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# Degradation of human hair by three soil fungi. An electron microscopic study.

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Degradation of hair keratin has been studied in three soil fungi differing in keratinolytic ability, viz. *Keratinophyton terreum*, *Dictyoarthrinopsis kelleyi* and *Fusarium moniliforme*. All fungi attacked the hair cuticle forming specialised mycelial organs, fronds, under the scale-like cuticular cells. The cortex was attacked by very thin "boring hyphae". Their growth was intracellular and perpendicular to the hair axis. In *Keratinophyton terreum* older boring hyphae branched into complex formations, displaying clear lytic action on keratin. In *Dictyoarthrinopsis kelleyi* branching was rare and lysis of keratin weaker. In *Fusarium moniliforme*, a fungus not regarded as keratinophilic, the growth of boring hyphae ceased early and the lytic action remained minimal. All fungi digested the less keratinised parts of the hairs (endocuticle, intercellular substance, interfibrillar matrix) prior to the lysis of hard keratin fibrils.

**Key words**: keratinophilic fungi, keratinolysis, human hair, electron microscopy

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Rozklad vlasového keratinu byl studován u tří půdních hub (*Keratinophyton terreum*, *Dictyoarthrinopsis kelleyi*, *Fusarium moniliforme*), lišících se keratinolytickými schopnostmi. Všechny houby rozkládaly kutikulu vlasu, kde tvořily specializované myceliální orgány („fronds") pod šupinovitými kutikulárními buňkami. Kortex byl prorůstán velmi tenkými hyfami, jejichž růst byl intracelulární a kolmý k podélné ose vlasu. U *K. terreum* se starší hyfy v korte větvily a tvořily složité útvary s jasným lytickým účinkem na keratin. U *D. kelleyi* bylo větvení vzácné a lýza keratinu slabá. U houby *F. moniliforme*, která není považována za keratinofilní, se růst hyf v korte brzy zastavil a keratinolýza zůstala minimální. Všechny houby rozpouštěly méně keratinizované části vlasu (endokutikulu, intercelulární hmotu, interfibrilární matrix) dříve než napadly fibrily tvrdého keratinu.

## INTRODUCTION

Keratinophilic fungi represent an ecological group of fungi that act as decomposers of keratinaceous materials of animal origin (epidermal scales, hairs,

nails or claws, hooves, feathers etc.) in soil. Whereas the term "keratinophilic" is conventionally used for all fungi found colonising keratinaceous remnants, the term "keratinolytic" should be reserved for species or strains displaying clear degradation of keratin, observable by microscopy or proven by physiological experiments (Filipello-Marchisio 2000).

The study of keratinophilic fungi was stimulated by the finding that some primitive species of dermatophytes (keratinolytic fungi causing diseases of the skin of humans and animals) may be found in soil (Vanbreuseghem 1952). Such "geophilic dermatophytes" have been isolated from human hair, feathers and other similar materials used as "bait". Microscopic observation of hair bait enhanced the knowledge of the morphology of hard keratin degradation by keratinolytic fungi. By the use of light microscopy, the decomposition of human hair by keratinophilic fungi has been most thoroughly investigated by English (1963) who described in detail the specialised organs formed by filamentous fungi for the degradation of hair cuticle ("fronds") and hair cortex ("perforating organs", "boring hyphae"). She also studied attack of non-keratinophilic fungi on human hairs and observed some morphological similarities (English 1965).

In vitro electron microscopic studies on the decomposition of human hair by the dermatophyte *Trichophyton mentagrophytes* were published by Mercer & Verma (1963), who observed only the first five days of the growth. The results of the above authors were expanded by Baxter & Mann (1969), Hsu & Volz (1975), Kunert & Krajčí (1981), Kaaman & Forslind (1985) and specifically by detailed studies of Kanbe & Tanaka (1982) and Kanbe et al. (1986). Scanning electron microscopy was also used for the study of keratinolysis by dermatophytes (Kunert & Hejtmánek 1976, Kanbe & Tanaka 1982, Kaaman & Forslind 1985, Filipello-Marchisio et al. 1994, Rashid et al. 1995, Wawrzkiewicz et al. 1998, Filipello-Marchisio et al. 2000). This method is especially suitable for illustrating the decomposition of the surface layers of hairs or nails.

In comparison to the dermatophytes, less attention has been paid to the degradation of hard keratin by other keratinophilic fungi. Cano et al. (1991) investigated three species of the genus *Aphanoascus* which attack human hair from the surface or cutting edges without forming perforating organs or the typical fronds. Fusconi & Filipello-Marchisio (1991, see also Filipello-Marchisio 2000) described the degradation of human hair by *Chrysosporium tropicum*. This fungus initially attacks the cortex of hairs by thin and long unbranched hyphae (boring hyphae) growing from appressoria-like cells found in the cuticle. Later on, the hyphae grow thicker, become septated and branched and turn into complex formations similar to true perforating organs. The lytic action of these formations on keratin is evident. A similar type of hair degradation was observed by light microscopy in other species of *Chrysosporium* (English 1969, 1976) and in *Keratinophyton terreum* (Kunert 1967). In *Scopulariopsis brevicaulis* only three

out of nine studied strains degraded the cuticle and cortex of hairs to some extent and sent off boring hyphae into the cortex. These hyphae degraded the structures of keratinized cells in their surroundings but did not swell and did not produce large lytic channels (Filipello-Marchisio et al. 2000). At the level of light microscopy, conventional (thin) boring hyphae and various types of "wide" or "swollen" boring hyphae have been repeatedly described in keratinophilic fungi with limited keratinolytic ability (see e.g. Filipello-Marchisio 1986, Filipello-Marchisio et al. 1994).

