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Trichaptum sector (Ehrenb.:Fr.) Kreisel (Polyporaceae s.l.)

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SUMMARY—*Trichaptum sector* (Polyporaceae s.l.) is tetrapolar (bifactoral) heterothallic. The common-B interaction can be detected grossly in culture by the presence of double hyphal ridges between confronting mycelia; the common-AB by a single ridge. The common-A cannot be distinguished grossly from the $A \neq B =$ reaction. The common-B reaction often shows pseudoclamps in the zone of confrontation, and subcultures from that zone undergo sectoring. Primary and secondary mycelia are mono- and dikaryotic, respectively.

In culture *T. sector* lacks fibre hyphae but shows sclerified segments of generative hyphae. No special odours develop in culture. Tests for enzymes indicate that *T. sector* is positive for peroxidase and laccase. Electron micrographs of hyphae from the secondary mycelium demonstrate that *T. sector* has dolipore septa of the O1/P2 type characteristic of the genus.

The basidiocarp is dimitic and bears incrustated cystidioles in the hymenium. This taxon is a member of the warm temperate-tropical flora where it is associated with a white-rot of angiosperm wood.

RÉSUMÉ — *Trichaptum sector* (Polyporaceae s.l.) est tétrapolaire. La ligne de confrontation des mycéliums présente deux bourrelets si les facteurs A et B sont différents, B communs; un seul bourrelet si les facteurs A et B sont communs; enfin, si les facteurs A sont communs, B différents ou A et B différents, les mycéliums s'interpénètrent et ne peuvent être distingués. Dans le premier cas, $A \neq B =$, on peut noter la présence de fausses boucles: des subcultures de cette région présentent des secteurs. Les mycéliums primaires et secondaires sont respectivement mono- et dicaryotiques.

La culture de *T. sector* est dépourvue de fibres mais des segments

d'hyphes génératrices sont sclérifiées. Les cultures ne dégagent aucune odeur. Les tests enzymatiques indiquent que *T. sector* produit de la laccase et de la peroxydase.

L'ultrastructure des dolipores de *T. sector* est de type O1/P2.

Les carpophores sont dimitiques avec des hyphes squelettiques et produisent cystidioles incrustées dans l'hymenium. Ce taxon est un élément caractéristique des pays chauds où il est associé à une pourriture blanche.

ZUSAMMENFASSUNG - *Trichaptum sector* (Polyporaceae s.l.) ist tetrapolar. Falls die Faktoren A und B verschieden sind, aber B gemeinsam, so entstehen an den Berührungsstellen der Myzelien zwei Linien. Nur eine Linie entsteht, wenn die Faktoren A und B gemeinsam sind. Sind die Faktoren A gemeinsam, aber B oder A und B verschieden, so durchdringen sich die Myzelien und können nicht unterschieden werden. Im ersten Fall, $A \neq$, $B =$, können Pseudoschnallen in den Berührungszonen beobachtet werden. Subkulturen dieser Region zeigen Sektoren. Die primären und sekundären Myzelien sind mono- respektive dikaryotisch.

Die Kulturen von *T. sector* entwickeln keine eigentlichen faserartigen Strukturen, aber Abschnitte der generativen Hyphen sind sklerotisiert. Die Kulturen sind ohne besonderen Geruch. Enzymatische Untersuchungen zeigen, dass *T. sector* Laccase und Peroxydase bildet.

Die Feinstruktur des Doliporus entspricht dem Typ O1/P2. Die Fruchtkörper sind dimitisch (mit Skeletthyphen) und entwickeln inkrustierte Cystidien.

Trichaptum sector ist ein charakteristisches Element der warm-gemäßigten bis tropischen Flora. Der Pilz wächst auf Angiospermen und erzeugt Weissfäule.

