Never change a functionally successful principle: The evolution of Boletales s.l. (Hymenomycetes, Basidiomycota) as seen from below-ground features*

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Summary:
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In the present study characteristics of substrate hyphae and of rhizomorphs have been applied as a completely new group of features to discern relationships of Boletales s.l. Rhizomorph structures have been shown to be very conservative. A so-called 'boletoid-rhizomorph type' is representative of Suillaceae, Rhizopogonaceae, Coniophoraceae, Strobilomycetaceae, Paxillaceae, Pisolithaceae, Astraeaceae, Boletaceae and Sclerodermataceae. These rhizomorphs possess 'runner hyphae' where backward oriented ramifications grow towards the main hypha, after they have originated above the first simple septum or the first clamp of a side-branch. Frequently, these hyphae fork close to the main hypha into a distally and a proximally growing branch. The 'runner hypha' and additional ones enlarge and become vessel-like. Gomphidiaceae, Tapinellaceae and Truncocolumellaceae have different types of rhizomorphs. Coniophoroineae and Tapinellineae are proposed as new suborders of Boletales s.l. Omphalotaceae remain provisionally placed in the Tricholomatales. The order Sclerodermatales with its families Sclerodermataceae, Pisolithaceae and Astraeaceae are included in Boletales.

Zusammenfassung:
In den vorliegenden Untersuchungen werden, um verwandtschaftliche Beziehungen der Boletales s.l. zu klären, Charakteristika von Substrathyphen und von Rhizomorphen als völlig neue Gruppe von Merkmalen verwendet. Es konnte aufgezeigt werden, daß die Merkmale der Rhizomorphen sehr konservativ sind. Ein sog. 'boletoider-Rhizomorphen-Typ' ist repräsentativ für Suillaceae, Rhizopogonaceae, Coniophoraceae, Strobilomycetaceae, Paxillaceae, Pisolithaceae, Astraeaceae, Boletaceae und Sclerodermataceae. Diese Rhizomorphen besitzen 'Läufer-Hyphen' an denen rückwärts gerichtete Verzweigungen gegen die 'Läufer-Hyphen' wachsen, nachdem sie oberhalb des ersten einfachen Septums oder oberhalb der ersten Schnalle eines Seitenzweiges entsprungen sind. Häufig gabeln sich diese rückwärts gerichteten Hyphen nahe der 'Läufer-Hyphe' in einen distal und in einen proximal orientierten, weiter wachsenden Hyphenast. Die 'Läufer-Hyphen' und weitere Hyphen verdicken sich und werden gefäßähnlich. Gomphidiaceae, Tapinellaceae und Truncocolumellaceae zeigen abweichende Rhizomorphen-Typen. Coniophoroineae und Tapinellineae werden als neue Unterordnungen der Boletales s.l. vorgeschlagen. Die Omphalotaceae bleiben provisorisch in den Tricholo-

* Dedicated to Univ.-Prof. Dr. Andreas Bresinsky, Regensburg, on the occasion of his 65th birthday.

matales. Die Ordnung Sclerodermatales, mit den Familien Sclerodermataceae, Pisolithaceae und Astraeaceae, wird in die Boletales einbezogen.

Introduction

The Boletales have attracted the interest of many mycologists, either with respect to their relation to Agaricales s.l., or with emphasis to the groupings within the order (comp. BRESINSKY 1996). The discussion of the order Boletales became particularly fascinating, since pigment data were used to include fungal families in the Boletales with deviating types of fruitbodies, e.g. Coniophoraceae (BRESINSKY 1973, BRESINSKY & BACHMANN 1971, STEGLICH et al. 1968, 1971)

During the last decade five contributions concerning the systematics of the Boletales in a more comprehensive way (BESL & BRESINSKY 1997, BRESINSKY 1996, HØILAND 1987, BRUNS et al. 1998, SINGER 1986) were published.

SINGER (1986) treats Boletales as a suborder within the Agaricales, and divides it into three families, viz. Boletaceae, Paxillaceae and Gomphidiaceae. Boletaceae are again subdivided into Gyroporoideae, Gyrodontoideae, Suilloideae, and Strobilomycetoideae. The taxa are primarily defined anatomically and morphologically. Almost exclusively pileate-stipitate members are included; neither resupinate forms (Coniophoraceae) nor gastroid species are considered (e.g. Rhizopogonaceae, Sclerodermataceae).

HØILAND (1987) applies chemical as well as anatomical characters with several character states, and uses parsimony and character compatibility analysis for phylogenetic conclusions. To distinguish plesiomorphic and apomorphic states, quite often Corner's *Clavaria*-theory (CORNER 1964) is quoted to assume that *Gomphus* is a possible predecessor of the Boletales, and consequently, *Gomphus* is used as an outgroup. The families Paxillaceae, Gyrodontaceae, Xerocomaceae, Boletaceae, Strobilomycetaceae, Gomphidiaceae, Rhizopogonaceae, Chamonixiaceae and Coniophoraceae are included in this treatment. Gyrodontaceae (with *Gyroporus* and *Gyrodon*) are proposed to be included in the Paxillaceae; *Chamonixia* is regarded as related to *Gyroporus,* but treated as a separate family; Xerocomaceae are suggested to be combined with Boletaceae; Rhizopogonaceae are regarded as probable derivatives of Boletaceae, and *Suillus* is included in the Gomphidiaceae.

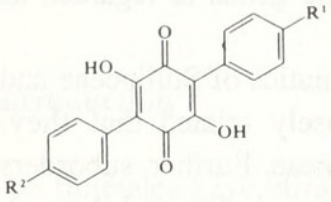
BRESINSKY (1996) puts emphasis on chemical characters, and in addition applies restriction fragment length polymorphism (RFLP) to several genera and species of the Boletales. His circumscription of Boletales includes gastroid, resupinate and pileate taxa. One main concern was the delimitation from other Hymenomycetes. Roughly four groups with a great deal of overlap have been distinguished. One group containing exclusively ectomycorrhizal fungi is provided only with pulvinic acid (**F3**) derivatives (e.g. *Boletus, Chalciporus* and *Truncocolumella*); a second shows the same pigment composition, but its constituents live saprotrophic as brown rot fungi (e.g. *Hygrophoropsis, Serpula* and *Tapinella*); a third entity encompasses mostly ectomycorrhizal fungi with cyclopentenones (**F17-F20**) as additional pigments to pulvinic acids (**F3**) (e.g. *Gyrodon* and *Paxillus; Leccinum* lacks pulvinic acids), and fourthly, again an ectomycorrhizal group with pulvinic acids, possesses terpenoids as accompanying compounds (**F4-F14**) (e.g. *Gomphidius, Rhizopogon* and *Suillus*). Others are regarded as closely related to these Boletales: Sclerodermatales (*Scleroderma*) and Omphalotaceae (*Lampteromyces, Omphalotus*) due to their pulivnic acids (**F3**), Scutigeraceae (*Albatrellus*) enriched with atromentin (**F1**), the basic compound of pulvinic acids (**F3**) biosynthesis and cyclopentenones (**F17-F20**) and Strobilomycetaceae (*Strobilomyces*) which do not contain

pulvinic acids, but DNA-characteristics indicate their membership of the Boletales. Further, *Boletopsis* appears in the scheme, but no explanation is given why this genus is regarded as being close to the Boletales.

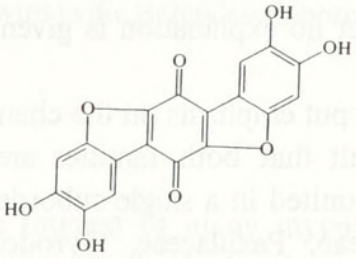
BESL & BRESINSKY (1997) mainly put emphasis on the chemosystematics of Suillaceae and Gomphidiaceae, with the main result that both families are so closely related that they, together with Rhizopogonaceae, are united in a single suborder, Suillineae. Further suborders are: Paxillineae (with Coniophoraceae, Paxillaceae, Gyrodontaceae, and Omphalotaceae), Boletineae (Boletaceae) and Strobilomycetineae (Strobilomycetaceae).

BRUNS et al. (1998) applied sequences of a small region of the mitochondrial large subunit rRNA gene for phylogentic analysis of several Hymenomycetes, and included particularly relationships with ectomycorrhizal fungi. Within the Boletales they distinguished six groups. The boletoid group comprises species of Boletaceae and Strobilomycetaceae, the *Paxillus* group contains one species each of *Chalciporus*, *Paxillus* and *Paragyrodon*; in the Coniophoraceae-group cluster *Tapinella, Serpula, Austropaxillus* and *Hygrophoropsis*; separate groups are formed by *Coniophora* and by *Gyrodon*, *Pisolithus*, *Phaeogyroporus* and *Gyrodon merulioides*, respectively; a large cluster, the suilloid group, contains members of Gomphidiaceae, Rhizopogonaceae and Suillaceae as well as some genera previously not incorporated in these families, for instance, one species each of *Melanogaster, Hymenogaster*, and *Truncocolumella*.

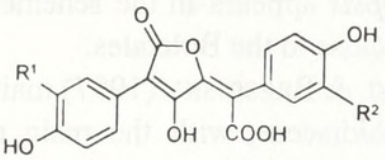
The present contribution considers a completely new complex of features to obtain new insights in the systematic relationships of and within the Boletales, namely characteristics of the substrate hyphae, i.e. the anatomy of rhizomorphs, and to some extent the structure of ectomycorrhizae. Thelephorales are also included, as both relationships have atromentin (**F1**) as a basic compound for the synthesis of their pigments, and because Thelephoraceae and Gomphidiaceae have been suggested as closely related (AGERER 1991a).



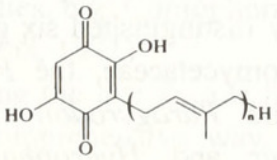
F1: Atromentin ($R^1 = R^2 = OH$)



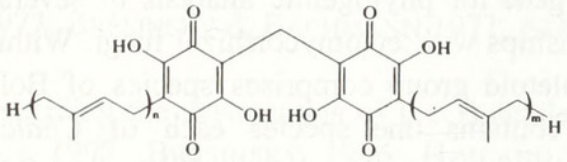
F2: Thelephoric acid



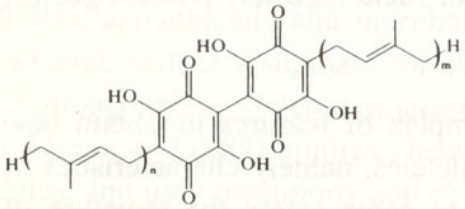
F3: Pulvinic acids



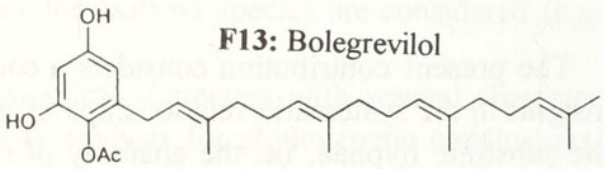
F4: Boviquinone-3 (n=3)
F5: Boviquinone-4 (n=4)



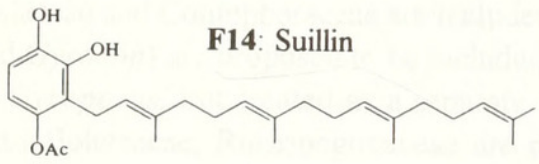
F8: Methylenediboviquinone-3,3 (n = 3, m = 3)
F9: Methylenediboviquinone-3,4 (n = 3, m = 4)
F10: Methylenediboviquinone-4,4 (n = 4, m = 4)



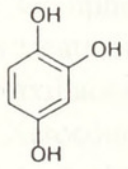
F6: Diboviquinone-3,4 (n = 3, m = 4)
F7: Diboviquinone-4,4 (n = 4, m = 4)

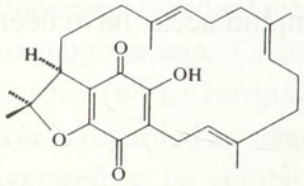


F13: Bolegrevilol



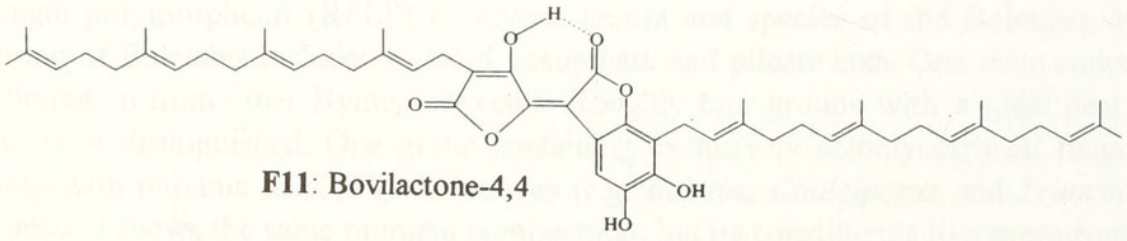
F14: Suillin



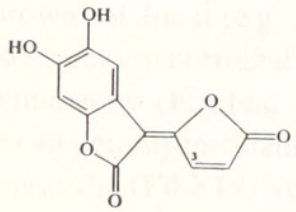


F12: Tridentoquinone

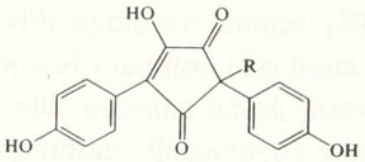
F16: 1,2,4-Trihydroxybenzene



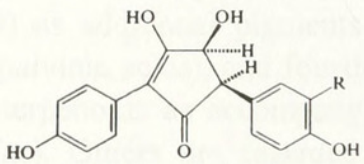
F11: Bovilactone-4,4



F15: Gomphilactone



F17: Gyrocyanin (R = H)
F18: Gyroporin (R = OH)



F19: Chamonixin (R = H)
F20: Involutin (R = OH)

Important anatomical characters

Three general groups of features are regarded as important for the evolution of Hymenomycetes and for interpretation of phylogenetic relations: the formation and reduction of clamps, evolution of substrate hyphae and occurrence of amyloidy.

A. Transport structures, important targets of evolution

Hyphae, as exploiting filaments, deplete their environment of nutrients close to their surface. Therefore, fungi continuously have to grow, and a crucial need arises to translocate the incorporated substances within their hyphal systems. Three structures can be involved in transport: clamps, backward growing hyphae, and rhizomorphs.

1. Clamps

The possession of clamps has been repeatedly considered as a plesiomorphic character (BOIDIN 1971, KÜHNER 1980, SINGER 1986). Since no conclusive arguments for this assumption are provided to date, some points are made herein.

Hitherto, clamps apparently are almost exclusively considered from a one-sided point of view. Many references emphasise their role for a regular, conjugated division of nuclei, or at least they do not attempt to explain the reasons for the presence of clamps, due to the lack of clamps in so many Basidiomycota (ALEXOPOULOS et al. 1996, CLEMENÇON 1997, GÄUMANN 1964, INGOLD & HUDSON 1993). The efficiency of clamps for a regular and simultaneous division and transmission of dikarya is sometimes explained by the small diameter of hyphae and by the nuclei's mutual impediment during mitosis (GÄUMANN 1964). But detailed analyses of hyphal systems of different fungal relationships clearly show that there is no correlation between hyphal diameter and the presence or absence of clamps, although the nuclear diameter can be regarded as fairly constant for Hymenomycetes with the range of 1–2 µm (comp. AGERER & RAMBOLD 1998).

For example, *Byssocorticium lutescens* Erikss. & Ryv. with hyphal diameters in the subhymenium of 2–3 µm forms clamps (ERIKSSON & RYVARDEN 1973), whereas *B. atrovirens* (Fr.) Bond & Sing.: Sing, does not produce them, although it possesses the same hyphal dimensions (BRAND 1991). There are some examples however, where a correlation of clamps with hyphal diameter could be given, but a causal interdependence has yet to be shown. For instance, *Ceraceomerulius serpens* (Fr.) Erikss. & Ryv. which possesses clamps, shows 2.5–3.5 µm thick hyphae (ERIKSSON & RYVARDEN 1973), whereas the clampless hyphae of *C. rubicundus* (Litsch.) Erikss. are 3–5 µm thick (ERIKSSON & RYVARDEN 1973). In some *Athelia* species, a further combination is realized. Here, within one and the same fruitbody, primarily thick, basal hyphae form clamps, whereas the thinner ones in the subhymenium are clampless (ERIKSSON & RYVARDEN 1973). But the opposite situation is also known. Most clamp-bearing species of the genus *Hyphoderma* form 3–4 µm wide hyphae (ERIKSSON & RYVARDEN 1975), but the clampless hyphae of *H. capitatum* Erikss. & Ryv. are 2–3 µm thick (ERIKSSON & RYVARDEN 1975). Among others, the species of the genus *Botryobasidium* possess hyphae with 6–10 µm diameter. They include members with clamps and without clamps (LANGER G 1994). The thinnest clampless hyphae possibly occur in the genus *Dendrothele*, for instance *Dendrothele acerina* (Fr.) Lemke, with diameters of 1–2 µm (ERIKSSON & RYVARDEN 1973).

Most of the Hymenomycetes, at least when "The Corticiaceae of North Europe" are evaluated, form hyphae of 3–4 µm diam., regardless, whether clamps are formed or not. Although the dikaryotic condition of their clampless hyphae has not been shown in most of the species, their presence in all of the above mentioned taxa can very likely be inferred from the formation of four spores per basidium.

Since, according to ALEXOPOULOS et al. (1996), also some homokaryotic mycelia can form clamps, these specialized structures are not necessarily involved in synchronous nuclear division. A similar situation is known about the formation of whirl-clamps, where the successively originating clamps are not always accompanied by the division of nuclei, and, quite importantly, clamps are formed even without a conjugated division of nuclei (CLEMENÇON 1997, GREIS 1937). In *Stereum hirsutum* (Willd.: Fr.) S.F.Gray however, several nuclei divide simultaneously, and the number of clamps corresponds with the number of nuclei involved (GÄUMANN 1964).

In *Coprinus disseminatus* (Pers.: Fr.) S.F.Gray low-temperature treatment decreased hyphal diameter and depressed clamp formation (BUTLER 1981), although the hyphae remained dikaryotic. This indicates an independence of clamp formation from the simultaneous mitosis of the dikaryon and from hyphal diameter. In this dikaryotic mycelium, although compatible nuclei, i.e. different A allels (clamp cells are formed) and different B allels (clamp cell fuses with subterminal cell) are present (CASSELTON & KÜES 1994), the formation of clamps is repressed by environmental conditions.

A completely different approach to explain clamp formation, lets nuclei for the moment out of account and emphasizes primarily cytoplasmic transport as the main reason for the formation of backward oriented, hook-like outgrowths, the future clamps.

AS shown by BULLER (1933) in sophisticated light microscopy observations based on the movements of cytoplasmic granules, the cytoplasm streams in all fungi investigated from older to younger portions of the hyphae, i.e. in most cases from the base to the growing hyphal tip. There was no support for the opinion that within one hypha bidirectional transport occurs. The mechanism for protoplasmic transport seems to be a turgor-driven mass flow of solutions (JENNINGS 1994), although this has been recently questioned by HEATH & STEINBERG (1999). A reversal transport, from tip to proximal parts, is evident when a tip forms an anastomosis with an older hyphal cell. Then the cytoplasm streams into this anastomosing tip down to older parts of the hypha (BULLER 1933).

Hyphal tips are not only sites of extension by production of wall material ('growth zone'), they are also, shortly behind the growth zone in the 'absorption zone', highly active areas of export of digesting enzymes and incorporation of ions and organic molecules (INGOLD & HUDSON 1993, JENNINGS & LYSEK 1996). Hyphal tips show intensive lysis of organic material, and they are sites of absorption, as is clearly indicated by haustoria, which are in many cases transformed hyphal tips (JENNINGS & LYSEK 1996).The molecules taken up have to be transported back to the 'storage zone' of the hyphae (JENNINGS & LYSEK 1996), or further back to comsumption areas, and this apparently is flowing against the tip-directed counter-current of cytoplasm (BULLER 1933). The mass flow towards hyphal tip is in fact important for extending hyphae, since cytoplasm is pushed forward the quicker the faster the hypha grows (BULLER 1933), and hyphae can save cytoplasm in an economical way (STEINBERG et al. 1998). But this flow cannot explain how the incorporated ions and molecules taken up in distal parts of the hyphae by endocytosis (HOFFMANN & MENDGEN 1998) are transported backward, against the counter-current mass flow of cytoplasm. Opposed streaming directions in one and the same hyphal compartment should at least occur down to those points, where

the first anastomosis occurs or where backward oriented branches can take charge of transport towards their tip, which is as a consequence oriented towards the base of the main hypha. On microtubules gliding vesicles have been demonstrated (LEHMLER et al. 1997, STEINBERG 1997, STEINBERG & SCHLIWA 1995), and regarded as important for transport; the vesicles are shown to perform a retrograde movement (STEINBERG et al. 1998). Recent studies provided evidence for a contemporary bidirectional transport of vesicles along microtubles in one and the same hypha, and at one and the same cytoplasmic site. Due to antiparallel orientation of microtubules, or to different kinds of motor molecules vesicles should be moved towards the hyphal tip as well as towards proximal cell regions (Steinberg., pers. comm.).

Clamps of Basidiomycota are regarded as by-pass hyphae for the transport of nuclei (HAWKSWORTH et al. 1985), and they can be formed in response to nuclear positions (CLÉMENÇON 1997). The hook of the later on formed clamp is undoubtedly a short, backward-oriented side-branch, with a Spitzenkörper, and vesicles have to be transported from the subapical Golgi bodies to the site of branch initiation (HEATH 1994) and the nuclei to the position of clamp formation (WEBER 1993). The role of microtubles in clamp formation (ORMEROD et al. 1976, SHEPHERD et al. 1993), nuclei movement with changing intensity and reversal of their direction of movement (SUELMANN et al. 1997, WEBER l.c.) have been shown and lastly, the entry of a single nucleus into the hook, as ALEXOPOULOS et al. (1996), CASSELTON & KÜES (1994), INGOLD & HUDSON (1993) and WEBER (1993) point out. Other authors however, refer to a daughter nucleus which enters the hook during mitosis (CLÉMENÇON 1997, HAWKSWORTH et al. 1995). This course of events during clamp formation and the necessary transport of incorporated molecules back to older hyphal compartments suggest a backward transport within cytoplasm (SHEPHERD et al. 1993).

Nuclear divisions are mostly combined with the formation of septa, which are positioned between the pairs of daughter nuclei of the dikaryon, resulting in the two septa of a mature clamp (GIRBARDT 1979). Both have a central pore. The backward oriented hook which appeared during clamp formation is possibly not only a by-pass for migration of nuclei (HAWKSWORTH et al. 1995), but also a general means to enable contemporary backward and forward cytoplasmic transport through the septa. SHEPHERD et al. (1993) found tubules moving in both directions through the dolipore septum. The movements appeared coordinated, and during the exchange between the terminal and the penultimate cells tubules transiently interconnected vacuoles in adjacent cells. Peristaltic movements appeared to transfer material beween them. If both the septa are used for transport, although tubules have been shown to move in the dolipores in both directions, a specialization of the dolipores of a clamp regarding transport directions could considerably facilitate bidirectional transport in a hypha. One septum could serve the forward pathway, the other could provide the by-pass for the backward transport. As the dolipores of the septa are very thin (CLÉMENÇON 1997), and parenthesomes encage the pore the countercurrents of transport will meet there in a bottleneck, and a piling up of vesicles could result. The inclusion of the second pore could relieve the cytoplasmic traffic.

This hypothesis therefore considers clamps firstly as appropriate aids to prevent congestion of two countercurrent movements at a septum. Secondly, the clamp formation is not a means for unimpeded synchronous nuclear division, but should rather be understood as the necessary prerequisite for formation of two septa and hyphal compartmentation. However, the inclusion of the genes for clamp formation and fusion in the mating type loci (CASSELTON & KÜES 1994) suggest a primary role of clamp formation in sexuality. A functional switch should have taken place.

Nuclear divisions also precede septa formation in simple septate hyphae, but only one septum is built. Bidirectional transport should therefore also be possible in simple septate hyphae. How this demand can be resolved, will be discussed further below.

2. Backwardly growing hyphae

Many Hymenomycetes do not establish clamps any more. Possibly others are primarily simple-septate. There are several examples in which the reduction of clamps is evident, and where the clamps can be reduced to different degrees. For instance, some species of the genus *Suillus* provide evidence for an almost complete reduction of clamps. Only the 'runner hypha' (rapidly growing main hypha with very distant septa and branches; different from 'leading hyphae' which grow rather slowly and form septa and branches in shorter distances), possesses clamps, which is later that hypha where the formation of rhizomorphs starts, e.g. *Suillus variegatus* (Swartz: Fr.) Kuntze (RAIDL 1997). The question arises, why several fungi can deny formation of clamps. This question is particularly relevant when clamps are considered by-passes for a bidirectional transport.

Since Falck (FALCK 1912, MELIN 1923) it has been repeatedly shown that backward growing ramifications of hyphae are a rather common feature of ectomycorrhizal (AGERER 1995, RAIDL 1997) and of saprotrophic fungi (Agerer, in prep.). AGERER (1992b) and CAIRNEY (1992) have hypothesized that this mode of ramification can facilitate bidirectional transport in a mycelial system.

Most of the rhizomorphic fungi studied form backward oriented ramifications (e.g. AGERER 1995, AGERER & RAMBOLD 1998). Only a few exceptions are known: *Cystoderma carcharias* (Agerer, in prep.), *Entoloma sinuatum* (Bull.: Fr.) Kummer (AGERER 1997), *Laccaria bicolor* (R.Mre.) Orton (RAIDL 1997), *L. amethystina* (Bull.: Hooker) Murr. (RAIDL & AGERER 1992), *Omphalotus olearius* (DC: Fr.) Sing. (fig. 8), *O. atraetopus* (Kalchbr. apud Thümen) Ch.Hahn (fig. 8) and *Ripartites tricholoma* (A. & S.: Fr.) P.Karst. (Agerer, in prep.). More often backward oriented branches are lacking in non-rhizomorphic fungi, e.g. *Pseudotomentella tristis* (P. Karst.) M.J.Larsen (AGERER 1994), *Rozites caperatus* (Pers.: Fr.) P.Karst. (AGERER 1999a), *Tomentella albomarginata* (Bourd. & Galz.) M.J.Larsen (AGERER 1996a) and *Tylospora asterophora* (Bonord.) Donk (RAIDL 1997). This possibly applies also to most species of the genus *Inocybe*. With the exception of *Pseudotomentella tristis* all the mentioned examples possess clamps.

A possible explanation of the evolution of backward growing hyphae is deducible from observations by NIEDERPRUEM et al. (1971) on mutants of *Schizophyllum commune* Fr.: Fr. Pseudoclamps delimited by a neck septum and with a cross-wall in the main hyphal axis could grow out in different directions, forward as well as rearward, to form a new branch. PARAG (1965) found uninucleate pseudoclamps growing out exclusively backward. It is tempting to speculate that, during evolution of Hymenomycetes, the origin of backward oriented ramifications was based on such mutations. This course of events can very likely also explain the co-evolution of backward oriented ramifications and simple septa, realized, for instance, in *Jaapia ochroleuca* (Bres.) Nannf. & J.Erikss. (figs. 13c, d). An outgrowing pseudoclamp lacking a neck septum could be the reason for the formation of backward oriented branches which refrain from clamp formation. Also young stages of whirl-clamps, not fused with the main hypha, can grow to normal hyphae (KEMPER 1937). This was exclusively attributed to higher air moisture.

Backward oriented branches would be able to support or replace the by-pass effect of clamps for bidirectional transportation within the hyphae, regardless as to whether clamps are formed or not. Consequently, the different transport directions can be distributed over different hyphae, as CAIRNEY (1992) hypothesized. This line of arguments can now be used for evolutionary considerations regarding specialization of substrate hyphae and evolution of rhizomorphs.

3. Rhizomorphs: conserved structures with a high diversity

As convincingly pointed out by OBERWINKLER (1985), the most primitive fruitbodies of Hymenomycetes belong to the corticioid type, i.e. resupinate with smooth hymenophore. Although such species are depicted at most exclusively with their hymenium, trama and hyphae connecting the fruitbodies to the substrate (e.g. BREITENBACH & KRÄNZLIN 1986, ERIKSSON & RYVARDEN 1973), i.e. the 'superficial substrate hyphae', all species in addition grow within wood, leaves, etc., on which the fruitbodies are formed. These 'internal substrate hyphae' have to exploit the organic matter, and they have to transfer energy-rich compounds and nutrients. The mycelia use them for the formation of reproductive structures. The 'internal substrate hyphae' are in particular targets of selection and evolution until they are functionally and anatomically adapted in their special ecological niche to the fungi's nutritional demands.

'Internal substrate hyphae' growing in soft substrate or in cavities, and 'superficial substrate hyphae', can aggregate into linear structures, which can be differently assembled. Such multihyphal linear organs are generally known as rhizomorphs (AGERER 1987–1998, CAIRNEY et al. 1991). According to RAYNER et al. (1999) rhizomorphs "minimize the dissipative free surface of hyphae and is engergy-saving and even energy-yielding". Besides transport functions, this might be an additional advantage of hyphal aggregation to rhizomorphs.

A screening of the series "Corticiaceae of North Europe" regarding 'superficial substrate hyphae' results in 91 genera, which exclusively form simple hyphae which are not bundled to any extent. Only 30 genera contain species which produce rhizomorphs. In total, only 65 species of the 342 fungi treated in 'Corticiaceae of North Europe' are rhizomorphic.

Most of these species form primitive rhizomorphs with often rather loosely bundled hyphae of uniform diameter. Quite infrequently some of the rhizomorph hyphae are formed as simple, thick-walled, sometimes slightly thinner skeletals. Only a few species show differentiated structures in so far as diameters of a few hyphae are enlarged. This latter situation is realized only in the following 19 species (a question mark indicates that literature data are not conclusive enough). *Byssocorticium terrestre* (Fr.) Bonord. & Sing. (ZAK & LARSEN 1978), *Jaapia ochroleuca* (figs. 13c, d), *Kavinia alboviridis* (Morgan) *Gilbertson* & Budington, *K. himantia* (Schw.) Eriksss., *Leucogyrophana pseudomollusca* (fig. 18), *L. mollusca* (?) (Parm.) Parm. (ERIKSSON & RYVARDEN 1976), *Lindtneria trachyspora* (Raidl, in prep.), *Phanerochaete calotricha* (?) (P. Karst.) Eriksss. & Ryv., *P. galactites* (?) (Bourd. & Galz.) Eriksss. & Ryv., *P. laevis* (?) (Fr.) Eriksss. & Ryv., *P. sanguinea* (?) (Fr.) Pouz. (ERIKSSON et al. 1978), *Phlebiella subflavidogrisea* (Litsch.) Oberw. (HJORTSTAM et al. 1988), *Phlebiella vaga* (Fr.) Karst (CAIRNEY & CLIPSON 1991), *Ramaricium alboochraceum* (Bres.) Jülich (HAHN et al. 2000, ERIKSSON & al. 1981), *Steccherinum fimbriatum* (Pers.: Fr.) J.Eriksss. (CAIRNEY et al. 1989), *Trechispora cohaerens* (?) (Schw.) Jülich & Stalpers, *T. microspora* (?) (P.Karst.) Liberta, *T. mollusca* (Pers.: Fr.) Liberta and *T. subsphaerospora* (Litsch.) Liberta (HJORTSTAM et al. 1988).

Kavinia, Ramaricium and *Trechispora* species form at most ampullate hyphae in their rhizomorphs. The most highly differentiated rhizomorphs occur in the few species *Byssocorticium terrestre*, *Jaapia ochroleuca, Leucogyrophana mollusca (?), L. pseudomollusca*, *Lindtneria trachyspora*, *Phlebiella vaga*, and *Steccherinum fimbriatum*.

The first conclusion therefore is that Hymenomycetes with primitive fruitbodies lack rhizomorphs, or when rhizomorphs are formed, they are frequently only slightly differentiated. Apparently, those species with highly elaborated rhizomorphs are often related to species which possess fruitbodies of a more advanced type: *Jaapia* to *Serpula* (see below), *Leucogyrophana* to *Hygrophoropsis* (see below) and *Lindtneria* to *Stephanospora* (OBERWINKLER & HORAK 1979). As will be shown later for the order Boletales, and below for the Gomphales, the main rhizomorph organization can persist during evolution, even when the fruitbodies have evolved to a very complex structure.

Many fungi of different relationships retain a primitive, undifferentiated organization of their rhizomorphs. Even when they have derived types of fruitbody. Other fungi do not form rhizomorphs at all, e.g. the genera *Chroogomphus* (AGERER 1990), *Inocybe* (AGERER 1995), some *Tomentella* species (DANIELSON & PRUDEN 1989), *Pseudotomentella tristis* (AGERER 1994), *Rozites caperatus* (AGERER 1999a) and many *Russula* species

A **'uniform-loose rhizomorph type'** (fig. 1, designated as type A according to AGERER 1987–1998) is represented by most of the rhizomorphic corticioid fungi, e.g. *Amphinema byssoides* (Pers.: Fr.) J.Erikss. (WEISS 1991), *Piloderma croceum* J.Erikss. & Hjortst. (BRAND 1991) and *Tomentella albomarginata* (AGERER 1994). It is also known for example in *Dermocybe* (AGERER 1995, AGERER & RAMBOLD 1998), *Entoloma sinuatum* (AGERER 1997), *Gomphidius* roseus (L.) Fr. (AGERER 1991a), a few *Tricholoma* species (AGERER 1987, AGERER & RAMBOLD 1998), and in *Melanophyllum echinatum* (Roth: Fr.) Sing. (Agerer, in prep.).

The 'uniform-compact rhizomorph type' (fig. 1, type B according to AGERER 1987–1998) is, for instance, realized in most *Lactarius* species (AGERER & RAMBOLD 1998), *Bankera fuligineo-alba* (Schmidt: Fr.) Pouz. (AGERER & OTTO 1997), *Cystoderma carcharias* (Pers.: Secr.) Fay. (Agerer, in prep.), *Entoloma clypeatum* (L.: Fr.) Kummer (Agerer, unpubl.), *Phellodon niger* (Fr.: Fr.) P.Karst. (AGERER 1992c), *Hydnellum peckii* Banker apud Peck (AGERER 1993), *Tometellopsis submollis* (Svrcek) Hortst. (AGERER 1998b), *Ripartites tricholoma* (Agerer, in prep.), *Omphalotus olearius* (fig. 8) and *O. atraetopus* (fig. 8).

A **'thelephoroid rhizomorph type'** (fig. 1, included in rhizomorph type C (AGERER 1987–1998)) can be designated as a further type. It is slightly differentiated with only the peripheral hyphae differing somewhat in diameter and structure. This type is typically shown, for example, by *Thelephora terrestris* Pers.: Fr. (AGERER & WEISS 1989), *Tomentella ferruginea* (Pers.: Fr.) Pat. (RAIDL & MÜLLER 1996), *Gomphidius glutinosus* (Schaeff.) Fr. (AGERER 1991a).

A **'russuloid rhizomorph type'** (fig. 1, type E according to AGERER 1987–1998) is characteristic of some species of the genus *Russula*, e.g. *Russula ochroleuca* (Pers.) Fr. (AGERER 1986) and *R. acrifolia* Romagn. (AGERER et al. 1994). Some thickened hyphae with thin branches and preponderantly complete septa are irregularly distributed in the rhizomorphs accompanied by ladder-like thick-walled hyphae with several septa in close distance (comp. MOYERSOEN 1996).

The **'phlegmacioid rhizomorph type'** (fig. 1, type D, according to AGERER 1987–1998) is similar to the 'russuloid rhizomorph'. A few randomly distributed slightly thicker hyphae, embedded in a matrix, can enlarge their septal pore; a distinct septal dissolution is mostly lacking. Such rhizomorphs are found in *Cortinarius* subg. *Phlegmacium* (e.g. AGERER 1988b)

or in *Albatrellus ovinus* (Schaeff.: Fr.) Kotl. & Pouz. (AGERER et al. 1996b) and *Polyporoletus sublividus* Snell (AGERER et al. 1998)..

Finally the **boletoid rhizomorph type** (fig. 1, included in rhizomorph type F, according to AGERER 1987–1998), so characteristic of boletes will be discussed in detail further below.

The fungal relationship that will be discussed below has maintained principally identical rhizomorphs, but evolved fruitbodies of great diversity. It conveys an impression as to how conservative rhizomorph characters can be, suggesting a high value of these organs for discerning fungal relationships of higher-level taxa.