In the present study three species of soil fungi, displaying moderate to weak keratinolytic ability, were studied by means of transmission and scanning electron microscopy (TEM, SEM). In *Keratinophyton terreum*, light microscopy (LM) showed the presence of swollen boring hyphae that turned into formations resembling true perforating organs (Kunert 1967). *Dictyoarthrinopsis kelleyi* produced numerous boring hyphae which only rarely thickened and branched. *Fusarium moniliforme* represents a fungus that is not regarded as keratinophilic. However, our strain was able to grow on human hairs and degrade them partially by fronds and boring hyphae.

## MATERIAL AND METHODS

Three species of soil fungi from the collection of dermatophytes and keratinophilic fungi at the Department of the first author were used: *Keratinophyton terreum* Randhawa et Sandhu (1963, type strain), *Dictyoarthrinopsis kelleyi* Dominik et Majchrowicz (1966, type strain) and *Fusarium moniliforme* Sheldon. The first two fungi were found on keratinaceous substances, the third one was isolated directly from agricultural soil. All strains were kept on 4 % glucose – 1 % peptone agar slants at 28 °C in the dark.

Fair children's hairs from a barber's were washed with warm water containing detergent, then washed repeatedly with distilled water, dried at room temperature and cut into pieces approximately 2 cm long. The hairs were sterilised by propylene oxide (6 hours at room temperature in an atmosphere saturated with vapourised oxide, Kunert & Krajčí 1981), placed on a layer of 1.5 % water agar in Petri dishes and inoculated with spores from the surface of 10-day old cultures on the glucose-peptone medium. In preliminary experiments with *F. moniliforme*, hairs sterilised by mild autoclaving (110 °C, 15 min.) and non-sterile hairs were also used.

After one to seven weeks of growth at 28 °C hairs at various stages of degradation were fixed in vapours of glutaraldehyde in Petri dishes for 24 hours. Then they were fixed in 2 % glutaraldehyde and 1 % formaldehyde in 0.1 M phosphate buffer pH 7.4 (24 hours) and postfixed in 1 % osmium tetroxide in the

same buffer (2 hours), dehydrated in acetone and embedded in Durcupan ACM (Fluka, Switzerland).

Thin sections were made on an Ultracut (Reichert, Austria) microtome using a glass knife, contrasted with uranyl acetate and lead citrate according to Reynolds and observed under a Zeiss Opton 109 (Germany) electron microscope operated at 80 kV. The primary magnification was within a range of 3,000 to 50,000 ×.

Fixation for SEM was performed with a mixture of 2 % glutaraldehyde and 1 % formaldehyde in 0.1 M phosphate buffer pH 7.4 (24 hours) and the samples were dehydrated in a graded acetone series. The samples were then dried using the critical point dryer CPD-030 (Bal-Tec, Liechtenstein), coated with a 5 nm layer of gold and palladium in the sputtering device Polaron E 5100 (Great Britain), and observed under a Tesla BS 340 (Czech Republic) scanning electron microscope.

## RESULTS

The morphology of keratin degradation by the fungus *Keratinophyton terreum* was, in most respects, similar to that of *Chrysosporium tropicum,* which was described by Fusconi & Filipello-Marchisio (1991). Its description and illustration is therefore presented in an abbreviated form. The degradation started at the hair surface, where the hyphae grew along the edges of cuticular cells and, thereafter, penetrated under the cuticular scales. There the hyphae were densely branched and composed of flat and lobose cells ("fronds", "fronded mycelium" – English 1963) (Fig. 1a, e). In advanced stages the hyphae were thick and circular in cross-section and evidently contributed to the mechanical decomposition of cuticular layers (Fig. 1d). The most easily decomposed layer of the cuticle cells was the endocuticle, an inner layer containing transformed remnants of the cytoplasm of keratinised cells. Its degradation could be observed up to several micrometers from the nearest hypha. Later on, blocks of amorphous keratin in the exocuticle (outer layer) were gradually digested. The most resistant layer was the A-layer of the exocuticle under the outer cytoplasmic membrane and a similar thinner layer facing the inner membrane. These layers remained mostly undegraded even in advanced stages of keratinolysis (Fig. 1d, e).

The cortex was attacked by hyphae growing perpendicularly to the longitudinal axis of the hairs. They arose by an inward growth of some cells of fronds at the border between cuticle and cortex. These hyphae ("boring hyphae", "borers" – English 1963) were very thin (under 0.5 $\mu$m) and penetrated the hair intracellularly across the cortical cells. At first, the boring hyphae were fully embedded in the keratinaceous mass of penetrated cells but, later on, lytic channels were visible around them (Fig. 1c). The hyphae then grew thick and divided into columns of short cells, similar to true perforating organs of dermatophytes. The component of the cortex degraded first was the complex of cytoplasmic membranes and

intercellular cementing substances between adjacent cells. The inter-macrofibrillar matrix inside the cells was digested next, followed by the keratin macrofibrils themselves. The latter were digested both from the surface and from the centre, where the packing of keratin microfibrils was less dense. In advanced stages of cortex degradation many macrofibrils disappeared, giving rise to extended lytic channels. In these channels a new type of mycelium ("erosive mycelium") was observed, produced by branching of swollen boring hyphae. It grew in parallel with the longitudinal axis and reminded of the fronds in the cuticle by its primarily intercellular growth and its morphology. The only undegraded component of the cortex was the melanin granules.