INTRODUCTION

Trichaptum Murr. is a genus of about thirty taxa, of which approximately eleven occur in the New World (Corner, 1987; Gilbertson & Ryvarden, 1987). These taxa are sessile to substipitate, have irpicoid, daedaloid, or poroid hymenophores, and produce hyaline, smooth, nonamyloid spores which are ellipsoid to subballantoid in shape. Hyphal construction is reported to be dimitic and trimitic. *Trichaptum sector* is a prominent member of the warm-temperate to tropical mycoflora of the Western Hemisphere. David (1970, as *Hirschioporus*) has studied

this species in culture, and we are in essential agreement with her results. We add to her studies additional remarks on culture morphology, compatibility behavior, and submicroscopic morphology.

BASIDIOCARP MORPHOLOGY (FIG. 1,A,E,G,H,P) AND DISTRIBUTION

Pileus sessile, dimidiate to flabelliform, thin, relatively flexible when dry; upper surface tomentose to velutinate, often rough to cristate toward base, zonate with alternating light and dark bands of brownish pink; adhymenial surface light greyish red brown to almost black, pores angular, thin-walled, dentate, 3-6/mm, -1.5 mm deep.

Spores 4.5-5 x 2-2.5 μ m, subcylindrical to cylindrical, thin-walled, hyaline, IKI-, acyanophilous, with an inconspicuous hilar appendage.

In section the context is of dense strands of brown skeletal hyphae held together by branching or twisting narrower hyaline hyphae; skeletals turn downward forming the pore walls held together as in the context; tubes lined with a hymenium of basidia and hyaline, slightly thick-walled incrustated cystidioles, usually with acute apices, on occasion skeletal hyphae protrude into the base of the hymenium with their apices rounded and slightly swollen; tomentum of mixed skeletal and generative hyphae; cuticle of a \pm compact hyphal layer.

Generative hyphae hyaline or faintly pigmented, clamped, thin-walled, ca. 2-3 μ m in diam with cells up to at least 130 μ m in length, others with capillary or no lumen, ca. 4 μ m in diam, both types branch frequently, thick-walled ones sometimes with short branching laterals, often from site of clamp-connection; skeletals hyaline to light brown, generally with lumina completely occluded, 4-7 μ m in diam, some pigmented ones form hyaline twisting extensions ca. 3 μ m in diam with one or more short spurs.

The twisting extensions from the skeletals and the branching solid lateral extensions from the generative hyphae perform the "binding" function. No truly binding hyphae such as those seen in some *Trametes* Fr. were observed. We are interpreting the structure of *T. sector* as dimitic with skeletal and generative hyphae.

This fungus is found throughout Mexico and Central America and occurs frequently in the bottomland hardwood forests of Louisiana, U.S.A. Gilbertson and Ryvarden (1987) report it as a characteristic element of such regions. With a spore print, from which to take measurements, the fungus can be identified by its usually darkened pore surface and its thin

flexible, tomentose pileus with its typical colours. It is found in our region on dead hardwoods, where it causes a white rot. Our collections are from Louisiana (ALW 4750, ALW s.n. 7 Sep 1985) and Mexico (P.A.Lemke 59143).

Table 1. Results of Spot Tests for Enzymes (1)

Reagent	Time in minutes					Overnight
	0	5	15	30	60	
Alpha-Naphthol (Laccase)	-	+	+	+	+	+
Alpha-Naphthol Phosphate (Phosphatase)	-	-	-	-	-	-
Guaiacol (Peroxidase)	-	-	+	+	+	+
P-Cresol (Laccase & Peroxidase)	-	-	+	+	+	+
Pyrogallol (Peroxidase)	-	-	-	-	-	+
Syringaldazine (Laccase & Peroxidase)	-	±	+	+	+	+
L-Tyrosine (Tyrosinase)	-	-	-	-	-	-
Tincture Gum Guaiac	+	+	+	+	+	+

(1) Four monokaryon and one dikaryon isolates per test.

CULTURES (Fig. 1,B) AND ENZYME SPOT TESTS

Cultures were examined by mounting hyphae in 3% aqueous KOH and staining in 1% aqueous phloxine.

Mycelial mats subfelty, white; hyphae of secondary mycelium clamped, thin-walled, hyaline, 3-5 µm in diam, some with sclerified segments which may be intercalary or terminal, with or without short branches, wider thin-walled hyphae often with empty cells; hyphae of advancing zone ca. 3 µm in diam, clamped; no special structures or swellings; no particular odour; reverse unchanged; plates covered in 3 weeks when grown at 25° C.

