

DACTYLOMYCES AND THERMOASCUS

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(With 2 Text-figures)

After rediscovery of *Dactylomyces thermophilus* Sopp in Sweden and in Britain the position of the genera *Thermoascus* Miehe (1907) and *Dactylomyces* Sopp (1912) is reassessed. The study of certain isolates of *T. aurantiacus* Miehe, *D. thermophilus* Sopp and *D. crustaceus* Apinis & Chesters indicates that the genera are not synonymous but represent different developmental and morphological types which justify their retention. The genus *Dactylomyces* is subdivided into two new subgenera *Dactylomyces* and *Paecilomyopsis* Apinis. A new family, the *Thermoascaceae*, is proposed to accommodate the two genera.

The type species of the genus *Thermoascus*, *T. aurantiacus*, was isolated from self-heating hay and carefully described by Miehe in 1907. Later, its ecology and physiology was extensively studied by Noack (1912, 1920). Sopp (1912) reported another thermophile from the wooden casing of a bath thermometer in Norway and placed it in a new genus *Dactylomyces*, represented by *D. thermophilus* Sopp. Because of its penicillioid conidiophore Biourge (1923) named the species *Penicillium thermophilus* (Sopp) Biourge, and Trotter (1931) provided the Latin diagnosis under *P. thermophilum* (Sopp) Saccardo.

In describing the genus *Dactylomyces* Sopp (1912) suggested that *D. thermophilus* might be identical with Miehe's *T. aurantiacus*. Despite obvious differences, this suggestion, coupled with the lack of authentic material available for comparison, made a considerable impact on the subsequent interpretation of both genera. Thus Raper & Thom (1949) examined Emerson's isolate from retting guayule, referred to *D. thermophilus*, and stated that it produced penicillioid conidia and *Thermoascus*-like ascocarps. This isolate was deposited by Fennell and Raper at the Centraal Bureau voor Schimmelcultures (CBS), Baarn, under *D. thermophilus* (cf. CBS *List of Cultures*, 1961). Furthermore, Cooney & Emerson (1964) suggested that their *D. thermophilus* isolate from retting guayule was representative of Sopp's species of that name, and also considered it to be identical with *Thermoascus* Miehe, assuming that absence of penicillioid conidiophores in Miehe's original description was due to the loss of conidial reproduction in the strain studied. However, personal examination of Emerson's isolate deposited at CBS, Baarn, by Fennell and Raper, and of Cooney and Emerson's strain M 206516, showed beyond any doubt that these isolates are neither *D. thermophilus* Sopp nor *T. aurantiacus* Miehe, but are identical with *D. crustaceus* Apinis & Chesters (1964) which was infrequently isolated from debris of coastal grasses. Despite the mounting evidence that the

species of both genera represent different fungi, Stolk (1965) accepted Cooney and Emerson's view that the genera are synonymous.

In 1952 *T. aurantiacus* was repeatedly isolated in this country from alluvial grassland soils from the Trent Valley near Nottingham (Apinis, 1963). All these isolates were identical with Noack's isolate deposited at CBS, Baarn, in 1931. However, during the summer of 1965, T. Nilsson, from The Royal College of Forestry in Stockholm, sent me some cultures of thermophilous fungi isolated from saw dust and chips stored at paper mills in Northern Sweden. Examination of these cultures showed that three isolates were identical with Sopp's description of *D. thermophilus* of which there was no authentic material in existence at that time. Subsequently, we succeeded (Apinis & Pugh, 1967) in isolating *D. thermophilus* from the debris of nests of blackbirds (*Turdus merula* L.) and thrushes (*Turdus* spp.) near Nottingham. This rediscovery of *D. thermophilus* presents an excellent opportunity of reassessing both genera and of clarifying some of the existing confusion.

DESCRIPTION OF GENERA AND SPECIES

THERMOASCUS Miede, *Die Selbsterhitzung des Heues*, pp. 70-73, fig. 8a-f, 1907. Non *Dactylomyces* Sopp (1912), fide Cooney & Emerson (1964, p. 39); non *Penicillium* Link, fide Cooney & Emerson (1964, p. 39); non *Thermoascus* Miede, fide Cooney & Emerson (1964, pp. 39-50, figs. 15-20).