In the cytoplasm of hyphal cells nuclei with nucleoli, mitochondria, vacuoles with granules and membrane debris, endoplasmic reticulum, lipid drops and various vesicles and granules were observed (Fig. 1a). Some vesicles showed a reticular structure at their surface (Fig. 1b).

Hair degradation by *Dictyoarthrinopsis kelleyi* was slower and its course indicated a weaker keratinolytic ability of this fungus. Typical fronds, proliferating in place of the digested endocuticle, were observed in the cuticular cells. The exocuticle was digested in some places. However, its overall degradation was slow and the A-layer remained mostly intact (Fig. 2a). The organs of cortex degradation were frequent and typical borers. They originated from swollen, appressoria-like cells of fronds in or under the cuticle (Fig. 2b, c) and penetrated the cortex directly, more or less perpendicularly to the long axis of the cells and their keratin fibrils. The exocuticle of the cuticular cells (Fig. 2b) and the elements of the cortex (Fig. 2c) looked like drilled through by the boring hyphae, in the vicinity of which no signs of mechanical deformation (e.g. bending and displacing of the fibrils) were observed. Young boring hyphae filled tightly the holes they produced but in later stages the lytic action on less keratinised elements (transformed cytoplasmic membranes with intercellular cement, cytoplasmic remnants, inter-macrofibrillar matrix) was evident. Because these parts were degraded faster than the hard keratin of macrofibrils, the line of lysis along the hypha was irregular and typically "festooned" (Fig. 2c, d). The keratin itself was also attacked, as demonstrated by the separation of keratin microfibrils and an increased osmiophilia of the attacked parts. However, the lytic holes around the boring hyphae increased only slowly. An erosive mycelium produced by the branching of swollen boring hyphae remained rare and the hair degradation stopped after six to eight weeks without decomposing most of the hair substance both in the cuticle and the cortex.

Hair degradation by the strain of *Fusarium moniliforme* capable of growing on human hairs was in most aspects similar to that of *Dictyoarthrinopsis kelleyi*. The cuticle layer was attacked first by morphologically normal hyphae, growing along the edges and penetrating into the spaces between cuticular scales (Fig. 3a). Later on, typical fronds were formed that spread in place of the digested endocuticle.

The exocuticle was degraded only slowly and its A-layer remained intact even in advanced stages of the growth on hairs. The main organs of hair degradation were numerous boring hyphae (Fig. 3b). They arose from swollen, appressoria-like cells of fronds found mainly at the border between cuticle and cortex and penetrated it mostly perpendicularly to the long axis of the hairs (Fig. 3c, d). The boring hyphae were thin and non-branched and their course was often tortuous due to changes of direction at the borders of cortical cells and layers. Young borers fitted tightly into the holes they produced in the resistant layers of the cuticle or the cortex. Later on, lytic action on less resistant components of the cortex was evident and typical "festooned" lines of lysis were observable both on cross and longitudinal sections (Fig. 4 a, b). Hard keratin fibrils were also attacked, as shown by desintegration of macrofibril margins and an increased osmiophilia of the attacked areas (Fig. 4c). However, no large lytic channels (observable by light microscopy) were formed and the boring hyphae remained thin. An eroding mycelium was formed only rarely. This was found predominantly in intercellular spaces and its effect remained limited to the less keratinised components of the cortex (the complex of plasmatic membranes and the inter-macrofibrillar matrix, Fig. 4d). After six to eight weeks further growth on hairs and their degradation ceased. Even in the regions of hairs attacked most strongly only approximately 20 % of the hair substance was digested.

In preliminary experiments hair degradation by *Fusarium moniliforme* was studied under different conditions of cultivation. The degradation was slightly stronger with autoclaved hairs compared to hairs sterilised by propylene oxide and non-sterile hairs. It was also faster with hairs on glucose-peptone agar than on agar without the added nutrients. However, the course and morphology of hair degradation was essentially the same under all conditions.

## DISCUSSION

Degradation of human hair was studied in three soil fungi differing in keratinolytic ability. Human hairs, belonging to the most resistant of mammalian hairs (Wawrzkiewicz et al. 1998) were chosen as the substrate. These hairs were also used in most of the previous studies.

In all three species the cuticle of the hairs was attacked first. Specialised hyphal organs were observed, described as "fronds" by English (1963) and found later by many authors studying hair degradation by keratinophilic fungi in vitro (see Introduction). Their morphology probably reflects an adaptation to growth in the flat and thin spaces formed by the degradation of the least resistant parts of cuticular cells (scales). Filipello-Marchisio et al. (1994) suggested that fronds are similar to the hyphopodia of phytopathogenic fungi formed at plant surfaces. The fronded mycelia grow oriented under the cuticular scales at the hair surface. They rapidly digest the complex of cytoplasmic membranes of adjacent cells and their