Spot tests for the presence of enzymes were performed according to Nobles (1958a), Stalpers (1978) and Marr (1979,1984). A drop of each reagent was applied to the mycelium and observed at intervals (see Table 1) for colour changes. These reactions are interpreted as showing the presence of laccase and peroxidase in the mycelium of this fungus. Growth and reaction of *T. sector* on Gallic and Tannic Acid agar after 8 days are:

Plate	G.A.A.	T.A.A.
1	50 mm diam +++++	50 mm diam +++++
2	50 mm diam +++++	50 mm diam +++++

GROWTH RATE STUDIES

Growth rate studies were made in triplicate on MPY (malt extract, peptone, yeast extract) agar and MEA (malt extract agar) at four temperatures. Growth is slightly faster on MPY agar than on MEA but not significantly so. The fastest growth occurred at 25° and 30° C. There was no growth at 45° C, but at 15° C the growth was slow relative to the median temperatures. At the median temperatures the plates were filled in three weeks.

KARYOLOGY

The nuclear condition of the hyphae was determined by staining with Giemsa stain (Boidin, 1958). Cells of the primary (homokaryotic) mycelium were uninucleate; those of the secondary (heterokaryotic) mycelium were dikaryotic. Therefore, the nuclear condition of the hyphae of *T. sector* is normal (Boidin, 1964).

COMPATIBILITY TESTS

Primary (homokaryotic) mycelia derived from single spores were opposed in all possible combinations on Malt Extract Agar in plastic Petri dishes held at 25° C. Our results (Table 2) confirm that *T. sector* has a tetrapolar (bifactoral) incompatibility system (David, 1970). Three different reactions were observed in these cultures. Reaction 1 was the formation of a thin common ridge of hyphae between opposing mycelia. Clamp-bearing hyphae were not observed. We interpret this reaction as the common-AB mating. Reaction 2 was the formation of double mycelial ridges between opposing mycelia. What appeared to be clamp-bearing hyphae were observed in the interaction zone. Subcultures from this zone exhibited sectoring, a characteristic of pseudo-clamped hyphae. We interpret this reaction as the common-B mating. Reaction 3 was, in fact, no reaction, that is, no ridges were formed and the opposing hyphae intermingled freely. One sub-set of the cultures showing this reaction had clamp-connections; the other sub-set did not. The former

represents a successful cross and is interpreted as a cross between mycelia carrying dissimilar A and B factors; the latter we interpret as the common A mating, although the cultures did not show reduced knobby hyphae predicted by some models (Raper, 1966).

The results of our tests, however, were complicated. Table 2 shows, according to our interpretation of the genotypes, three anomalies. Crosses 1 x 9, 3 x 6, and 6 x 8 do not yield the expected results. In every other cross 9 acts like 1, and 4 and 6 act like 2. We cannot explain these results. Also, we could demonstrate clamp-connections only in the zone between confronting hyphae. Either nuclear migration does not occur (a defective B factor ?) or it is so slow that the homokaryons filled the

Table 2. Incompatibility Tests Results

A1 B1			A2 B2		A2 B1			A1 B2	
1	4	9	2	6	3	5	10	7	8
1	a	*	+	+	*	*	*	-	-
	4	a	+	+	*	*	*	-	-
		9	+	+	*	*	*	-	-
			2	a	-	-	-	*	*
				6	a	-	-	*	a
					3	a	a	+	+
						5	a	+	+
							10	+	+
								7	a

Plus signifies clamp-connections in zone of confrontation; minus indicates mycelia intermingling without ridge formation or clamp-connections; a indicates formation of a single ridge in zone of confrontation; and * indicates formation of two ridges with false clamp-connections. Crosses 1 x 9, 3 x 6, and 6 x 8 are anomalous.

plates before the introduced nuclei could affect the growth of the resident mycelia.