Recently, it has been shown that the ectomycorrhizae, including rhizomorphs, of *Gomphus clavatus* (Pers.: Fr.) S.F.Gray and of several *Ramaria* species have ampullate hyphae in their rhizomorphs, produce acanthocystidia with yellowish contents and plasmatically yellowish, irregularly roundish, inflated, thin-walled cells (AGERER 1996b, 1998a). In addition, the ecological niche of their ectomycorrhizae is identical. They form dense mats predominantly in the mineral soil layer and become greyish or blackish when they senesce (AGERER & RAMBOLD 1998). Almost the same features could be found for *Geastrum fimbriatum* Fr. (AGERER & BEENKEN 1998). But in addition very thin, thick-walled dextrinoid hyphae could be detected on the mycorrhizal mantle and on the surface of the rhizomorphs of this species. Acanthocystidia and the yellowish, inflated cells could however, only be found on the mycorrhizal mantle. It was concluded (AGERER & BEENKEN 1998) that all three genera are systematically rather closely related due to these unique features. This reasoning has been corroborated by results from comparison of DNA sequences (HIBBETT et al. 1997a, 1997b), and by ultrastructural studies, for continuous parenthesomes could be found in all these genera (HAHN et al. 2000, Bauer, pers. comm.). *Ramaricium alboochraceum* (Bres.) Jülich, regarded as a member of Gomphaceae (GINNS 1979, OBERWINKLER 1977a), shows the same organization of rhizomorphs; only the acanthocystidia are lacking (HAHN et al. 2000). As an additional feature, *Ramaricium* and *Ramaria* hyphae are covered by lens-shaped wall appositions (AGERER & RAMBOLD 1998), which admittedly are lacking in the studied *Gomphus* and *Geastrum* species.

BRESINSKY (1996) and PEGLER et al. (1993) regard the genus *Gautieria* as related to the order Boletales, apparently referring to the argument that, as many Boletales, *Gautieria* is parasitized by the genus *Sepedonium* (BESL et al. 1996, PEGLER et al. 1993) and *Gautieria* and *Chamonixia* possess similar spores, as SMITH & SINGER (1959) had already pointed out. OBERWINKLER (1977a) however, regarded Gautieriales as a separate gastroid order with unknown connections to other fungi. Our own investigations clearly show that *Gautieria* spec. nov., from Chile (Palfner, in prep.) forms all the typical below-ground features of *Ramaria*: ampullate rhizomorph hyphae, acanthocystidia, roundish, thin-walled, plamatically yellowish cells, hyphae with lens-shaped appositions (fig. 4), and mat-like ectomycorrhizae which are formed in mineral soil layer, and become blackish when old. All these features shift the genus *Gautieria* close to the *Ramaricium-Ramaria-Gomphus-Geastrum* complex. Though ultrastructrual results are lacking yet, there cannot be much doubt that *Gautieria* is more a member of this complex, and not a member of Boletales, particularly as BRUNS et al. (1998) could show that mitochondrial rDNA sequences indicate a monophyletic relationship of *Gomphus, Ramaria, Kavinia* and *Gautieria*.

The diversity of the fruitbodies of this relationship could not be greater than demonstrated by these fungi. *Ramaricium* is typically corticioid, *Ramaria* is clavarioid, *Gomphus* forms stipitate-pileate fruitbodies, *Geastrum* is an epigeous earth-star with powdery spore masses, and *Gautieria* a hypogeous fungus with a chambered gleba until maturation and during spore

dispersal (OBERWINKLER 1977a). *Kavinia*, also a member of this group (BRUNS et al. 1998), contributes to this diversity with resupinate hydnoid fruitbodies. Whereas the spores of *Ramaricium, Ramaria,* and *Gomphus* are very similar in their shape and in their brownish colour with rough surface, those of *Geastrum* are small, globose and warty, and the epispore of *Gautieria* is longitudinally ribbed. It is apparent that not only the fruitbodies and the spores changed their shape during evolution considerably, but that also the form and function of basidia as *Gautieria* and *Geastrum* have adapted the gastroid organization of the fruitbodies.

The relationship which includes Gomphales, Geastrales and Gautieriales suggests that structures of the rhizomorphs comprise of highly conserved features. Their conservatism seems to be of a similar level as that of the parenthesome-dolipore type and of rDNA sequences. The reason why these structures are so highly conserved can only be speculated. The ampullate hyphae possibly enhance nutrient transport in the special ecologcial niche where mycorrhizae and hyphal mats are in close contact to mineral soil layers. There, the dense mats of hyphae often dry out the soil almost completely. Whether the yellowish contents of acanthocystidia and/or globular cells play a role for defence against soil organisms is as yet unknown.

Similar rhizomorphs, but without the decisive acanthocystidia and without inflated cells with yellowish contents (they are also lacking on the mycorrhizal mantle), are typical of *Hydnum repandum* L.: Fr. and *H. rufescens* Fr. (AGERER et al. 1996c, RAIDL & AGERER 1992).

Rhizomorphs with ampullate hyphae are henceforth, due to their characterization capacity of the Gomphales-Geastrales-Gauteriales complex, designated as **'ramarioid rhizomorph type'** (fig. 1, included in rhizomorph type C according to AGERER 1987–1998)

4. Structure and evolution of the 'boletoid rhizomorph type' (figs. 37, 38)

The **'boletoid rhizomorph type'** (fig. 1, included in tpye F (AGERER 1987–98)) is one of the most highly elaborated conducting organs of fungi. It is characterized firstly, when mature by very thick, often centrally arranged hyphae, with partially or even completely dissolved septa (= vessel-like hyphae). A fast growing 'runner hypha' with often very distant septa is the first hypha which increases considerably its diameter over its whole length; and this hypha is consistently the first one to dissolve septa. Exceptions are *Jaapia ochroleuca* (figs.13c, d) and *Leucogyrophana pseudomollusca* (fig. 18a) with septa remaining complete. A similar final organization of rhizomorphs is also true for the **'agaricoid rhizmorph type'**(fig. 1, also included in type F (AGERER 1987–98)), (fig. 5), but its ontogeny is completely different (Agerer, in prep.). Fast growing 'runner hyphae' are lacking, 'leading hyphae' can precede mycelial extension, but they are not the first to be enlarged, and when they become inflated, only a portion of their cells do so (fig. 38a).

Secondly, in the 'boletoid rhizomorph type' backward oriented ramifications grow towards the main hypha, after they have originated above the first simple septum or the first clamp of a side-branch. There, in many species, it forks into two hyphae, one takes the growth direction of the main hypha, the other grows towards its proximal end (figs.13d, 15a, 18d, 19a, 22a, b, 23d, 24d, 26d, e, 27b, 28b, 29d-f, 30a, 31e, 34b, 35a, 36c). In some species however, no fork is formed. In the latter case the unramified, reversely oriented hypha grows directly towards the proximal end of the main hypha (figs. 13c, 23a,d, 24e, 30c,d, 32c, 33b, 35a, 36a). When young, these hyphae are distinctly thinner than the main hypha and keep in touch with it. Such hyphae in *Serpula lacrymans* (Wulf. In Jacq.: Fr.) Schroeter have been called 'Rankenfäden' by FALCK (1912). The 'agaricoid rhizomorph' develops backward oriented hyphal

ramifications, too, but they do not originate from the proximal end of a side branch and do not grow towards the main hypha and do not keep in intimate contact with it over considerable distances. They are direct derivatives of a main hypha, and are of similar diameter. The same type of hyphal branching as in 'boletoid rhizmorphs' is known in some *Tricholoma* species and *Amanita muscaria* (L.: Fr.) Hooker (RAIDL 1997).

Thirdly, most species are characterized by peculiar nodes at branching points of rhizomorphs (figs. 15c-e, 17b, 18a, 22c, 23g, 27a, b, 34c). Such thickenings can also be evident without ramification, e.g. in *Serpula lacrymans*. At any rate, the nodes occur at positions of septa or clamps of the main hypha. There, several thin hyphal branches divide repeatedly in an irregular manner resulting in a knot-like structure. Bent and tortuous shapes of these hyphae increase the distinctiveness of this structure. Such nodes are known, e. g. in *Amanita muscaria* (RAIDL 1997), *Leccinum scabrum* (Bull.: Fr.) S.F.Gray (MÜLLER & AGERER 1990), *Tomentella* spec. (AZUL et al. 1999) and *Tricholoma vaccinum* (Pers.: Fr.) Kummer (RAIDL 1997). Hyphae form many anastomoses within this node, and also close to it. The anastomoses probably facilitate transfer at this rhizomorph branching point, since it is known that vessel-like hyphae of rhizomorphs of some taxa, e.g. *Suillus bovinus*, are also repeatedly connected to the mantle by many short branches and anastomosing hyphae (AGERER 1990). Anastomoses with the main hypha can be found only as exceptions, for instance in *Chalciporus piperatus* (Bull.: Fr.) Pat. (fig. 31f).

Fourthly, conical side-branches are obvious in several species (AGERER & RAMBOLD 1998), (figs.20c, 22g, 26h, 29h, 33c, 34e, 35b, 36d). The ontogeny of these structures is studied in detail in *Paxillus involutus* (Fr.) Batsch (AGERER 1988a). A hypha, branching off from a 'runner hypha', becomes enveloped primarily at its base by thin hyphae from the main rhizomorph, leaving the distal part of the hypha naked over a longer distance (figs. 20c, 26h, 33c, 34e). Besides members of the Boletales, these conical side-branches occur in *Tomentella ferruginea* (RAIDL & MÜLLER 1996), and very distinctly in *Tomentella* spec. (fig. 7e, f).

'Boletoid rhizomorphs' are, from a phylogentic point of view, very old. They are already formed by species with a supposed primitive fruitbody type, for instance by *Jaapia ochroleuca*. This extant species can help to understand the evolution of the 'boletoid rhizomorph type'.

In *Jaapia ochroleuca*, long, tubular cystidia without septa (150–200 µm long, according to ERIKSSON & RYVARDEN 1976) which originate in the trama project through the hymenium (figs. 13a, 14a), but they can also grow radially over the substrate at the margin of the corticioid fruitbody (fig. 13b). Cystidia can reach extreme lengths of 360 µm (ROGERS 1943). Apically thin-walled cystida are sometimes able to grow out, and continue their growth with a clamp and a normal thin-walled hyphal extension, as is shown for tubular cystidia in aculei of *Hyphodontia floccosa* (Bourd. & Galz.) J.Erikss. by LANGER E. (1994). A similar procedure appears conceivable for the evolution of the rhizomorphs of *Jaapia ochroleuca* predecessors. Tubular cystidia could have become longer and thicker, and at the clamps the second important characteristic of the boletoid rhizomorph appeared, namely backward growing hyphae above the first septum of a side-branch (figs. 13c, d). Although the fruitbody consistently possesses clamps, sidebranches and reversely oriented hyphae can forego of clamps and form simple septa (figs. 13c, d). The central 'runner hypha' is only enveloped with a few additional hyphae, and the rhizomorph is therefore barely differentiated. The septa do not dissolve, neither those of the 'runner hypha' nor the septa of the enveloping ones (figs. 13c, d), although some 'internal substrate hyphae' show disintegrated septa (fig. 14c).

Coniophora arida (Fr.) P.Karst. bears several clamps on its considerably long 'runner hypha' with very distant septa (figs. 15e, 16a). No simple septa occur in it. The whirl-clamps are formed consecutively, i.e. older 'runner hyphae' increase their number of clamps in the whirl consecutively in comparison to younger hyphae. This is in accordance with the observations of KEMPER (1937). First side-branches can originate even on simple septa (fig. 15a), and are generally not formed by outgrowth of clamps (figs. 15e, 16c, d, 17e). Even thicker rhizomorphs do not show any sign of septal dissolution in the 'runner hyphae'; pores are at most only slightly enlarged (figs. 16a, b). The 'runner hypha, is the first to exploit the substrate, and is possibly also the first to transport substances back for support of hyphal growth. It is therefore remarkable that its septa are not dissolved. Whether the multiple clamps per septum provide the hypha with more transport facilities is difficult do demonstrate, but the enlarged and thick-walled 'runner hypha' suggests an effective transport, in spite of the missing septal disintegration. The simple septate enveloping hyphae however, dissolve the septa (fig. 17a). The 'runner hypha' of *Coniophora arida*, remind therefore of the 'runner hypha' of *Jaapia ochroleuca* (figs. 13c, d). *Leucogyrophana pseudomollusca* possesses also very long 'runner hyphae' with distant clamps (fig. 18a), no whirl-clamps are formed, and the clamp septa are dissolved to variable degrees (fig. 18a). Enveloping hyphae show clamps and simple septa as well, and their septa are disintegrated to a higher extent (fig. 18b), similar to those of *Coniophora arida* (fig. 17a). *Hygrophoropsis aurantiaca* (Wulf.: Fr.) R.Mre. (figs. 20, 21) reveals the same ontogeny as *L. pseudomollusca*, but simple septa are apparently not formed. The 'runner hypha' has its clamps not so distant, and most of the septa are at least in part dissolved, resulting in very long vessel-hyphae with a possibly unimpeded transport system of more than 1.7 µm (fig. 21). *Serpula lacrymans* (fig. 19) rhizomorph ontogeny has already been studied in detail by FALCK (1912); his observations on early stages agree completely with our own. Mature rhizomorphs have a similar structure as those of *Hygrophoropsis aurantiaca*, but in addition skeletal hyphae are evident (FALCK 1912, HORNUNG & JENNINGS 1981).

The 'boletoid rhizomorphs' of *Leucogyrophana pseudomollusca, Hygrophoropsis aurantiaca* and *Serpula lacrymans* are plesiomorphic regarding clamps in comparison to *Jaapia ochroleuca* and *Coniophora arida*, which frequently develop simple septa. Rhizomorphs with consistent clamps are also known, for instance in *Alpova trappei* Fogel (fig. 26), *Austropaxillus boletinoides* (Sing.) Bresinsky & Jarosch (Palfner, in prep.), *Boletinus cavipes* (Opat.) Kalachbr. (RAIDL 1997, TREU 1990), *Gyrodon lividus* (Bull.: Fr.) Sacc. (AGERER et al. 1993), *Gyroporus cyanescens* (Bull.: Fr.) Quél. (AGERER 1999b), *Melanogaster variegatus* (Vitt.) Tul. (fig. 26), *Paxillus involutus* (AGERER 1988a), *Phaeogyroporus beniensis* Sing. & Dig. (fig. 24), *Pisolithus tinctorius* (Mich.: Pers.) Coker & Couch (AGERER 1991b) and *Scleroderma citrinum* Pers. (RAIDL 1997).

Several species with 'boletoid rhizomorphs' have reduced the clamps in the rhizomorphs, but occasionally occur on the 'runner hypha', for example, in *Rhizopogon roseolus* (Corda in Sturm) Th.M.Fr. (RAIDL & AGERER 1998), *Scleroderma areolatum* Ehrenb. (fig. 36), *Suillus variegatus* (RAIDL 1997). Many species reduce clamps in rhizomorphs completely, e.g. *Afroboletus luteolus* (Heinem.) Pegler & Young (fig. 23), *Austroboletus gracilis* (Peck) Wolfe (fig. 28), *Austropaxillus statuum* (Speg.) Bresinsky & Jarosch (Hahn, unpubl.), *Boletellus pruinatus* (Fr. & Hök) Klofac & Krisai-Greilhuber (fig. 29), *Boletus erythropus* (Fr.: Fr.) Pers. (fig. 30), *Chalciporus piperatus* (Bull.: Fr.) Pat. (fig. 31), *Chamonixia caespitosa* Rolland (fig. 32), *Leccinum scabrum* (Bull.: Fr.) S.F.Gray (MÜLLER & AGERER 1990), *Phylloporus rhodoxanthus* (Schw.) Bres. (fig. 33), *Porphyrellus pseudoscaber* (Secr.) Sing. (fig. 34), *Pulveroboletus*

cramesinus (Secr.) Sing. (fig. 35), *Rhizopogon vinicolor* A.H.Smith in Smith & Zeller (fig. 25), *Strobilomyces floccopus* (Vahl: Fr.) P.Karst. (fig. 22), *Suillus tridentinus* (Bres.) Sing. (TREU 1990), *Tylopilus felleus* (Bull.: Fr.) P.Karst. (UHL 1988a) and *Xerocomus subtomentosus* (L.: Fr.) Quél. (PALFNER & AGERER 1995).

For the evolution of the 'boletoid rhizomorph type' a progression can therefore be seen from rhizomorphs with consistent clamps to clamps only present on 'runner hyphae' to a complete loss of clamps.

A further argument for an early evolution of this rhizomorph type comes from an unidentified parasite of *Strobilomyces floccopus* rhizomorphs. A highly differentiated and very specialized 'soaking organ' could be found within the rhizomorphs (fig. 6). A clampless, thick-walled, brown hypha inflates subterminally balloon-like. Several very thin and bent hyphae grow out of the inflation and protrude between the rhizomorph hyphae. At the transition zone from the inflated part to the thick-walled hypha, an internal slightly dextrinoid calotte is formed into which a rostrum developed. This anatomically highly differentiated organ probably also functions in a highly specialized manner. The dextrinoid calotte is perhaps a poorly dissolvable carbohydrate synthesized from soluble carbohydrates possibly soaked up by the thin, maccaroni-like hyphae. Due to this fixation, the soluble carbohydrates are re-moved from the osmotically effective pool to ensure further uptake of sugars. The rostrum might dissolve the carbohydrate again, and transport it away. Such a highly sophisticated haustorium should have a rather long evolutionary history, also indicating 'boletoid rhizomorphs' as ancient organs. Such an organ has previously never been found (comp. JEFFRIES & YOUNG 1994).

B. Amyloidy

Amyloidy is a characteristic which has been used in systematics of Basidiomycota for a long time, particularly in the Agaricales s.l. (e.g. SINGER 1986), and in the so-called Aphyllophorales (JÜLICH 1981, 1984). In Hymenomycetes, spores or hyphae can be amyloid (JÜLICH 1981, 1984, SINGER 1986), whereas in Urediniomycetes and Ustilaginomycetes, amyloid structures are unknown (comp. JÜLICH 1981, 1984).

Several families of Hymenomycetes (family affiliation of genera according to HAWKSWORTH et al. 1995) have genera with at least a few species with amyloid spores: Agaricaceae (*Cystoderma*, *Lepiota*), Aleurodiscaceae (*Acanthobasidium, Aleurocystidiellum, Aleurodiscus*), Amanitaceae (*Amanita*), Amylocorticiaceae (*Amyloathelia, Amylocorticium, Hypochniciellum, Irpicodon, Melzericium, Plicatura*), Asterostromataceae (*Asterostroma*), Atheliaceae (*Hypochnopsis*), Auriscalpiaceae (*Auriscalpium, Dentipellis*), Bondarzewiaceae (*Bondarzewia*), Boletaceae (*Tubosaeta*, HEINEMANN & RAMMELOO 1989), Clavariadelphaceae (*Ceratellopsis*), Clavicoronaceae (*Clavicorona*), Coriolaceae (*Anomoporia, Heterobasidion, Postia, Tyromyces* (Watling, pers. comm.)), Dichostereaceae (*Dichostereum*), Elasmomycetaceae (*Elasmomyces, Gymnomyces, Macowanites, Martellia, Zelleromyces*), Gloeocystidiellaceae (*Boidinia, Gloeocystidiellum, Gloiodon, Laxitextum, Megalocystidium, Pseudoxenasma, Scytinostromella, Vesiculomyces*), Hericiaceae (*Arthomyces, Creolophus, Dentipratulum, Hericium, Mucronella*), Hygrophoraceae (*Neohygrophorus*), Lachnocladiaceae (*Scytinostroma, Vararia*), Lentariaceae (*Lentaria*), Lentinellaceae (*Lentinellus*), Lentinaceae (*Panus*), Rhizopogonaceae (*Rhizopogon*, SMITH & ZELLER 1966), Russulaceae (*Lactarius, Russula*), Schizophyllaceae (*Plicaturopsis*), Scutigeraceae (*Albatrellus*), Stereaceae (*Amylostereum, Laurilia, Stereum, Xylobolus*), Tricho-

lomataceae (*Armillaria*, *Baeospora*, *Cantharellula*, *Catathelasma*, *Clitocybula*, *Dermoloma*, *Dictyopanus*, *Fayodia*, *Filoboletus*, *Hydropus*, *Leucopaxillus*, *Melanoleuca*, *Mycena*, *Porpoloma*, *Pseudoarmillariella*, *Pseudoclitocybe*, *Pseudoomphalina*, *Xeromphalina*), Typhulaceae (*Typhula*) and Xenasmataceae (*Aphanobasidium*).

Only a few genera are reported to possess species with amyloid hyphal walls: *Albatrellus* (AGERER et al. 1996a, JÜLICH 1984; Scutigeraceae), *Amylocystis*, *Antrodia* (JÜLICH 1984; Coriolaceae), *Boletopsis* (AGERER 1992a; Bankeraceae, STALPERS 1993), *Boletellus* (IMLER 1950; Boletaceae), *Boletus* sect. *Luridi* and *Calopodes* (IMLER 1950, SINGER 1986; Boletaceae); *Boletinellus* (Bruns, pers. comm.), *Chroogomphus* (AGERER 1990, SINGER 1986; Gomphidiaceae), *Deigloria* (SINGER 1986; Tricholomataceae), *Dentipellis* (JÜLICH 1984; Auriscalpiaceae), *Descolea*, *Descomyces* (Agerer, in prep.; Bolbiliaceae), *Gastroboletus* (MILLER 1971; Boletaceae), *Gomphidius* (AGERER 1991a, SINGER 1986; Gomphidiaceae), *Hericium* (HARRISON 1964, IMLER 1950, JÜLICH 1984; Hericiaceae), *Macrolepiota* (Agerer, in prep., Agaricaceae), *Mycena* (SINGER 1986; Tricholomataeae), *Omphalotus* (MILLER 1971, SINGER 1986; Omphalotaceae), *Paragyrodon* (IMLER 1950; Gyrodontaceae), *Polyporoletus* (AGERER et al. 1998; Scutigeraceae), *Polyporus* (SINGER 1986; Polyporaceae), *Pulveroboletus* (IMLER 1950, Boletaceae), *Pseudotomentella* (AGERER 1994; Thelephoraceae), *Rhizopogon* (AGERER et al. 1996a; Rhizopogonaceae), *Rozites* (AGERER 1999a, SINGER 1986; Cortinariacae), *Scleroderma* (INGLEBY 1999; Sclerodermataceae), *Thelephora* (AGERER 1991a, Thelephoraceae), *Tomentella* (AGERER 1996a; Thelephoraceae), *Tricholoma* (MILLER 1971; Tricholomataceae), *Tubosaeta* (HEINEMANN & RAMMELOO 1989; Boletaceae), *Xerocomus* (IMLER 1950; Boletaceae).

Sometimes (additional) amyloid hyphae can be found in fruitbodies of *Rhizopogon*, and in ectomycorrhizae of some *Suillus* species. But these hyphae originate from *Chroogomphus* and *Gomphidius* growing as foreign hyphae in these genera (AGERER 1990, 1991, AGERER et al. 1996a). These hyphae are not considered in the above compilation, *Gastroboletus* possibly being an exception.

Amyloidy could therefore be proven in 14 orders consisting of 36 different families of Hymenomycetes: Agaricales s.l. (Agaricaceae, Amanitaceae, Bolbiliaceae, Cortinariaceae, Hygrophoraceae, Tricholomataceae), Boletales s.l. (Boletaceae, Gomphidiaceae, Gyrodontaceae, Omphalotaceae, Rhizopogonaceae, Sclerodermataceae), Bondarzewiales (Bondarzewiaceae), Cantharellales s.l. (Clavariadelphaceae, Scutigeraceae, Typhulaceae), Hericiales (Auriscalpiaceae, Clavicoronaceae, Gloeocystidiellaceae, Hericiaceae, Lentinellaceae), Gomphales (Lentariaceae), Hymenochaetales (Asterostromataceae), Lachnocladiales (Dichostereaceae, Lachnocladiaceae), Poriales (Coriolaceae), Polyporales (Polyporaceae), Russulales (Elasmomycetaceae, Russulaceae), Schizophyllales (Schizophyllaceae), Stereales (Aleurodiscaceae, Amylocorticiaceae, Atheliaceae, Stereaceae, Xenasmataceae) and Thelephorales (Bankeraceae, Thelephoraceae). Some of the mentioned orders form a natural relationship, viz. Bondarzewiales, Hericiales, Russulales (comp. OBERWINKLER 1977a). The order Agaricales is according to KÜHNER (1980) possibly heterogeneous. As Tricholomatales and Pluteales are segregations of Agaricales s.l., 13 different relationships possess species with amyloid structures.

Provided that the amyloid reaction is consistently based upon the same chemical compound, the question arises whether this feature has evolved convergently in Hymenomycetes several times, or whether it is a plesiomorphic character and has been lost repeatedly during evolution.

Analysis of spore walls and amyloid hyphae of the Hericiales-Russulales complex (DODD & MCCRACKEN 1972), and of some additional Hymenomycetes (BLACKWELL et al. 1985) revealed a wall bound, short-chain starch as the amyloid substance (DODD & MCCRACKEN

1972). They suggested that the amyloid spore wall inhibits oxygen uptake resulting in a slow metabolism within the dormant spores, and the cold-water solubility of the short-chain compound should guarantee that the spores are able to germinate only after enough rainfall (DODD & MCCRACKEN 1972). This hypothesis however, does not take into account that many spores have only amyloid warts or ridges and therefore no continuous amyloid protecting shield, and it does not explain why in some fungi walls of undifferentiated hyphae and of cystidia are amyloid.

An additional hypothesis might claim the amyloidy primarily as a feature of hyphae. Since starch is a substance well courted, utilized by many organisms, it could, as a consequence of evolution, be withdrawn from substrate hyphae and transferred to cystidia or spores, to keep it from competing organisms. In this case, starch in spore walls could be a triggering food for microorganisms which, after biological degradation, might enable the spores to germinate. This hypothesis of starch retraction from hyphae is confirmed by partially amlyoid hyphae which show the blue reaction only in septa, or in central swellings of septa. This feature is realized by hyphae of mycorrhizal mantles or/and rhizomorphs in several species, e.g. *Gomphidius* species (AGERER 1990, 1991), *Thelephora terrestris* (AGERER 1991a), *Albatrellus ovinus* (AGERER et al. 1996b), *Pseudotomentella tristis* (AGERER 1994). Mycorrhizal hyphae are distinctly amyloid in, e .g. *Albatrellus ovinus* (AGERER et al. 1996b), *Polyporoletus sublividus* (AGERER et al. 1998), *Rhizopogon subcaerulescens* A. H. Smith (AGERER et al. 1996a), and *Scleroderma sinnamarense* Mont. (INGLEBY 1999). In *Rozites caperatus* the whole gelatinous mantle is strongly amyloid, but soil hyphae only partially (AGERER 1999a).

A possible, perhaps step-wise loss of amyloidy is shown when substrate hyphae are compared to stipe base hyphae and hyphae of remaining parts of the fruitbodies. For instance, all members of the Thelephoraceae with amyloid portions of soil or mycorrhizal hyphae (as above mentioned) do not show any amyloidy in their fruitbodies. *Albatrellus ovinus* and *Polyporoletus sublividus* have in comparison to mycorrhizal hyphae less distinctly amyloid hyphae in their stipe base (AGERER et al. 1996b, 1998). *Gomphidius* species ought to have no amyloid structures in their fruitbodies (MILLER 1964, SINGER 1986), but they show amyloid septa or some amyloid walls in mycorrhizal and soil hyphae (AGERER 1991a), and even in cap tissue of *G. maculatus* (AGERER 1991a). *Chroogomphus* has distinctly amyloid fruitbody, but soil hyphae and mycorrhizal hyphae are less amyloid (AGERER 1990). In some *Boletus* species, fruitbody plectenchyma are amyloid, e.g. in *B. calopus* Fr. and *B. luridus* (ENGEL et al. 1983), whereas the rhizomorphs are amyloid only in *B. calopus* (s. below). Although the mycorrhizae of *R. caperatus* are distinctly amyloid, the soil hyphae are less amyloid, and even less amyloid than the stipe base hyphae (AGERER 1999a); the remaining fruitbody hyphae are only partially amyloid (MOSER 1987).

In this context, amyloid substrate hyphae of Thelephoraceae, *Gomphidius*, *Scleroderma*, and *Polyporoletus sublividus*, appear to be remnants of formerly more pronouced amyloidy. In *Albatrellus ovinus* amyloidy has been retained in substrate and stipe base hyphae, in *Boletus luridus* amyloidy is, in contrast to *B. calopus* and *Rhizopogon subcaerulescens*, completely retracted to the fruitbody.

Besides amyloidy, also the distribution of clamps over mycorrhizae, soil hyphae, stipe base and remaining parts of fruitbodies show that substrate hyphae, i.e. mycorrhizal hyphae in ectomycorrhizal species, are equiped with rather plesiomorphic characters (AGERER 1991a, RAIDL 1997). But mycorrhizal mantles appear often in a more advanced state regarding reduction of clamps than substrate or emanating hyphae. This is apparent in ectomycorrhizae

of *Rozites caperatus* and of *Inocybe* spp., where mantle hyphae are clampless, but emanating and soil hyphae form them still (AGERER 1999a, BEENKEN et al. 1996).

According to SWANN & TAYLOR (1995) Hymenomycetes can based upon sequences of 18S rDNA be divided into two subclasses: subclass Tremellomycetidae characterized by extracellular amyloid substances (EAS) of their yeast stages, and Hymenomycetidae not producing such substances, if yeasts are formed at all (PRILLINGER et al. 1991, TAYLOR & SWANN 1995). Studying the phylogenetic classification of pore-forming fungi utilising mitochondrial DNA, HIBBETT & DONOGHUE (1995) found several clusters, with *Stereum* at the base, followed by a cluster including *Polyporus*, which is a sister group of all other species with the Bondarzewiales-Hericiales-Russulales complex as a basal group. *Stereum* is known to form amyloid spores as is true of the Bondarzewiales-Hericiales-Russulales complex. The cluster containing *Polyporus* (with amyloid stipe hyphae, see above) comprises no further examples of known amyloidy. The heterogeneous assemblage of the sister group of the Bondarzewiales-Hericiales-Russulales complex contains members of the Boletales. The basal clustering of *Stereum* and of the Bondarzewiales-Hericiales-Russulales complex might therefore indicate that amyloidy could be regarded as a rather old character (comp. also HIBBETT et al. 1997b, BRUNS et al. 1998).
All these considerations lead to the conclusion that, firstly, amyloidy can most likely be regarded as plesiomorphic at least in the Hymenomycetidae and lost several times during evolution, but in other species amyloidy is, secondly, an erratic feature, which possibly hints at atavisms or an convergent development. As amyloidy is representative of Tremellomycetidae yeasts, it is tempting to speculate that amyloidy of Hymenomycetidae is derived from EAS of Tremellomycetidae. *Rozites caperatus* is particularly interesting with reference to its gelatinous, strongly amyloid mantle, reminiscent of EAS of Tremellomycetidae. As amyloidy is hitherto unknown in the heterobasidomycetous lineage of the Hymenomycetidae and in the groups with continuous parenthesomes (comp. BRUNS et al. 1998, HAHN et al. 2000, HIBBETT et al. 1997b, OBERWINKLER 1977a, SWANN & TAYLOR 1995), amyloidy could perhaps also exclusively be a plesiomorphic feature of the homobasidiomycetous lineage of Hymenomycetidae with perforate parenthesomes. In either case, amyloidy seems to represent a plesiomorphic character in the orders of the present contribution inclusive of the Russulales, Hericiales, Bondarzewiales, and Stereales complex (BRUNS et al. 1998, HIBBETT et al. 1997b).

C. Plesiomorphic versus apomorphic anatomical characters

Phylogenetic progressions within Boletales have already been compiled by BRESINSKY & WITTMANN-BRESINSKY (1995), which can completely be accepted here. Some features have to be repeated. Others are added and arranged in an evolutionary sense from the plesiomorphic (left) to the apomorphic state (right). For evolution of ectomycorrhizal features compare also AGERER (1996c).

Rhizomorphs lacking (outgroup)	→ rhizomorphs present
Rhizomorphs undifferentiated	→ rhizomorphs differentiated
Rhizomorphs of the 'uniform-compact type'	→ rhizomorphs of the 'phlegmacioid type'
Rhizomorphs of the 'uniform-compact type'	→ rhizomorphs of the 'boletoid type'
Backward oriented ramifications lacking	→ backward oriented ramifications present

Rhizomorphs without a 'runner hypha'	→ 'runner hypha' present
Backward oriented hypha above the septum of a hyphal sidebranch growing only towards proximal end of 'runner hypha'	→ this backward growing hypha forking into a distally and a proximally oriented branch
Rhizomorphs without nodes	→ nodes formed
Rhizomorphs with clamps throughout	→ only running hypha with clamps → → clamps completely lacking
Rhizomorph septa complete	→ septa dissolving
Rhizomorph marginal hyphae undifferentiated	→ with inflated cells
Substrate hyphae amyloid	→ substrate hyphae inamyloid
Saprotrophic	→ ectomycorrhizal
Mycorrhizal mantle plectenchymatous	→ pseudoparenchymatous
Mycorrhizal mantle undifferentiated (type B, AGERER 1987–1998)	→ with ring-like hyphal bundles (type A)
Mycorrhizal mantle undifferentiated (type B)	→ with inflated cells (type F)
Mycorrhizal mantle undifferentiated (type B)	→ with cystidia (type D)
Fruitbodies with exposed hymenium (ballistosporic)	→ fruitbodies gastroid (statismosporic)
Fruitbodies resupinate	→ as consoles → excentrically stipitate → → centrally stipitate
Fruitbodies amyloid	→ amyloidy lacking (→ amyloidy present)
Set of metabolites complete	→ not complete

The Relationships of Boletales s. l.

A. The outgroup (fig. 2)

Rozites caperatus is chosen as an outgroup, because this species combines several features which are regarded as plesiomorphic.

Rhizomorphs are lacking, substrate hyphae form clamps, simple septa occur only in the mycorrhizal mantle. The walls of mantle hyphae and the gelatinous matrix are distinctly amyloid, emanting hyphae are only in patches or in septa amyloid. The stipe base possesses amyloid hyphae, too; in the trama amyloid hyphae occur sporadically (AGERER 1999a). The formation of ectomycorrhizae however, is apomorphic. The fruitbody morphology is derived (SINGER 1986) as are the ornamented, brown, dextrinoid spores (SINGER 1986). Clamps in the fruitbody, the lack of cystidia and a regular gill trama (SINGER 1986) are plesiomorphic characters.

B. The Atromentin-Group (fig. 2)

For Omphalotaceae, Thelephorales, and Boletales atromentin (**F1**) is the uniting compound, which has been detected in several species (BESL & BRESINSKY 1997, GILL & STEGLICH 1987), and it holds a key position for the biosynthesis of cyclopentenones (**F17-F20**), thelephoric acid (**F2**) and pulvinic acids (**F3**) (BESL & BRESINSKY 1997). Atromentin (**F1**) could not be found in Gomphidiaceae. Since atromentin is known as a precurser compound of pul-

vinic acids (**F3**) (BRESINSKY 1977, KÄMMERER et al. 1985), the absence of this substance from the pulvinic acids containing Gomphidiaceae is not of great importance.

The occurrence of sesquiterpenoids in Omphalotaceae and of similar ones in Russulales was mentioned by KÄMMERER et al. (1985) without any further systematic considerations. As amyloidy is characteristic of Russulales, and this relationship clusters with respect to DNA-sequences close to Boletales and Thelephorales (BRUNS et al. 1998, HIBBETT et al. 1997b), the Russulales should have also been included in the present comparison, but this would clearly be beyond the scope of the present contribution. The basal connection of Thelephorales and Boletales as shown in fig. 1, might possibly have to be modified somewhat in this case.

1. Omphalotaceae (fig. 2)

In *Omphalotuis olearius,* besides atromentin (**F1**), a rich diversity of pigments could be found, characteristic are thelephoric acid (**F2**) (GILL & STEGLICH 1987), pulvinic acids (**F3**) (GILL & STEGLICH 1987), and the cyclopentenone gyroporin (**F18**) (GILL & STEGLICH 1987). *Lampteromyces japonicus* (Kawamura) Sing. contains in addition gyrocyanin (**F17**) (KÄMMERER et al. 1985). This saprotrophic family causes a white rot, the test for phenoloxidases and peroxidases being positive (KÄMMERER et al. 1985, Agerer et al., in prep.).

The family Omphalotaceae was suggested by Bresinsky (KÄMMERER et al. 1985), and founded basically on the presence of pulvinic acids (**F3**) and sesquiterpenes and on the production of a white rot. All Boletales are either ectomycorrhizal or cause a brown rot (KÄMMERER et al. 1985, NILSSON & GINNS 1979). The occurrence of thelephoric acid (**F2**), was apparently rated as of minor importance. A possible relation to Thelephoraceae was not discussed.