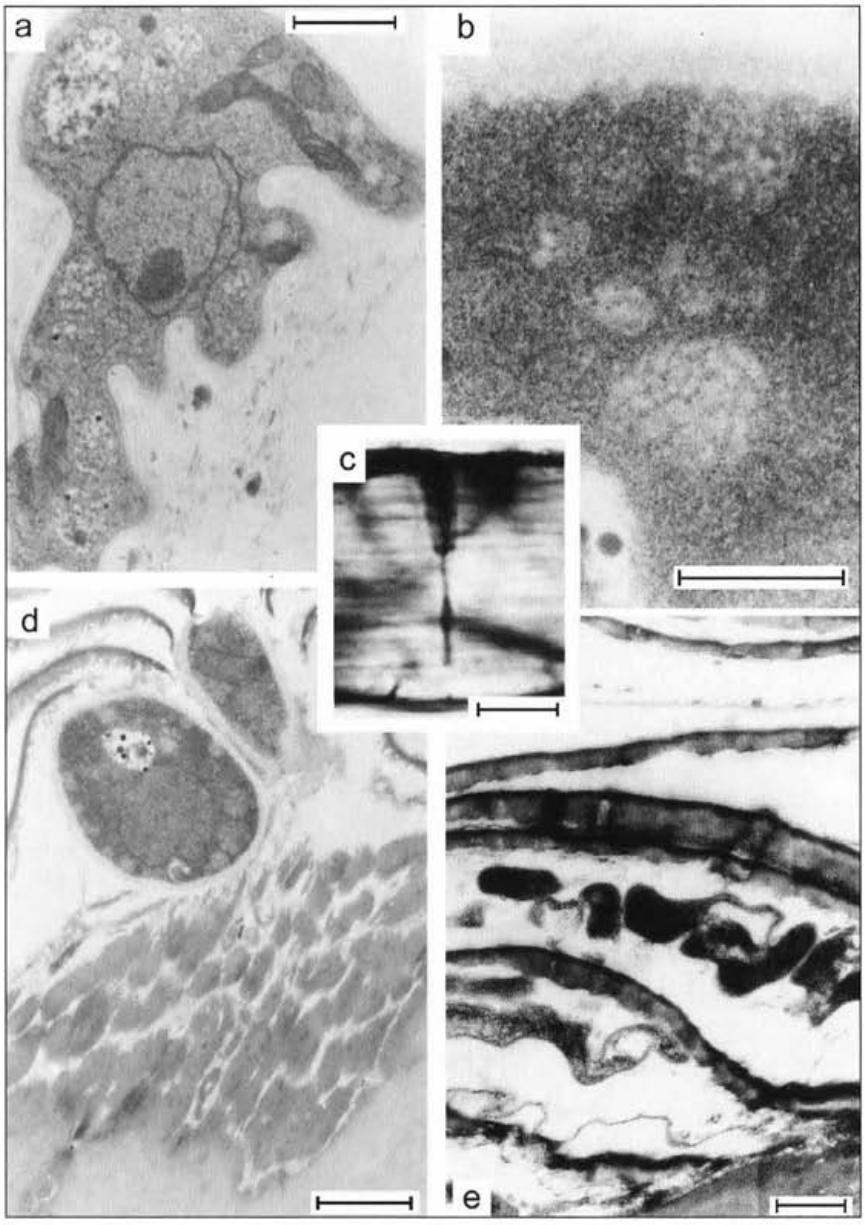


**Fig. 1.** *Keratinophyton terreum*. **a** Lobose cells ("fronds") in the cuticle. Tangential section of the hair. TEM, scale bar = 1 $\mu$m; **b** Coated vesicles in the cytoplasm of older hyphal cells. TEM, scale bar = 0.2 $\mu$m; **c** "Boring hypha" in the hair cortex. Note the lytic hole around the older (upper) part of the hypha. LM, scale bar = 20 $\mu$m; **d** Older hyphae in the cuticle. Cross section of the hair. Partly digested cuticle (upper part) and cortex (lower part of the picture). TEM, scale bar = 1 $\mu$m; **e** Cross sections of lobose cells in the cuticle. TEM, scale bar = 1 $\mu$m.