Mycelium consists of hyaline, thin (1.5-3.0 μ) and thick (up to 20 μ), septate, branched, rapidly spreading hyphae which may form intercalary chlamydospores and loose strands on the surface of the substratum. *Conidia* terminal on shorter or longer branches, \pm hyaline, clavate to somewhat spindle-shaped, aseptate or septate, of *Aphanoascus*-, *Leveillula*- and *Microsporum*-type (cf. Dangeard, 1907; Miede, 1907; Nour, 1957). *Ascocarps* superficial, cream, orange-yellow to brown, \pm globose to irregular, relatively small, solitary or confluent; on certain media rich in carbohydrates more or less continuous crust-like structures may be formed. *Peridium* consists of an outer layer of larger, hyaline to yellow-brown, pseudoparenchymatous cells with a slightly thicker cell wall, and of an inner layer of smaller pseudoparenchymatous cells. *Asci* are formed in small clusters and are enclosed in an irregularly thick peridium; they are subglobose to oval, 8-spored and evanescent. *Ascospores* colourless or slightly yellow, non-septate, oval or elliptical.

Type species: *Thermoascus aurantiacus* Miede (1907).

THERMOASCUS AURANTIACUS Miede, *Die Selbsterhitzung des Heues*, pp. 70-73, fig. 8a-f, 1907. Non *D. thermophilus* Sopp, fide Cooney & Emerson (1964, p. 39); non *Penicillium thermophilus* (Sopp) Biourge, fide Cooney & Emerson (l.c. p. 39); non *P. thermophilum* (Sopp) Saccardo (Trotter, 1931), fide Cooney & Emerson (l.c. p. 39); non *T. aurantiacus* Miede, fide Cooney & Emerson (l.c. pp. 39-50, figs. 15-20).

Mycelium consists of thin and thick (up to 20 μ), hyaline, septate and branched hyphae (Fig. 1A) which may produce loose strands with anastomoses. *Conidia* develop terminally on long or short hyphal branches singly (seldom 2-3 conidia are clustered on a single hyphal tip) and are

clavate or somewhat spindle-shaped, smooth, 0-3 (5)-septate, $12-35 \times 5-10 \mu$ diam. (Fig. 1 B-I). *Ascocarp* initials vary and appear as small branching knots of hyphae formed either by two conjugating hyphae (Fig. 1, J, K) or arise from a network of hyphae winding around the thicker trailing hyphae as in *P. vermiculatum* (cf. Dangeard, 1907); such clusters subsequently produce fine radiating hyphae with spirally twisted ends as in *Aphanoascus cinnabarinus* (cf. Dangeard, 1907) which, after re-