The rhizomorphs of *Omphalotus olearius* and *O. atraetopus* belong to the 'uniform-compact type', clamps are present throughout, simple septa and backward ramifications of hyphae are lacking. Rhizomorphs are very infrequent and only formed outside the woody substrate (Agerer, pers. obs.). This features label Omphalotaceae as very primitive. The presence of a large set of pigments (thelephoric acid (**F2**), atromentin (**F1**), pulvinic acids (**F3**), gyroporin (**F18**)), is according to BRESINSKY & WITTMANN-BRESINSKY (1995) also an indication of plesiomorphy. Amyloid hyphae in culture (MILLER 1971, SINGER 1986) corroborate this assumption.

Since the rhizomorphs are of a very primitive type, without any apomorphic character, it is difficult to find relatives of this family, if the Boletales are not regarded as related. Such rhizomorphs are also known in the Tricholomatales (e.g. *Laccaria*, RAIDL & AGERER 1992; *Ripartites*, Agerer, in prep.; *Cystoderma*, Agerer, in prep.), and Agaricales ss. Kühner (*Coprinus*, *Psathyrella*, Agerer, in prep.). On the other hand, several Thelephorales form 'uniform-compact rhizomorphs'. But all produce backward branching hyphae, when rhizomorphs are formed.

2. Thelephoric acid group (fig. 2)

The order Thelephorales is equipped with thelephoric acid (**F2**) (BRESINSKY & RENNSCHMID 1971, GILL & STEGLICH 1987), but this compound can also be sporadically found in the Boletales, Omphalotaceae (s. above), and Coriolaceae (GILL & STEGLICH 1987, BESL & BRESINSKY 1997). In addition, Thelephorales are traditionally characterized, as far as the families Thelephoraceae and Bankeraceae ss. Stalpers (STALPERS 1993) are considered, by mostly brown spores with a diversity of ornamentations, i.e. warts, double-warts, spines (OBERWINKLER 1977a, 1977b, STALPERS 1993). The latter family was erected by DONK (1961) for genera with white spores, even in outline, and a fenugreek odour. OBERWINKLER

(1977a) desired a more precise definition and delimitation of Bankeraceae, if considered separate from Thelephoraceae. STALPERS (1993) interprets this family in a wider sense and includes all genera with stipitate fruitbodies. Based on the presence of thelephoric acid and great similarities in mycorrhizal features between *Albatrellus ovinus* and *Thelephora terrestris*, AGERER et al. (1996b) discussed a closer relationship between Scutigeraceae and Thelephorales.

When below-ground-features of Thelephorales are included, five different groups can be distinguished. However, very limited data are available to attempt more detailed systematical conclusions.

All members of Thelephoraceae are, as far as investigated, ectomycorrhizal and characterized by brown or brownish, rather thick-walled soil hyphae (AGERER 1996, AGERER & Weiss 1989, AGERER et al. 1995, AZUL et al. 1999, DANIELSON & PRUDEN 1989, JAKUCS et al. 1997, JAKUCS & AGERER 1999a, KÖLJALG 1992, RAIDL & MÜLLER 1996); *Pseudotomentella tristis* is an exception (AGERER 1994). In ectomycorrhizal mantle structure this family is rather heterogeneous. Three main groups can be designated (fig.2). One group is made up by some *Tomentella* species (DANIELSON & PRUDEN 1989) and *Pseudotomentella tristis* (AGERER 1994) which do not form backward oriented hyphal branches and rhizomorphs. They have a variety of ectomycorrhizal mantles. Pseudoparenchymatous mantles with cystidia are realized and plectenchymatous ones which lack both a hyphal pattern and cystidia. The second group possesses 'uniform-loose'or 'thelephoroid rhizomorphs', but no nodes and conical side-branches. Representatives of this group are *Thelephora terrestris* (AGERER & WEISS 1989), *Tomentella albomarginata* (AGERER 1996a), *T. crinales* (Fr.) M.J.Larsen (KÖLJALG 1992), *T. galzinii* (Burt) Bourd. & Galz. (JAKUCS et al. 1997, Jakucs et al., in prep.). Plectenchymatous and pseudoparenchymatous mantles and cystidia can be found. The third group reveals nodulose rhizomorphs (*Tomentella ferruginea* (Pers.: Fr.) Pat., RAIDL & MÜLLER 1996; *T. pilosa* (Fr.) Bourd. & Galz., JAKUCS & AGERER 1999a), and conical side-branches are in addition known from an unidentified *Tomentella* species (fig. 7; "*Quercirhiza nodulosomorpha*", AZUL et al. 1999). Cystidia occur exclusively on mycorrhizal mantle and rhizomorphs of *T. pilosa*.

The rhizomorph ontogeny of some Thelephoraceae reminds one of that of the Boletales. This has been studied in detail in *Thelephora terrestris* (AGERER 1988a) and in "*Quercirhiza nodulosomorpha*" (fig. 7). A backward oriented hypha is growing out above a clamp of a side-branch. It forks and one branch grows in proximal and the other in distal direction of the main filament. This is not a typical 'runner hypha' with distant clamps, and it does not inflate during later ontogenetic phases, possibly because these hyphae thicken their brown walls very early, and therefore impeding an enlargement. KÖLJALG (1996) lays emphasis on rhizomorphs of tomentelloid fungi. He demonstrated both monomitic and dimitic examples and regards this feature as important on genus or subgenus level.

Some of the Thelephoraceae possess amyloid hyphal portions, seen in *Thelephora terrestris* (AGERER 1991a), *Pseudotomentella tristis* (AGERER 1994), *Tomentella albomarginata* (AGERER 1996a). Unfortunately this is a feature tested only by a few authors and for a very limited number of species.

Apart from rhizomorphs of Thelephoraceae which show considerable heterogeneity, mantle types of ectomycorrhizae must also be regarded as possible determinants of relationships within this family. An example for a probably necessary systematical transfer from Thelephoraceae to Bankeraceae based on mycorrhizal features is *Tomentellopsis submollis* (see below).

Bankeraceae, which have been examined for ectomycorrhizae and rhizomorphs all possess plectenchymatous mantles without pattern (*Boletopsis leucomelaena*, AGERER 1992a; *Hydnellum peckii*, AGERER 1993) or ring- or star-like arranged hyphal bundels (*Bankera fuligineo-alba*, AGERER & OTTO 1997; *Phellodon niger*, AGERER 1992c; *Sarcodon imbricatum*, AGERER 1991c). The Rhizomorphs are either of the 'uniform-compact type'(*Bankera fuliginea-alba*, AGERER & OTTO 1997, *Phelldon niger*, AGERER 1992c) or of the 'phlegmacioid type' (*Boletopsis leucomelaena*, AGERER 1992a; *Hydnellum peckii*, AGERER 1993; *Sarcodon imbricatum*, AGERER 1991c). 'Phlegamcioid rhizomorphs' and ring- or star-like hyphal bundles of mantles are hitherto unknown in Thelephoraceae. The mycorrhizae of *Tomentellopsis submollis* fit to the Bankeraceae with their 'uniform-compact rhizomorphs' and ringlike organized mantles (AGERER 1998b).

Amyloidy is known only exceptionally in Bankeraceae. Amyloid points are found on substrate hyphae of *Boletopsis leucomelaena* (AGERER 1992a). IMLER (1950) reports on an "apparent amyloidy" of some Bankeraceae, but this amyloidy is based on intracellular amyloid particles and not in cell walls.

Interesting is the systematic position of *Pseudotomentella tristis*. As mentioned above, this species does not form thick-walled, dark brown substrate hyphae. It therefore is not well placed in the Thelephoraceae/Scutigeraceae-cluster of fig. 2, but would better be grouped within the Bankeraceae. A confirmation of such a position is provided by BRUNS et al. (1998), who could show a closer connection with the Bankeraceae *Sarcodon* than with all Thelephoraceae studied. With *Pseudotomentella tristis*, a member with amyloid septa and hyphal walls and lacking rhizomorphs, would be included in Bankeraceae. Generally, the rhizmorphs and mycorrhizae of Thelephoraceae and Bankeraceae are too little known to get a more detailed impression of their possible role in discerning relationships within this group.

The mycorrhizal features of the Scutigeraceae *Albatrellus ovinus* (AGERER et al. 1996b), *A. subrubescens* (Pillukat, in prep.) and *Polyporoletus sublividus* (AGERER et al. 1998) are so simliar to those of *Thelephora terrestris* (WEISS & AGERER 1989) that an inclusion in Thelephorales appears justified (AGERER et al. 1996b) in spite of the smooth, colourless spores and their phlegmacioid rhizomorphs. Colourless (and warty) spores are however, also known in Bankeraceae. The pigment composition also hints at such a relationship, since thelephoric acid (**F2**) could be detected (AGERER et al. 1996b), and atromentin (**F1**) occurs (GILL & STEGLICH 1987). The synthesis of cyclopentenones indicates a possible relation to the Boletales (BRESINSKY 1996), but pulvinic acids (**F3**) have not been found (BRESINSKY 1996, GILL & STEGLICH 1987). Amyloid substrate hyphae (AGERER et al. 1996b) put Scutigeraceae close to Thelephoraceae.

HIBBETT et al. (1997b) show a basal position of *Hydnellum* sp. and *Thelephora* sp. to the Boletales. *Albatrellus syringae* however, is in a different cluster, but not very distant from *Hydnellum* sp. and *Thelephora* sp. According to BRUNS et al. (1998) *Albatrellus* and *Polyporopletus* form a sister cluster to the Thelephorales.

3. The pulvinic acid group (fig. 2, 3)

Different pulvinic acids (**F3**) occur in this group (GILL & STEGLICH 1987), although in some species they are lacking (comp. Strobilomycetaceae, *Leccinum*). A general feature are backward growing hyphal branches.

The Boletales suborder Suillineae is basically only hold together by DNA data (BRUNS & SZARO 1990, BRUNS et al. 1998, KRETZER & BRUNS 1999). A great diversity of below-ground

features is realized. This suborder includes the Truncocolumellaceae, Gomphidiaceae, Suillaceae and Rhizopogonaceae.

a. The group with 'uniform-compact rhizomorphs' (Truncocolumellaceae) (fig. 2)

Truncocolumella, is regarded by BRESINSKY (1996) together with *Boletus* and *Xerocomus* in one group. *Truncocolumella citrina* is the type species, whilst the second one, *T. rubra*, has been transferred to *Gastroboletus* (comp. BESL & BRESINSKY 1997). HAWSKWORTH et al. (1995) include this genus in Rhizopogonaceae.

The rhizomorphs are undifferentiated of the 'uniform-compact type' (figs. 9, 10), unlike those of Rhizopogonaceae and Boletaceae (s. below). Undifferentiated rhizomorphs have also been described and depicted by EBERHART & LUOMA (1996). Short-celled, thick-walled hyphae on thicker rhizomorphs and at the growing tip are hitherto unique. Clamps as a primitive feature are consistently present; amyloidy is lacking. *Truncocolumella citrina* forms ectomycorrhizae and chlamydospores (EBERHART & LUOMA 1996).

The spores of *T. citrina* are short-ellipsoid (ZELLER 1939), thick-walled and dextrinoid (SMITH & SINGER 1959) whereas those of *Rhizopogon* are mostly thin-walled, elongate and mostly not dextrinoid (MARTIN 1996, SMITH & ZELLER 1966), they are amyloid in *R.* sect. *Amylopogon* (SMITH & ZELLER 1966). The shape and dextrinoidy of *T. citrina* spores reminds one of the spores of *Tapinella atrotomentosa* and *T. panuoides* (HAHN & AGERER 1999a); *Tapinella* spp. also produce chlamydospores (HAHN & AGERER 1999a). Chlamydospores are known in the tuberculate extomycorrhizae of *Rhizopogon vinicolor,* too (Müller & Agerer, in prep.).

The basal position of *T. citrina* in comparison to *Rhizopogon* is corroborated by sequences of the ITS region of rDNA (KRETZER et al. 1996), whereas in other DNA-studies a clear distinction from *Rhizopogon* and *Suillus* was impossible (BRUNS et al. 1998, KRETZER & BRUNS 1999). The primitive organization of the rhizomorphs of *T. citrina* separate Truncocolumellaceae systematically from Suillaceae and Rhizopogonaceae and Boletaceae (see below).

b. The amyloid, episymbiotic group with 'thelephoroid' or lacking rhizomorphs (Gomphidiaceae) (fig. 2)

The Gomphidiaceae is with respect to substrate hyphae a well defined taxon. Members form mycorrhizae with plectenchymatous mantles with differently, species-specifically shaped cystidia. Cystidia and thick-walled cells or septa of mantle or emanating hyphae and/or rhizomorphs are amyloid (AGERER 1990, 1991). Emanating hyphae of mycorrhizae and rhizomorph hyphae are often thick-walled and slightly brownish. Rhizomorphs are only produced by ectomycorrhizae of *Gomphidius glutinosus* and *G. roseus* and are at most slightly differentiated of the 'uniform-loose type' or of the 'thelephoroid type'(AGERER 1991a). Fruitbodies lack rhizomorphs. Stipe base cystidia are similarly shaped to those of mycorrhizae and are slightly amyloid, even in *Gomphidius glutinosus, G. maculatus* and *G. roseus* (AGERER 1991a). The pileus trama of *G. maculatus* is furnished with a few amyloid hyphae. *Gomphidius* ought to be, in contrast to *Chroogomphus,* inamyloid (SINGER 1986, MILLER 1964).

Similar mycorrhiza-cystidia are only known from *Albatrellus ovinus* (AGERER et al. 1996b), *A. subrubescens* (Pillukat, in prep.), *Thelephora terrestris* (AGERER & WEISS 1989) and some *Tomentella* species (Agerer, unpubl.). The cystidia of *Strobilomyces floccopus* (fig. 22) and of *Rhizopogon vinicolor* (fig. 25) are produced on 'boletoid rhizomorphs', reveal a deviating ontogeny and lack amyloid reactions (see below).

Clamps are frequent in mycorrhizal mantles and rhizomorphs of Gomphidiaceae, they become infrequent at the stipe base and are lacking in the fruitbody. This is an evident indi-

cation that features of mycorrhizae and rhizomorphs are plesiomorphic in comparison to those of fruitbodies (see above). The gradual reduction of amyloidy in *Gomphidius* from mycorrhizae to fruitbodies parallels this situation.

A general feature of all Gomphidiaceae (five species tested, AGERER 1991a, 1996d) is their aibility to grow their hyphae within mantles and/or rhizomorphs of *Rhizopogon* and *Suillus* species (AGERER 1990, 1991, 1996d, AGERER et al. 1996a). *Gomphidius glutinosus* differs strikingly from *G. maculatus, G. roseus, Chroogomphus helveticus* (Sing.) Mos. and *C. rutilus* (Schaeff.: Fr.) O.K.Miller, in growing in foreign rhizomorphs only inamyloid hyphae, whereas the latter four species produce amyloid, coil-like haustoria within cortical cells, which are enveloped by the Hartig net of the *Suillus* or *Rhizopogon* ectomycorrhizae. Primordia of *Gomphidius glutinosus* and of *Chroogomphus helveticus* ssp. *tatrensis* (Pilat) Kuthan & Sing. are found to be formed directly on rhizomorphs of a *Suillus* and *Rhizopogon* species, respectively (AGERER 1991a, 1990).

Similar pigment compositions of *Suillus* (Suillaceae) and *Gomphidius* (Gomphidiaceae) urged to postulate a closer relationship between these two genera, and "based on the evidence..., the close relations between the genus *Suillus* and Gomphidiaceae (and *Rhizopogon*) cannot be disputed" (BESL & BRESINSKY 1997). The authors provided detailed compilations of pigments of these two genera.

Gomphidius glutinosus, G. maculatus and *G. roseus* have 1,2,4-trihydroxybenzene (**F16**) as a characteristic pigment. It is lacking in *G. subroseus* Kauffm. (BESL & BRESINSKY 1997). This compound and its dimerisation products (e.g. gomphilactone (**F15**)) could not be detected in *Chroogomphus* (BESL & BRESINSKY l.c.). *Chroogomphus* species are, instead of, provided with boviquinones (BESL & BRESINSKY l.c., GILL & STEGLICH 1987, GILL 1999: *C. helveticus*: boviquinone-3 and -4 (**F4, F5**); *C. rutilus*: boviquinone-3 and -4 (**F4, F5**), diboviquinone-3,4 and -4,4 (**F6, F7**), methylenediboviquinone-3,3, -3,4- and -4,4 (**F8-F10**), and *C. tomentosus* (Murr.) O.K. Miller: 'boviquinones'), which lack *Gomphidius* (BESL & BRESINSKY l.c.).

The main argument (except for DNA-data, see above) to accept a close relationship between Gomphidiaceae and *Suillus* is the presence of boviquinones (**F4-F10**) in *Chroogomphus* and in *Suillus*. The pigment survey for Gomphidiaceae and *Suillus* given by BESL & BRESINSKY (l.c.) indicate that boviquinones and the related prenylated phenols (suillin (**F14**), bolegrevilol (**F13**) and tridentoquinone (**F12**)) occur only infrequently in the 38 *Suillus* species tested. Bolegrevilol (**F13**) could be detected in *S. granulatus* (L.) Kuntze and *S. grevillei* (Klotzsch: Fr.) Sing., suillin (**F14**) in *S. collinitus* (Fr.) Kuntze, *S. granulatus, S. bellinii* (Inzenga) Watl. and *S. variegatus*, bovilactone (**F11**) in *S. americanus* (Peck) Snell in Slipp & Snell, *S. bovinus* (L.) Kuntze and *S. collinitus*, boviquinone-3 (**F4**) in *S. collinitus*, boviquinone-4 (**F5**) in *S. bovinus* and *S. spraguei* (Berk. & M.C.A.Curtis in Berk.) Kuntze, diboviquinone-4,4 (**F7**) in *S. americanus* and *S. bovinus*, methyl-boviquinone-4,4 (**F10**) in *S. bovinus*, tridentoquinone (**F12**) (related to boviquinone-4 (**F5**)) in *S. tridentinus* (Bres.) Sing. In summary, from 38 *Suillus* species tested, in 9 species boviquinones occur. In *Boletinus asiaticus* Sing. and *B. paluster* (Peck) Peck the related asiaticusins could be detected (GILL 1999). *Gastrosuillus laricinus* (Singer & Both) Thiers and *Boletinus cavipes* (Fr.) Kalchr. lack boviquinones. Calculated for Suillaceae, boviquinones and their derivatives are found only in 11 of 42 species whereas thelephoric acid (**F2**) is present in four of these 42 species.

Boviquinone-4 (**F5**) in *Suillus bovinus* is formed by geranygeranylation of 3,4-dihydroxybenzoic acid in position 5 of the phenyl nucleus, whereas boviquinone-3 (**F4**) of *Chroogomphus rutilus* origiantes by farnesylation of this compound in position 2 (GILL 1999). These are two different biosynthesis pathways. It would be necessary to compare the biosynthesis of

the boviquinones of all *Chroogomphus* and of the boviquinone-positive *Suillus* species. Possibly, this difference could indicate a convergent evolution of boviquinones in *Chroogomphus* and *Suillus*.

BESL & BRESINSKY (1997) isolated not further characterized 'lipolytic pigments', i.e. prenylated phenols and quinones (e.g. boviquinones (**F4-F10**)) in *Suillus* (not in *Boletinus*) and regard them as indicators of a relationship between *Suillus* and Gomphidiaceae/Rhizopogonaceae and they "have not been found in any single bolete species (i.e. Boletales with tubulate hymenophore) outside the genus *Suillus*" (BESL & BRESINSKY 1997). (For further discussion see Suillaceae and Rhizopogonaceae, below).

The value of *Chroogomphus* pigments in *Suillus* species is relativized by the episymbiotic feature of Gomphidiaceae. According to AGERER (1991, 1996d; Agerer, unpubl.) amyloid hyphae of Gomphidiaceae (of *Chroogomphus* and *Gomphidius*) could be found in rhizomorphs and/or mycorrhizal mantles and roots of ectomycorrhizae of *Suillus bovinus* (episymbiotic with *G. roseus*), *S. collinitus* (*C. rutilus*), *S. granulatus* (*C. rutilus*), *S. grevillei* (*G. maculatus)*, *S. plorans* (Rolland) Kuntze (*C. helveticus*), *S. sibiricus* (Sing.) Sing. (*C. helveticus*) and *S. variegatus* (*C. rutilus*). The situation gets even more complicated by the fact that Gomphidiaceae hyphae can not only grow in rhizomorphs and mycorrhizae of *Suillus*, but they might also be found in fruitbodies. This could definitely be proven in fruitbodies of *Rhizopogon subcaerulescens* (AGERER et al. 1996a) and other *Rhizopogon* spp. (SMITH & ZELLER 1966). At least *Gomphidius roseus* and *S. bovinus* can form united stipe bases. But it is not known how far the *G. roseus* hyphae reach into the fruitbody of *Suillus*. A microscopical differentiation is impossible, as Gomphidiaceae hyphae become gradually inamyloid the denser they are embedded between those of *Suillus* (AGERER 1990). The great dependence of *G. roseus* hyphae for growth from *Suillus bovinus* is indicated by the fact that mycelial cultures of *G. roseus* could only be obtained when trama pieces of both species were coinoculated on agar plates (AGERER 1991a).

Presently, the most favoured feature for delimitation and recognition of relationships are sequence studies of DNA. BRUNS & SZARO (1990) and BRUNS et al. (1998) report a close relationship between Boletaceae subf. Suilloideae and Gomphidiaceae with respect to sequences of nuclear and mitochondrial RNA genes. These results are consistent with those published by BRUNS & SZARO (1992). Aslo ATPase 6 data indicate a closer relationship between *Suillus* and *Brauniellula*, a hypogeous Gomphidiaceae (KRETZER & BRUNS 1999). ITS sequences of nuclear rDNA indicate however, that the genus *Suillus* forms one group, basal to it appears *Rhizopogon subcaerulescens*, basal *to R. subcaerulescens* stands *Truncocolumella citrina* and again basal to it *Chroogomphus vinicolor* (Peck) O. K. Miller and *Gomphidius glutinosus* together (KRETZER et al. 1996). The position of *Truncocolumella citrina* between *Suillus* and Gomphidiaceae might indicate a greater separation of *Suillus* and Gomphidiaceae, as earlier suggested. But the DNA-tree (KRETZER et al. 1996) is unrooted or at least arbitrary rooted (Bruns, pers. comm.). Therefore this tree should not be overinterpreted; and ITS sequences are said to be only useful for differentiation of species and genera, whereas sequences of nuclear rDNA could be applied for higher level taxa analysis (BRUNS et al. 1991).

The plesiomorphic characters of the substrate hyphae (no or undifferentiated rhizomorphs, clamps) group Gomphidiaceae and Truncocolumellaceae together and basal to Suillaceae and Rhizopogonaceae which have highly developed rhizomorphs and almost completely reduced clamps (see below); and this conflicts with some DNA-data (s. below). Whether the great similarities between ectomycorrhizae of some Thelephoraceae, Scutigeraceae and Gomphidia-

ceae, are the consequence of a common ancestor or the result of convergent evolution is still an open question.

c. The group with boletoid rhizomorphs (Suillaceae, Rhizopogonaceae) (fig. 2)

'Boletoid rhizomorphs' are the most elaborated conducting organs of fungi (s. above) and are likely to be the reason for rapid evolution of fruitbodies and possibly a prerequisite for production for such voluminous fruitbodies as *Boletus* spp.(see also 'Boletales ceteri'). Two main functions can be attributed to these rhizomorphs with their rapidly growing 'runner hyphae'. They provide after READ (1992) "an extremely effective structure with which to scavenge for resources and the rapid onset of infection following contact between unifected roots" (or more general: substrate) "and the advancing mycelial front confirms ... a very high inoculum potential." In the case of saprotrophs, rhizomorphs are preferentially formed between larger substrate gaps, whereas dispersed mycelium prevails within a nutritive substrate (comp. RAYNER et al. 1985).

The families Suillaceae and Rhizopogonaceae appear well characterized by some special features of their 'boletoid rhizomorphs' and of their mycorrhizae. 'Boletoid rhizomorphs' have been proven for all *Rhizopogon, Suillus* and *Boletinus* species studied to date: *Rhizopogon vinicolor* (fig. 25), *R. luteolus* Fr. (UHL 1988b), *R. melanogastroides* M. Lange (RAIDL 1998), *R. roseolus* (RAIDL & AGERER 1998), *R. subcaerulescens* (AGERER et al. 1996a), *R. vulgaris* (Vitt.) M. Lange (JAKUCS et al. 1998), *Suillus bovinus* (DUDDRIDGE et al. 1980), *S. collinitus* (UHL 1988a), *S. flavus* (RAIDL 1997, TREU 1990), *S. granulatus* (RAIDL 1997), *S. laricinus* (Berk.) Kuntze (TREU 1990), *S. luteus* (RAIDL 1997), *S. placidus* (Bon.) Sing. (Agerer, unpubl.), *S. plorans* (TREU 1990), *S. sibiricus* Sing. (TREU 1990), *S. tridentinus* (TREU 1990), *S. variegatus* (RAIDL 1997) and *Boletinus cavipes* (RAIDL 1997, TREU 1990). All species, hitherto studied exactly enough, possess crystals, which reflect in Normarski's interference contrast microscopy light strongly (possibly oxalate crystals) and brownish exuded drops of pigment (e.g. *Suillus laricinus*, TREU 1990). Such crystals and drops of pigment occur also in *Rhizopogon* (e.g. *Rhizopogon roseolus*, RAIDL & AGERER 1998). Drops of pigments are lacking in *Boletinus cavipes* (TREU 1990). The brownish drops of pigment are possibly the "lipophilic pigments" (prenylated phenols), isolated by BESL & BRESINSKY (1997), which are "clearly the substances that form the characteristic incrustation of the fasciculated cystidia which are coloured by KOH .... and considered to be indicator substances for the genus *Suillus* (and for the Gomphidiaceae/ Rhizopogonaceae)" (BESL & BRESINSKY 1997). A colouration of the exuded drops of pigment of the rhizomorphs in KOH is also apparent (TREU 1990). Both, drops of pigment and these crystals, are unknown in any other family of Boletales.

The genera *Suillus* and *Rhizopogon* are both receptors of Gomphidaceae hyphae, which penetrate rhizomorphs, mantle and Hartig net (see Gomphidiaceae). This is possibly also true of *Boletinus cavipes* (Agerer, unpubl.). Gomphidaceae therefore similarly indicate fungal relationships as has been shown for the ascomycete *Hypomyces chrysospermus* Tul. *(Sepedonium)*, which reveals fungi as being a member of the Boletales (GILL & WATLING 1986, HELFER 1991). That also non boletalean fungi can be hosts of *H. chrysospermus* has already been discussed (see *Gautieria*, above.)

Terpenoids are regarded as important pigments of Suillaceae and Rhizopogonaceae as well (BRESINSKY 1996, BESL & BRESINSKY 1997). Some *Suillus* species are characterized by boviquinones (**F4-F10**) and derivatives (comp. Gomphidiaceae). A specific derivative has been detected in *Rhizopogon*, the ansaquinone rhizopogone, a similar compound as tridentochinone (**F12**) from *Suillus tridentinus* (BRESINSKY & STEGLICH 1989, GILL 1999, GILL & STEGLICH

1987). A close relationship between *Suillus* and *Rhizopogon* has been generally accepted (BRESINSKY 1996, BESL & BRESINSKY 1997, BRUNS et al. 1998); but there is much to be said for and also against a close relationship between Suillaceae and Gomphidiaceae.

The pros regard similarities in pigment composition (BESL & BRESINSKY 1997), DNA-sequences (BRUNS & SZARO 1990, BRUNS et al. 1998) and ATPase 6 structrue (Kretzer & Bruns 1999). This has already been discussed in some detail above. In addition, the spores of Gomphidiaceae and Suillaceae are similarly shaped and reminiscent of Boletaceae. Their gill trama is bilateral, again as in Boletaceae (SINGER 1986). The contras concern fundamental differences in the structrue of rhizomorphs and mycorrhizae, the lack of amyloidy in Suillaceae and the consistent presence of clamps in mycorrhizae of Gomphidiaceae.

The 'thelephoroid' or 'uniform-loose' rhizomorphs in Gomphidiaceae are even more primitive than some of the genus *Tomentella* or *Thelephora*. No forking of backward growing hyphae could be found in Gomphidiaceae. The genus *Chroogomphus* lacks rhizomorphs on fruitbodies and on ectomycorrhizae. The absence of rhizomorphs could be interpreted as a reduction, or as an original state. The 'thelephoroid' rhizomorphs of *Gomphidius* could have theoretically emerged by reduction from 'boletoid' ones. But two facts contradict this assumption. Firstly, if they should have developed by reduction, at least the earliest - in an ontogenetical and in a phylogenetical sense - characteristics of boletoid rhizomorphs should still be found, namely 'backward oriented ramifications growing towards a main hypha, after they have originated above the first clamp of a side-branch', and the runner hyphae. This is not the case. Runner hyphae of *Suillus* betray, due to their occasional clamps and their early formation during ontogeny, their plesiomorphic character (RAIDL 1997) and can hence, after Heckel's 'biogenetic rule', be considered phylogenetically as most primitive. And there is no reasonable ground, why such a functionally successful organ, as a 'boletoid rhizomorph', should be reduced at all, even when these fungi have evolved to grow in rhizomorphs of Suillaceae and Rhizopogonaceae. The very complicated ontogeny of 'boletoid rhizomorphs' should be governed by several genes. A mutation could lead to a loss of this functionally highly sophisticated organ and would be detrimental for the evolution of these fungi. 'Boletoid rhizomorphs' should have been retained in spite of the fruitbodies' access to nutrients via foreign rhizomorphs and mycorrhizae at least on the ectomycorrhizae of *Gomphidius*. Secondly, rhizomorphs are very important for the function of the symbiosis in the ectomycorrhizae. Highly elaborated rhizomorphs have better access to nutrients of the substrate than 'thelephoroid' ones (KAMMERBAUER et al. 1989). There is again no explanation, why such a highly specialized symbiotic relation should be reduced in its functional capability by disorganization of its transport organs. 'Boletoid rhizomorphs' are structurally identical whether they are organs of fruitbodies or mycorrhizae. In Gomphidiaceae, typical rhizomorphs are retained on the ectomycorrhizae, but reduced on the fruitbodies, when they are developed on foreign rhizomorphs.

Gomphidiaceae mycorrhizae form very frequent clamps in their mantles and rhizomorphs, they are only occasionally present on the runner hyphae of some *Suillus* species, but occur frequently in *Boletinus*. The loss of clamps and the lack of amyloidy, both indicate only a distant relation of *Suillus* to Gomphidiaceae as do the cystidia of Gomphidiaceae, unknown in *Suillus*. Several features of below-ground structures in Gomphidiaceae reveal apparently a 'plesiomorphy syndrome' of independent characters.

The episymbiotic life-style opened for the Gomphidiaceae a stabile ecological niche, withdrawn from competition by other fungi. This was likely the reason for rapid evolution to pileate-lamellate fruitbodies, in spite of their hardly differentiated or lacking rhizomorphs. And they contemporarily developed bilateral gill trama and fusoid spores. Convergent evo-

lution of this fruitbody type is not uncommon. Tapinellaceae and Paxillaceae provide in our context the best example.

The conclusion is that, if there is a closer relationship between Gomphidiaceae and Suillaceae as DNA-data suggest, Gomphidiaceae should be like Truncocolumellaceae, at the base of the cluster which is called the 'suilloid group' by BRUNS et al. (1998) or 'suilloid radiation' by KRETZER & BRUNS (1999). The terpenoids of *Chroogomphus* and of *Suillus* and the 'lipophilic pigments' of Suillaceae and Gomphidiaceae could therefore be regarded, inspite of their infrequent occurrence, as characteristic of Boletales subord. Suillineae, if boviquinones in *Suillus* are genuine compounds and if there is no distinct difference in biosynthesis of boviquinones in *Chroogomphus* and *Suillus* (GILL 1999).

The similar modifications of four different, independent DNA-regions of Gomphidiaceae, Suillaceae, Rhizopogonaceae (and Truncocolumellaceae) point at a monophyletic group (Bruns, pers. comm.), with the consequence that the 'boletoid rhizomorphs' of Suillaceae/ Rhizopogonaceae have evolved independently from those of 'Boletales ceteri' (see below, and fig. 2, 3). A convergent evolution of these four different DNA-regions and their parallel divergence in comparison to those of 'Boletales ceteri' is very unlikely (Bruns, pers. comm.). Convergent changes in DNA-sequences however - which should not be excluded per se - would on the one hand relativize the importance of DNA-data sets, and on the other, could designate 'boletoid rhizomorphs' as a character of a monophylum Boletales s.str., including only and all families with 'boletoid rhizomorphs'. The boletoid rhizomorphs of Suillaceae/ Rhizopogonaceae on the one hand and those of 'Boletales ceteri' (figs. 2, 3) might then parallel the situation in the Gomphales-Geastrales-Gautieriales complex, where identical rhizomorph structures indicate a close relationship (s. above; HAHN et al. 2000). But, as 'boletoid rhizomorphs' are also known in *Trichloma batschii* Gulden (RAIDL 1997), a convergent evolution of this rhizomorph type also within Boletales can not be excluded.

Another example which proves rhizomorphs as owners of conservative characters is demonstrated by the Agaricaceae and their relatives. HIBBETT et al. (1997, 1997b) found from DNA-sequences, close similarities between the Agaricaceae (*Agaricus*, *Lepiota)*, and the Lycoperdaceae (*Calvatia* and *Lycoperdon)*. The studies on rhizomorphs *of Lepiota, Macrolepiota, Leucoagaricus, Leucocoprinus, Agaricus, Podaxis, Calvatia* and *Lycoperdon*, again revealed the same structures, which are different from those, for instance, of the Strophariaceae (*Hypholoma* and *Stropharia)*, or the Coprinaceae (*Coprinus*, *Psathyrella)*. All the above mentioned genera of Agaricaceae, Lycoperdaceae and Strophariaceae have 'agaricoid' rhizomorphs. Dextrinoid, thick-walled marginal rhizomorph hyphae however, occur only in the Agaricaceae (Agerer, in prep.). *Tulostoma*, also found in the same DNA-cluster as Agaricaceae and Lycoperdaceae, differs however, in lacking these dextrinoid hyphae (Agerer, in prep.). This difference has to be discussed in more detail, but is beyond the scope of this contribution.

Rhizopogonaceae contains, according to BRESINSKY (1996) and PEGLER et al. (1993), the two genera *Rhizpogon* and *Alpova*. TRAPPE (1975) regards *Alpova* as a link between *Rhizopogon* and *Melanogaster*, and includes *Alpova* in Melanogastraceae.

As stated above, *Rhizopogon* forms typical 'boletoid rhizomorphs'. Some species possess cysti-dia. They are either terminal and colourless (*Rhizopogon subcaerulescens*, AGERER et al. 1996a) or they can be geniculate by including several portions of a branched hypha (*Rhizopogon vinicolor*, fig. 25). *Alpova trappei* (fig. 26) and *Melanogster variegatus* (fig. 27), the only species' of these genera studied in detail, form 'boletoid rhizomorphs', too. The

mycorrhizal mantles of *Rhizopogon* show a high diversity. Ring-like hyphal bundles can occur (e.g. *R. subcaerulescens*, AGERER et al. 1996a), the mantle can be built by multiply branched hyphae (*R. luteolus*, UHL 1988b), or the whole mycorrhizal system can be enveloped by an irregular tomentum of cystidia-like hyphae (ZAK 1971.). *Alpova diplophloeus* (Zeller & Dodge) Trappe & A.H.Smith forms ring-like hyphal bundles on the mantle surface (MASSICOTTE et al. 1989), amorphous material and bulbous cystidia (MILLER et al. 1988). The mycorrhizae of *Melanogaster* are not known in detail. BRESINSKY (1996) places *Melanogaster broomeianus* close to *Gyrodon* and *Paxillus* due to the presence of involutin (**F20**) (BESL et al. 1996), and includes it in the Paxillaceae (BRESINSKY et al. 1999). In the investigations of BRUNS et al. (1998) *Melanogaster tuberiformis* clusters with the 'sulloid group'.