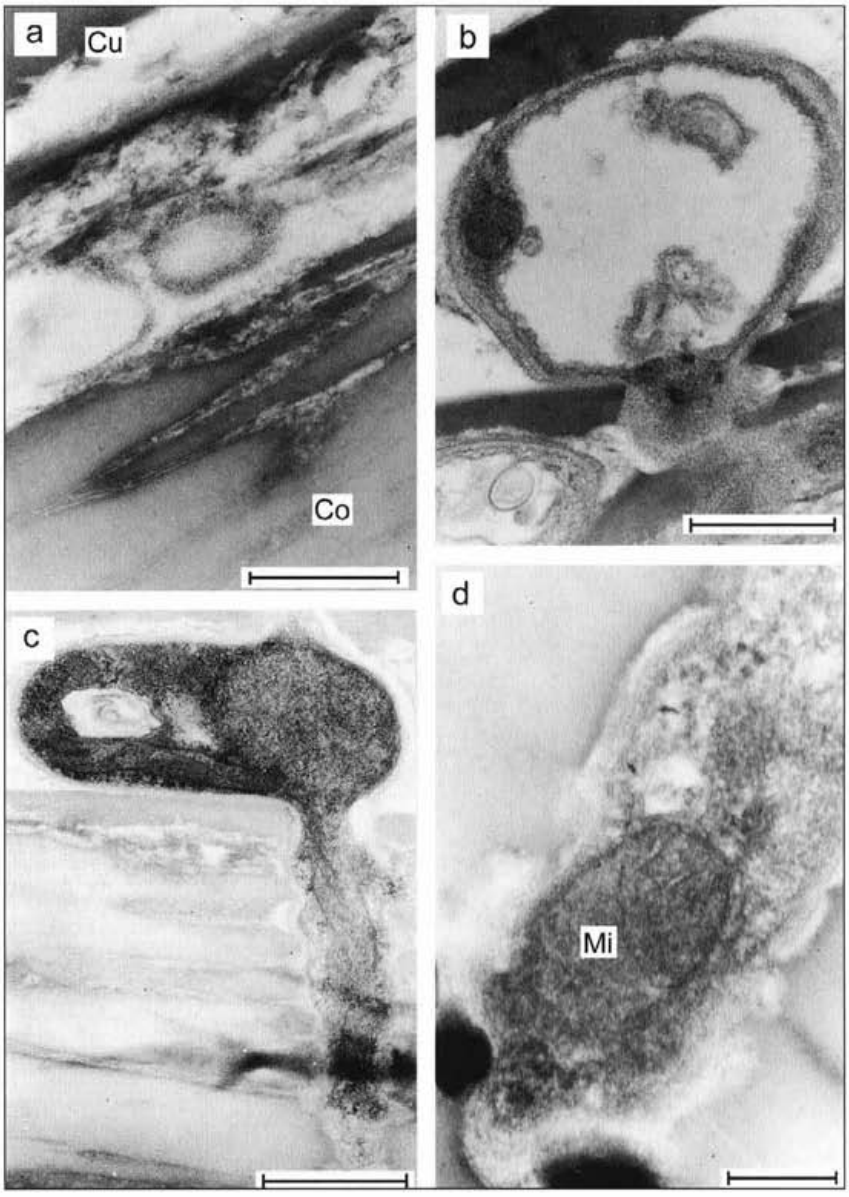


**Fig. 2.** *Dictyoarthrinopsis kelleyi*, TEM. **a** Cross sections of hyphae in the cuticle (Cu). Degradation of endocuticle and exocuticle. Lower part: lytic action on intercellular substance in the cortex (Co). Scale bar = 0.5 $\mu$m. **b** Appressorium-like cell in the cuticle with a boring hypha penetrating innermost cuticle cells. Scale bar = 0.5 $\mu$m. **c** Appressorium-like cell under the cuticle with a boring hypha penetrating the hair cortex. Scale bar = 1 $\mu$m. **d** Part of a boring hypha in the cortex. Note the signs of lysis of surrounding keratinaceous substance. Mi = mitochondrion. Scale bar = 0.2 $\mu$m.