KEY CODE (Nobles, 1965; Boidin, 1966) for *T. sector*
2a.3c.7.32.36.38.43.54.60.61

TEM OBSERVATIONS

Plugs of agar bearing the mycelium of *T. sector* were fixed in gluteraldehyde, sectioned, mounted unstained, and observed with a Philips 410 LS electron microscope. The hyphae have imperforate parenthesomes (Fig. 2) characteristic of *Trichaptum*. The dolipore structure is that of the O1/ P2 type (Moore, 1985).

COMPARISONS WITH OTHER *TRICHAPTUM* SPECIES

Trichaptum sector has been reported as trimitic (Fidalgo & Fidalgo, 1967, as *Coriolus*; Gilbertson & Ryvarden, 1987), but our interpretation of hyphal structure is that it is dimitic, agreeing with Corner (1987), which enhances its similarities to other *Trichaptum* species. Of the eleven taxa presently recognized as occurring in the New World, seven are tetrapolar (David, 1970; Gilbertson & Ryvarden, 1987; also *T. byssogenum* (Jungh.) Ryv., teste David, pers. comm.). Again, the tetrapolarity of *T. sector* follows the generic pattern. In comparing the results of our culture study of *T. sector* with those of David (1970) we failed to find fibre hyphae (she observed them only rarely) and cystidia. Her key pattern (Nobles, 1965; Boidin, 1966) for *T. sector* is similar to those for *T. abietinum* (Dicks.:Fr.) Ryv. and *T. bifforme* (Fr.) Ryv. in Nobles (1965), but her key pattern for *T. perrottetii* (Lév.) Ryv. is quite similar to our pattern for *T. sector* except the latter species grows more rapidly. Those species producing fibre hyphae fall into Group 45 of Nobles (1958b). Rather, *T. sector* produces generative hyphae with sclerified segments, some of which may branch.

Our electron micrographs of the parenthesome show the imperforate structure that has come to be associated with *Trichaptum*. Other fungi known to possess such a parenthesome are in Hymenochaetaceae and in some heterobasidiomycetaceous fungi (see Moore, 1985 for literature).

INTRARELATIONSHIPS IN *TRICHAPTUM*

Although compatibility and culture studies are wanting in a number of *Trichaptum* species, particularly those occurring in Asia, some

evolutionary trends within the genus seem evident. Of the north temperate and boreal species, three, *T. abietinum*, *T. fuscoviolaceum* (Fr.) Ryv. and *T. laricinum* (Karst.) Ryv., are exclusively conifer inhabitants. These three are closely related, so closely that their status has been confused in the literature. (Gilbertson & Ryvarden, 1987). *Trichaptum bifforme* and *T. subchartaceum* (Murr.) Ryv. grow on hardwoods; the former occurs on conifers rarely. *Trichaptum abietinum*, *T. fuscoviolaceum*, *T. subchartaceum*, and *T. bifforme* are circumglobal (Gilbertson & Ryvarden, 1987). We can reasonably assume that the widely distributed species originated earlier and were associated with conifers. There seems to be a tendency among these species to adopt the hardwood habitat.

The warm north temperate and tropical species show a similar trend in substrate specialization. *Trichaptum byssogenum* grows on Bald Cypress and Junipers and sometimes on hardwoods. *Trichaptum sector* is found mainly on hardwoods and *T. perrottetii* exclusively on hardwoods. Also, all three species occur in the tropics. It seems clear that the hardwood specialization has allowed those species possessing it to maintain themselves in warmer regions. The only exception, *T. subchartaceum*, is specialized for restricted hardwood substrates not found at lower elevations in warm and tropical areas.

If we are allowed to take our speculation one step farther, it is not unreasonable to postulate the following evolutionary scenario for *Trichaptum* species. It is likely that *Trichaptum* was a characteristic member of the mycoflora of the Arcto-tertiary flora specializing in coniferous substrates. From this element arose those partially and exclusively hardwood inhabitants, *T. bifforme* and *T. subchartaceum*. As this flora retreated after the last glaciation, other taxa evolved which were able to remain at the southern extremities of this flora by adapting to other coniferous substrates (Bald Cypress) and to hardwoods. The hardwood-inhabiting species were enabled to invade the Neotropical flora.