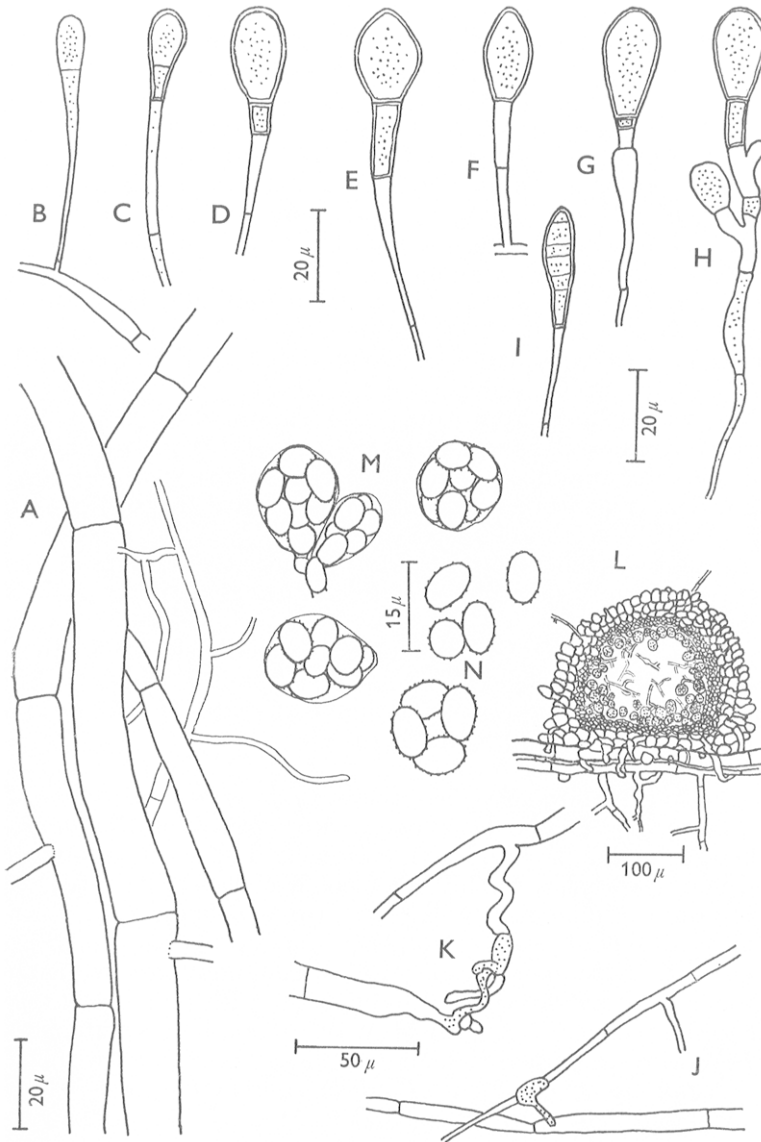


Fig. 1. *Thermoascus aurantiacus* Mieh. A, Hyphae; B-I, conidia; J, K, conjugating hyphae; L, section through the cleistothecium; M, asci; N, ascospores.

branching, take part in the formation of the peridium and produce the ascogenous hyphae. *Ascocarps* brown-coloured, superficial irregular, more or less spherical to oval, single, clustered or confluent; on certain media rich in carbohydrate (e.g. oatmeal agar) extensive pseudoparenchymatous tissue and large cavities with asci are produced as continuous crust-like structures; the size of a single ascocarp may reach 1 mm diam. *Peridium* is irregular and consists of two more or less distinctly formed layers: the inner layer consists of small, closely packed isodiametric cells with cell walls slightly thickened while the outer peridium is composed of larger cells with the walls more strongly thickened and deeply coloured (Fig. 1 L). The outer peridium of larger, less thickly packed cells, may be covered by a layer of very loose, reticulate mycelium which may produce another layer of asci above it which subsequently is enclosed again by the peridium. In this way another superimposed ascocarp is produced, thus making the fertile crust more or less multilocular on the surface of the agar medium. *Asci* in clusters, subglobose to oval, evanescent, 8-spored, *c.* 8–15 × 7–10 μ (Fig. 1 M). *Ascospores* hyaline, non-septate elliptical, thin-walled, slightly rough, *c.* (4) 5–7 × (3) 4–5 μ diam. (Fig. 1 N).

Neotype: **BDUN** 343, **IMI** 91787, isolated from alluvial grassland soil near Attenborough, Notts., England in 1951.

Three isolates were studied upon which the above description is based:

- (a) **CBS** isolate, probably deposited by Noack, and received in 1953;
- (b) **IMI** 67936, isolated from sawdust of Parana pine, Forest Products Research Laboratory S. 748;
- (c) **BDUN** 343 (= **IMI** 91787), the neotype.

All the isolates produced conidia of *Aphanoascus*-*Microsporum* type on malt extract agar and other media as is mentioned by Miehe (l.c. p. 70, fig. 8d).

T. isatschenkoi Malchevskaya (1939) is regarded as a doubtful species of which no satisfactory description exists and no material is available for examination.

D. crustaceus Apinis & Chesters (1964) was transferred to the genus *Thermoascus* by Stolk (1965) as *T. crustaceus* (Apinis & Chesters) Stolk on the assumption that *Dactylomyces* is synonymous with *Thermoascus*; because of this the transfer is not accepted here.

DACTYLOMYCES Sopp, *Skr. VidenskSelsk. Christiania Math.-naturw. Kl.* **II**, 35–42, fig. 20, pl. III and IV (figs. 21–30), 1912. Non *Penicillium* Link, fide Biourge (1923, p. 106); non *Penicillium* Link, fide Trotter (1931, p. 671); non *Thermoascus* Miehe, fide Cooney & Emerson (1964), 39–50; non *Thermoascus* Miehe, fide Stolk (1965, pp. 270–275).

Mycelium consists of hyaline, branched, septate hyphae which produce either robust, dichotomously branched conidiophores with palmate anellophores or *Paecilomyces*-like conidiophores with phialides. *Conidia* are hyaline to subhyaline, i.e. slightly brown or green, non-septate, in chains. *Ascocarps* red-brown, superficial, more or less globose or irregular, firm, single, gregarious or confluent. *Peridium* consists of brick-red pseudoparenchymatous cells with brown and hyaline hyphae attached on the surface. *Asci* subglobose to oval, evanescent, 8-spored. *Ascospores* hyaline to subhyaline non-septate, subglobose to elliptical.