At least *Rhizopogon* sect. *Amylopogon* appears with respect to amyloid spores distinct form the other sections. However, SMITH & ZELLER (1966) could find in other sections amlyoid spores, at least in the early stages of spore development, cautioning them not to describe a separate genus (SMITH & ZELLER 1966). Amyloidy in this genus appears to be either an atavism, similar to that found in the genus *Boletus* (see below) or a hint for a closer relationship to Gomphidiaceae and hence a primitive character, although the Suillaceae, the possibly older family in comparison to Rhizopogonaceae, does not show any amyloidy. A more detailed discussion of the genus *Rhizopogon* is beyond the scope of this contribution, but the occurrence of thelephoric acid (**F2**) exclusively in *Rhizopogon* sect. *Villosuli* (GILL & STEGLICH 1987, Müller et al., in prep.) aspires after more detailed systematic studies.

d. The group with 'phlegmacioid/agaricoid rhizomorphs' (Tapinellaceae) (fig. 2)

Tapinella J.-E. Gilbert is a segregate of *Paxillus* which is meanwhile widely (e.g. BRESINSKY et al. 1999, REDHEAD & GINNS 1985, SUTARA 1992), but not generally accepted (e.g. HAWKSWORTH et al. 1995). Many differences justify the separate genus, as comprehensively discussed by HAHN & AGERER (1999b): *Tapinella* possesses in contrast to *Paxillus* smaller spores, lacks cystidia, forms bidirectional not gelatinous gill trama (unidirectional with gelatinous lateral strata in *Paxillus*), rhizomorph structure is 'phlegmacioid' or 'agaricoid' in *Tapinella* (boletoid in *Paxillus*), chlamydospores occur only in *Tapinella* but sclerotia are unknown, caulohymenium and involutin are lacking, and twin-clamps occur only in *Tapinella*. *Paxillus* is ectomycorrhizal in contrast to *Tapinella* which forms a brown rot. The similar habit of e.g. *Paxillus involutus* and of *Tapinella atrotomentosa* (Batsch: Fr.) Sutara is hence the result of convergent evolution. The frequent asymmetric shape of *T. atrotomentosa* is reminiscent of the less advanced fruitbody type still realized by *T. panuoides*.

These differences suggest also the existence of a separate family Tapinellaceae. *Tapinella* comprises *T. atrotomentosa* (fig. 11) with agaricoid rhizomorphs whereas those of *T. panuoides* (Fr.: Fr.) Gilb. are phlegmacioid (HAHN & AGERER 1999b) and are therefore fundamentally different from those of Boletales proper. DNA-sequence data place both species on a common branch basal to all the species of Boletales tested (BRESINSKY et al. 1999, HIBBETT et al. 1997b), and supports LOCQUIN (1981, 1984) who proposed already this family name. According to BRESINSKY et al. (1999) this name is however, invalidly published.

Whether the genus *Pseudomerulius* belongs to this family, which JÜLICH (1984) included in the Coniophoraceae, needs further studies. Similarities to *T. panuoides* can be seen in the same type of 'phlegmacioid rhizomorphs' of *P. aureus* (Fr.) Jülich (fig. 11), in the existence of knobby outgrowths with very thin hyphae, a gelatinous trama, and as a causal agent of brown rot (JÜLICH 1984). As the spores are thin-walled, not dextrinoid and at most slightly yellow there is no evident relation to *Tapinella*; furthermore, backward ramifying hyphae are lacking

in *P. aureus* (fig. 12). An affiliation to Coniophoraceae therefore can be rejected. Pulvinic acids (**F3**) have not been detected (comp. GILL & STEGLICH 1987), but these compounds are lacking also in the Coniophoraceae member *Jaapia* (BESL et al. 1986).

e. The saprotrophic group with 'boletoid rhizomorphs' (Coniphoraceae) (figs. 2, 3)

As discussed above, possibly the first 'boletoid rhizomorphs'which originated during evolution were similar to those found in *Jaapia ochroleuca* (fig. 13). Although pulvinic acids (**F3**) have not been detected (BESL et al. 1985), and the spores are colourless or at most slightly yellowish, their dextrinoidy places this genus in the proximity of the brown-rot genera *Coniophora, Leucogyrophana* and *Serpula*. The genus *Hygrophoropsis*, another brown-rot fungus (LINDEBERG 1948) with colourless and dextrinoid spores, is suggested to be transferred from Paxillaceae or Hygrophoropsidaceae to Coniophoraceae (BRESINSKY et al. 1999). Hence Paxillaceae comprises, after the exclusion of *Hygrophoropsis* and *Tapinella*, only ectomycorrhizal symbionts. Whether *Jaapia ochroleuca* is a brown-rot fungus has still to be substantiated; both collections examined, grew on white-rotten wood (Agerer, pers. observ.). Even the suggested brown-rot fungus *Tapinella atrotomentosa* is able to form peroxidases, but phenoloxidases cannot be detected (Agerer, unpubl.). This composition of oxidative enzymes is shown by almost all ectomycorrhizal fungi amongst the Boletales s.l. (Agerer et al., in prep.).

f. The ectomycorrhizal group with 'boletoid rhizomorphs'(figs. 2, 3)

Strobilomycetaceae differ from the remaining families by the lack of pulvinic acids (**F3**) (GILL & STEGLICH 1987, BRESINSKY 1996). They synthesize DOPA from tyrosine (GILL & STEGLICH 1987), and do not go further to atromentin (**F1**) or pulvinic acids (**F3**). Several pulvinic acids containing species do not produce atromentin any more, although this compound is known as a semifinished product of pulivinic acids (GILL & STEGLICH 1987). At least they do not enrich it in the fruitbodies. The same could be possible for *Strobilomyces*. A second interpretation might be that most of the tyrosine, allocated to secondary metabolism, is consumed for the synthesis of DOPA. Both explanations consider therefore the lack of pulvinic acids for systematic affiliation of minor importance.

The rhizomorphs are brownish grey and completely lack clamps: a combination of possibly apomorphic characters. *Strobilomyces floccopus* forms cystidia (figs. 22e, f), which originate internally, and are not formed as terminal ends of the outermost rhizomorph hyphae. *Afroboletus luteolus*, has basically the same rhizomorphs. Typical cystidia are lacking, but terminal ends of peripheral hyphae are distally slightly inflated and their walls are somewhat thickened (fig. 23g).

In spite of many attempts, it was not possible yet to prove whether *Strobilomyces* is ectomycorrhizal. But a tenacious resistance against growth in culture (BRESINSKY 1996) is supposed as a hint for being mycorrhizal. Attempts to culture it were according to Bruns (pers. comm.) exceptionally successful.

This family is characerized by thick-walled spores with reticulations or prominent ribs as ornament, and is therefore accepted as a separate family (BESL & BRESINSKY 1997). PEGLER & YOUNG (1981) however, propose a very broad definition mainly based on spore-print colour and they include even the genus *Suillus*, an inclusion, which has not been accepted (e.g. HAWKSWORTH et al. 1995, HØILAND 1987).

Paxillaceae (i.e. excl. Hygrophoropsidaceae and Tapinellaceae, incl. Gyrodontaceae and Melanogastraceae, comp. BRESINSKY et al. 1999) are, regarding to their rhizomorphs, difficult to distinguish from the other families with exception of the mostly consistent presence of

clamps. Some south hemispheric species are possibly an exception with an apomorphic lack of clamps. In addition, sclerotia which are formed frequently on rhizomorphs, and brownish colours are evident.

Sclerotia are documented for *Austropaxillus boletinoides* (Palfner, in prep.), *Boletinellus merulioides* (Schwein.) Murrill (COTTER & MILLER 1985), *Gyrodon lividus* (Bull.: Fr.) Sacc. (AGERER et al. 1993), *Paxillus involutus* (e.g. LAIHO 1970), *P. rubicundulus* Orton, *P. validus* Ch. Hahn in Hahn & Agerer (HAHN & AGERER 1999a) and *Phlebopus sudanicus* Har. & Pat. (THOEN & DUCOUSSO 1989). This is perhaps an apomorphic character which unites these genera, but this character has to be looked for in several more genera and species. In Coniophoraceae however, sclerotia are known, too, namely in *Hygrophoropsis aurantiaca* (e.g. ANTIBUS 1989) and *Leucogyrophana* spp. (GINNS 1976).

Clamps in below-ground hyphae have been proven in *Boletinelleus merulioides* (COTTER & MILLER 1985), *Gyrodon lividus* (AGERER et al. 1993), *Gyrodon cyanescens* (AGERER 1999b), *Melanogaster variegatus* (fig. 27), *Paxillus involutus* (AGERER 1988a, MLECZKO 1997), *P. obscurosporus* Ch.Hahn, *P. rubicundulus, P. validus* (HAHN & AGERER 1999a), *Phaeogyroporus beniensis* (fig.24) and *Phlebopus sudanicus* (THOEN & DUCOUSSO 1989). Clamps are lacking in rhizomorphs of *Austropaxillus statuum* (Hahn, unpubl.).

According to BRESINSKY (1996) and BESL et al. (1996), the members of Paxillaceae possess cyclopentenones (**F17-F20**), with the exception of *Austropaxillus*, a segregate from *Paxillus* (BRESINSKY et al. 1999). It does not have involutin (**F20**), the typical cyclopentenone of *Paxillus* (BRESINSKY et al. 1999). Therefore, this chemical character is not a consistent marker for Paxillaceae. 28S rDNA-sequences, distribute Paxillaceae with two separate clades amongst the Boletales, one clade with *Paxillus, Gyrodon* and *Melanogaster*, the other contains exclusively *Austropaxillus* species (BRESINSKY et al. 1999). *Austropaxillus* forms a sister cluster to *Serpula*, and the *Paxillus-Gyrodon-Melanogaster* clade a sister group to *Rhizopogon, Suillus* and others. Only the latter cluster is a sister group to *Coniophora-Leucogyrophana-Hygrophoropsis*. Hence Paxillaceae overlap with respect to DNA-sequences different, anatomically defined groups.

Sclerotia and clamps in brown rhizomorphs occur also in *Pisolithus tinctorius* (AGERER 1991b, GODBOUT & FORTIN 1985, WEISS 1992). Clamps occur in *Pisolithus aurantioscabrosus* Watl., but sclerotia are unknown and the rhizomorphs are more orange (WATLING et al. 1995). Rhizomorphs and mycorrhizae of *Paxillus* and *Pisolithus* are very similar (comp. HAHN & AGERER 1999a, MLECZKO 1997, WATLING et al. 1995, WEISS 1992) all possessing inflated cells on the rhizomorph margin. A relationship between Paxillaceae and Pisolithaceae is therefore more likely than a relation between Pisolithaceae and Sclerodermataceae (s. below). Pisolithaceae do not produce cyclopentenones (**F17-F20**) (GILL 199, GILL & WATLING 1986, GILL & STEGLICH 1987) unlike most Paxillaceae, but these compounds are also lacking in *Austropaxillus* as mentioned above. Unfortunately at present there are no DNA-comparisons between these two families.

The main difference between Paxillaceae and Pisolithaceae regards the special shape of peridiole forming fruitbodies in Pisolithaceae, and lamellate (or tubular) hymenophores in Paxillaceae as well as the shape and ornamentation of the spores. Fruitbody as well as spore evolution is strongly dependent upon selection resulting from environmental influences. A similar situation with very high diversity of fruitbody types and spores could already be shown for the Gomphales-Geastrales-Gautieriales complex (see above).

All Boletaceae and Sclerodermataceae hitherto studied, posses 'boletoid rhizomorphs' (figs. 37, 38): *Austroboletus gracilis* (fig. 28), *Boletellus ananas* (Curt.) Murr. (fig. 29a, b), *B. pruinatus* (fig. 29d–i), *B. russellii* (Forst.) Gilb. (fig. 29c), *Boletus calopus* (Agerer, unpubl.), *B. edulis* Bull.: Fr. (GRONBACH 1988), *B. erythropus* (fig. 30), *Chalciporus piperatus* (fig. 31), *Chamonixia caespitosa* (fig. 32, RAIDL 1999), *Leccinum holopus* (Rost.) Watl., *L. scabrum, L. variicolor* Watl. (MÜLLER & AGERER 1990), *Phylloporus rhodoxanthus* (fig. 33), *Porphyrellus pseudoscaber* (fig. 34), *Pulveroboletus cramesinus* (fig. 35), *Scleroderma areolatum* (fig. 36), *S. bovista* (RICHTER & BRUHN 1989), *S. citrinum* (RAIDL 1997), *S. sinnamarense* (INGLEBY 1999), *Tylopilus felleus* (UHL 1988a), *Xerocomus armeniacus* (Quél.) Quél. (PALFNER & AGERER 1995), *X. badius* (Fr.) Kühn.: Gilb. (GRONBACH 1988), *X. chrysenteron* (Bull.: St. Amans) Quél (BRAND 1989) and *X. subtomentosus* (PALFNER & AGERER 1995).

All rhizomorphs are light coloured, mostly white, sometimes yellow. Crystals are not formed, but peripheral hyphae can be distinctly warty. Quite frequently, inflated, roundish cells, nodes and conical side-branches of rhizomorphs occur. Only the rhizmorphs of *B. calopus* are amyloid, and very distinctly so. *Scleroderma sinnamarense* shows amyloid rhizomorphs and ectomycorrhizal mantles (INGLEBY 1999).

Most species posses mycorrhizal mantles with ring-like arranged hyphal bundles (mantle type A, according to AGERER 1987–1998, AGERER & RAMBOLD 1998): *Boletellus pruinatus* (Agerer, unpubl.), *Boletus edulis* (GRONBACH 1988), *B. luridus* Schaeff.: Fr. (BRUNNER et al. 1992), *Chalciporus piperatus* (Agerer, unpubl.), *Chamonixia caespitosa* (RAIDL 1999), *Leccinum aurantiacum* (Bull.: St.Amans) S.F.Gray (GODBOUT & FORTIN 1985), *L. holopus, L. scabrum, L.variicolor* (MÜLLER & AGERER 1990), *Scleroderma bovista* (JAKUCS & AGERER 1999a), *S. citrinum* (WALLER et al. 1993), *Tylopilus felleus* (UHL 1988a), *Xerocomus armeniacus* (PALFNER & AGERER 1995), *X. badius* (GRONBACH 1988), *X. chrysenteron* (BRAND 1991) and *X. subtomentosus* (PALFNER & AGERER 1995).

All hitherto studied members of Boletaceae do not form clamps, neither in the rhizomorphs nor in the mycorrhizal mantle. The genus *Scleroderma* however, contains species with consistent clamps (*S. citrinum*, RAIDL 1997, WALLER et al. 1993), or clamps occurring occasionally only on the 'runner hyphae' (*S. areolatum*, fig. 36).

With reference to pigments, BRESINSKY (1996) grouped *Leccinum, Chamonixia* and *Gyroporus* together. They contain cyclopentenones (**F17-F20**), in contrast to the remaining Boletaceae, *Boletellus, Boletus, Chalciporus, Phylloporus, Tylopilus* and *Xerocomus*. (But *Leccinum* does not contain pulvinic acids). *Scleroderma* produces pulvinic acids (**F3**) (ARNOLD et al. 1996). The consistent formation of clamps by *Gyroporus cyanescens* (AGERER 1999b) indicates that this genus is rather a member of Paxillaceae than of Boletaceae.

Porphyrellus pseudoscaber, frequently regarded as a member of Strobilomycetaceae (MOSER 1987, PEGLER & YOUNG 1980, HAWKSWORTH et al. 1995), belongs, when the light coloured rhizomorphs are taken into account, to Boletaceae.

From the great similarities between rhizmorphs and ectomycorrhizae of Boletaceae and Sclerodermataceae and the presence of pulvinic acids (**F3**) in both families, Sclerodermataceae are transferred into Boletales. The roundish, warty or reticulated spores, known in Sclerodermataceae (SIMS et al. 1995), but not in Boletaceae is of minor importance, as spores with complicated spore ornamentation occur also in Strobilomycetaceae, a family generally accepted in the Boletales. The spore ornamentation can possibly change during gasteromycetation, as is obvious also for Geastrales and Gautieriales in comparison to the spores of the related Gomphales (s. above.)

Astraeus hygrometricus (Pers.) Morgan forms 'boletoid rhizomorphs', too (GAIE & HEINEMANN 1980, RICHTER & BRUHN 1989, SCHRAMM 1966). The mycorrhizal structure is insufficiently known to draw conclusions on the mantle type. The consistent presence of clamps in rhizomorphs and the dark brown colour of hyphae (SCHRAMM 1966) suggest rather a relation to Pisolithaceae than to Sclerodermataceae.

Synopsis of the atromentin-containing relationships
(emended under consideration of BESL & BRESINSKY 1997, BRESINSKY et al. 1999)

Order (Tricholomatales Kühner) ?
- Family Omphalotaceae Bresinsky

Order Thelephorales Corner: Oberw.
- Family Bankeraceae Donk emend. Stalpers
- Family Thelephoraceae Chev.
- Family Scutigeraceae Bond.& Singer: Singer

Order Boletales Gilbert emend. Agerer

Suborder Suillineae Besl & Bresinsky
- Family Truncocolumellaceae Agerer
- Family Gomphidiaceae R.Maire: Singer

  Truncocolumellaceae and Gomphidiaceae are exclusively placed in this suborder due to the DNA-data (see above). On anatomical reasons, both families should have been separated at least at suborder level. Such a rearrangement should be done after it has been shown that DNA-sequences of Gomphidiaceae and Truncocolumellaceae have evolved more rapidly in comparison to their functionally crucial anatomical features. In the latter case, both families would be basal to Suillaceae and Rhizopogonaceae
- Family Suillaceae (Singer) Besl & Bresinsky
- Family Rhizopogonaceae Dodge

Suborder Tapinellineae Agerer
- Family Tapinellaceae Ch.Hahn

Suborder Coniophoroineae Agerer & Ch.Hahn
- Family Coniophoraceae Ulbr. (incl. Hygrophoropsidaceae Kühner)

Suborder Paxillineae Feltgen
- Family Paxillaceae R.Maire (incl. Gyrodontaceae (Singer) Heinem., incl. Melanogastraceae Tul., excl. Chamonixiaceae Jülich)
- Family Pisolithaceae Ulbr.
- (Family Astraeaceae Zeller: Jülich) ?

Suborder Strobilomycetineae Gilbert
- Family Strobilomycetaceae Gilbert

Suborder Boletineae Rea emend. Gilbert
- Family Boletaceae Chev. (incl. Xerocomaceae Pegler & Young, incl. Chamonixiaceae Jülich)
- Family Sclerodermataceae Corda
- (Family Astraeaceae Zeller: Jülich) ?

New Taxa

Coniophoroineae Agerer & Ch.Hahn, subordo nova

Typus subordinis: Coniophoraceae Ulbr. 1928

Diagnosis latina: Hymenomycetes, Basidiomycota. Sporis dextrinoideis; rhizomorphis boletoideis, saprotrophis.

Tapinellineae Agerer, subordo nova

Typus subordinis: Tapinellaceae Ch.Hahn in HAHN & AGERER (1999) Studien zur Systematik der Paxillaceae. Sendtnera 6: 115–133.

Diagnosis latina: Hymenomycetes, Basidiomycota. Carposomata pileata, stipitata vel laterale adnexa. Sporis brunneis, ellipsoideis, laevibus, dextrinoideis; chlamydosporis praesentibus; rhizomorphis unifomibus vel phlegmacioideis vel agaricoideis, non boletoideis. Involutin deficiens, aceta pulvinica formantes.

Truncocolumellaceae Agerer

Typus familiae: *Truncocolumella* ZELLER (1939) New and noteworthy Gasteromycetes, Mycologia 31: 6.

Diagnosis latina: Hymenomycetes, Basidiomycota. Carposomata gastroidea; columellis truncoideis vel dendroideis, glebis brunneis; sporis brunneis, laevibus, ellipsodeis, dextrinoideis, crassitunicatis; chlamydosporis praesentibus; rhizomorphis uniformibus. Involutin deficiens, aceta pulvinica formantes.

LOQUIN (1984) mentioned the family Truncocolumellaceae and refers to his earlier publication LOQUIN (1981). Sinces intensive searches for the latter publication were not successful and Truncocolumellaceae are not included in HAWKSWORTH et al. (1995) as a valid family, Truncocolumellaceae are described and validly published in the present paper.

Omphalotus atraetopus (Kalchbr. in Thümen) Ch.Hahn, comb. nov.

Basionym: *Paxillus atraetopus* Kalchbr. in THÜMEN, F. (1878) Diagnosen zu Thümen's "Mycotheca universalis". Flora 61: 87. – Lectotypus in M.

According to REID (1975) "*Paxillus*" *atraetopus* is synonymous to *Omphalotus olearius*. The pallid spores, the paxilloid fruitbodies and the anatomy of the rhizomorphs (fig. 8h) confirm the categorization into *Omphalotus*. The difference in spore colour - *Omphalotus olearius* possess a white sporeprint, "*Paxillus*" *atraetopus* on the other hand possess a yellowish sporeprint - is a reason to deny this conspecifity. The occurrence in the Capensis on native wood as a special habitat emphasize the seperation of "*Paxillus*" *atraetopus* as an own species. Unfortunatly the original description is quite short and no recent collections are available. So the macroscopical characters are difficult to discuss. Possibly there are further distinctive features to distinguish these two species. Due to the difference in sporeprint colour, we believe that it is justified to suggest *Omphalotus atraetopus* as an own taxon on species level.

Collection data of the used specimens

Some 60 rhizomorphic genera of different families of Hymenomycetes have been studied to date and they contributed to the results of the present paper, but only the below mentioned genera are actually included.

Afroboletus luteolus: Burundi, Rumonge, under *Brachystegia microphylla* in hill miombo, 12.3.1991, *Buyck 4238* (PC). – ***Agaricus bisporus***: Germany, Bayern, Weilheim-Schongau, Grasleitener moor between Schöffau and Huglfing, eastern margin of the Schwein-Moos, ca. 690 m asl, 21.10.1998, *Hahn & Beenken LB1047* (M). – ***Alpova trappei***: USA, Oregon, Sinn County, Willamette National Forest, Andrew's Experimental Forest, Mill creek 2, ca. 750 m asl, stand ca. 45–60 years old, 20.6.1995, *Agerer RA12199* (M). – ***Austroboletus gracilis***: USA, Michigan, north-west corner of Montmorency County, 30.7.–28.8. 1967, *Bresinsky 67/1015* (M). – ***Boletellus ananas***: USA, Florida, Gainesville, 26.8.1977, *Bresinsky 77–36* (M). – ***Boletellus pruinatus***: Germany, Bayern, Regensburg, Vorderer Bayerischer Wald, Forstmühle, in forest district 'Rabenzipfl', 14.10.1997, *Agerer RA12350* (M). – ***Boletellus russellii***: USA, Florida, Gainesville, 26.8.1977, *Bresinsky 77–35* (M). – ***Boletus erythropus***: Germany, Bayern, Oberstdorf, on the Fellhorn close to middle station of Fellhornbahn, ca. 1400–1500 m asl, 19.8.1998, *Agerer RA12385* (M). – ***Chalciporus piperatus***: Germany, Bayern, Regensburg, Vorderer Bayerischer Wald, Forstmühle, in forest district 'Rabenzipfl', 14.10.1997, *Agerer RA12348* (M). – ***Chamonixia caespitosa***: Germany, Bayern, district Bad Tölz-Wolfratshausen, in the valley of the river Isar between Vorderriß and Wallgau, 47°33'N 11°24'E, app. 800 m asl, 19.10.1998, *Raidl SR720* (M). – ***Coniophora arida***: Germany, Bayern, Regensburg, Forstmühle, in forest district 'Rabenzipfl, 31.7.1998, *Hahn SR511* (M). – ***Gautieria* sp.**: Chile, X. region, Province Osorno, Cordillera de los Andes, National Park Puyehue, Refugio Antillanca, 40°42'S 72°18'W, ca. 1100 m asl, in *Nothofagus pumilio* wood with *Drimys andina* understorey, shortly below tree borderline, thin humus layer on vulcanic ash, 27.3.1998, *Palfner GP4901* (M). – ***Hygrophoropsis aurantiaca***: Germany, Bayern, Aichach, zwischen Odelzhausen und Mering, im Höglwald near Tegernbach, 20.9.1998, *Agerer RA12408* (M). – ***Jaapia ochroleuca***: Germany, Bavaria, Allgäu, Oberjoch, northern slope of Iseler, 1800–1900 m asl, on *Pinus mugo*, 4.9.1984, *Oberwinkler FO35659* (TUB). – Switzerland, Graubünden, Val brevere, on *Larix*, 1820 m asl, 9.9.1976, *Oberwinkler FO24019* (M). – ***Leucogyrophana pseudomollusca***: Germany, Baden-Württemberg, Tübingen, Spitzberg, 1.10.1977, *Oberwinkler FO25068* (TUB). – ***Melanogaster variegatus***: Italy, Emilia Romana, Parma, from Borgotaro direction Bardi, close to Borgotaro shortly behind Brunelli, close to the crossing direction Lame, *Quercus-Castanea* wood, *Beenken LB1014* (M). – ***Omphalotus atraetopus***: South Africa, Boschberg, near of Somerset-East, Febr. 1876, *Mac Owen & Tuk 1216*, type (M). – ***Omphalotus olearius***: Italy, Emilia Romana, Parma, Tagli close to Borgotaro, 20.9.1994, *Agerer RA12132* (M). – ***Phaeogyroporus beniensis***: Chile, Escuadron, Gregario, rara vez solitario, sobre suelo o entre corteza de tocones podridos de *Pinus radiata*, *Garrido 196* (M). – ***Phylloporus rhodoxanthus***: USA, Michigan, Montmorency County, northwest corner, 30.7.–28.8.1967, *Bresinsky 67/1173* (M). – ***Porphyrellus pseudoscaber***: Poland, Gorce Mountains, western slope of Gorc mountain, ca. 1200 m asl, in acid rocky clay soil, in mixed beech and spruce forest (Fagetum carpaticum), *Mleczko RA12768* (M). – ***Pseudomerulius aureus***: Czech Republic, Prachatice, Husinec, dam of Blanice, mountain Hradec, on laying pine branch, 13.9.1996, *Hahn CH89/96*. – ***Pulveroboletus cramesinus***: Germany, Bayern, Hartschimmelhof, Goaslweide, MTB 80333/31, Cephalanthero-Fagetum, 17.9.1998, *Karasch RA12407* (M). – "***Quercirhiza noduloso-morpha***" *(=Tomentella* sp): Portugal, Grândola, district Setúbal, 38°5'N 8°33'W, on *Quercus suber*, 31.10.1998, myc. isol. *Azul AAM3/98* (M). – ***Rhizopogon vinicolor***: USA, Oregon, Sinn County, Willamette National Forest, Andrew's Experimental Forest, Mill creek 2, ca. 750 m asl, stand ca. 45–60 years old, 20.6.1995, *Agerer RA12202a* (M). – ***Scleroderma areolatum***: Italy, Emilia Romana, Parma, from Borgotaro direction Bardi, close to Borgotaro

shortly behind Brunelli, close to the crossing direction Lame, *Quercus-Castanea* wood, 2.10.1998, *Hahn RA12485* (M). – ***Serpula lacrymans***: Strain collection of the Institut für Botanik, Regensburg, *Besl 697*. – ***Strobilomyces floccopus***: Germany, Bayern, Regensburg, Vorderer Bayerischer Wald, Forstmühle, in forest district 'Rabenzipfl', 31.7.1998, *Agerer RA12377* (M). – ***Tapinella atrotomentosa***: Germany, Bayern, Starnberg, Gauting, forests around Buchendorf, 22.9.1998, *Agerer RA12420* (M). – Germany, Bayern, Regensburg, Forstmühle, Rabenzipfel, *Hahn CH164/98*. – ***Truncocolumella citrina***: USA, Oregon, Jackson Co., Rogue River National Forest, just east of milepost 64 on highway 62 along southside of road, 42°54'N 122°18'W, ca. 1400 m asl, under *Pinus contorta, Pseudotsuga menziesii*, 15.10.1997, *Castellano (Trappe 21123)* (OSC).

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Legend of figures

Fig. 1: Schematical drawings and explanations of the different rhizomorph types (further explanations in the text).

Fig. 2: **Dendrogram showing relations between Omphalotaceae, Thelephorales, and Boletales (see also above: 'Plesiomorphic versus apomorphic anatomical characters')**. The 'uniform-compact rhizomorph type' of Omphalotaceae, a 'full set of pigments', the saprotrophic behaviour and amyloid hyphae in culture are plesiomorphic (2). The sister group of Omphalotaceae is supported by different types of rhizomorphs and by different ecological states. A closer connection could only be expected to Bankeraceae with the same rhizomorph type, but with ectomycorrhizae and lacking pulvinic acids. - Ectomycorrhizae (1) are regarded as apomorphic in comparison to a saprotrophic life-style and have been developed at least three times. - The two sister clades, the

'thelephoric acid group' and the 'pulvinic acid group' (3), are connected by the common compound atromentin, the primary product of the synthesis of thelephoric acid and pulvinic acids. No pulvinic acids are known in the 'thelephoric acid group', whereas thelephoric acid has been detected in several species of the 'pulvinic acid group' (Suillaceae, Rhizopogonaceae, Tapinellaceae). - Backward oriented hyphal branches (4) are apomorphic, resulting from their contribution in bidirectional transport and developed twice. - Brown thick-walled soil hyphae (5) are considered as apomorphic, providing resistence. - "Loss" of amyloidy (6) is apomorphic. It is repeatedly lost in the 'thelephoric acid group' (Bankeraceae, Thelephoraceae), but present in some species of *Rhizopogon* (Rhizopogonaceae), *Boletus* (Boletaceae), and *Scleroderma* (Sclerodermataeae). The occurrence at least in the two latter genera is interpreted as atavism. - (7) These three sister clades miss an apomorphic/ plesiomorphic differentiation. A broad range of rhizomorph types is demonstrated. Whether terpenoids are suited to be used as differentiation against the sister clades is uncertain, due to their infrequency in Suillaceae and Rhizopogonaceae (s. above). - The genus *Rhizopogon* is heterogeneous with respect to several features: amyloidy, formation of rhizomorph cystidia, and presence of thelephoric acid. This genus within Rhizopogonaceae might therefore be paraphyletic. - Loss of atromentin and pulvinic acids (8) appears apomorphic, although DOPA might prevent or mask the synthesis of pulvinic acids. The great diversity and elaboration of spore ornamentation and the formation of cystidia on the rhizomorphs are also regarded as apomorphic. It is uncertain, whether Strobilomycetaceae are ectomycorrhizal or saprotrophic. - (9) Scutigeraceae are characterized by phlegmacioid rhizomorphs, in Bankeraceae uniform, thelephoroid and phlegmacioid ones can occur. (F1, F2, F3 refer to chemical formula of atromentin, thelephoric acid and pulvinic acids, respectively; comp. above).

Fig. 3: **Dendrogram showing relations within Boletales (see also above: 'Plesiomorphic versus apomorphic anatomical characters')**. Ectomycorrhizae (1) are regarded as apomorphic in comparison to a saprotrophic life-style. - Loss of atromentin and pulvinic acids (2) appears apomorphic, although DOPA might prevent or mask the synthesis of pulvinic acids. The great diversity and elaboration of spore ornamentation and the formation of cystidia on the rhizomorphs are also regarded as apomorphic. It is uncertain, whether Stobilomycetaceae are ectomycorrhizal or saprotrophic. - The presence of clamps (3) is plesiomorphic and characteristic of all genera, with the exception of a few species of *Austropaxillus*. The loss in the latter genus is interpreted as an apomorphy in an otherwise plesiomorphic group. - Cystidia on the soil mycelium (4) are apomorphic. Possibly such cystidia are also present on mycelia of *Melanogaster* and Pisolithaceae, but so far not studied. It might therefore be a synapomorphy of Pisolithaceae and Paxillaceae. Cyclopentenones could be used for position (4), but they are less frequently present than mycelium cystidia; they are not found in Pisolithaceae and are lacking in *Austropaxillus*.- Ring-like bundles of hyphae of mycorrhizal mantles (5) are apomorphic due to a higher differentiation in comparison to the mostly rather undifferentiated mantles of Suillaceae and of Rhizopogonaceae, although ring-like hyphal bundles can also occur, e.g.. in *R. subcaerulescens* with amyloid mantles. Possibly, this *Rhizopogon* group is more closely related to amyloid *Boletus* species (Boletaceae) or *Scleroderma* species (Sclerodermataceae). - (6) The position of Astraeaceae is as yet uncertain. Dark brown, clamp-bearing mycelia put however, Astraeaceae closer to the Pisolithaceae/ Paxillaceae group. Further studies are necessary. - Four monophyletic groups are evident: Co-niophoraceae, Strobilomycetaceae, Paxillaceae/Pisolithaceae, and Sclerodermataceae/Boletaceae.

Fig. 4: *Gautieria* spec.: **a**. Emanating hyphae of a rhizomorph; note lens-shaped appositions of some thick-walled hyphae, and short, coral-like outgrowths (drawing divided into two parts; point of conitinuation in x - x). **b**. Crystal-bearing hyphae of a rhizomorph, below thick-walled ones. **c, d**. Acanthocystidia and thin-walled, inflated cells with yellowish contents of a rhizomorph surface. **e**. Optical section through a rhizomorph with ampullate inflations. (GP4901, material fixed in FEA = mixture of formadelyde, ethanol and acetic acid, comp. AGERER 1987–1998).

Fig. 5: *Agaricus bisporus*: **a**. Young rhizomorph with some inflating hyphae, no 'runner hypha' present; the thin, unthickened branches in their variable arrangement on the vessel-like hypha indicate the lack of a 'runner hypha'. **b**. Vessel-like hyphae with dissolved septa (drawing divided into two parts, point of continuation in x - x). **c**. Portion of a vessel-like hypha with dissolved septum and possibly proteinaceous crystals enveloped by a cytoplamic membrane. (LB1047; material fixed in FEA).

Fig. 6: Unknown parasite in rhizomorphs of *Strobilomyces floccopus*: **a**. Highly differentiated 'soaking organ' A clampless, thickwalled, brown hypha inflated subterminally balloon-like. Several very thin and bent, 'maccaroni-like' hyphae grow out of it. At the transition zone of the inflated part to the thick-walled hypha, an internal, slightly dextrinoid calotte is formed, into which a rostrum is developed. **b**. Brown thick-walled hypha growing out of (or into) the rhizomorph of *Strobilomyces floccopus*; a conical structure is formed at the entrance (exit ?) to the rhizomorph.(In RA12377, material fixed in FEA).

Fig. 7: "*Quercirhiza nodulosomorpha*" *(= Tomentella sp.)*: **a, b**. Terminal end of rhizomorphs with backward oriented hyphae at the side-branch (drawing 'a' divided into two parts, point of continuation in x - x). **c. d**. Hyphae enveloped by thin, irregularly banched hyphae. **e, f**. Conical side-branch of a rhizomorph with a naked hypha.(AAM3/98, material fixed in FEA).

Fig. 8: *Omphalotus olearius (a-g), O. atraetopus (h)*: Undifferentiated rhizomorphs of the 'uniform-compact' type. **a**. Terminal end of a thin rhizomorph; growing hyphae become gradually enveloped from behind. **b**. Uniting rhizomorphs; backward ramifications of hyphae could not be found. **c**. Side-branch of a rhizomorph; some, evenly thick hyphae form the young branch. **d**. A hypha bows back within the rhizomorph. **e**.Undifferentiated rhizomorph with a reversely oriented clamp. **f**. Hypha with a side-branch. **g**. Formation of a rhizomorphal branch. **h**. Longitudinal cryo-section of a rhizomorph.(a-g from RA12132, h from type; herbarium material of fruitbody with adhering rhizomorphs).

Fig. 9: *Truncocolumella citrina*: **a**. Part of a hyphal system in a rhizomorph with backward oriented hyphal ramifications. **b**. Terminal end of some hyphae which form a thin, rhizomorph. **c**. Terminal end of a thicker rhizomorph with thick-walled cells and anastomoses of terminal cells of neighbouring hyphae. **d**. Optical section through a rhizomorph with partially irregularly arranged hyphae, all hyphae of the same kind regarding diameter and wall thickness, only marginal hyphae with somewhat thicker walls. **e**. More central hyphae of a rhizomorph with slightly enlarged septal pores, no distinct dissolution of septa discernible.(Trappe 21123, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 10: *Truncocolumella citrina*: **a**. Optical section through a thin rhizomorph, with a slightly inflated hypha containing browinsh, cystoplasmic substances. **b**. Point of ramification of a rhizomorph, in 'x' the side-branch emerges. **c**. Hypha of a thicker rhizomorph with backward oriented hyphal branching (clustered arrows represent main growth directions of hyphae at ramification points). **d, e**. Thick-walled terminal ends of hyphae of thicker rhizo-

morphs and of fruitbody-base, with oil drop contents, reminiscent of chlamydospores. (Trappe 21123, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 11: *Tapinella atrotomentosa*: **a**. Terminal end of a thin rhizomorph; a first hypha becomes gradually enveloped by hyphae from behind; no typical 'runner hypha' is formed. **b**. Vessel-like hyphae with dissolved septa, right one with a backward oriented branch. **c-f**. Different modes of hyphal ramifications. **g**. Arthroconidia formed by a distal hyphal end. **h**. Intercalar chlamydospores. (Fig.' a' in two parts, point of continuation in x - x; fig. 'b' from RA12420, herbarium material of fruitbody with adhering rhizomorphs; figs. a, c–h from CH164/98, culture).