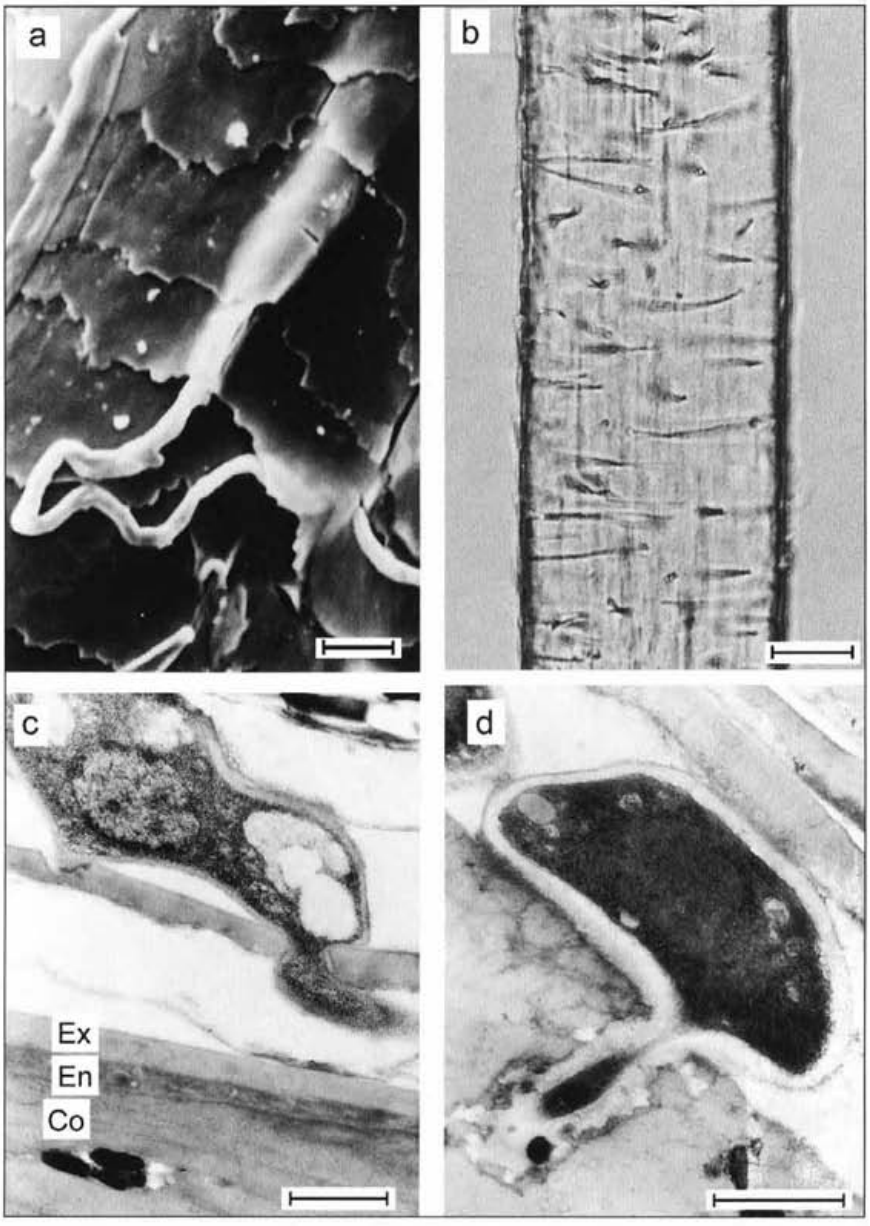


**Fig. 3.** *Fusarium moniliforme*. **a** Hyphae penetrating under the cuticular cells of the hair. SEM, scale bar = 5 $\mu$m. **b** Numerous boring hyphae in the attacked human hair. LM, scale bar = 20 $\mu$m. **c** Appressorium-like cell with a boring hypha penetrating the exocuticle. In the intact cuticle cell endocuticle (En) and exocuticle (Ex) are visible. Co = cortex. TEM, scale bar = 1 $\mu$m. **d** Appressorium-like cell with a boring hypha penetrating the hair cortex. Note the signs of cortex degradation around the boring hypha. TEM, scale bar = 1 $\mu$m.

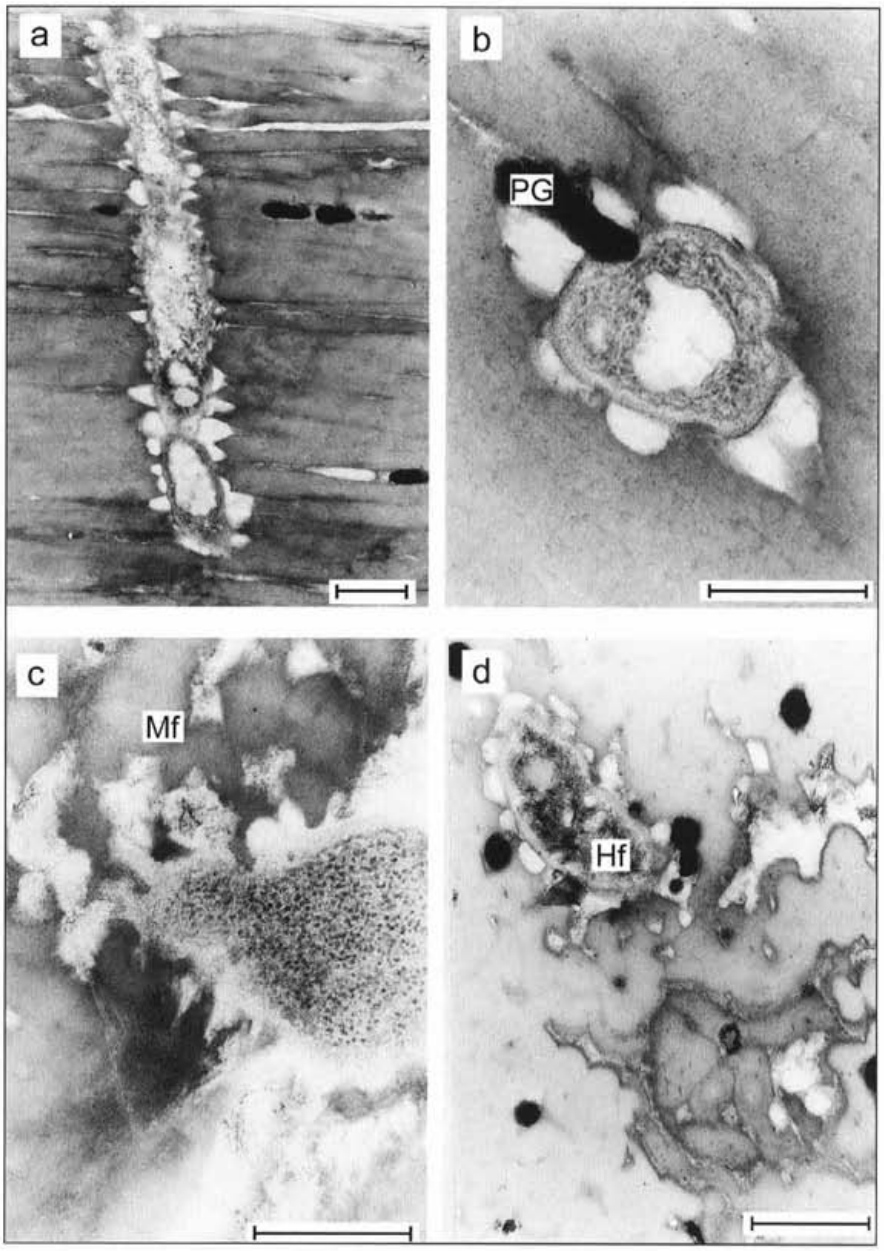


**Fig. 4.** *Fusarium moniliforme*, TEM. **a** Boring hypha in the hair cortex with a "festooned" line of lysis around it. Longitudinal section of the hair. Scale bar = 1 $\mu$m. **b** Cross-section of a boring hypha in the cortex with a surrounding irregular zone of lysis. PG = pigment granule. Scale bar = 0.5 $\mu$m. **c, d** Older boring hyphae (Hf) in the cross-sectioned hair cortex. Degradation of interfibrillar matrix separating individual hair keratin macrofibrils (Mf). Scale bar = 0.5 $\mu$m.