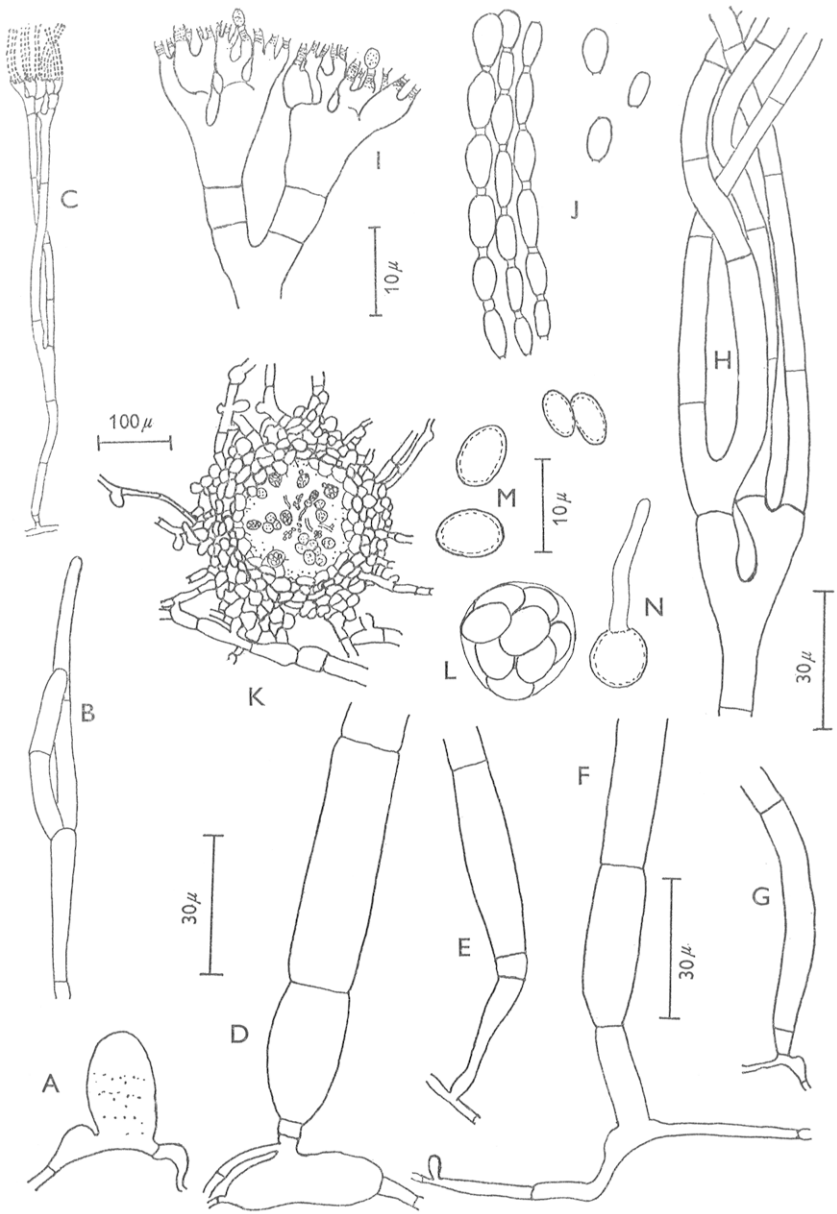


Fig. 2. *Dactylomyces thermophilus* Sopp. A, Conidiophore initial; B, young conidiophore; C, mature conidiophore; D-G, base of the conidiophores; H, dichotomous branching of the conidiophore; I, anellophores; J, conidia; K, section through the cleistothecium; L, ascus; M, ascospores; N, germinating ascospore.

Type species: *D. thermophilus* Sopp (1912).

Two new subgenera are proposed for this genus:

(a) Conidiophores more or less dichotomously branched with palmate anellophores (*Conidiophora per dichotomiam ramosa*, *anellophora ad apices palmatis*)—subgenus **Dactylomyces** based on *D. thermophilus* Sopp (1912).