Fig. 12: *Pseudomerulius aureus*: **a**. Optical section through a rhizomorph; thickend, thick-walled, hyphae are embedded in a gelatinous matrix. **b**. Thickened hypha with partially dissolved septa. **c**. Optical section of a rhizomorph; two hyphae have considerably thickened walls, causing an asymmetrical shape of the hyphal lumen. **d**. Hyphae of the fruitbody margin adnexed to the substrate; only forward oriented branches could be found. **e–g**. Several tiny hyphae are growing out from stout, irregularly shaped branches. **h**. Anastomoses between two hyphae, one hypha shows reversely oriented clamps. (All figs. from CH98/96, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 13: *Jaapia ochroleuca:* **a**. Section through a fruitbody with a basidia, spores and cystidium (cystidium in two parts, point of continuation in x - x). **b**. Marignal area of a fruitbody with a long cystidium growing approximately radially (perhaps representing a young stage of rhizomorph development) with a thin-walled acompanying hypha (or young basidium). **c, d**. Ramifiaction points of rhizomorphs (enveloping hyphae of the 'runner hyphae' not shown). **e**. 'Internal substrate hyphae' with intrahyphal hyphae, one with outgrowing hyphal tips. (Clustered arrows represent main growth directions of hyphae at ramification points; FO24019, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 14: *Jaapia ochroleuca*: **a**. Section through a fruitbody with 'superficial substrate-hyphae', basidia, spores and cystidia. **b**. Three 'internal substrate-hyphae' growing within a tracheid. **c**. 'internal substrate hypha' with a dissolved septum. **d** 'Internal substrate hypha' with reversely oriented clamps.(FO35659, herbarium material).

Fig. 15: *Coniophora arida*: **a**. Ramification at a septum of a 'runner hypha'; only simple septa present. **b**. Young rhizomorph at a clamp of the 'runner hypha'; only one clamp formed, several enveloping hyphae with terminal cell. **c**. 'Runner hypha' with twin-clamps; beginning of a node formation. **d**. 'Runner hypha' with twin-clamps; one clamp is growing out to enveloping hyphae of a node. **c**. 'Runner hypha' with three clamps; side-branches formed by hyphae with simple septa, even at their base; beginning formation of a node. (Clustered arrows represent main growth directions of hyphae at ramification points; SR511; culture material).

Fig. 16: *Coniophora arida*: **a**. Old 'runner hypha' of a thicker rhizmorph with lacking septal dissolution where clamps had been formed (drawing divided into several parts, points of continuation in x - x, y - y, etc.). **b**. 'Runner hypha', position of clamps; no septal dissolution present. **e**. 'Runner hyphae' with five clamps. **d**. Thickened 'runner hypha' with four clamps and the formation of a side-branch with a basal simple septum (left). (Clustered arrows represent main growth directions of hyphae at ramification points; SR511 in M; herbarium material of fruitbody with adhering rhizomorphs).

Fig. 17: *Coniophora arida*: **a**. One accompanying hypha of the 'runner hypha' with several dissolved septa (drawing divided into several parts, points of conitnuation in x - x, y - y, etc.). **b**. thickened 'runner hypha' with an inflation at the whirl-clamps; at least with four

clamps and two side-branches with basal simple septa, and reversely oriented branches. (SR511, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 18: *Leucogyrophana pseudomollusca*: **a**. Central hypha of a thin rhizomorph, rhizomorph approximately as thick as indicated at nodes, septa at nodes partially dissolved (drawing divided into several parts, points of continuation in v - v, x - x, etc.). **b**. Vessel-like hypha with dissolved septa, developed from an accomanying one of a 'runner hypha'. **c**. Dissolved septum of a vessel-like hypha. **d**. Point of ramification of a 'runner hypha'. **e**. Conical side-branch of a rhizomorph. (Clustered arrows represent main growth directions of hyphae at ramification points; FO25068, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 19: *Serpula lacrymans*: Very early ontogenetical stages of rhizomorph development. **a-d**. different modes of hyphal branching at a main hypha. (Drawing 'a'divided into several portions; point of continuation in w - w, x - x, etc.; clustered arrows represent main growth directions of hyphae at ramification points; Besl 697, culture).

Fig. 20: *Hygrophoropsis aurantiaca*: **a-b**. Ramifications at branching points of a main hypha. **c**. Conical side-branch formed on a rhizomorph; a hypha becomes cone-like enveloped by hyphae. **d**. Vessel-like hypha at a branching point of a rhizomorph, optical section. (Drawing 'a' and 'b' in several parts; points of continuation in u - u, v - v; etc., clustered arrows represent main growth directions of hyphae at ramification points; RA12408, material fixed in FEA).

Fig. 21: *Hygrophoropsis aurantiaca:* One central hypha of a thin rhizomorph; rhizomorph approximately double as thick as the hypha; cells with possibly proteinaceous crystals. (Drawing divided into several portions; points of continuation in,. a - a, b - b, etc.; RA12409, material fixed in FEA).

Fig. 22: *Strobilomyces floccopus:* **a-c**. Ramifications of a 'runner hypha'. **d**. Cryo-section of a rhizomorph showing the basal portions of cystidia originating internally. **e**. Plan view of a rhizomorph with two cystidia originating on the rhizomorph surface, one cystidium drawn in two portions (point of continuation in x - x). **f**. Cryo-section of a rhizomorph with a cystidium. **g**. Conical side-branch of a rhizomorph. **h**. Vessel-like hyphae with dissolved septa. (Clustered arrows represent main growth directions of hyphae at ramification points; RA12391, material fixed in FEA).

Fig. 23: *Afroboletus luteolus*: **a-d**. Ramifications of 'runner hyphae'. **e**. Thin rhizomorph with a thickened, central hypha with still undissolved septa. **f**. Vessel-like hypha with dissolved septa (drawing divided into two parts, point of continuation in x - x.). **g**. Surface view of a ramification point of a rhizomorph; note inflated, slightly thick-walled cells, and terminal inflations of cystidia-like hyphae (asterisk show the two rhizomorph branches). (Clustered arrows represent main growth directions of hyphae at ramification points; Buyck 4238; herbarium material of fruitbody with adhering rhizomorphs).

Fig. 24: *Phaeogyroporus beniensis:* **a**. Thin rhizomorph; drawing divided into several portions (points of continuation in p - p, q - q). **b**. One vessel-like hypha of a thick rhizomorph drawing divided into several portions (points of continuation in x - x and y - y). **c**. Clamp area of a vessel-like hypha with partially dissolved septum. **d-e**. Ramifications of a main hypha. (Clustered arrows represent main growth directions of hyphae at ramification points; Garrido 196, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 25: *Rhizopogon vinicolor*: **a,b**. Ramifications of a 'runner hypha'. **c**. Cystidium; note the geniculate appearance caused by unthickened, collapsed hyphal branches. **d-f**. Connections of cystidia with thin-walled hyphae.g. Cystidia close to thin hyphae with blue granules. **h**.

Vessel-like hyphae with dissolved septa. (Clustered arrows represent main growth directions of hyphae at ramification points; RA12202a, tuberculate mycorrhizae fixed in FEA).

Fig. 26: *Alpova trappei*: **a-e**. Ramifications of 'runner hyphae'. **f**. Surface view of a thicker rhizomorph with thick-walled, short, inflated, cells. **g**. Portions of vessel-like hyphae with dissolved septa. **h**. Conical side-branch of a rhizomorph terminating in two naked hyphae. (Clustered arrows represent main growth directions of hyphae at ramification points; RA12199, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 27: *Melanogaster variegatus*: **a, b**. Ramifications of thin rhizomorphs. **c**. Ramification of a 'runner hypha' with one dissolved septum. **d**. Portions of vessel-like hyphae with dissolved septa. **e**. Surface view of a thicker rhizomorph with thick-walled, inflated cells. (Clustered arrows represent main growth directions of hyphae at ramification points; LB1014, material fixed in FEA).

Fig. 28: *Austroboletus gracilis*: **a**. Thin rhizomorph, drawing divided into two portions (points of continuation in x - x). **b, c**. Ramifications of a main hypha. (Clustered arrows represent main growth directions of hyphae at ramification points; for fig. 'a' clustered arrows at the left side indicate hyphal growth directions above the vessel-like hypha, at the right side below it; Bres 67/1015, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 29: *Boletellus ananas (a,b), B. russellii (c), B. pruinatus (d-i):* **a**. First appearance of a backward oriented hypha at the base of a side-branch. **b**. Portion of a vessel-like hypha with dissolved septum. **c**. First appearance of a backward oriented hypha at the base of a side-branch. **d–g**. Ramifications of 'runner hyphae'. **h**. Conical side-branch of a rhizomorph. **i**. Portions of vessel-like hyphae with dissolved septa. (Clustered arrows represent main growth directions of hyphae at ramification points; a,b Bres 77-36; c Bres. 77-35; d-i RA12350; a-c herbarium material of fruitbody with adhering rhizomorphs; d-i material fixed in FEA).

Fig. 30: *Boletus erythropus*: **a–e**. Ramifications at a main hypha of a rhizomorph. **f**. Portions of vessel-like hyphae at partially dissolved septa. (Drawing 'a' in two parts; point of continuation in x - x; clustered arrows represent main growth directions of hyphae at ramification points; RA12385, material fixed in FEA).

Fig. 31: *Chalciporus piperatus:* **a–e**. Ramifications of 'runner hyphae'. **f**. Thin rhizomorph with a vessel-like hypha showing a dissolved suptum; an anastomosis of enevloping hyphae with the vessel-like one is apparent (dotted circle). (Clustered arrows represent main growth directions of hyphae at ramification points; RA12389, material fixed in FEA).

Fig. 32: *Chamonixia caespitosa*: **a–d**. Ramifications at main hyphae of thin rhizomorphs; in 'b' and 'd' backward oriented hyphae of two side-branches form an anastomosis, resulting in a triangular structure. **e**. Vessel-like hypha. (Clustered arrows represent main growth directions of hyphae at ramification points; SR720, material fixed in FEA).

Fig. 33: *Phylloporus rhodoxanthus*: **a, b**. Ramifications of a main hypha. **c**. Conical side-branch of a rhizomorph. **d**. Vessel-like hypha of a rhizomorph with dissolved septa (drawing divided into two parts, point of continuation in x - x). **e**. Surface view of a thicker rhizomorph. (Clustered arrows represent main growth directions of hyphae at ramification points; Bres 67/1173, herbarium material of fruitbody with adhering rhizomorphs).

Fig. 34: *Porphyrellus pseudoscaber:* **a**. Terminal end of an emanating hypha. **b**. Ramification of a 'runner hypha'. **c**. Vessel-like hypha within a node of a rhizomorph; note dissolving septum and formation of a side-branch (optical section). **d**. Vessel-like hyphae with dis-

solving septa. **e**. Formation of a conical side-branch of a rhizomorph. **f**. Surface view of a thicker rhizomorph with thick-walled, inflated cells and soil particles. (Clustered arrows represent main growth directions of hyphae at ramification points; RA12768, material fixed in FEA).

Fig. 35: *Pulveroboletus cramesinus:* **a**. Branching types of a terminal end of a young rhizomorph, depicted in three portions (points of continuation in x - x, and y - y). **b**. Conical side-branch of a rhizomorph. **c**. Vessel-like hyphae with dissolved septa. (Clustered arrows represent main growth directions of hyphae at ramification points; RA12407, material fixed in FEA).

Fig. 36: *Scleroderma areolatum*: **a-c**. Ramification of 'runner hyphae'. **d**. Young conical side-branch of a rhizomorph. **e**. Portions of vessel-like hyphae with dissolved septa. **f**. Bead-like inflated hyphae of a flat rhizomorph close to fruitbody base. (Clustered arrows represent main growth directions of hyphae at ramification points; RA12485, material fixed in FEA).

Fig. 37: Schematic drawings of rhizomorphs formed without backward oriented ramifications (a), and with backwardly growing hyphae (b, c). *Omphalotus* is an example of 'uniform-compact rhizomorphs', *Pseudomerulius* of 'phlegmacioid' rhizomorphs; all are based exclusively on forward oriented hyphal branches (a). - Backward oriented hyphae which do not originate from the proximal end of a side branch and which do not grow towards the main hypha and do not keep in intimate contact with it over considerable distances (b) are characteristic of *Truncocolumella citrina* ('uniform-compact' rhizomophs), *Tapinella atrotomentosa* and *Agaricus bisporus* ('agaricoid' rhizomorphs), and of *Tapinella panuoides* ('phlegmacioid' rhizomorphs). - Backward oriented hyphal branches which grow towards the main hypha after they have originated above the first simple septum or the first clamp of a side-branch (c) are typical of all species of Boletales tested ('boletoid' rhizomorphs), exclusive of the families Gomphidiaceae, Truncocolumellaceae and Tapinellaceae. In many species they fork into two hyphae, one takes the growth direction of the main hypha, the other grows towards its proximal end. At the origin of the side-branches, node-like inflations are formed.

Fig. 38: Comparison of mature 'agaricoid' and 'boletoid' rhizomorphs (those hyphae formed at the beginning of the ontogeny are depicted with thicker lines): In the 'agaricoid rhizomorph type'(a), the first hyphae to become inflated are those which are developed in the beginning of the rhizomorph ontogeny and usually only after a thicker hyphal bundle developed. A main hypha is enlarged as well as side-branches, but frequently not to their whole extent; step by step the diameter of additional hyphae enlarge and are added to the first ones. Rhizomorph side-branches can be connected to any hyphae of the main rhizomorph; a connection to those hyphae which are formed at the beginning is not necessarily realized. There are no preferential areas of side-branch development. - In the 'boletoid rhizomorph type' (b) the first hypha to become inflated is the 'runner hypha' and its diameter is enlarged through its complete length. Inflated hyphae are added, preferentially those which grew alongside the 'runner hypha'. Side-branches of the rhizomorphs are directly connected to the 'runner hypha' via the firstly developed hyphal branch. There, additional thickened hyphae are added. Irregular branching in the ramification area of the original 'runner hypha' causes the node-like appearance.

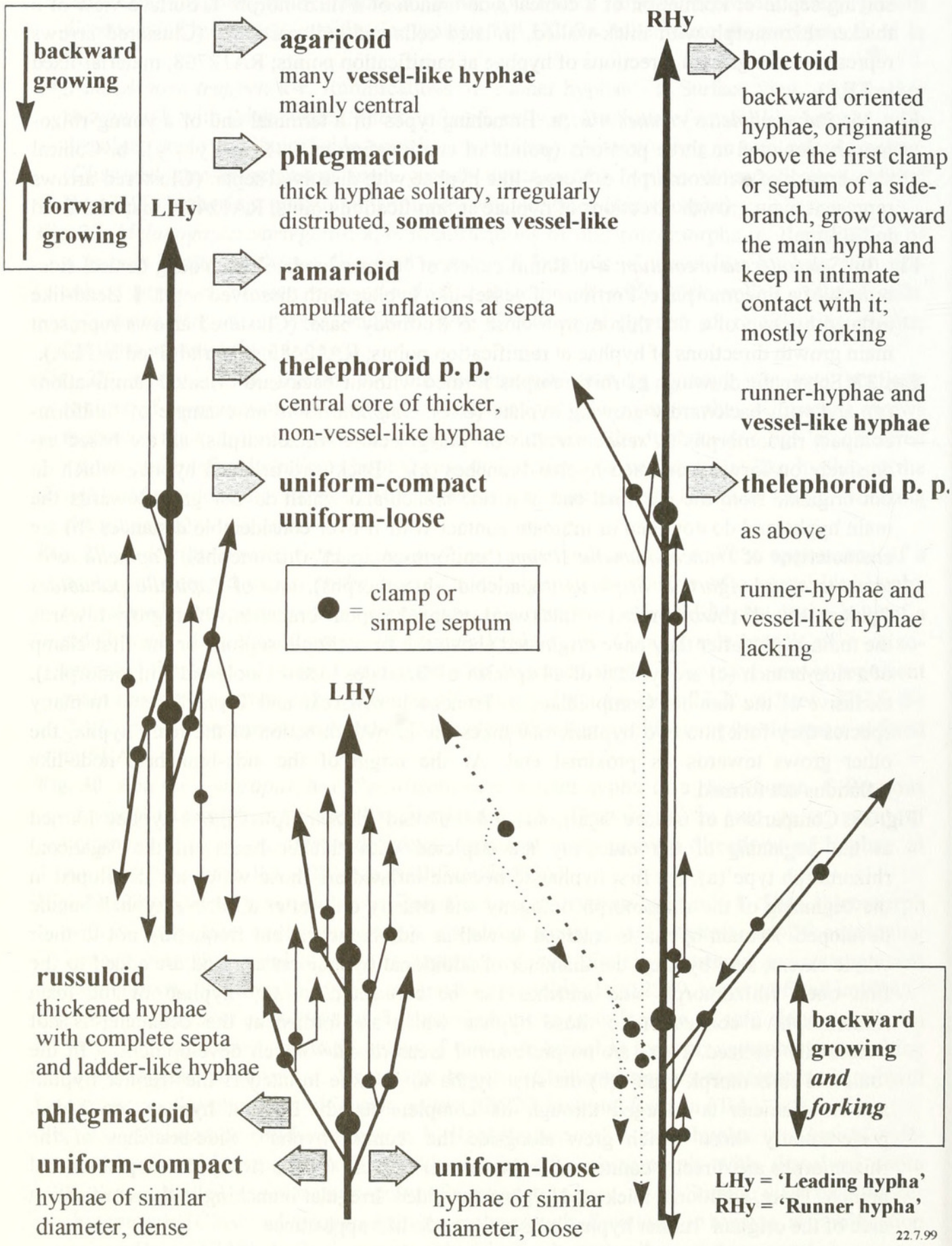
backward growing
forward growing
LHy
agaricoid
many vessel-like hyphae
mainly central
phlegmacioid
thick hyphae solitary, irregularly distributed, sometimes vessel-like
ramarioid
ampullate inflations at septa
thelephoroid p. p.
central core of thicker, non-vessel-like hyphae
uniform-compact
uniform-loose
= clamp or simple septum
LHy
russuloid
thickened hyphae with complete septa and ladder-like hyphae
phlegmacioid
uniform-compact
hyphae of similar diameter, dense
uniform-loose
hyphae of similar diameter, loose
RHy
boletoid
backward oriented hyphae, originating above the first clamp or septum of a side-branch, grow toward the main hypha and keep in intimate contact with it; mostly forking
runner-hyphae and vessel-like hyphae
thelephoroid p. p.
as above
runner-hyphae and vessel-like hyphae lacking
backward growing and forking
LHy = 'Leading hypha'
RHy = 'Runner hypha'
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Fig. 1

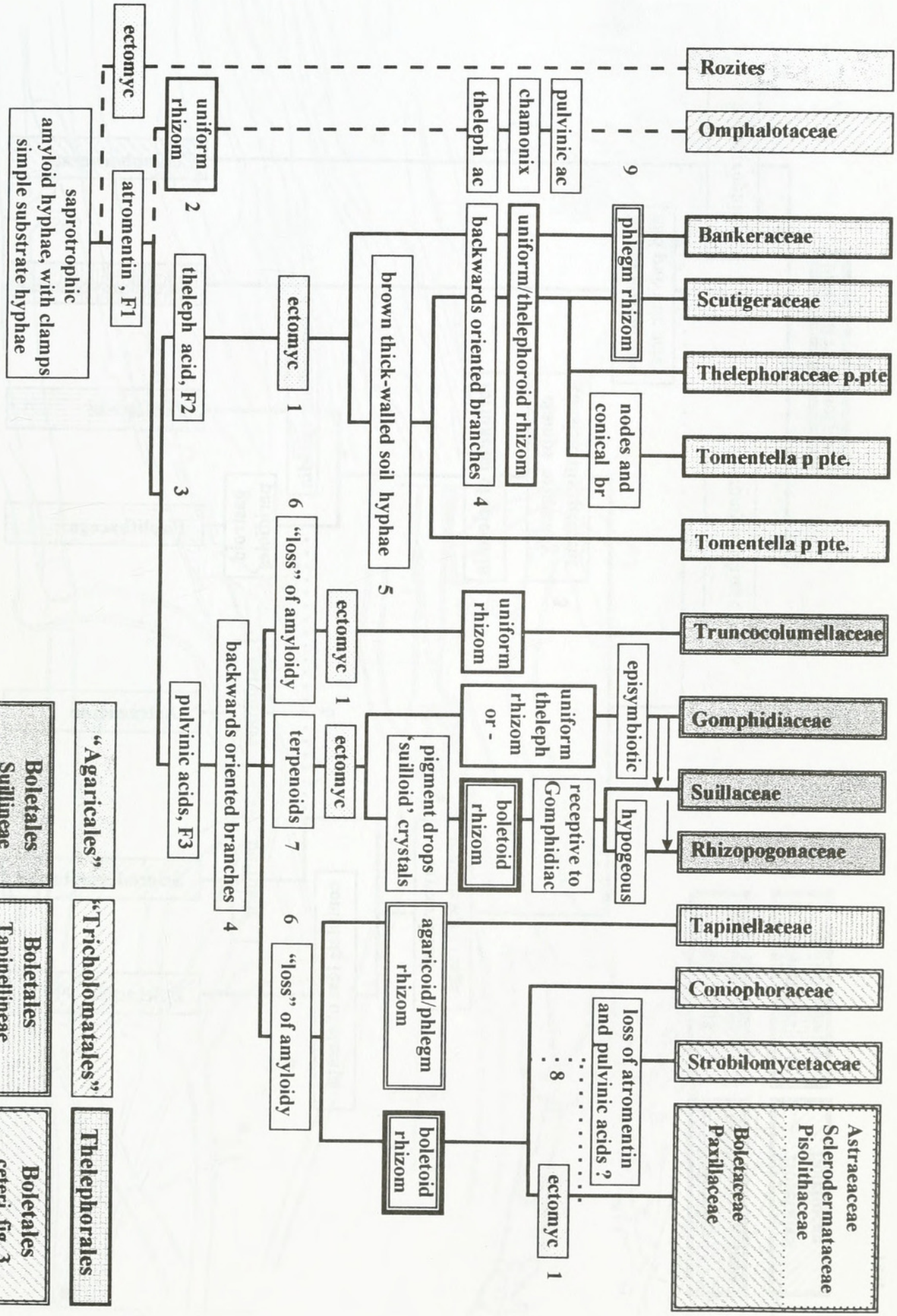
Rozites
Omphalotaceae
9
pulvinic ac
chamonix
theleph ac
phlegm rhizom
uniform/thelephoroid rhizom
backwards oriented branches
4
Bankeraceae
Scutigeraceae
Thelephoraceae p.pte
nodes and conical br
Tomentella p pte.
Tomentella p pte.
1
ectomyc
uniform rhizom
2
atromentin , F1
saprotrophic
amyloid hyphae, with clamps
simple substrate hyphae
theleph acid, F2
3
ectomyc
1
brown thick-walled soil hyphae
5
uniform rhizom
ectomyc
1
6
"loss" of amyloidy
backwards oriented branches
4
pulvinic acids, F3
terpenoids
7
ectomyc
pigment drops
'suilloid' crystals
uniform theleph rhizom or -
boletoid rhizom
receptive to Gomphidiac
episymbiotic
hypogeous
Truncocolumellaceae
Gomphidiaceae
Suillaceae
Rhizopogonaceae
Tapinellaceae
6
"loss" of amyloidy
agaricoid/phlegm rhizom
boletoid rhizom
Coniophoraceae
Strobilomycetaceae
loss of atromentin and pulvinic acids ?
8
ectomyc
1
Astraeaceae
Sclerodermataceae
Pisolithaceae
Boletaceae
Paxillaceae
"Agaricales"
"Tricholomatales"
Thelephorales
Boletales
Suillineae
Boletales
Tapinellineae
Boletales
ceteri fig. 3
22.7.99

Fig. 2

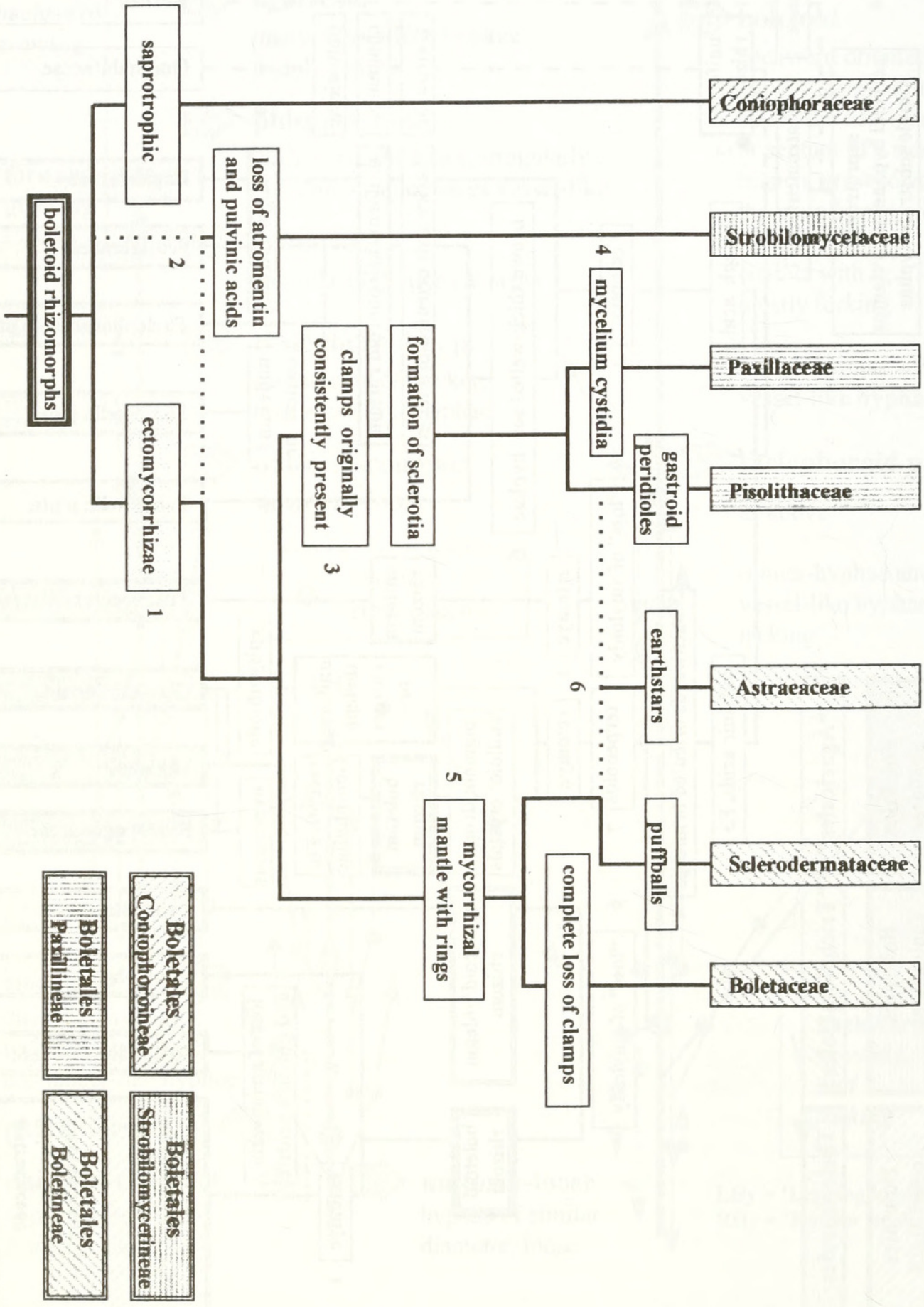
Coniophoraceae
Strobilomycetaceae
Paxillaceae
Pisolithaceae
Astraeaceae
Sclerodermataceae
Boletaceae
4
mycelium cystidia
gastroid peridioles
6
earthstars
puffballs
5
mycorrhizal mantle with rings
complete loss of clamps
formation of sclerotia
clamps originally consistently present
3
loss of atromentin and pulvinic acids
2
saprotrophic
boletoid rhizomorphs
ectomycorrhizae
1
Boletales Coniophoroineae
Boletales Strobilomycetineae
Boletales Paxillineae
Boletales Boletineae
1.6.99

