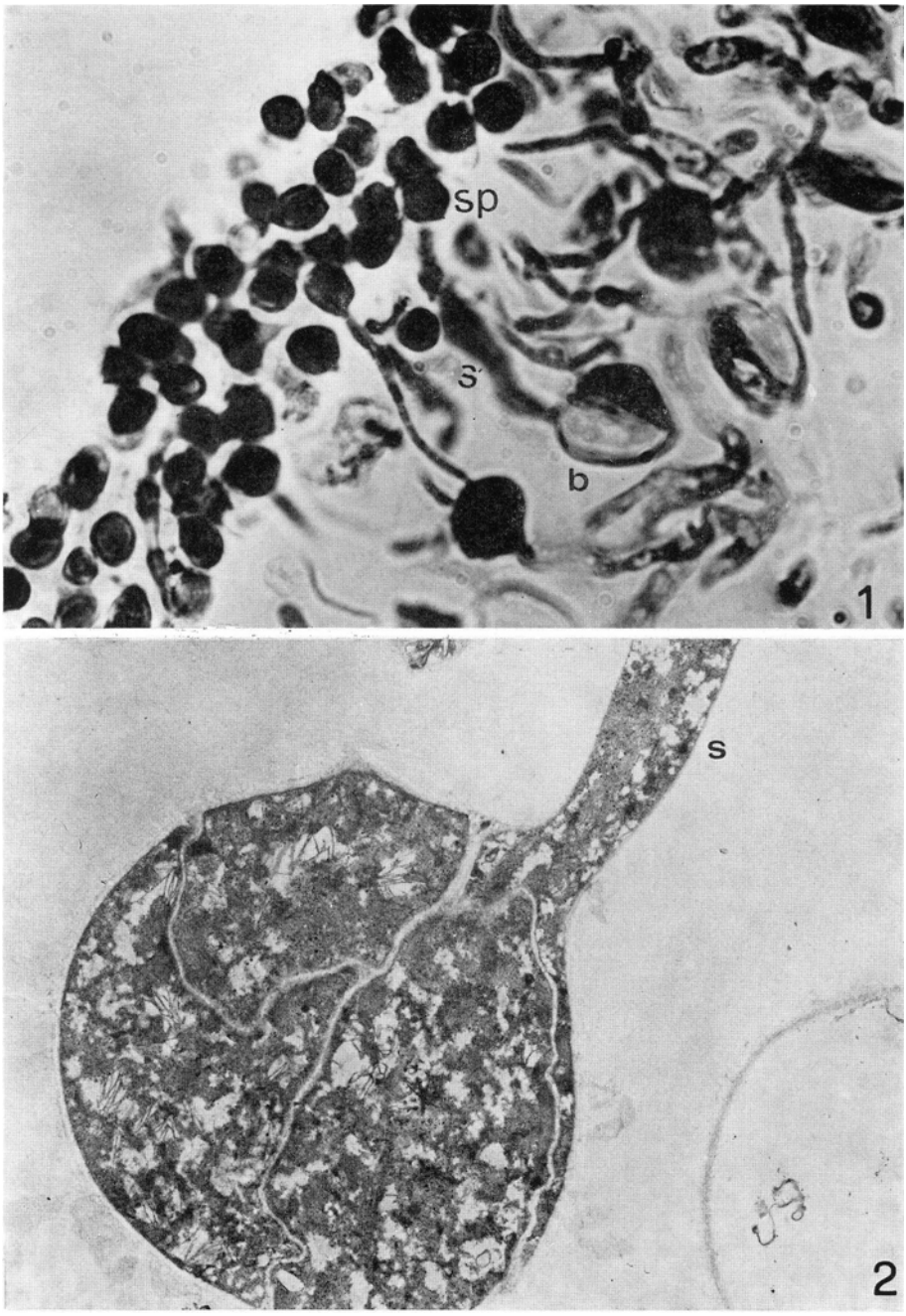
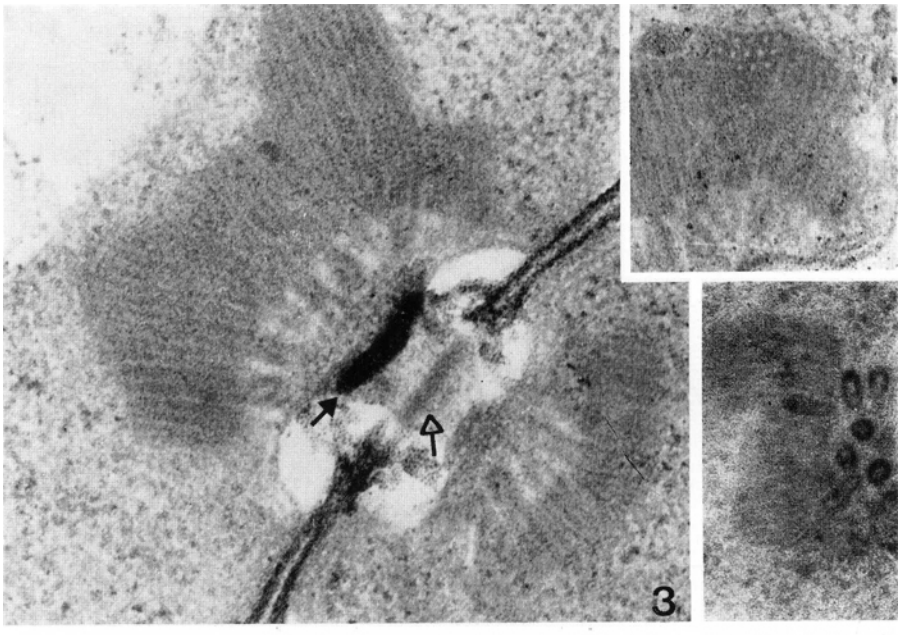