growth becomes intracellular. The sequence of degradation of cellular components corresponds to their degree of keratinization, paralleled by the content of sulphur (cystine). The endocuticle, containing remnants of cellular cytoplasm, is digested first, followed by the exocuticle, containing blocks of amorphous keratin. The A-layers, which are very rich in cystine (and perhaps also in other cross-linking bonds, e.g. isopeptides, Rice et al. 1994), remain mostly undegraded, especially in the less keratinolytic species, *Dictyoarthrinopsis kelleyi* and *Fusarium moniliforme*.

Whereas the hyphae grew parallel to the long axis of hairs in the cuticle, in the cortex the growth was perpendicular to this axis and intracellular from the very beginning. This is typical of all keratinophilic fungi. In the dermatophytes and other strongly keratinolytic species the organs of cortex degradation are perforating organs, columns of short cells producing rapidly large lytic channels and branching soon into the complex formations, described in detail by Kanbe & Tanaka (1982). Weakly keratinolytic fungi form only thin and unbranched boring hyphae (English 1963, 1965), usually without lytic channels discernible under the light microscope. Their ultrastructure was studied in detail by Fusconi & Filipello-Marchisio (1991) in *Chrysosporium tropicum* and by Filipello-Marchisio et al. (2000) in *Scopulariopsis brevicaulis*. Our results are in agreement with those of the above authors: the formation of boring hyphae from appressoria-like cells, their passage through tight holes in the exocuticle and cortex, and "festooned" lines of hair substance degradation around them were observed. The presence of appressoria-like cells suggests the concerted action of mechanical pressure and enzymatic lysis in cortex penetration. The lysis is probably more important, as shown by the absence of keratin fibril deformation in the surroundings of boring hyphae including their apices. In *Keratinophyton terreum* older boring hyphae produced large lytic channels, grew thick and densely septated, and were transformed into formations similar to perforating organs. This intermediary type (present also in species of the genus *Chrysosporium*, see Introduction) probably demonstrates the origin of perforating organs from boring hyphae in the evolution of keratinophilic fungi.

Also in the cortex, the first attacked elements are those that do not represent a true keratin (intercellular complex, remnants of cell organelles). Hard alpha-keratin is digested later and keratinaceous intermediate filaments are probably dissolved faster than the osmiophilic matrix found among them (Kunert & Krajčí 1981, Fusconi & Filipello-Marchisio 1991, Filipello-Marchisio 2000). This corresponds again to their content of sulphur (cystine). The sulphur content reflects the amount of disulphide (cystine) bridges that are the main source of keratin resistance. Truly keratinolytic fungi are able to cleave these cross-links by means of excretion of sulphite formed during intracellular oxidation of cystine sulphur (sulphitolytic theory of keratinolysis – Kunert 1972, for review see

Kunert 1995, 2000). At the level of electron microscopy sulphitolysis may be the cause of an increase in osmiophilia of the attacked keratin, observed by several authors (Kunert & Krajčí 1981, Kanbe & Tanaka 1982, Kanbe et al. 1986, Fusconi & Filipello-Marchisio 1991) and also in this study. Wickett & Barman (1985) described namely similar effects during the reduction of disulphide bonds of the hairs by dithiols.

The only component of the hairs that remains completely intact during hair degradation by keratinolytic fungi are the non-proteinaceous pigment granules (Mercer & Verma 1963, Hsu & Volz 1975, Kunert & Krajčí 1981, Cano et al. 1991, Fusconi & Filipello-Marchisio 1991).

Some fungi of the genus *Fusarium* are capable of growing on keratinaceous substrates and are mentioned among primary colonisers of such substrates in soil. These members of fungal succession were thought to use only non-keratins of hairs, nails etc. However, in the experiments of Oyeka & Gugnani (1998) a strain of *Fusarium solani* digested up to 20 % of powdered keratin suspension. Among eight strains of *Fusarium* spp. only one isolate of *F. moniliforme* attacked human hairs in a way comparable to keratinophilic fungi (Kunert, non-published results). In the present study it degraded the hairs nearly as intensively as *Dictyoarthrinopsis kelleyi*, originally described as a keratinophilic fungus (Dominik & Majchrowicz 1966). In contrast to *D. kelleyi* cuticle decomposition was slower and more incomplete, and the boring hyphae stopped grow earlier, mostly without branching and producing further mycelia. However, even here the boring hyphae in the cortex displayed a clear lytic, obviously enzymatic, activity. It is therefore highly probable that even the most weakly keratinophilic fungi penetrate keratinised tissues by a lytic action and cannot solely use mechanical pressure.

## REFERENCES

BAXTER M. and MANN P. (1969): Electron microscopic studies of the invasion of human hair in vitro by three keratinophilic fungi. – Sabouraudia 7: 33–37.

CANO J., GUARRO J. and FIGUERAS M. J. (1991): Study of the invasion of human hair in vitro by Aphanoascus spp. – Mycoses 34: 145–152.