Fig. 3

Fig. 4

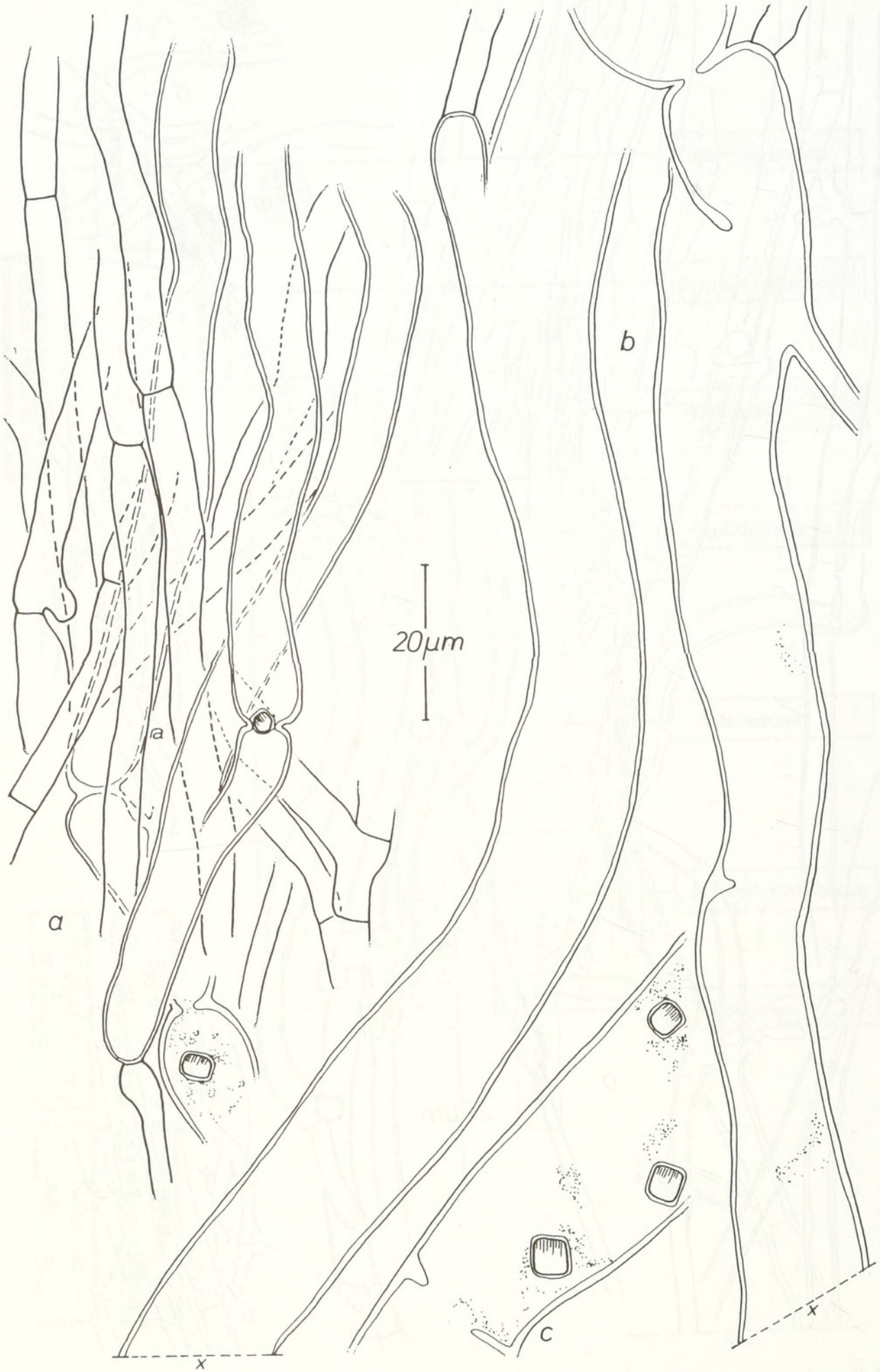

Fig. 5

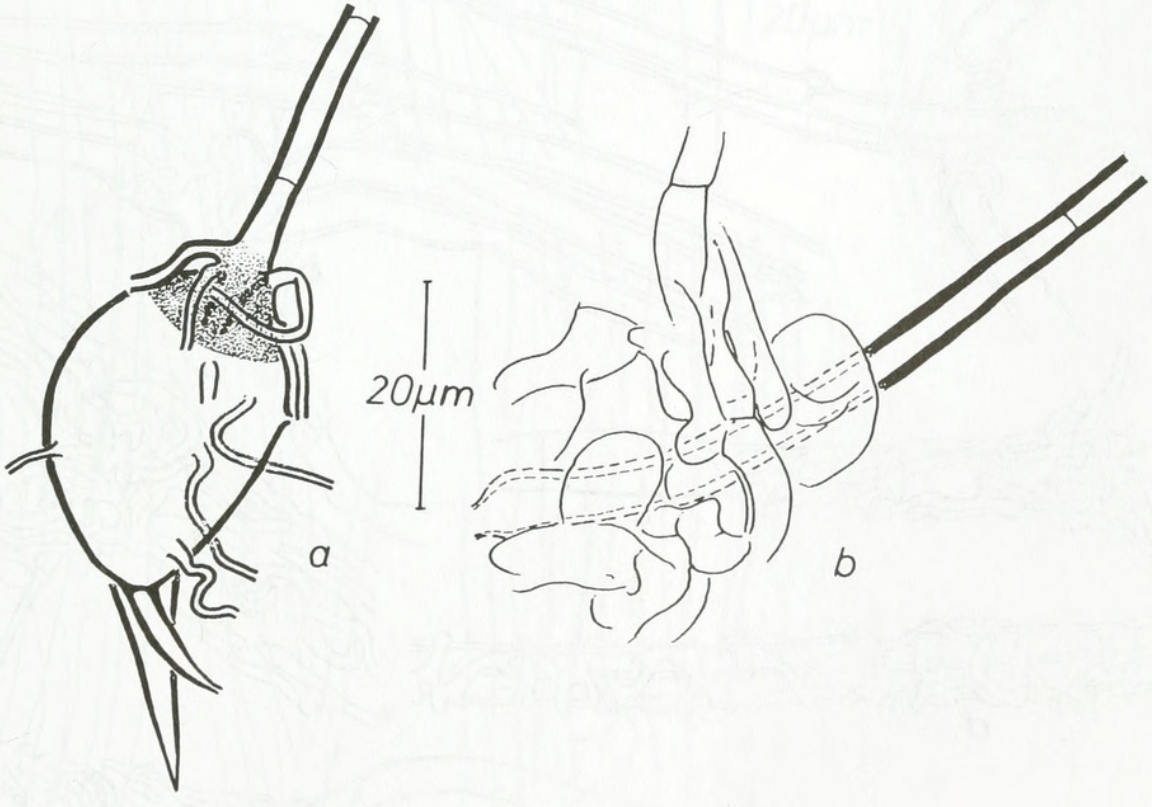

Fig. 6

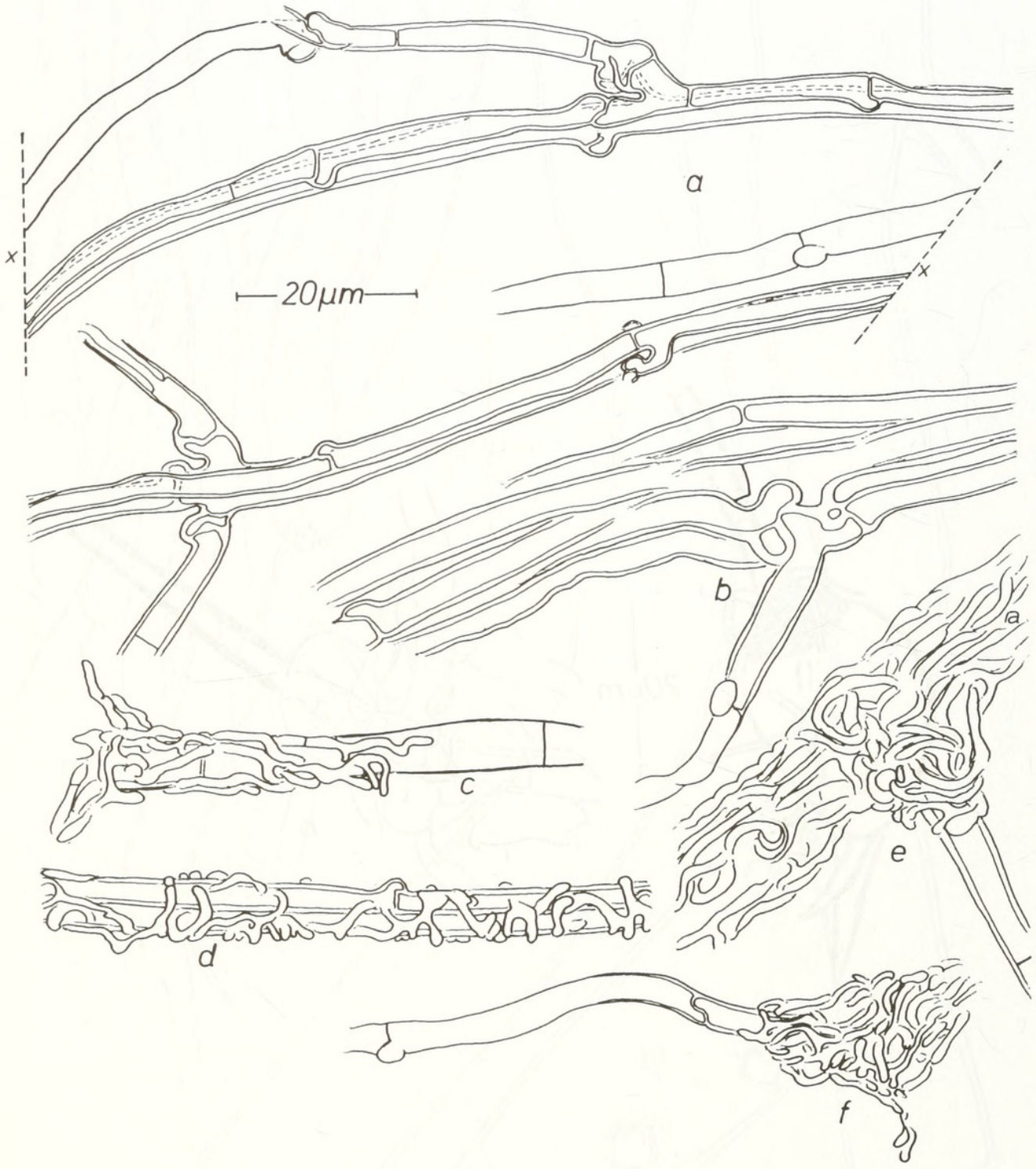

Fig. 7

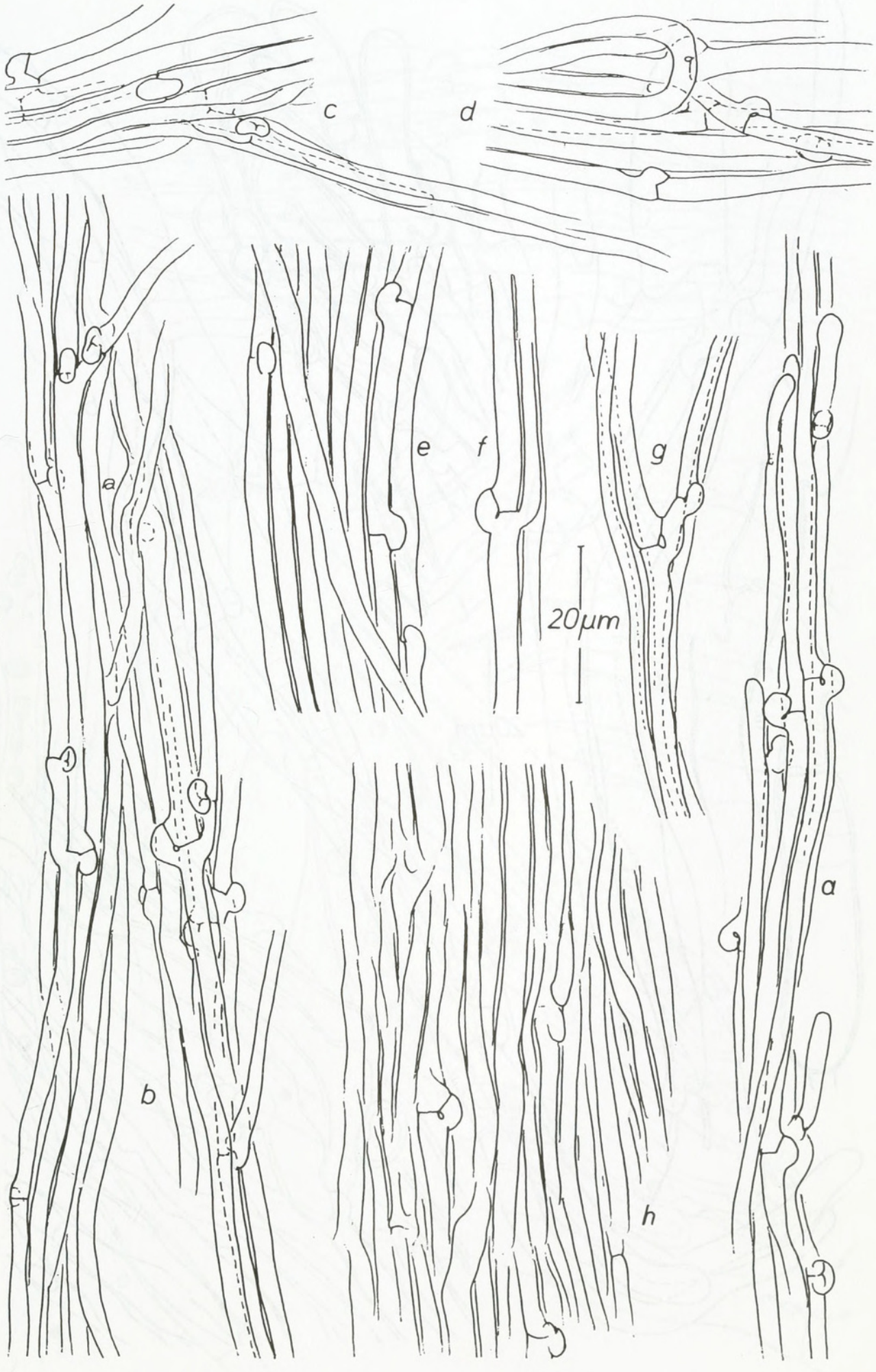

Fig. 8

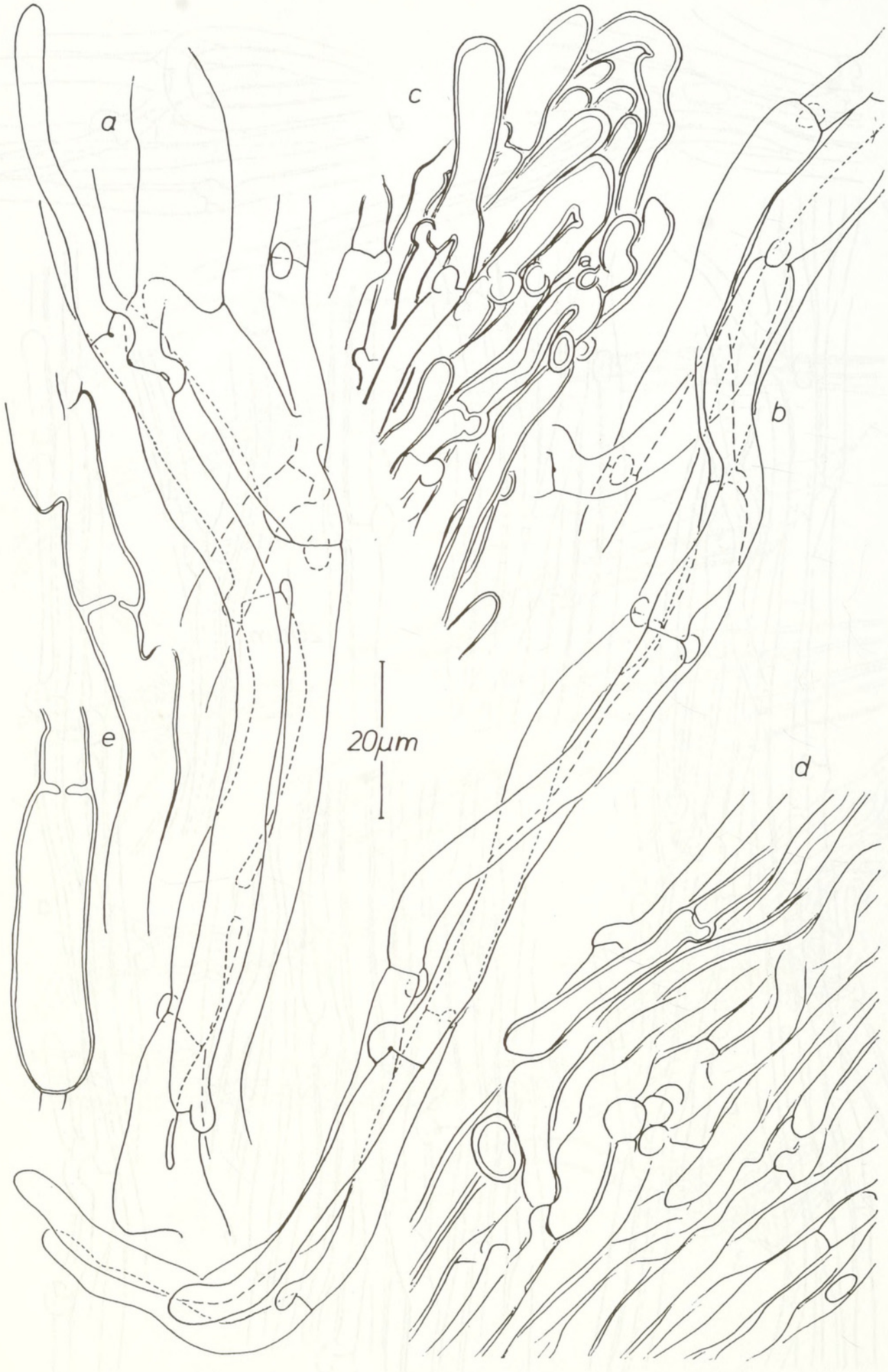

Fig. 9

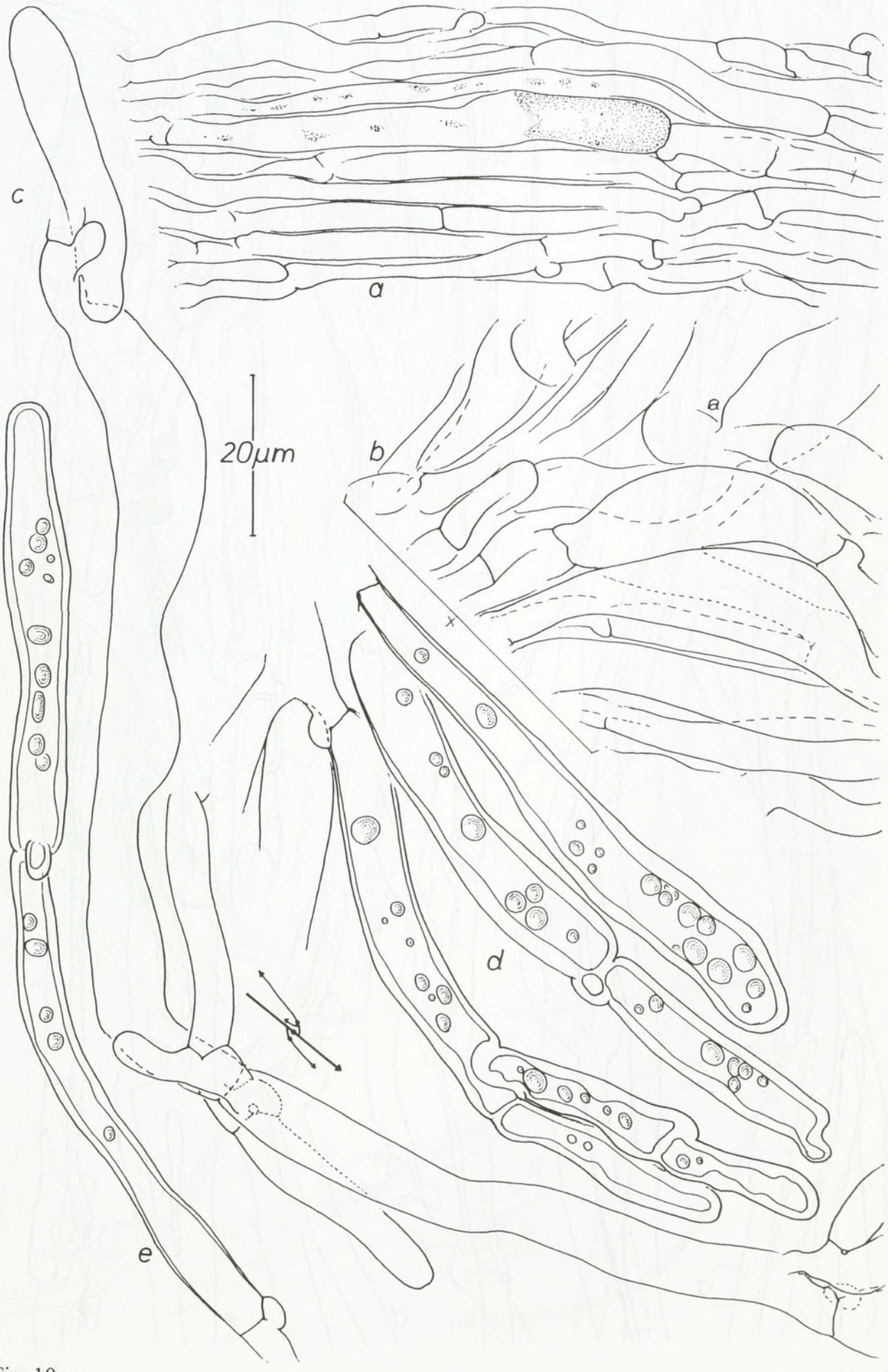

Fig. 10

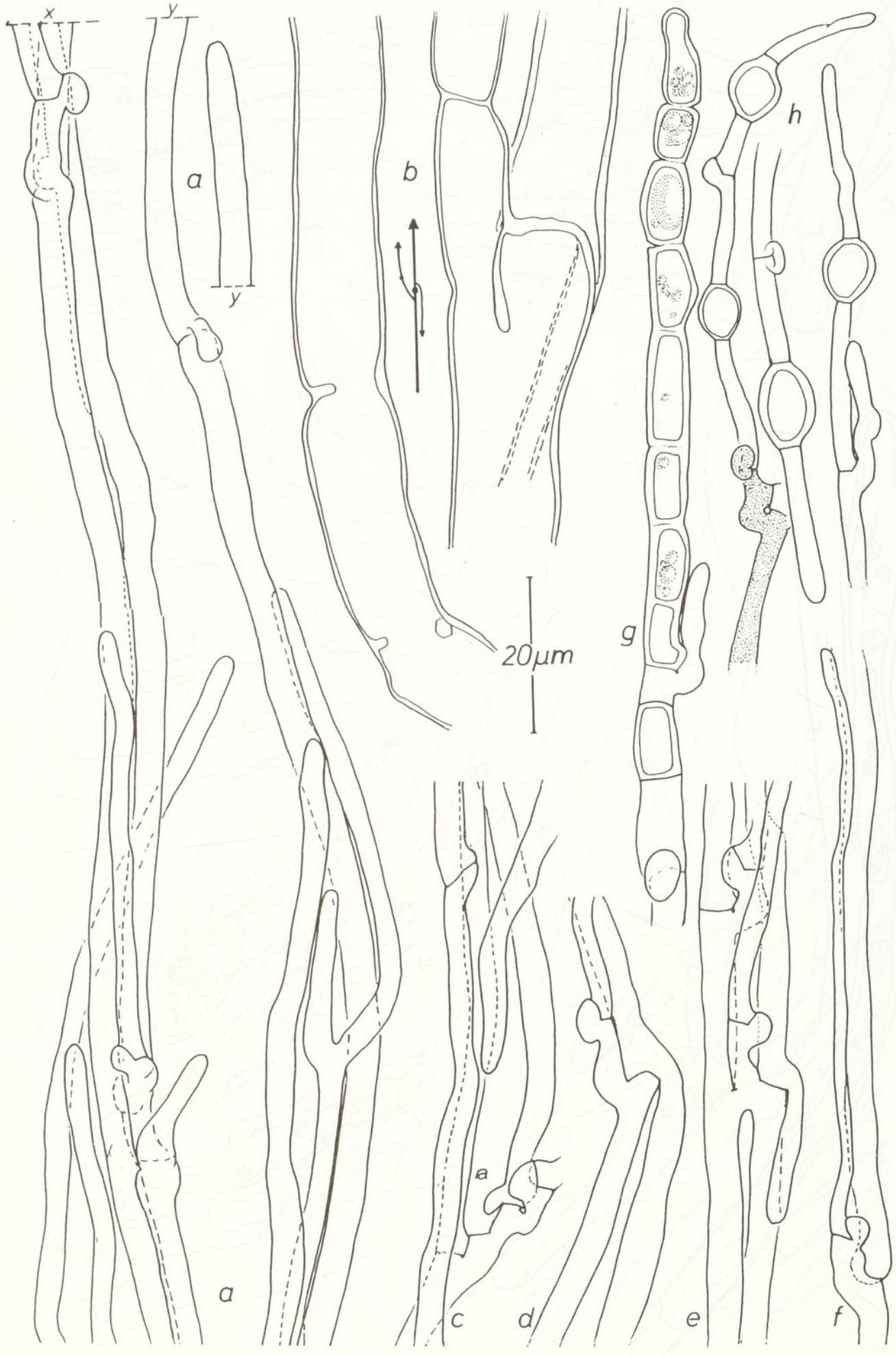

Fig. 11

Fig. 12

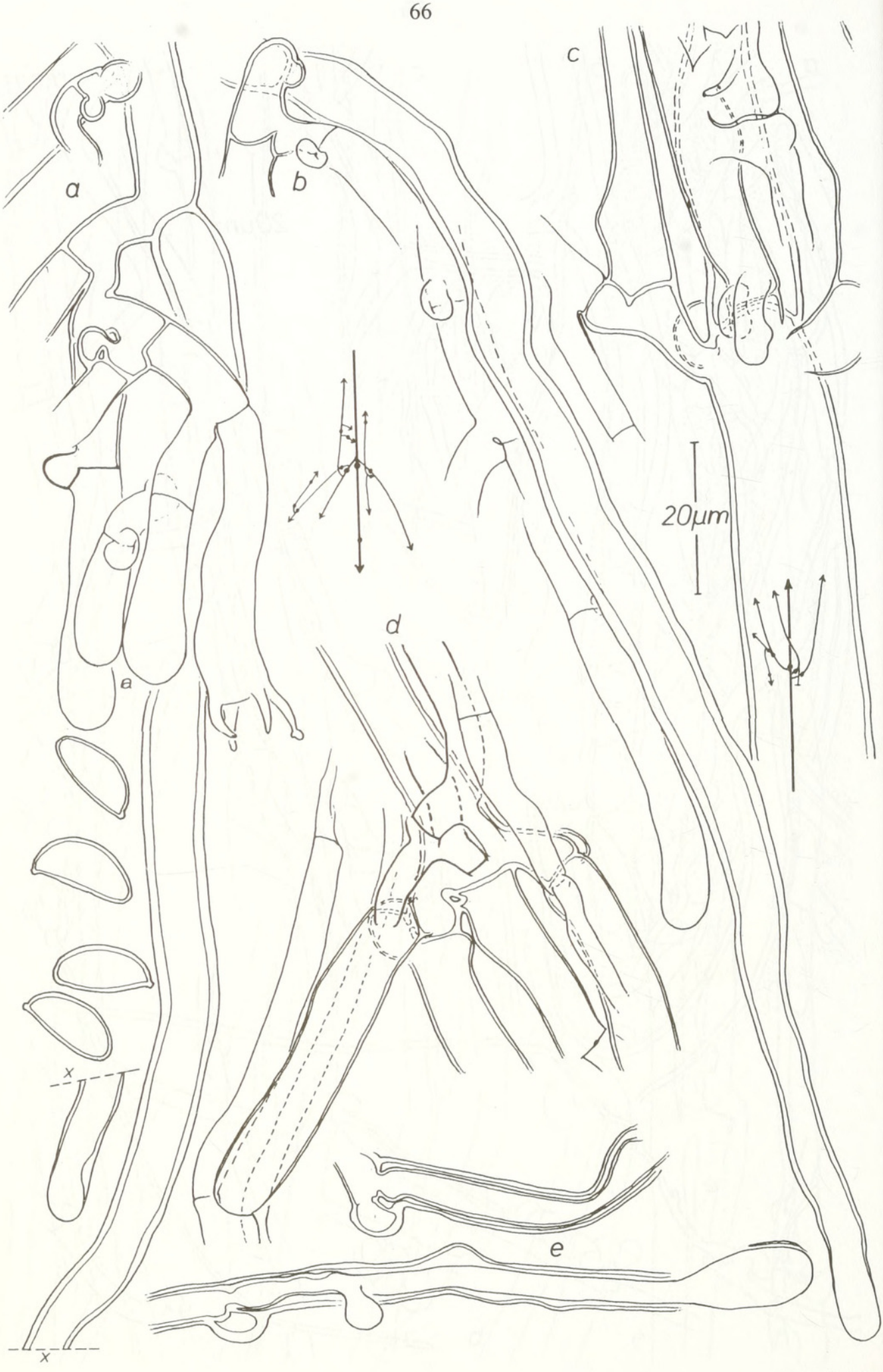

Fig. 13

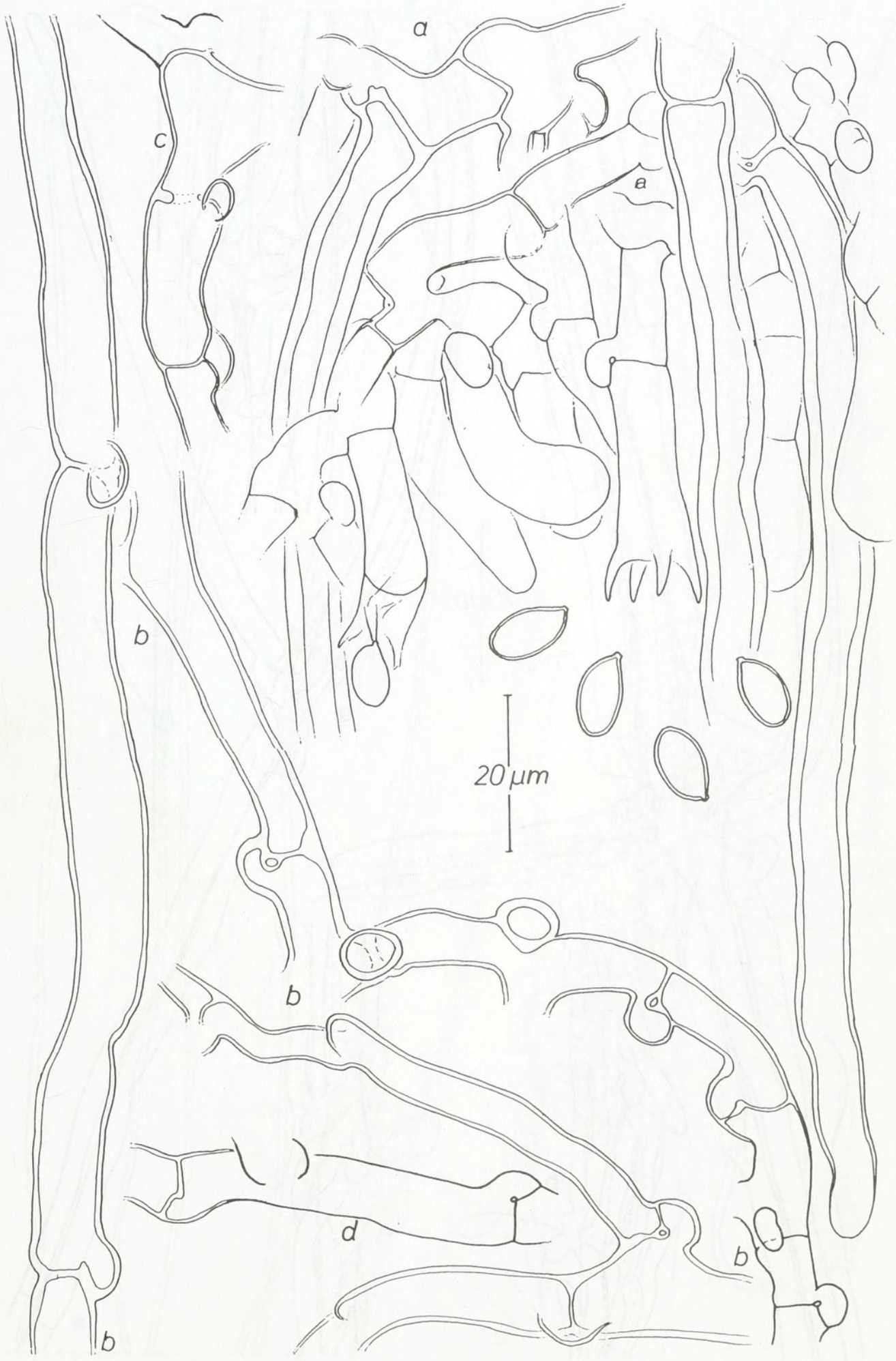

Fig. 14

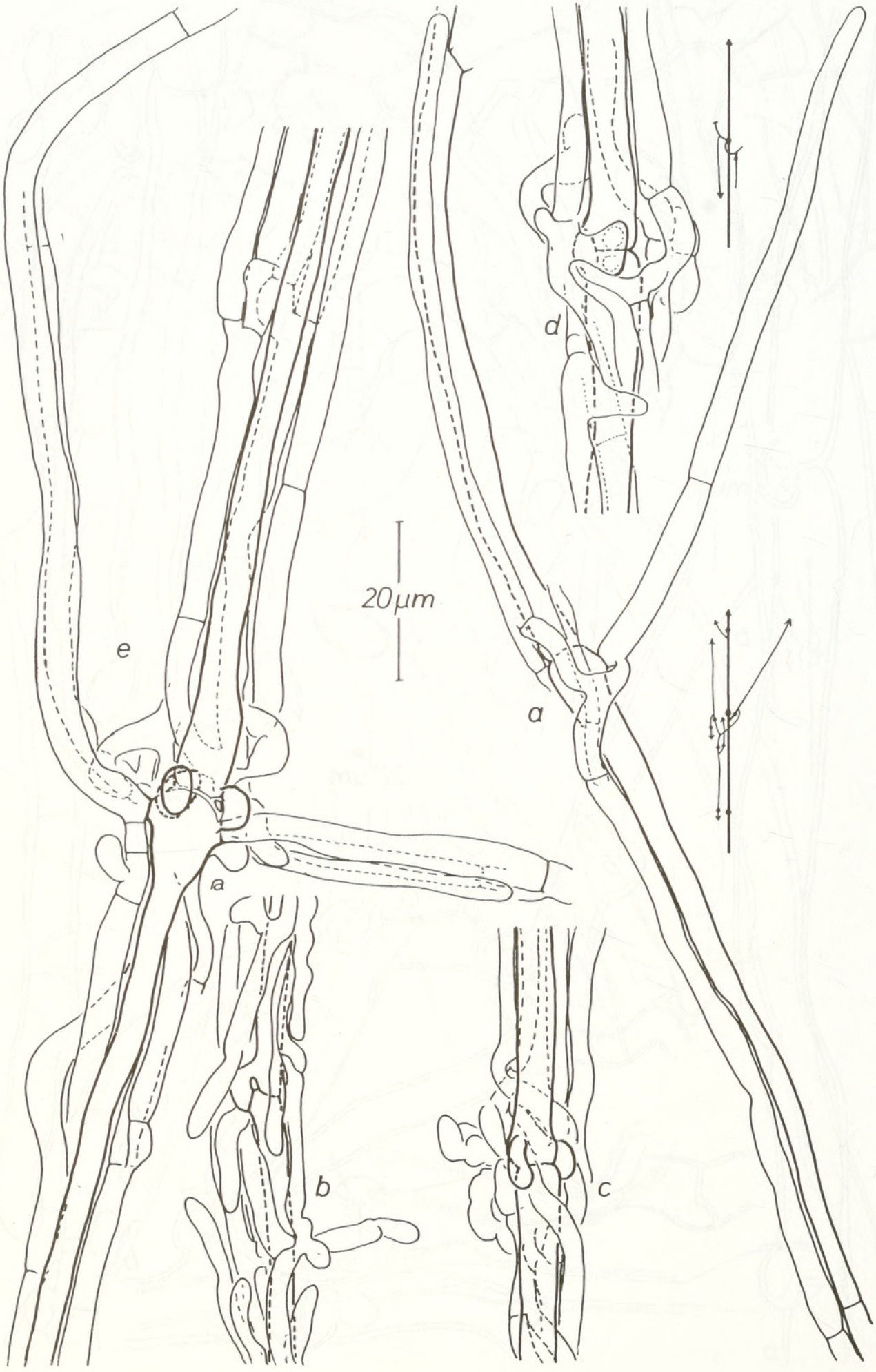

Fig. 15

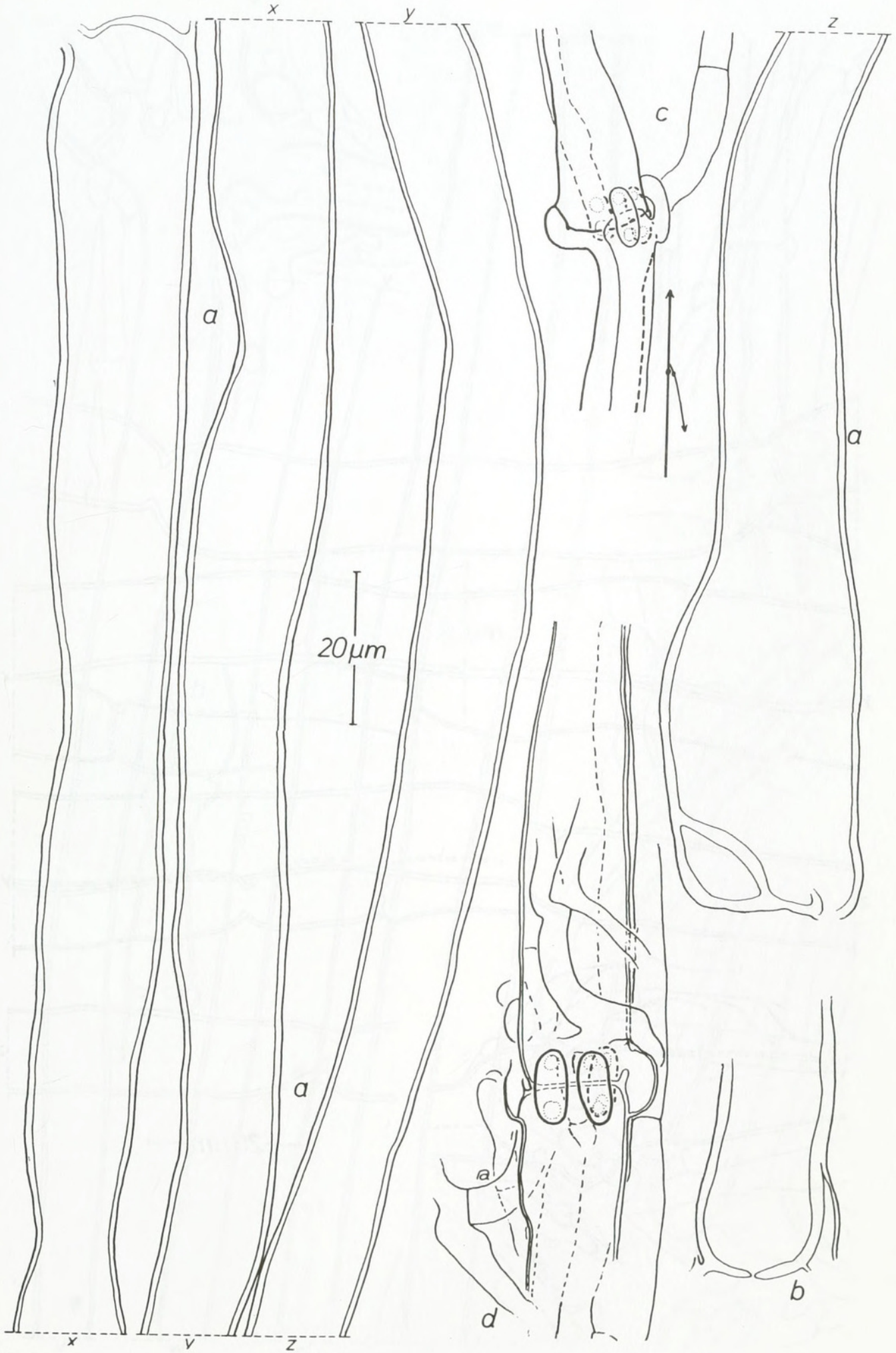

Fig. 16

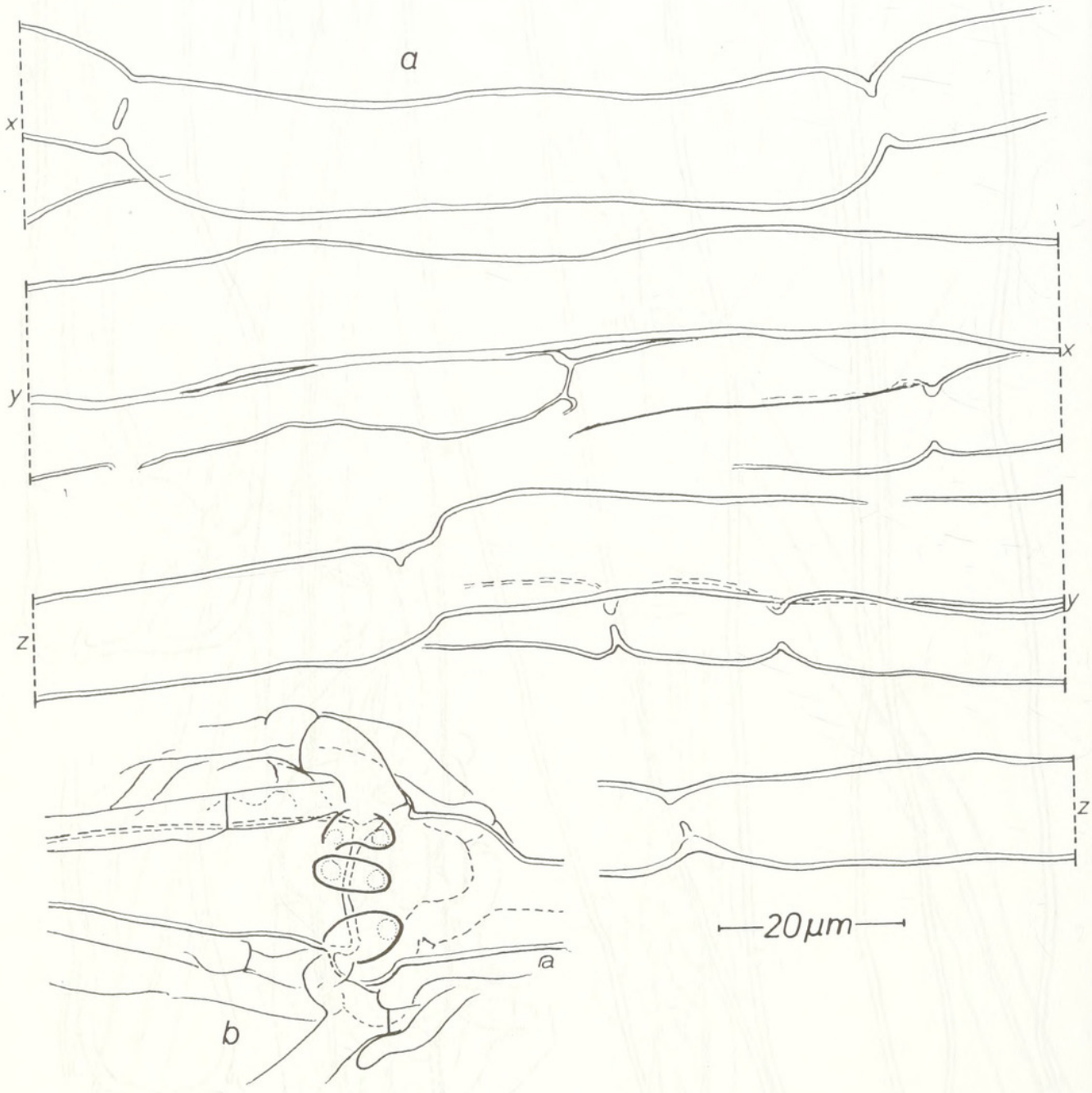

Fig. 17

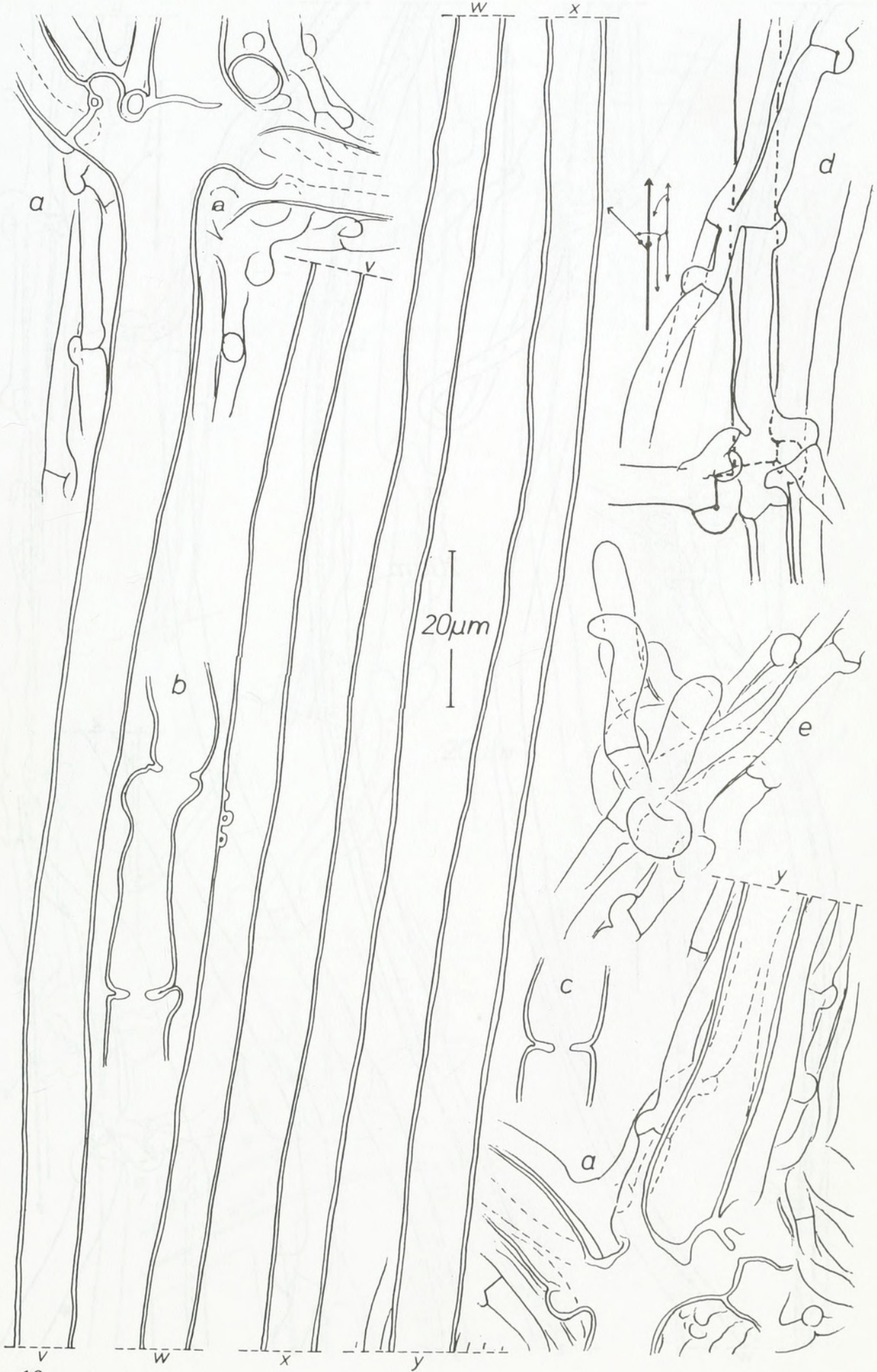

Fig. 18

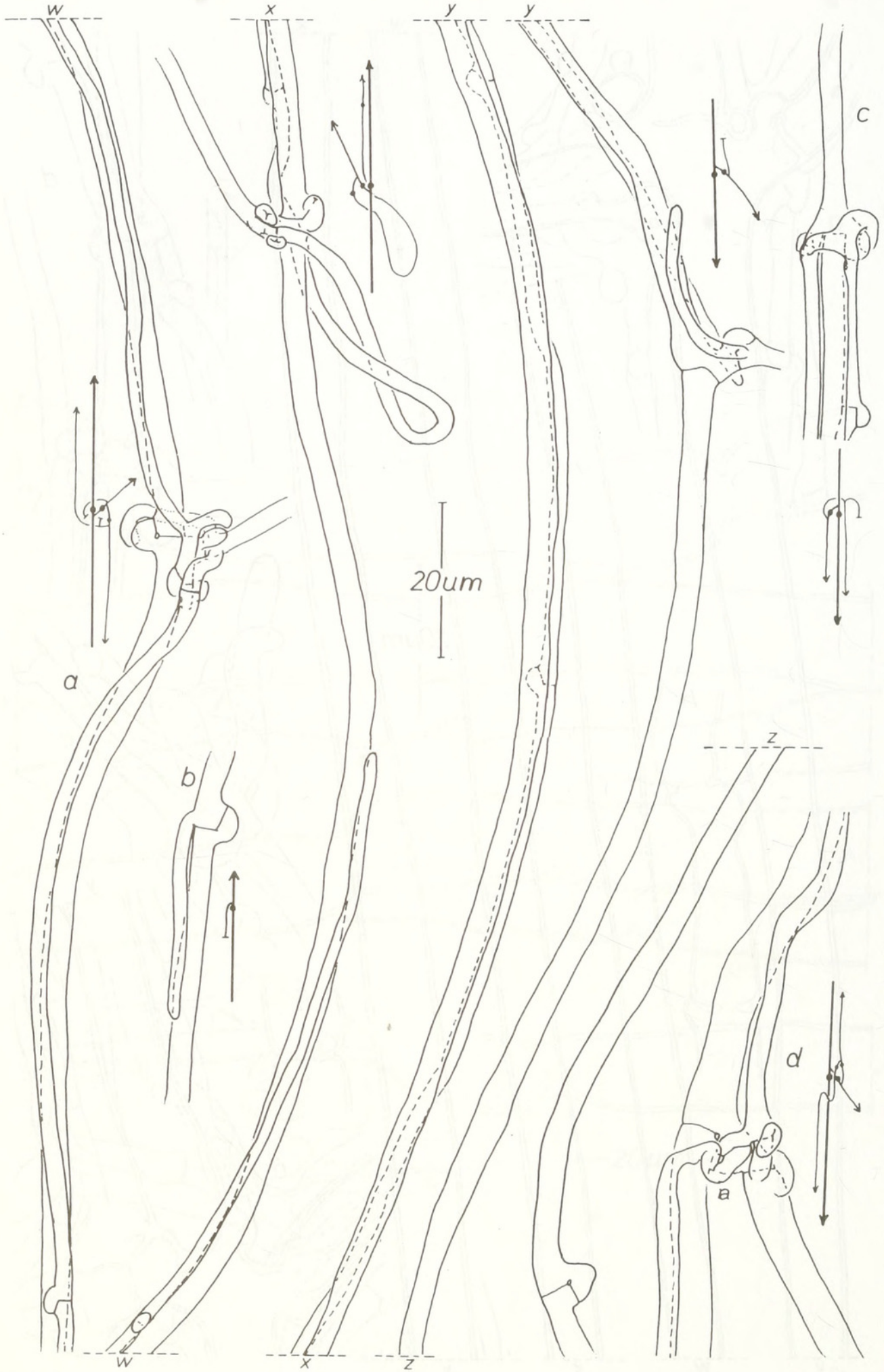

Fig. 19

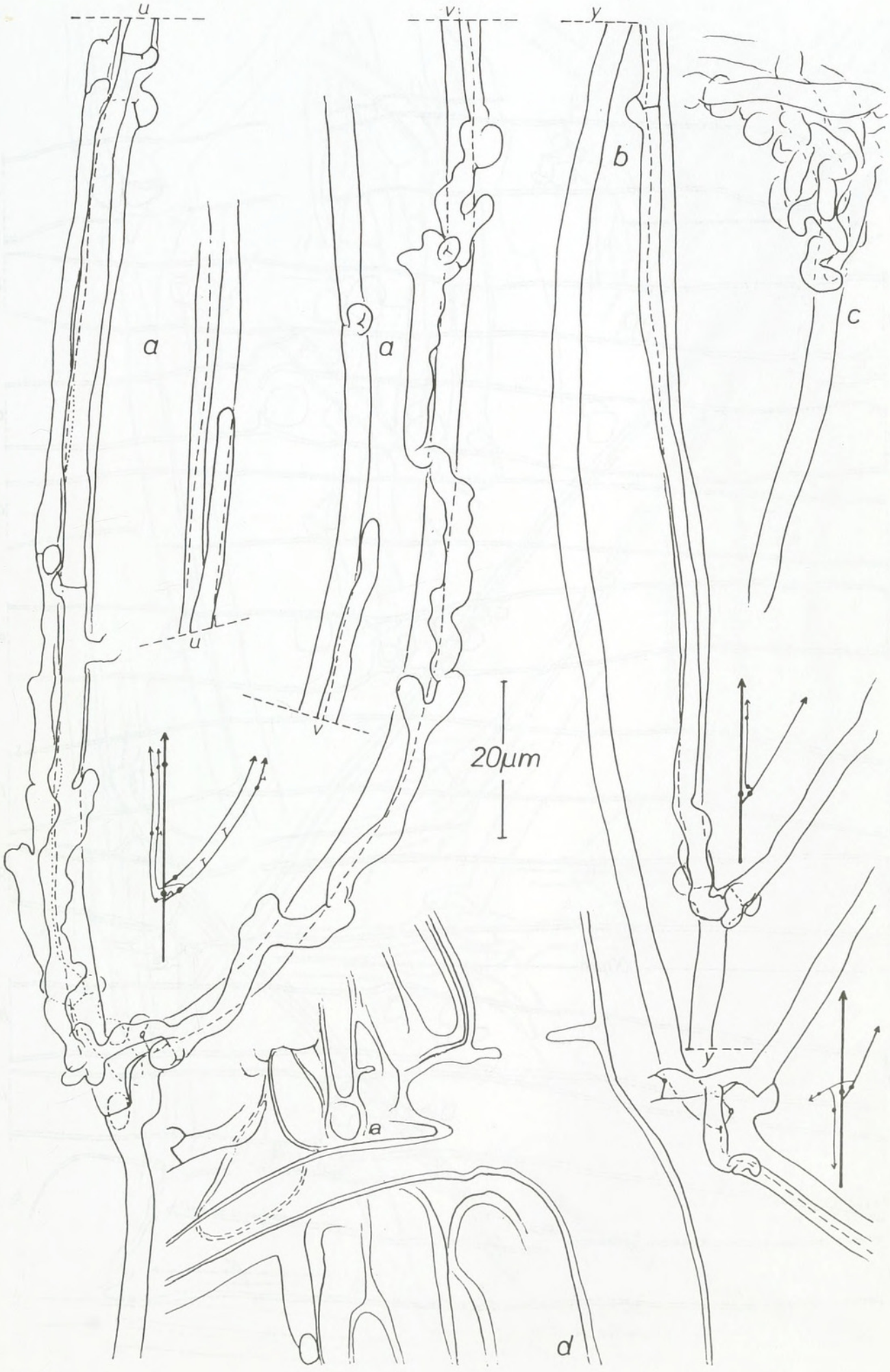

Fig. 20

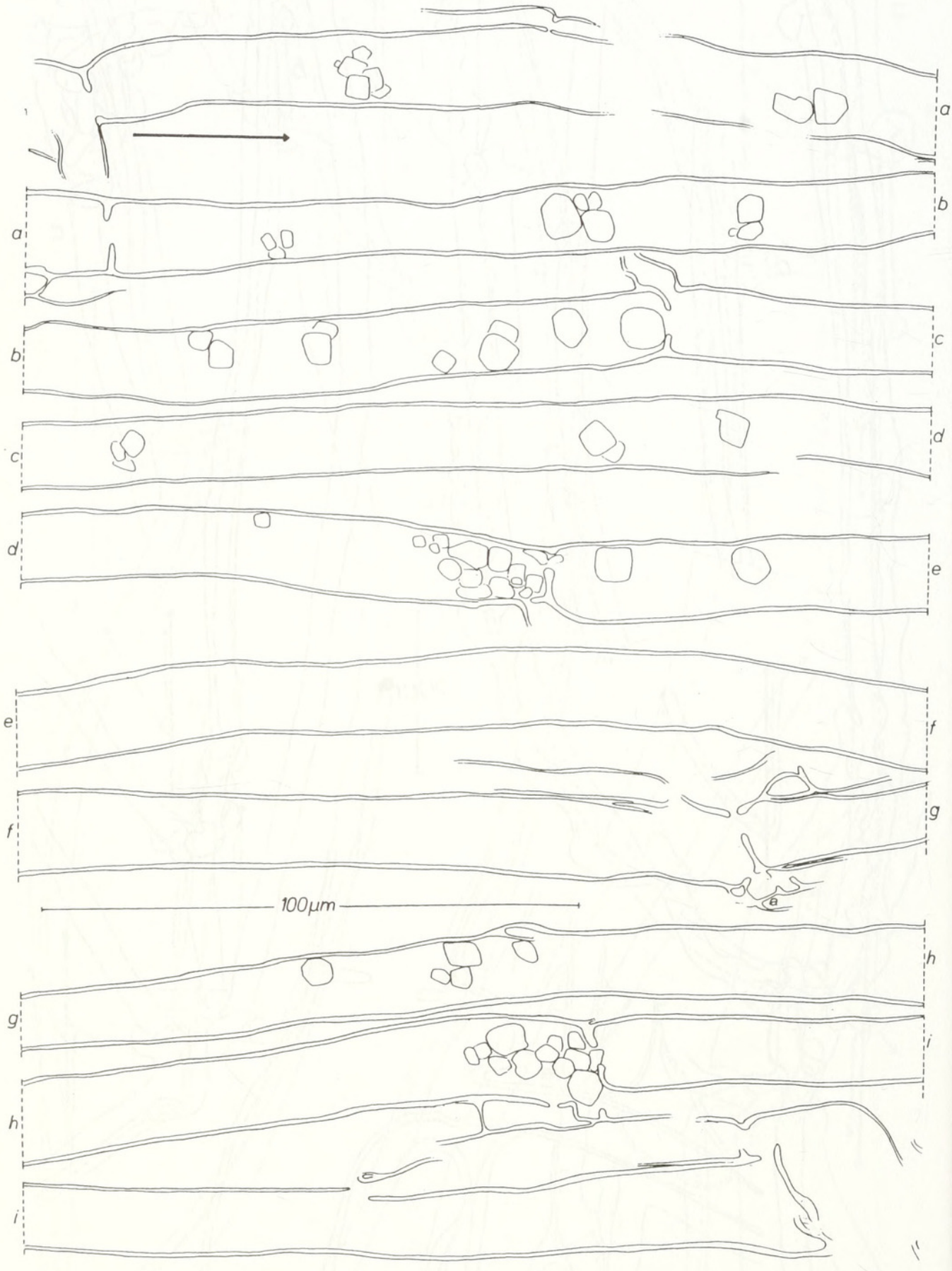

Fig. 21