(b) Conidiophores of *Paecilomyces* type (*Conidiophora ut in genere Paecilomyce*)—subgenus **Paecilomyopsis** Apinis based on *D. crustaceus* Apinis & Chesters (1964).

DACTYLOMYCES THERMOPHILUS Sopp, *Skr. VidenskSelsk. Christiania Mat.-naturv. Kl.* **11**, 31–42, fig. 20, pl. III and IV (figs. 1–30), 1912.

Syn.: *Penicillium thermophilus* (Sopp) Biourge, *Cellule* **33**, 106, 1923.

P. thermophilum (Sopp) Saccardo, fide Trotter, *Sylloge Fungorum*, **25**, Suppl. 10, 671, 1931.

Non *Thermoascus aurantiacus* Miede, fide Cooney & Emerson (1964, pp. 39–50, figs. 15–20); non *Thermoascus crustaceus* (Apinis & Chesters) Stolk (1965, pp. 270–275, fig. 2a–f).

Mycelium consists of hyaline, branched, septate, spreading hyphae *c.* 2–15 μ thick which may be somewhat restricted at septa. The smooth, dichotomously branched, robust and hyaline conidiophores are usually twisted and arise from either creeping surface hyphae or trailing aerial hyphae and are up to 25 μ in diameter (Fig. 2A–H). The dichotomous rebranching of the conidiophores may occur several times producing 16 to 32 or more branches each of which bear on their tip a lobed or palmate anellophore (Fig. 2I). The anellophores produce numerous conidia in chains which adhere in columns. *Conidia* non-septate, cylindrical to oval, smooth, green or yellow-green in mass, singly hyaline or subhyaline, *c.* 3–11 \times 2.5–5.5 μ (Fig. 2J). *Ascocarp* initials variable and consist of a small knot of branched, swollen and anastomosed hyphae which subsequently produce a larger cluster of pseudoparenchymatous structure in which the central cells are dissolved or absorbed as in *Eurotium* during the formation of the asci while the outer layer of the pseudoparenchyma produce the peridium. *Ascocarps* (Fig. 2K) superficial, firm, irregularly globose, red-brown, more or less solitary, *c.* 150–600 μ diam. *Peridium* consists of several layers of irregularly branched and swollen hyphae which produce the red-brown, more or less uniform, pseudoparenchymatous tissue covered by various brown and hyaline, branched and racquet-like hyphae. *Asci* 8-spored, evanescent, subglobose to oval (Fig. 2L), *c.* 12–15 μ diam. *Ascospores* hyaline, nonseptate, smooth, more or less oval, *c.* 5.5–8.0 \times 3.5–6.0 μ (Fig. 2M, N).

Neotype: T. Nilsson's isolate P4–IV from pine chips and pine bark at Lövholm's Paper Mill in Northern Sweden, 1963/4; **BDUN** 394, **IMI** 123298.

Other isolates studied: T. Nilsson's isolate BB 10–II from birch chips and isolate P 3–V from pine chips, both from Northern Sweden, 1963/4; both are predominantly conidial. Isolate **BDUN** 395, **IMI** 123299 is from the plant debris of a blackbird's nest near Nottingham, England, 1965. Three further isolates from the nest debris of thrushes near Nottingham, England, 1965, were also examined (Apinis & Pugh, 1967).

The morphology and the development of these thermophilous fungi studied in culture led to the conclusion that they undoubtedly represent Sopp's *D. thermophilus*. There is a general agreement with the original description, drawings (Plates III and IV), cultural characters as well as their temperature relations (cf. Bergman & Nilsson, 1966). The only exception, as compared with the original description, is the size of the conidia which are given as $12-14 \times 6-8 \mu$ by Sopp, whereas the above-mentioned isolates developed on agar media conidia *c.* $3-11 \times 2.5-5.5 \mu$ diam.

DACTYLOMYCES CRUSTACEUS Apinis & Chesters, *Trans. Br. mycol. Soc.* **47**, 428-429, fig. 2A-F, 1964. Stat. con.: *Paecilomyces crustaceus* Apinis & Chesters (l.c.).

Syn.: *Thermoascus aurantiacus* Miede, fide Cooney & Emerson, *Thermophilic Fungi*, pp. 39-50, figs. 15-20, 1964.