Fig. 1. — Longitudinal 1 μm thin section of *Tremella foliacea* hymenium. b = septate basidium; s = sterigmata; sp = spores. × 1,200.
Fig. 2. — Septate basidium of *Tremella foliacea*. s = sterigmata. × 8,800.



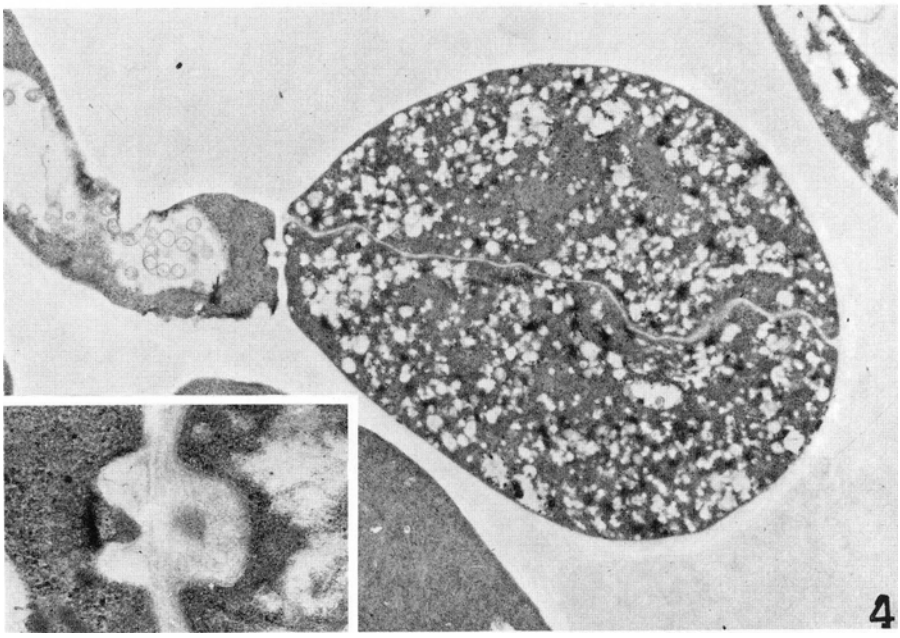


Fig. 3. — Dolipore septum in vegetative hypha of *Tremella foliacea*. The pore cap (or parenthesome) consists of a radiating array of tubular-like-structures. Each opening of the pore shows a limiting membrane and a band of electron dense material, though, in this imperfectly middling section, the band of electron dense material is visible only on the superior side (black arrow). In the middle of the pore channel is present a band of electron dense material (white arrow). In transverse section, the diameter of the elements, which constitute the pore cap, differs measuring 250 Å, in the distal part (1st inset), but much more in the portion near the pore opening (2nd inset). × 66,000; Insets × 72,000.

Fig. 4. — *Tremella foliacea*: septal pore apparatus between basidium and the lower hypha (× 6,000). Tubular structures are absent, bat a microfibrillar arrangement is visible (inset, × 42,000).

of each pore cap, similar to that described by KHAN and KIMBROUGH (1980). A very large plasmalemmasome is always present just near the pore caps (Fig. 6).