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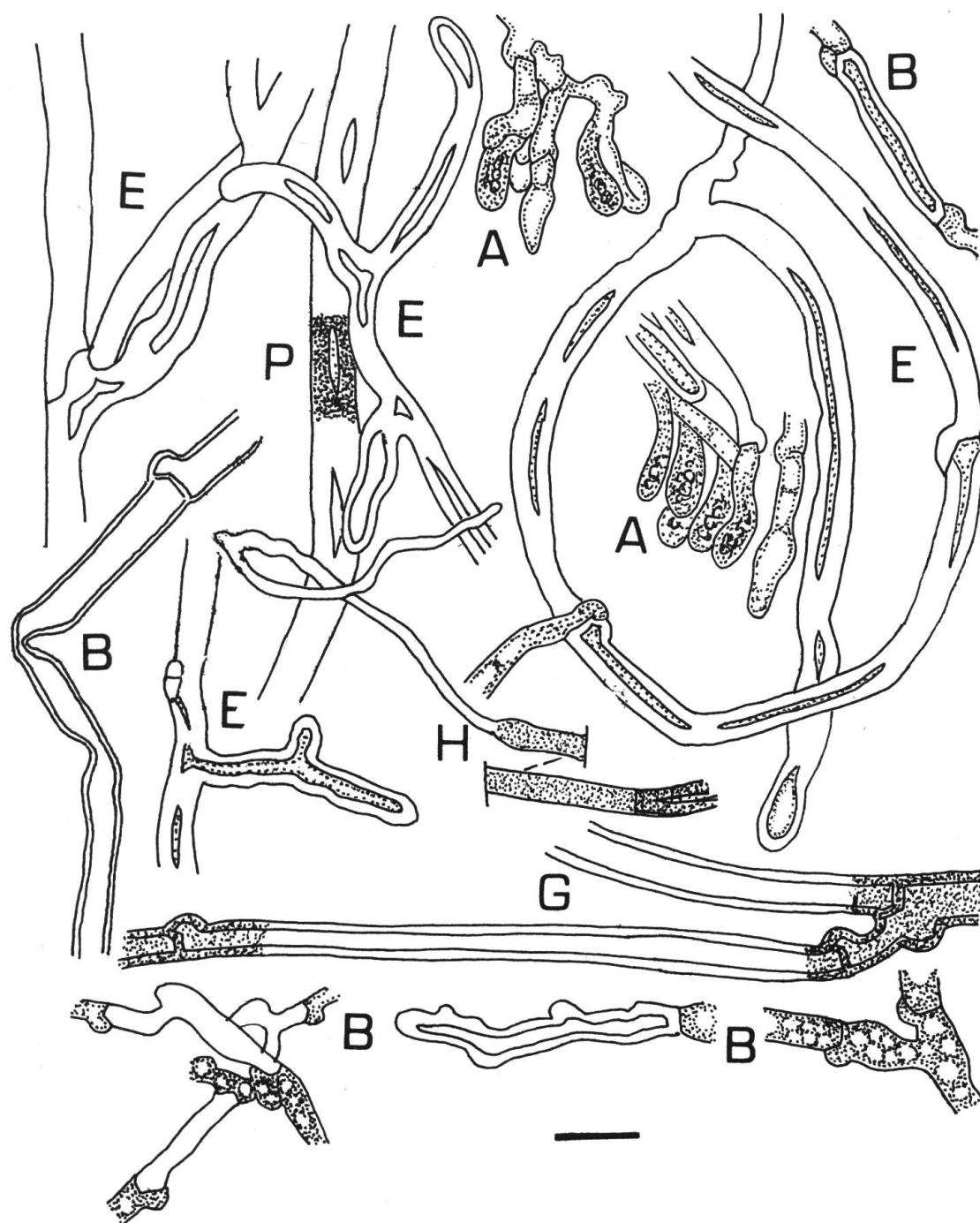


Fig. 1 *Trichaptum sector*. A. Hymenium with basidioles and young cystidioles. E. Sclerotized contextual hyphae, mostly generatives. P. Pigmented skeletal hypha from context. G. Pigmented contextual generative hyphae. H. Contextual hypha with hyaline twisted end; deleted portion = 30µm. B. Hyphae from culture. Line scale = 10µm.