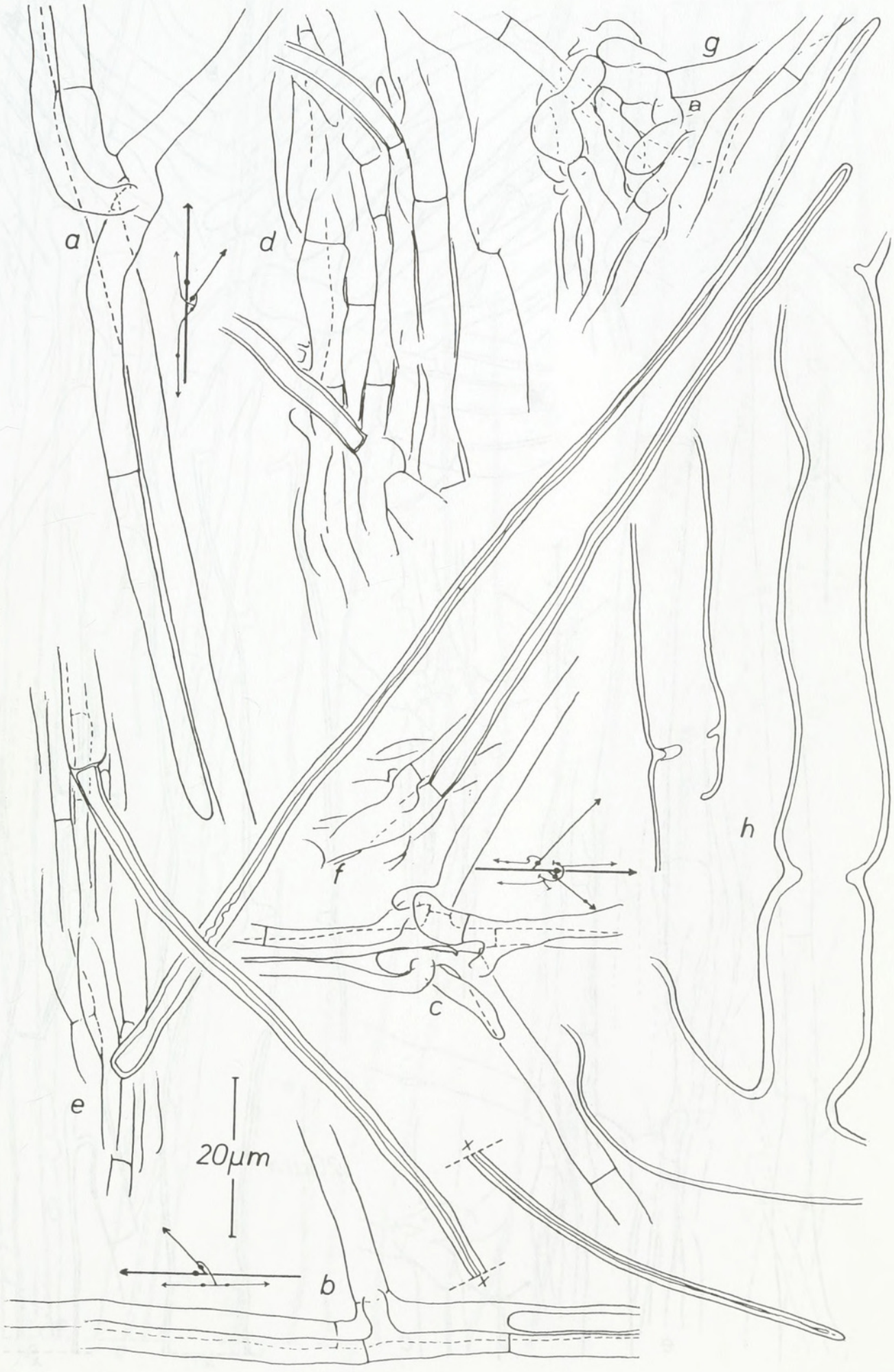

Fig. 22

Fig. 23

Fig. 24

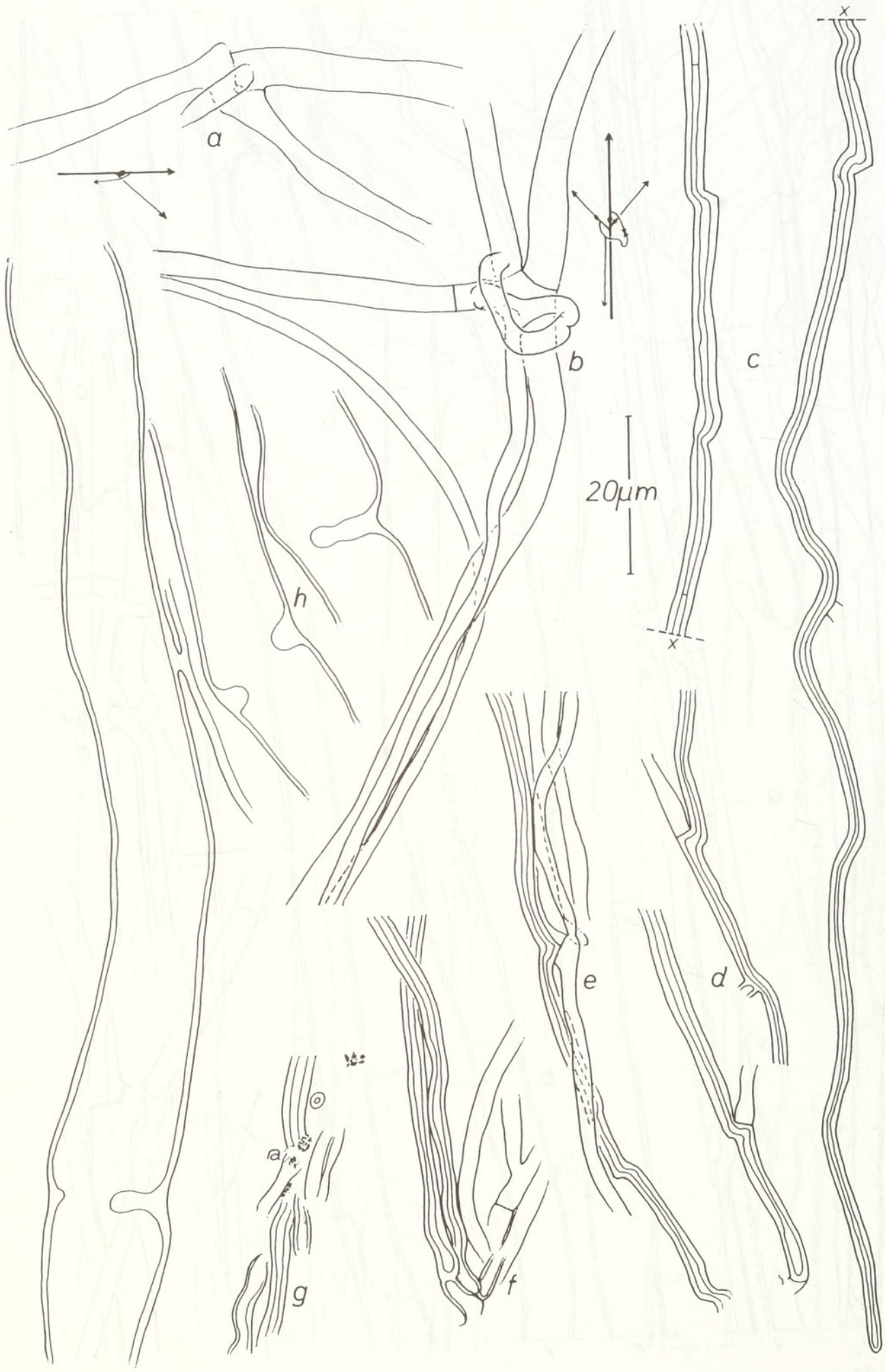

Fig. 25

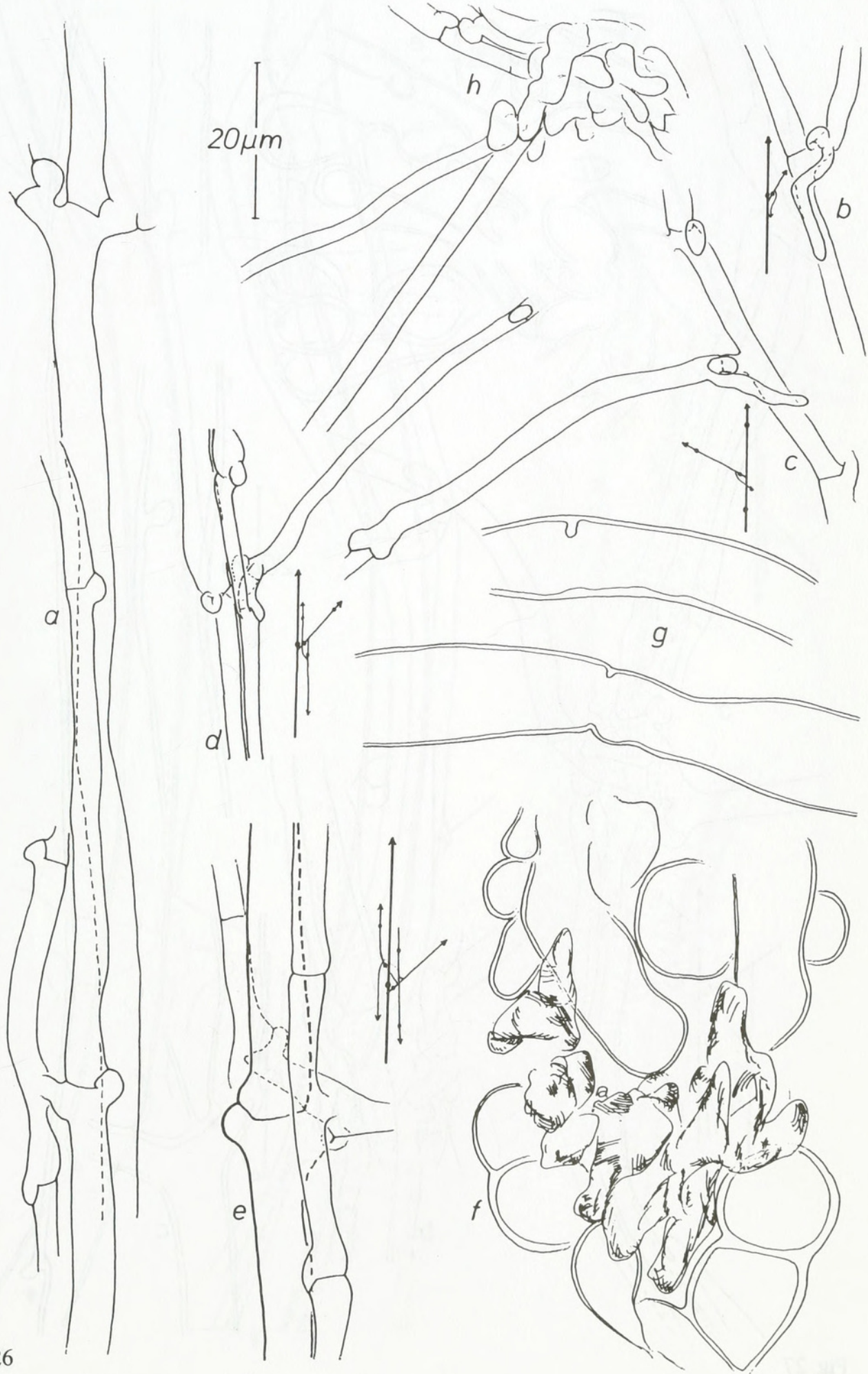

Fig. 26

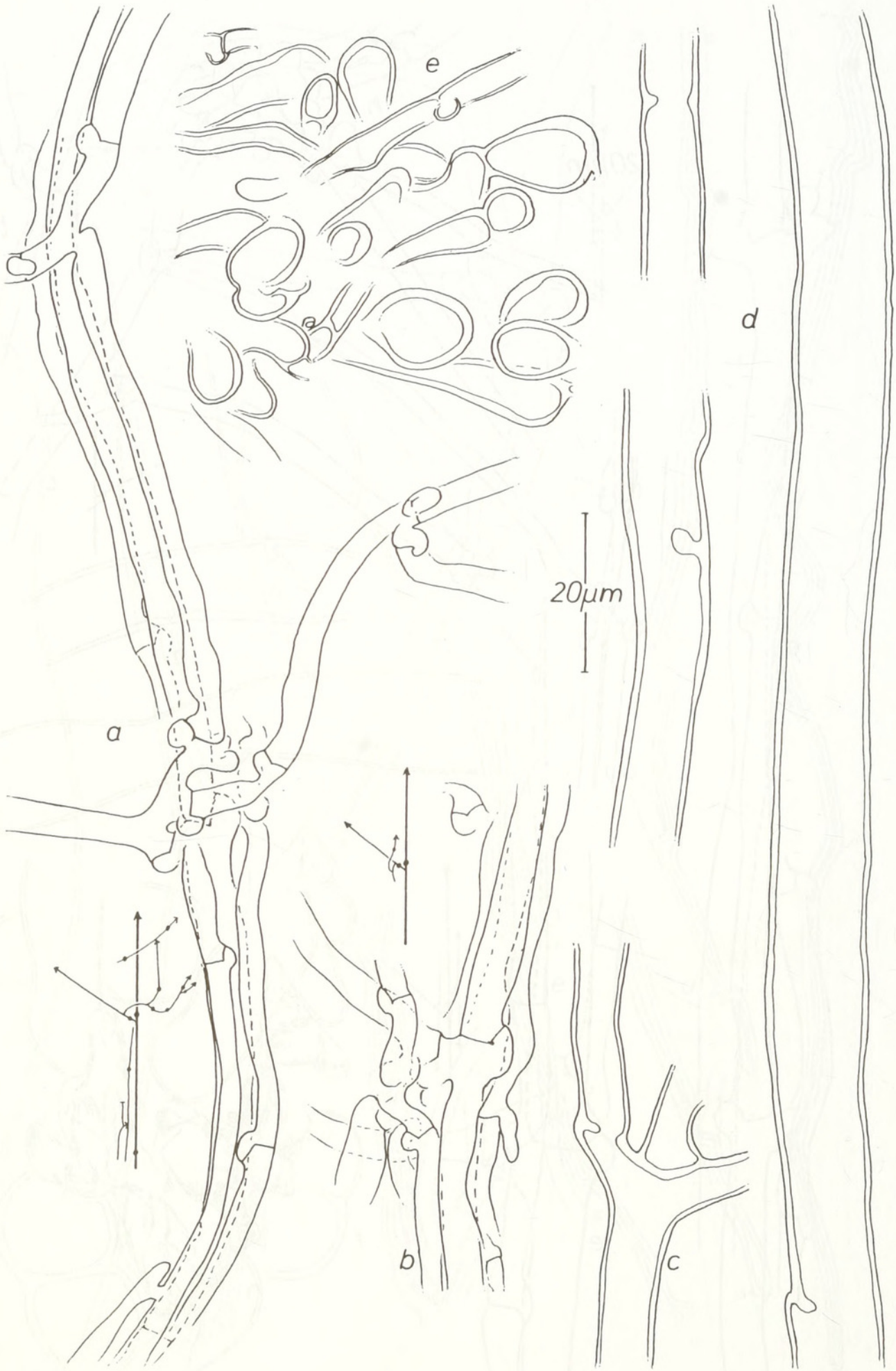

Fig. 27

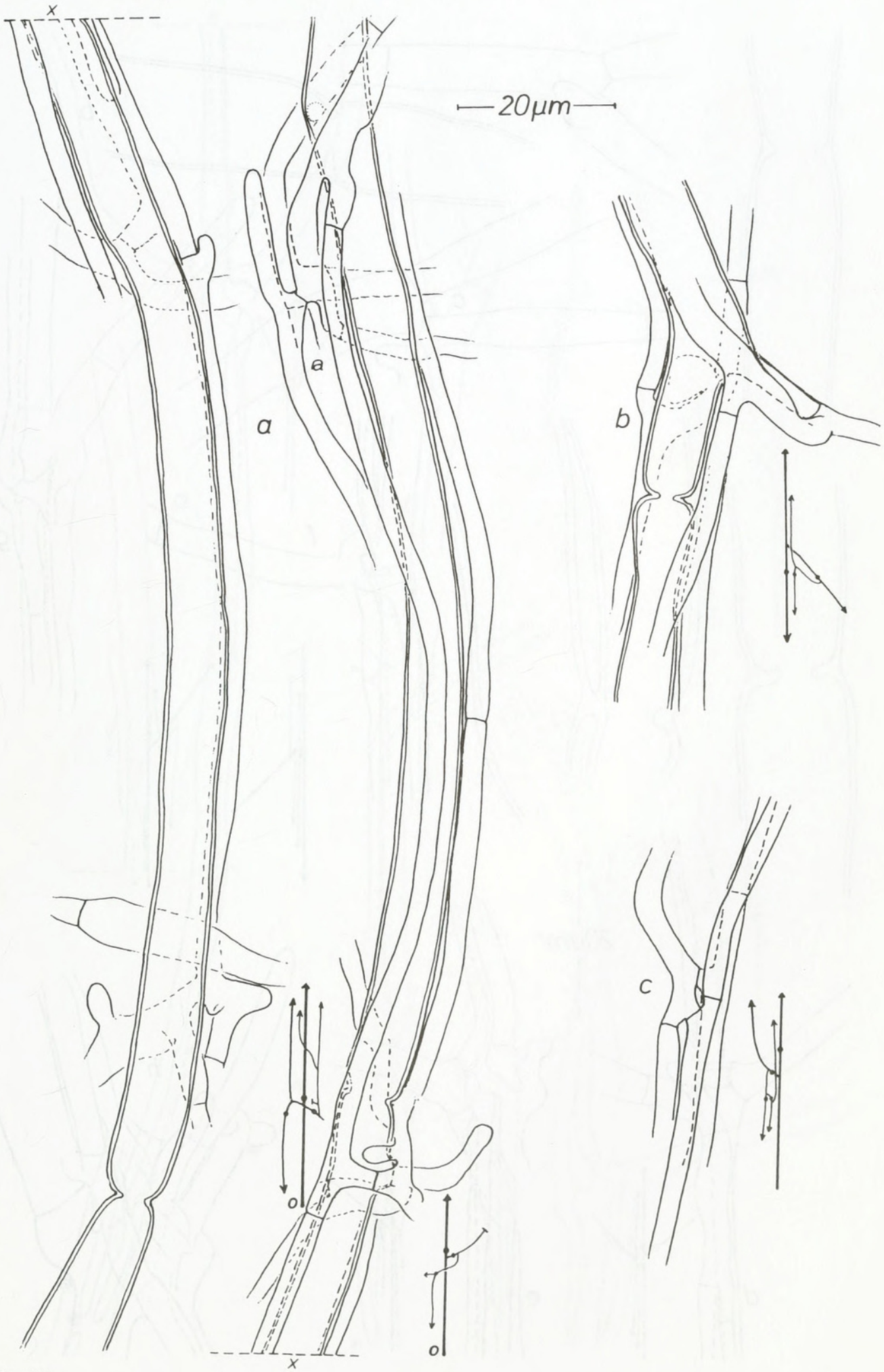

Fig. 28

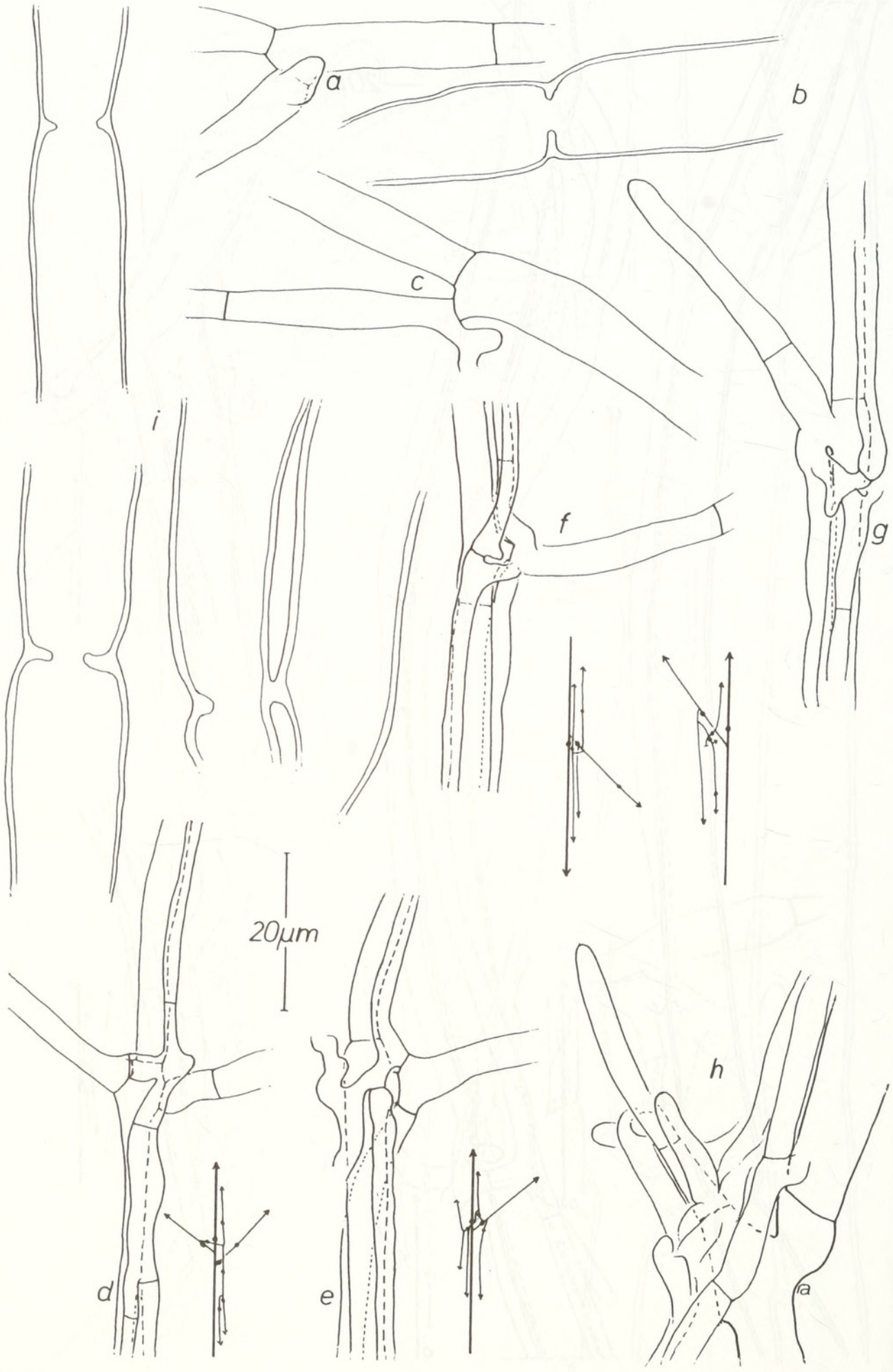

Fig. 29

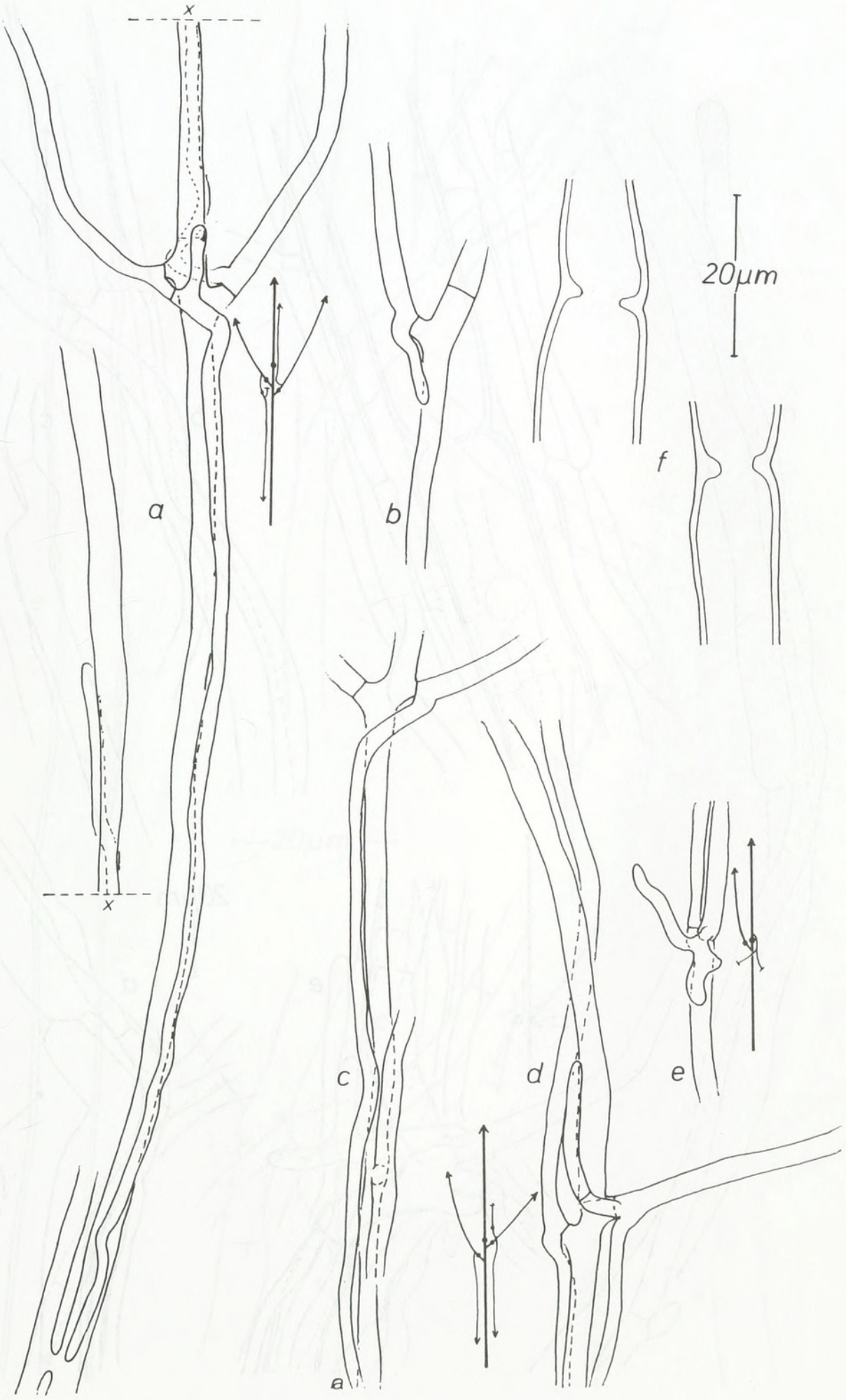

Fig. 30

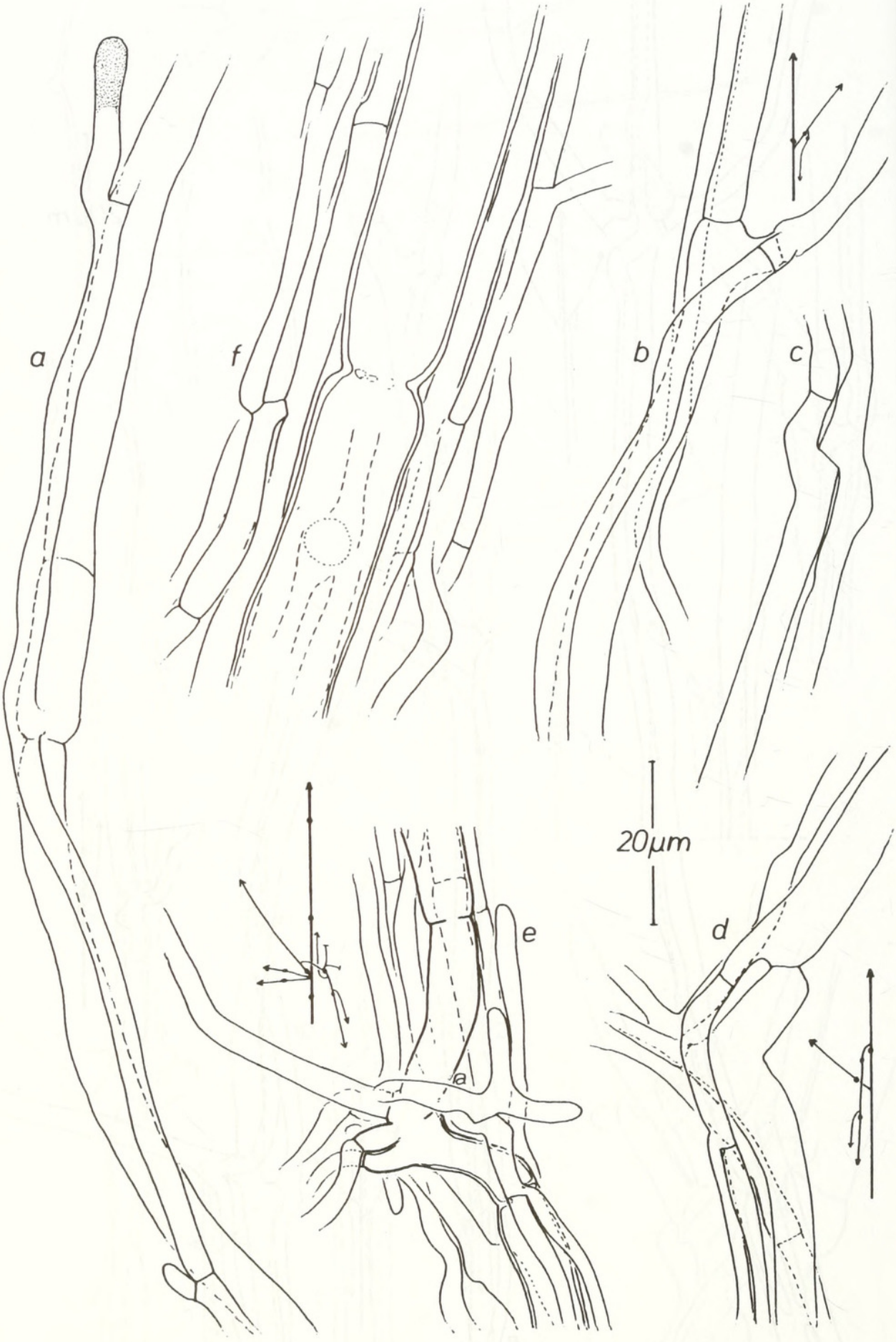

Fig. 31

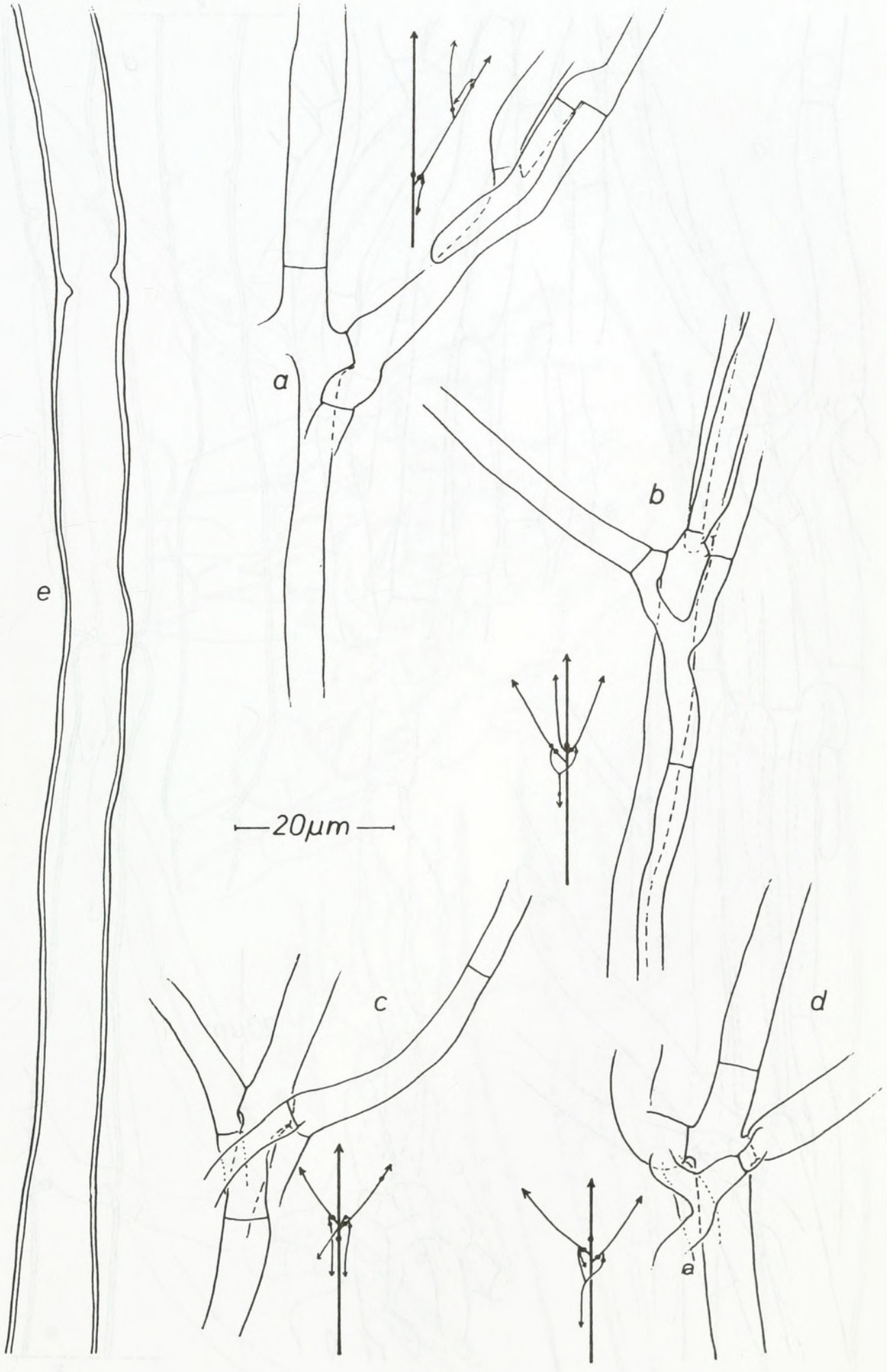

Fig. 32

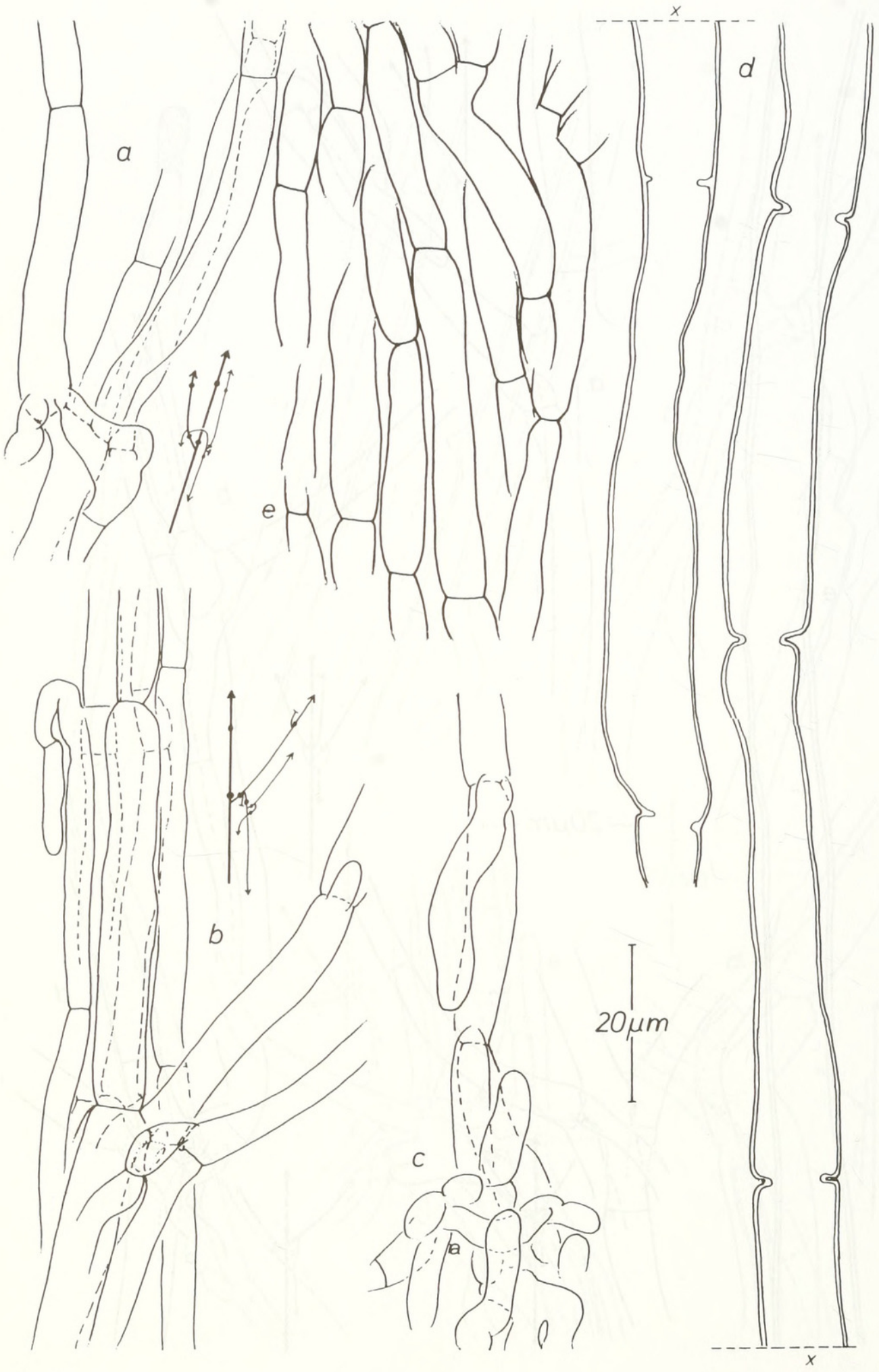

Fig. 33

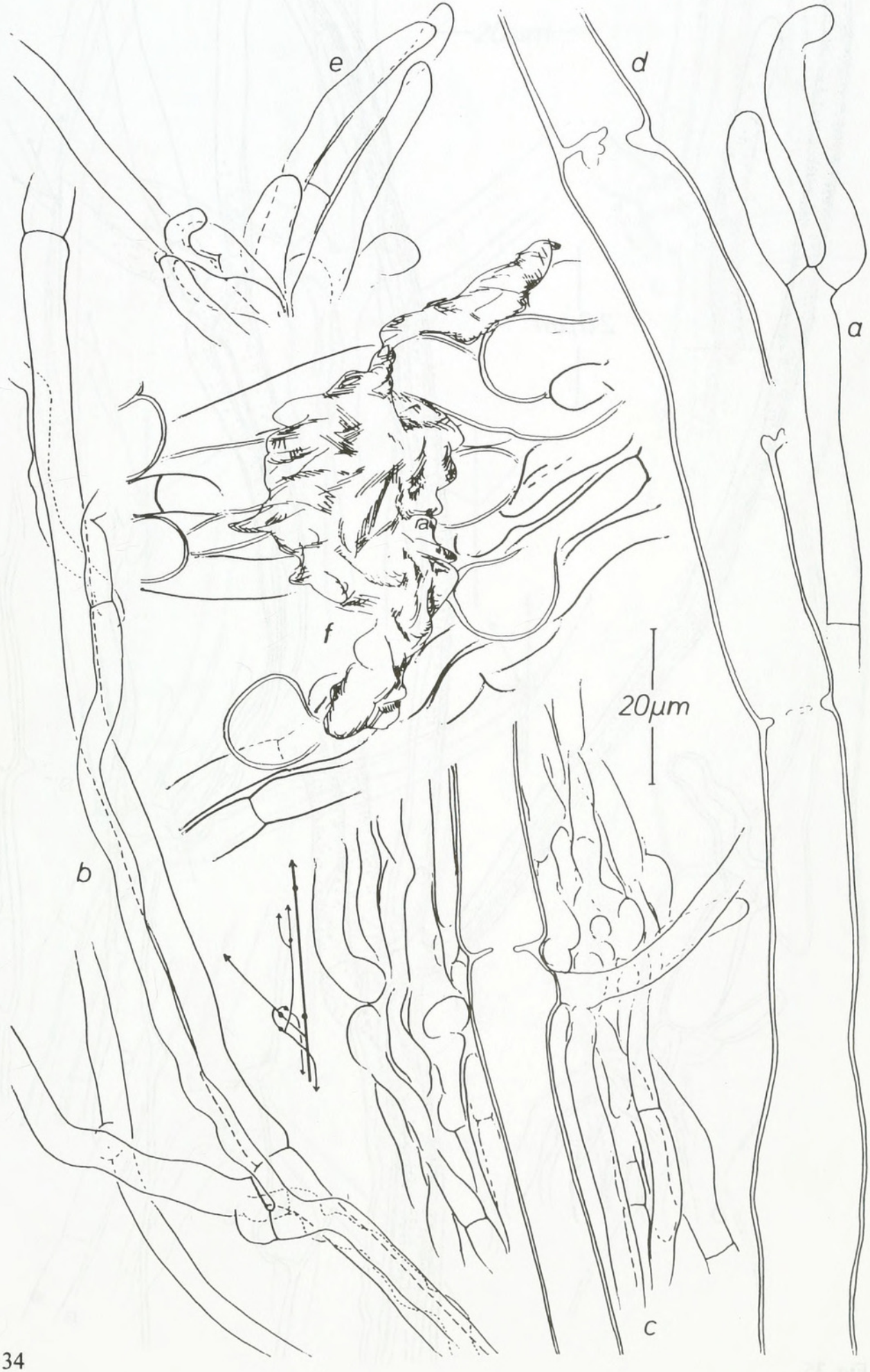

Fig. 34

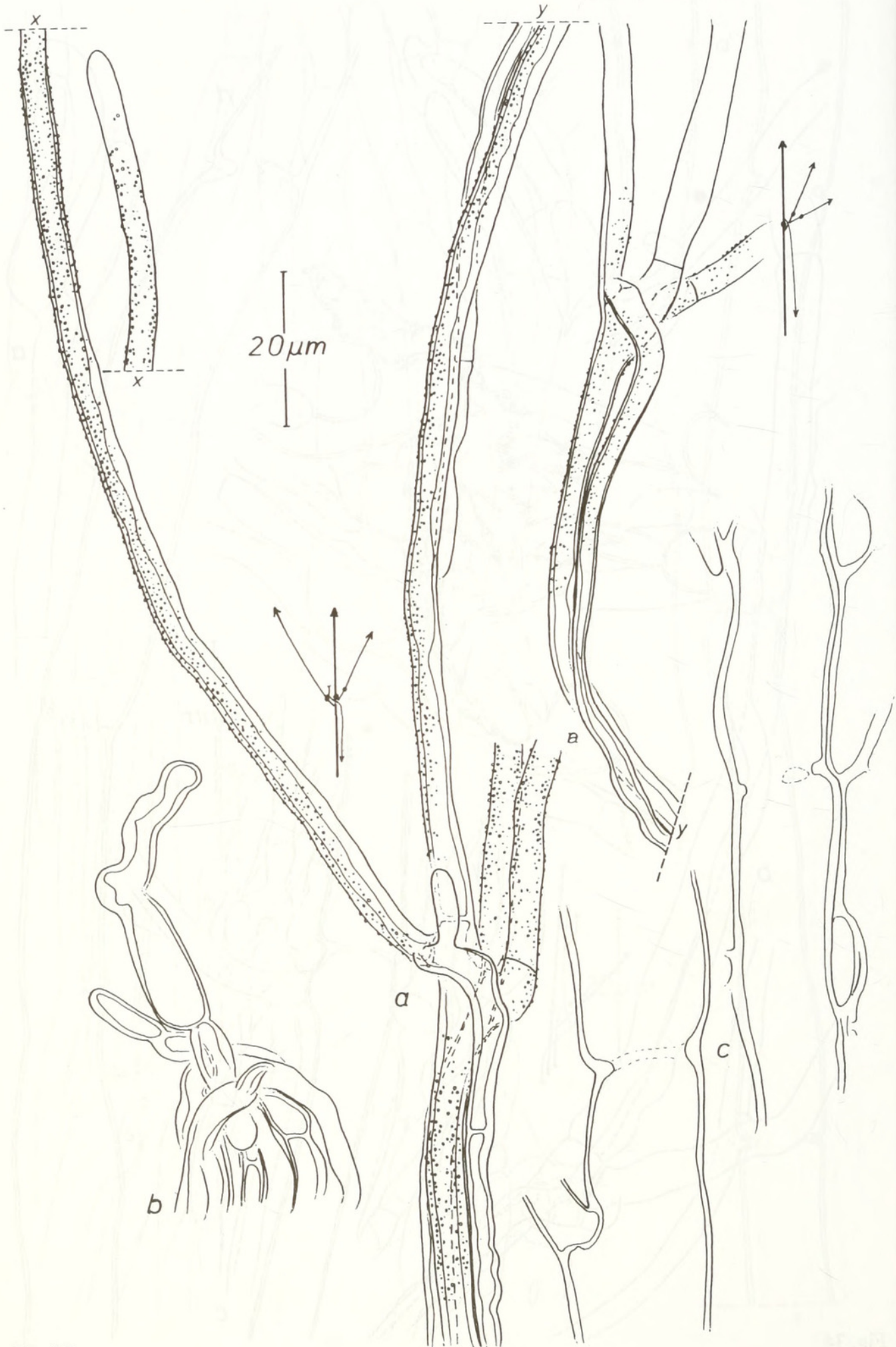

Fig. 35

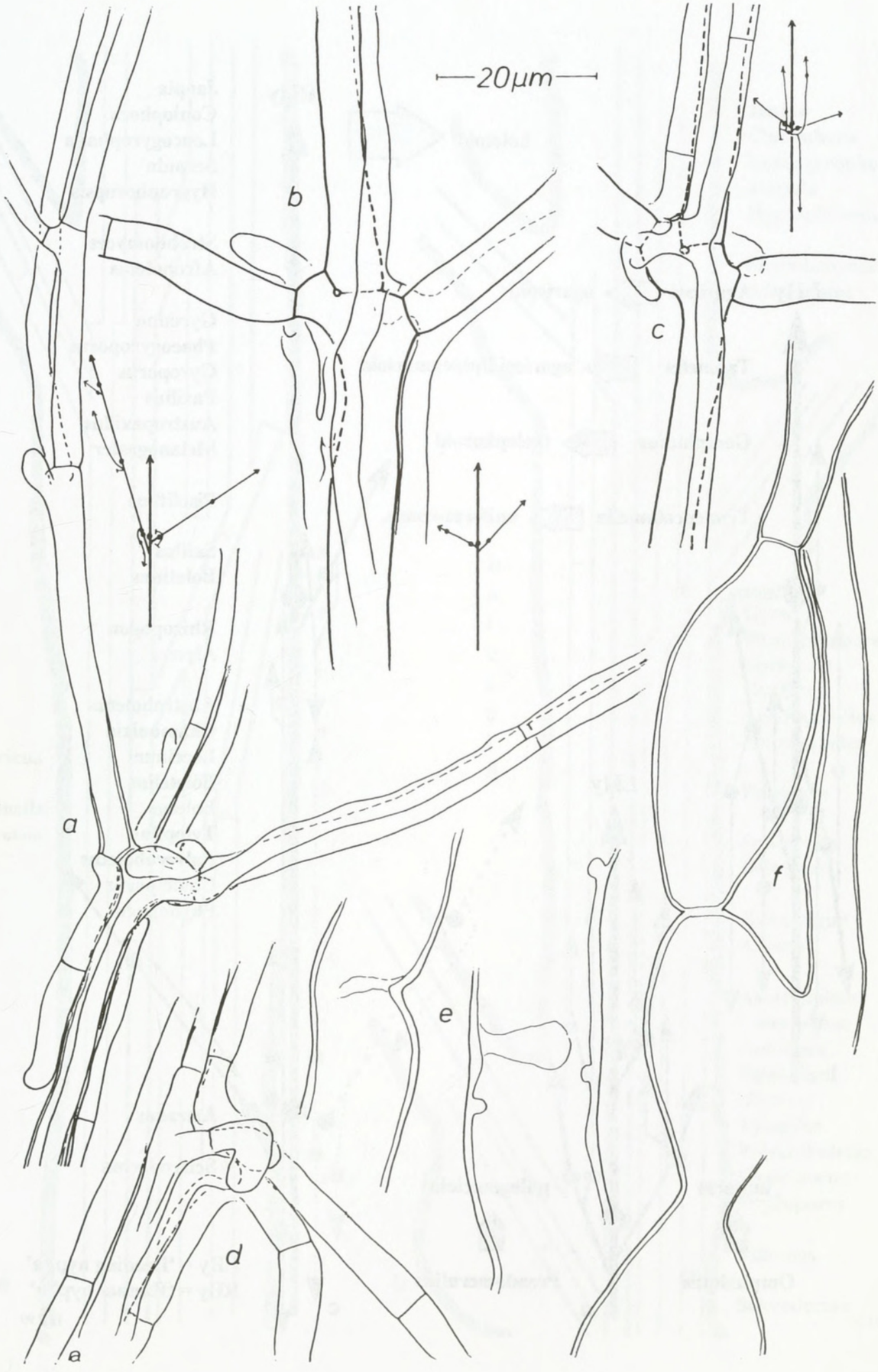

Fig. 36

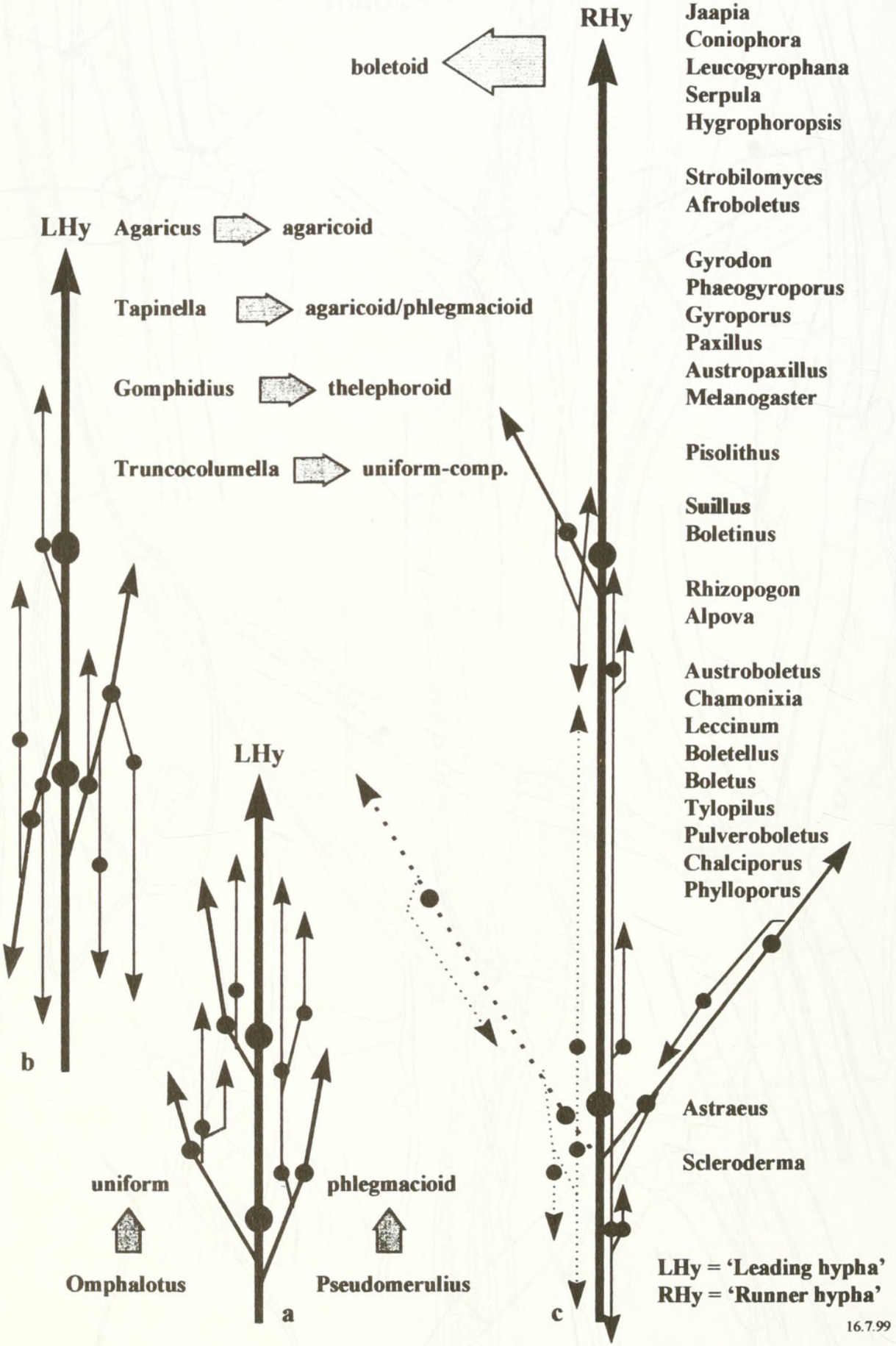
RHy
boletoid
Jaapia
Coniophora
Leucogyrophana
Serpula
Hygrophoropsis
Strobilomyces
Afroboletus
LHy
Agaricus
agaricoid
Gyrodon
Phaeogyroporus