DISCUSSION

The Ascomycetes generally possess simple perforate septa with associated Woronin bodies, although the occurrence of septa with expanded pore margins has been demonstred in *Wallemia sebi* (Deuteromycetes, TERRACINA 1974) and in some ascomycetous yeasts (KREGERVAN-RIJ 1969*a* and 1969*b*; WALT 1972). Only the Basidiomycetes, with the exception of the Uredinales, show elaborate septa named by MOORE and MARCHANT (1972) the dolipore-parenthesome.

According to several authors, the dolipore with imperforate pore caps are the most primitive, afterwards the pore caps become pauciperforate or vesiculate (PATTON and MARCHANT 1978). In different families, the structure and modification of septal pores, particularly the pore cap modifications, is believed to have a phylogenetic significance.

As regards the Tremellales, two types of septal pore apparatus have been described: imperforate pore caps in *Exidia glandulosa* (PATTON and MARCHANT 1978) and vesiculate ones in *Tremella* sp., *Tr. mesenterica* and *Tr. brasiliensis* (KHAN 1976; MOORE 1978). On the basis of these differences, MOORE (1978) proposed to establish two suborders into the Tremellales: the Tremellineae and the Exidineae.

Our observations confirm that, amongst Tremellales, the septa show common characteristics in their pore channels but remarkable differences in the mode of occlusion of the dolipore openings and in the pore cap structures. In fact, in *Tremellodon gelatinosum*, each dolipore opening is occluded by electron dense granular material, while in *Tremella foliacea* we observed barred material, as described in *Tremella mesenterica* (MOORE 1978).

In addition, the parenthesome of *Tremellodon gelatinosum* appears imperforate, as observed by a few authors in some Tremellales, Dacrymycetales and Auriculariales. By contrast, the parenthesome of *Tremella foliacea* is similar, but not identical to that of *Tremella mesenterica, Tr. brasiliensis* (MOORE 1978) and *Tremella* sp. (KHAN 1976), because the closed, tubular-like-structures are not identical with the cluster cupulate units which MOORE and KHAN described in the vegetative hyphae of the *Tremella* spp. mentioned above.

However, the regular array of tubular-like-structures is not detectable in the septal pore apparatus between the basidium and the adjacent hypha, even though we observed dolipores with the characteristic band of the Tremellales. Here, however, a radiating orientation of microfibrils is scarcely visible.