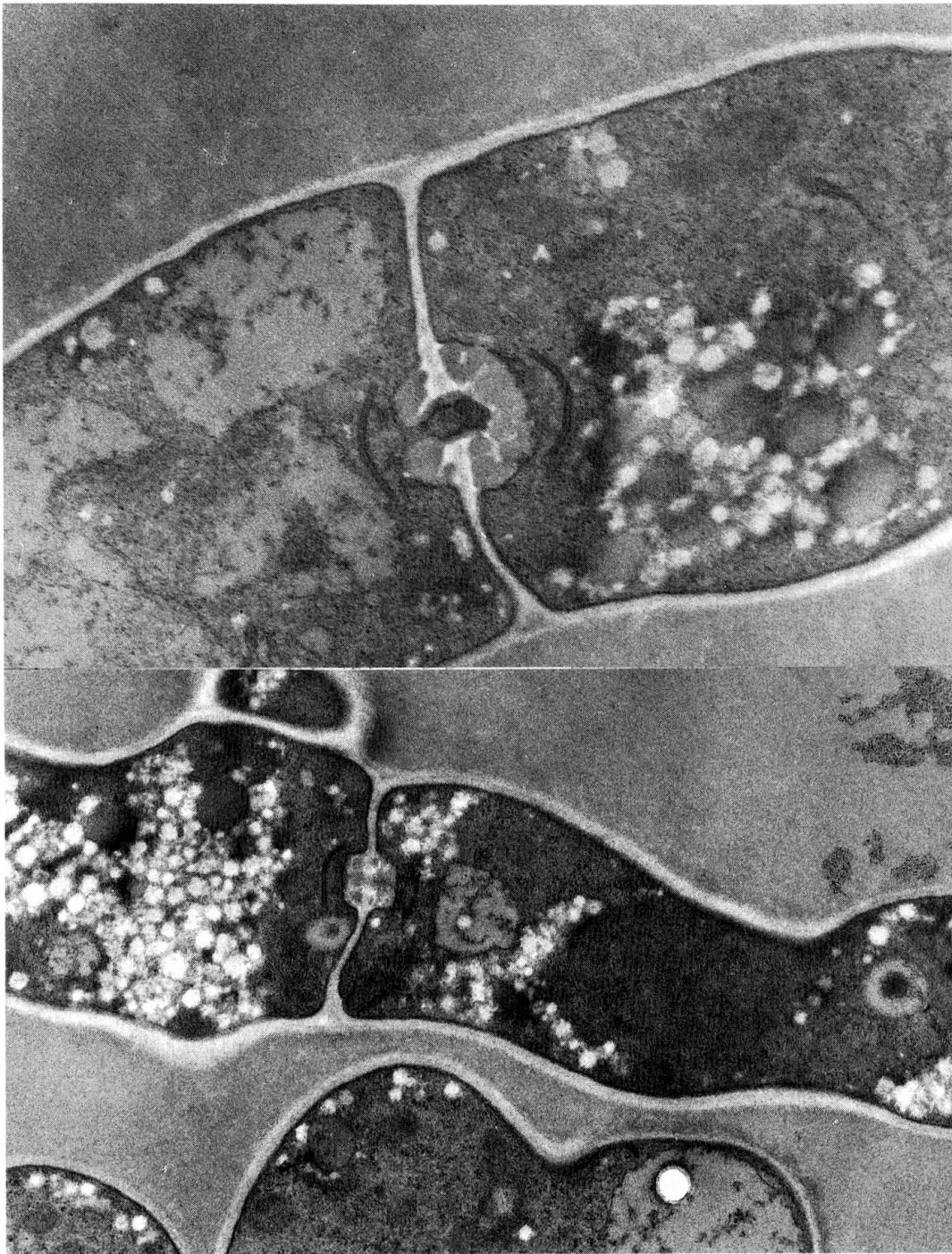


Fig. 2. *Trichaptum sector*. Both micrographs show the imperforate parenthosomes characteristic of this genus. Upper photo X ca. 30600; lower photo X ca. 18300.