DOMINIK T. and MAJCHROWICZ I. (1966): Some new species of fungi from the soil of Conakry. – Mycopathologia 28: 209–219.

ENGLISH M. P. (1963): The saprophytic growth of keratinophilic fungi on keratin. – Sabouraudia 2: 115–130.

ENGLISH M. P. (1965): The saprophytic growth of non-keratinophilic fungi on keratinized substrata and a comparison with keratinophilic fungi. – Trans. Brit. Mycol. Soc. 48: 219–235.

ENGLISH M. P. (1969): Destruction of hair by Chrysosporium keratinophilum. – Trans. Brit. Mycol. Soc. 52: 247–255.

ENGLISH M. P. (1976): Destruction of hair by two species of Chrysosporium. – Trans. Brit. Mycol. Soc. 66: 357–358.

FILIPELLO-MARCHISIO V. (1986): Keratinolytic and keratinophilic fungi of children's sandpits in the city of Turin. – Mycopathologia 94: 163–172.

FILIPELLO-MARCHISIO V., FUSCONI A. and RIGO S. (1994): Keratinolysis and its morphological expression in hair digestion by airborne fungi. – Mycopathologia 127: 103–115.

FILIPELLO-MARCHISIO V. (2000): Keratinophilic fungi: their role in nature and degradation of keratinic substrates. – In: Kushwaha R. K. S. and Guarro J. (eds.), Biology of dermatophytes and other keratinophilic fungi. – Rev. Iberoamer. Micol. , Bilbao, p. 86–92.

FILIPELLO-MARCHISIO V., FUSCONI A. and QUERIO F. L. (2000): Scopulariopsis brevicaulis: a keratinophilic or keratinolytic fungus ? – Mycoses 43: 281–292.

FUSCONI A. and FILIPELLO-MARCHISIO V. (1991): Ultrastructural aspects of the demolition of human hair in vitro by Chrysosporium tropicum Carmichael. – Mycoses 34: 153–165.

HSU Y. C. and VOLZ P. A. (1975): Penetration of Trichophyton terrestre in human hair. – Mycopathologia 55: 179–183.

KAAMAN T. and FORSLIND B. (1985): Ultrastructural studies on experimental hair infections in vitro caused by Trichophyton mentagrophytes and T. rubrum. – Acta Dermatol. Venereol. 65: 536–539.

KANBE T. and TANAKA K. (1982): Ultrastructure of the invasion of human hair in vitro by the keratinophilic fungus Microsporum gypseum. – Infect. Immunity 38: 706–715.

KANBE T., SUZUKI S. and TANAKA K. (1986): Structural differentiation in the frond and boring hypha of the dermatophyte Microsporum canis invading human hair in vitro. – J. Electron Microsc. 35: 38–46.

KUNERT J. (1967): Zur Mikromorphologie des Haarabbaues durch Dermatophyten in vitro. – Dermatol. Wschr. 153: 1141–1150.

KUNERT J. (1972): Keratin decomposition by dermatophytes: evidence of the sulphitolysis of the protein. – Experientia 28: 1025–1026.

KUNERT J. and HEJTMÁNEK M. (1976): Raster-Elektronenmikroskopie der menschlichen Haare, befallen durch den Dermatophyten Microsporum gypseum. – Mykosen 19: 329–336.

KUNERT J. and KRAJČÍ D. (1982): An electron microscopy study of keratin degradation by the fungus Microsporum gypseum in vitro. – Mykosen 24: 485–496.

KUNERT J. (1995): Biochemical mechanism of keratin degradation by keratinophilic fungi. – J. Indian Bot. Soc. 74A: 89–98.

KUNERT J. (2000): Physiology of keratinophilic fungi. – In: Kushwaha R. K. S. and Guarro J. (eds.), Biology of dermatophytes and other keratinophilic fungi. – Rev. Iberoamer. Micol., Bilbao, p. 77–85.

MERCER E. H. and VERMA B. S. (1963): Hair digested by Trichophyton mentagrophytes. An electron microscope examination. – Arch. Dermatol. 87: 357–360.

OYEKA C. A. and GUGNANI H. C. (1998): Keratin-Degradation durch Scytalidium-Arten und Fusarium solani. – Mycoses 41: 73–76.

RANDHAWA H. S. and RANDHU R. S. (1964): Keratinophyton terreum gen. nov., spec. nov.: a keratinophilic fungus from soil in India. – Sabouraudia 3: 252–256.

RASHID A., SCOTT E. and RICHARDSON M. D. (1995): Early events in the invasion of human nail plate by Trichophyton mentagrophytes. – Brit. J. Dermatol. 133: 932–940.

RICE R. H., WONG V. J. and PINKERTON K. E. (1994): Ultrastructural visualization of cross-linked protein features in epithelial appendages. – J. Cell Sci. 107: 1985–1992.

VANBREUSEGHEM R. (1952): Keratin digestion by dermatophytes: a diagnostic method. – Mycologia 44: 176–182.

WAWRZKIEWICZ K., ZIOLKOWSKA G. and WAWRZKIEWICZ J. (1997): In vitro biodegradation of hair from different animal species by Microsporum canis. – Int. Biodeteriation Biodegradation 39: 15–25.

WICKETT R. R. and BARMAN B. G. (1985): Factors affecting the kinetics of disulfide bond reduction in hair. – J. Soc. Cosmet. Chem. 36:75–86.