Gyroporus
Paxillus
Austropaxillus
Melanogaster
Tapinella
agaricoid/phlegmacioid
Gomphidius
thelephoroid
Truncocolumella
uniform-comp.
Pisolithus
Suillus
Boletinus
Rhizopogon
Alpova
Austroboletus
Chamonixia
Leccinum
Boletellus
Boletus
Tylopilus
Pulveroboletus
Chalciporus
Phylloporus
LHy
b
Astraeus
Scleroderma
uniform
phlegmacioid
Omphalotus
Pseudomerulius
a
c
LHy = 'Leading hypha'
RHy = 'Runner hypha'
16.7.99

Fig. 37

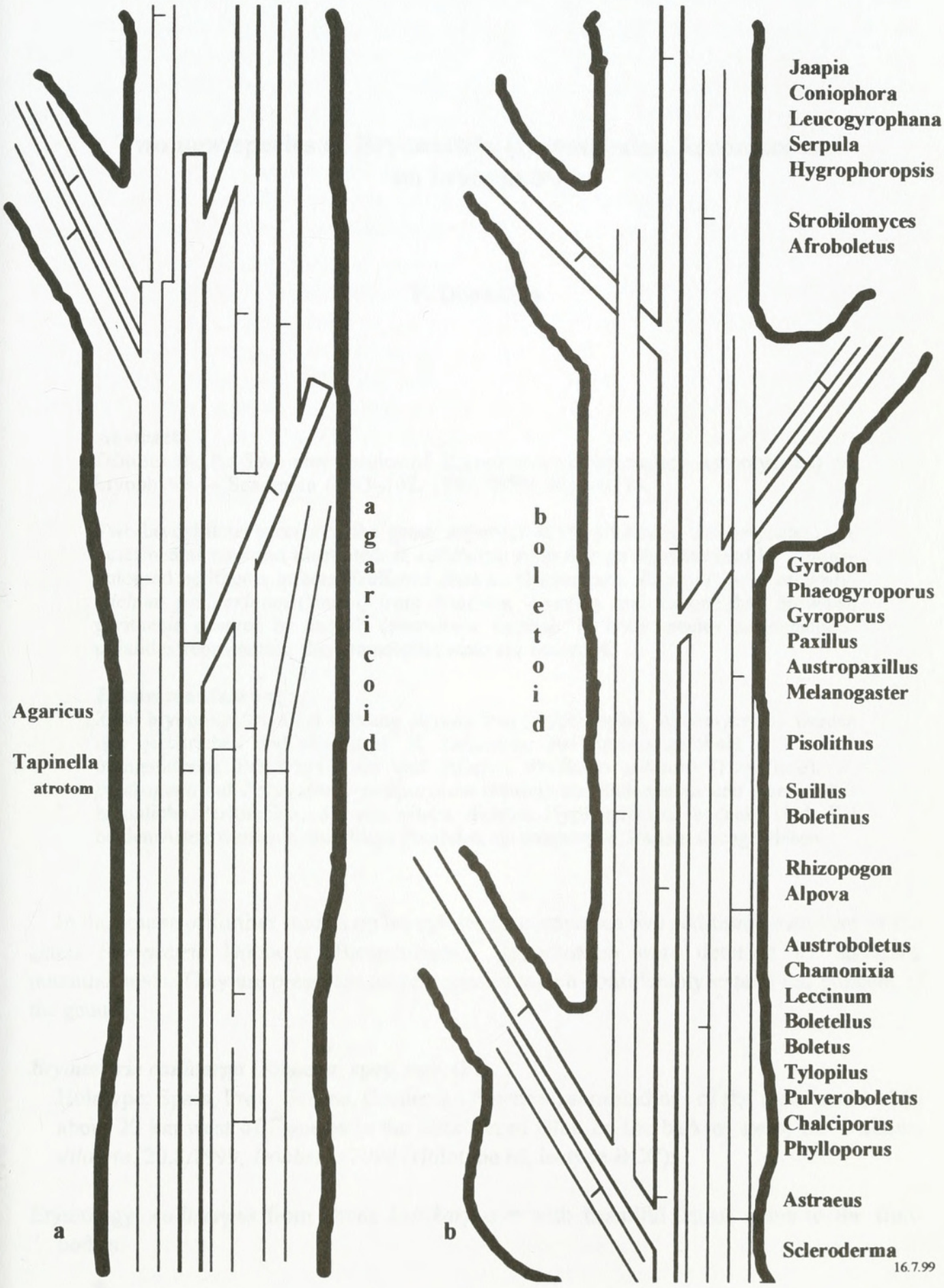
agaricoid
Agaricus
Tapinella
atrotom
a
boletoid
Jaapia
Coniophora
Leucogyrophana
Serpula
Hygrophoropsis
Strobilomyces
Afroboletus
Gyrodon
Phaeogyroporus
Gyroporus
Paxillus
Austropaxillus
Melanogaster
Pisolithus
Suillus
Boletinus
Rhizopogon
Alpova
Austroboletus
Chamonixia
Leccinum
Boletellus
Boletus
Tylopilus
Pulveroboletus
Chalciporus
Phylloporus
Astraeus
Scleroderma
b
16.7.99

Fig. 38