T. crustaceus (Apinis & Chesters) Stolk, *Antonie van Leeuwenhoek*, **31**, 262-276, fig. 2a-f, 1965.

Non *D. thermophilus* Sopp, fide Cooney & Emerson (1964, p. 39); non *Penicillium thermophilus* (Sopp) Biourge, fide Cooney & Emerson (l.c. p. 39); non *Penicillium thermophilum* (Sopp) Saccardo, fide Cooney & Emerson (l.c. p. 39).

Mycelium consists of rapidly spreading, hyaline, branched, septate, hyphae up to 12μ diam. The hyaline, septate, smooth conidiophores arise from submerged or trailing hyphae and are *c.* $10-12 \mu$ at the base, slightly tapered towards the apex, producing shorter or longer side branches. The phialides are of *Paecilomyces* type (cf. Brown & Smith, 1957) and occur as short side branches or are irregularly clustered on the tips of the conidiophore branches; they are with a slender neck and broadened base, *c.* $10-30 \times 2-7 \mu$. *Conidia* form shorter or longer, tangled, divergent chains; they are hyaline to pale brown, cylindrical to oval, smooth, *c.* $3-10 \times 2.5 \mu$ diam. *Ascocarps* superficial, red-brown irregular or somewhat globose, single, and tend to become confluent or crusty, *c.* $200-900 \mu$ diam. *Peridium* consists of several layers of slightly thick-walled, brown, pseudo-parenchymatous cells covered by brown, subhyaline or hyaline hyphae. The interior of the ascocarp is composed of a network of hyaline hyphae which produce clusters of globose to oval, 8-spored (infrequently 2-6-spored), evanescent *asci*, *c.* $15-21 \times 10-17 \mu$ diam. *Ascospores* non-septate, hyaline, may become slightly yellowish or tinged red-brown; subglobose to elliptical, finely pitted and echinulated, $7-9 \times 5-7 \mu$ diam.

Type: **BDUN** 378, **IMI** 102470, isolated from *Agropyron pungens* debris at Gibraltar Point, Lincs., England, March 1960.

Other material examined: **NRRL** 1563 from the Northern Utilization Research and Development Division in Peoria; specimen **UC M** 206516 from University of California Herbarium, Berkeley, U.S.A., under *Thermoascus aurantiacus* Miede, fide D. G. Cooney and R. Emerson; culture 1357 isolated from stored barley, Sharlow, G.B. 1965. Both cultures and the specimen examined were identical.

DISCUSSION

In addition to the morphological studies on the cultures of fungi mentioned above their growth pattern on various media was also compared. Observations made during the 10 days of culture at 38 °C are compiled in Table 1.

Table 1. *Growth patterns on agar media*

	<i>Thermoascus aurantiacus</i>	<i>Dactylomyces crustaceus</i>	<i>Dactylomyces thermophilus</i>
Cellulose	Thin, colourless mycelium with brown, scattered ascomata	Thin, conidial mycelium with few ascomata	Thin mycelium with central and marginal areas conidial and few ascomata
Czapek	Thin, colourless mycelium with initials of ascomata	Grey-green conidial mycelium with some ascomata; reverse green-brown	Thin, green conidial mycelium
Malt extract	Colourless mycelium with conidia and brown ascomata later	Green-brown conidial areas and many red-brown ascomata; reverse brown	Mycelium with green conidial areas and brick-red areas with ascomata
Oatmeal	Vigorously growing mycelium with numerous brown, confluent ascomata	Yellow-green conidial areas and brick-red, confluent ascomata	Thin mycelium conidial with brick-red ascomata
Potato dextrose	Numerous brown, confluent ascomata formed along the radially growing hyphae	Conidial areas yellow-green and numerous red-brown ascomata	Mycelium with numerous conidiphores and brick-red ascomata
Soil extract	Thin mycelium with brown, scattered ascomata	Thin, conidial mycelium with some brown ascomata	Thin, conidial mycelium with brown, scattered ascomata

None of the isolates was capable of dissolving the fine particles of cellulose suspended in agar. In contrast to the *T. aurantiacus* cultures those of both *Dactylomyces* species produced on Czapek and malt extract agars some grey-green or brown-green colours in the colony, especially in the conidial areas as well as in the agar (cf. Table 1). Both *T. aurantiacus* and *D. crustaceus* produced confluent or crust-like ascomata on oatmeal agar and some other media rich in carbohydrates. *T. aurantiacus* tended to produce on such media a more or less continuous basal layer near the surface of the agar consisting of slightly brown coloured pseudoparenchymatous cells above which a fertile layer with asci was formed subsequently.