We believe that the tubular-like-structures, observed in *Tremella foliacea*,

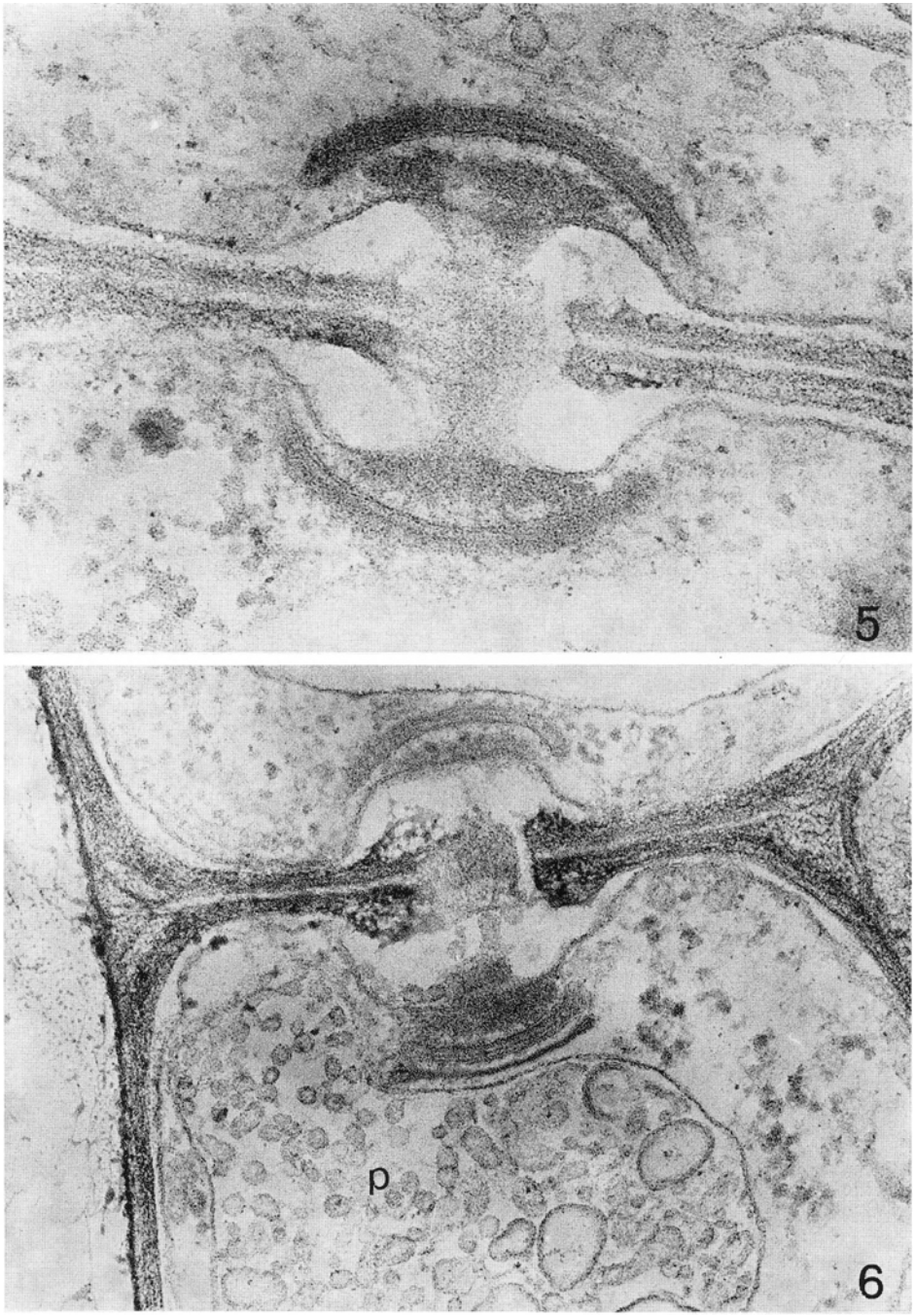


Fig. 5. — Septal pore of *Tremellodon gelatinosum*. The pore cap is imperforate. Granular electron dense material appears to occlude the dolipore opening. × 80,000.
Fig. 6. — Septal pore of *Tremellodon gelatinosum*. In the lumen of each pore cap an electron dense lamella is clearly observable. P = plasmalemmasome. × 80,000.

prevent the passage of cellular organelles, even permitting protoplastic exchange between two contiguous cells. But, this interpretation does not explain why these tubular-like structures are absent at the septum at the basidium base, that is, the cell which needs to control precisely the dikaryon migration. Tubular-like-structures, similar to those we have described in *Tremella foliacea*, have been observed by CARROLL (1967) in *Ascodesmis sphaerospora*, between the ascus and adjacent hypha. Nevertheless, it is difficult to explain in the structural resemblance of the septal pore in *Tremella foliacea* and in *Ascodesmis*. It may indicate either a phylogenetic link between these Ascomycetes and the Basidiomycetes mentioned or a similarity due to functional convergence.

In fact, all authors agree that the Basidiomycetes originate from the Ascomycetes. Some agree that some Ascomycetes reach morphological and ultrastructural organizations, comparable with that among the Basidiomycetes, e.g. the clamp-conjugation of the dikaryotic hyphae in *Sclerotinia trifoliorum* (GÄUMANN 1964), or the development of fruiting bodies differentiated into a sterile stalk and a fertile pileus (*Morchella, Helvella*) and so on.

It seems, therefore, of interest to investigate if some Ascomycetes possess a septal pore apparatus showing ultrastructural features which suggest a primordial dolipore-parenthesome. In this respect, two important structures have already been described among the Ascomycetes: a) the septa, in *Endomycopsis platypodis* have an expanded pore margin. The plasmalemma borders the septal swelling and extends through the pore. At first the pore is an open connection between two adjacent hyphal cells, later it becomes plugged with two dark bodies connected with ER-membrane (KREGER VAN RIJ and VEENHUIS 1969*a* and *b*). b) in *Ascodesmis nigricans* « a striate apparatus occupies some of the septal pores and, in the basal pores of asci, dome shaped inclusions (interpreted as tubules) protrude into the ascal protoplast » (CARROLL 1967; BRACKER 1967).

Therefore, it seems probable that the most primitive dolipore, among the Basidiomycetes, is that of *Tremella*, considering its resemblance to that of *Ascodesmis*.

In opposition to the suggestion of PATTON and MARCHANT, we think that dolipores with an imperforate parenthesome originate from the vesiculate ones of *Tremella* and not vice versa. Such a derivation appears to be supported, according to GÄUMANN (1964), by the observation that basidiocarps of Tremella are more primitive than those of *Tremellodon* one which possess basidiocarps more or less irregularly cap-shaped often with a lateral stalk, the hymenial surface formed by spines.

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