The asexual reproduction of the three fungi described above differ considerably. In *T. aurantiacus* asexual reproduction, as already stated by Mische (1907, p. 70), is by terminal conidia which are similar to those of *Microsporium* species, and they are provided with a separating cell at the base of the conidium. In *D. thermophilus* the chains of conidia are produced by branched anellophores as in *Polypaecilum* Smith (1961) and *Angulimaya* Subramanian & Lodha (1964) while in *D. crustaceus* conidial chains are formed by phialides of *Paecilomyces* type (cf. Brown & Smith, 1957).

Freezing microtome sections of agar cultures at various stages of develop-

ment showed also certain differences in development and morphology of the sexual states in the type species of both genera. Thus in *D. thermophilus* the central part of the ascocarp at an early stage of development is filled by hyaline pseudoparenchymatous tissue as in *Eurotium* which undergoes resorption by ascogenous hyphae while the asci are formed. In *T. aurantiacus*, however, the central part of the ascocarp is plectenchymatous and the formation of asci and the ascocarp wall is similar to *Aphanoascus* (cf. Dangeard, 1907). The structure of the peridium differs too. In *D. thermophilus* it is more or less uniform but in *T. aurantiacus* it consists of two layers.

For the classification of such fungi two criteria may be adopted: (1) to accept the perfect state characters as an exclusive guide; or (2) to accept the viewpoint that the full cycle of asexual and sexual state development is of importance for the generic classification of these ascomycetes. The latter viewpoint is applied here, bearing in mind also that each of the three fungi investigated shows different relationships to other genera of Plectascales. So *T. aurantiacus* shows morphological characters similar to *Aphanoascus* (Cephalothecaceae) but *D. thermophilus* in this respect is related to certain Microascaceae while *D. crustaceus* is close to *Paecilomyces* (Eurotiaceae). For this reason the latter species is retained in *Dactylomyces* under the new subgenus *Paecilomyopsis*.

Considerable uncertainty exists in regard to the position of the two genera in relation to the known families of Plectascales (cf. Fischer, 1896; Gäumann, 1926; Arx & Müller, 1954), because none of the present families possess the essential characters of the genera mentioned. To resolve this problem, it is proposed to place both the genera in question into the new family Thermoascaceae which is defined as follows:

Thermoascaceae fam.nov.

Hyphae hyalinae, ramosae, anastomosae vel septatae, non-fasciculatae vel etiam fasciculatae. Conidiophora diversa ad hyphas mycelii; conidia plus minusve hyalina. Cleistothecia firma, astoma, irregulariter globosa, solitaria, aggregata, confluentia vel crustosa, superficialia. Peridium irregulare, pseudoparenchymaticum, plus minusve tomentosum. Asci evanescentes, irregulariter dispositi, 2-8 sporis. Ascosporae continuae, plus minusve hyalinae.

Typus: *Thermoascus* Miehe (1907). Differt aliis familiis ordinis Plectascalearum quod habet peridium irregulare, pseudoparenchymaticum.

Penicillioopsis Solms-Laubach (1886) is another genus related to this family but more information about it is required to make any decisions. Thus the new family comprises at present the genera *Dactylomyces* and *Thermoascus* which represent certain thermophilous plectascales with rapidly spreading mycelium consisting of coarse and delicate, hyaline to subhyaline, anastomosing and branched, septate hyphae. The asexual reproduction is by single, terminal aleuriospores, anellospores or phialospores. The common, essential character of the genera of the family is their firm, somewhat sclerotoid, irregularly globose, pseudoparenchymatous cleistothecium which may become confluent or merge into a crust. Furthermore, species of both genera share in common the chief characteristics of Plectascales, such as the irregular arrangement of asci

within the cleistothecium, globose to oval shape of asci, evanescence of the ascus wall, the hyaline to subhyaline, nonseptate and more or less isodiametrical or elliptical ascospores.

I am indebted to Prof. C. G. C. Chesters, Department of Botany, for criticism and to Mr G. R. Watson, Department of Classics, The University of Nottingham, for the Latin of the diagnosis and Mr T. Nilsson, The Royal College of Forestry in Stockholm, for the isolates of *Dactylomyces thermophilus* placed at my disposal.

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(Accepted for publication 10 November 1966)