# The taxonomy of *Penicillium* species from fermented cheeses

R. A. SAMSON[1], CHRISTIANE ECKARDT[1,3] AND R. ORTH[2,4]

[1] *Centraalbureau voor Schimmelcultures, Baarn, The Netherlands, and*
[2] *Bundesforschungsanstalt für Ernährung, D-7500 Karlsruhe, Germany*

SAMSON, R. A., ECKARDT, C. and ORTH, R. 1977. The taxonomy of *Penicillium* species from fermented cheeses. Antonie van Leeuwenhoek **43**: 341–350.

The taxonomy of the *Penicillium camemberti* and *P. roqueforti* series is re-investigated. *P. caseicolum* Bainier is regarded as a synonym of *P. camemberti* Thom on the basis of morphological characters. *P. casei* Staub is considered to be identical with *P. verrucosum* Dierckx var. *cyclopium* (Westling) Samson, Stolk et Hadlok. Descriptions and illustrations of *P. camemberti* and *P. roqueforti* Thom are given. The occurrence and mycotoxin production of both species are shortly discussed.

## INTRODUCTION

Members of the genus *Penicillium* are commonly found in food products. Several species are known to cause spoilage (e.g. *P. digitatum* Sacc. and *P. expansum* Link ex S. F. Gray) or to produce toxic substances (e.g. *P. griseofulvum* Dierckx and *P. rubrum* Stoll). Some other species like *P. roqueforti* and *P.camemberti* have long been used in the production of such cheeses as Roquefort, Gorgonzola, Camembert and Brie. As early as the turn of the century Johan-Olsen (= Sopp) (1898), Dierckx (1901) and Thom (1906) and others reported on these fungi, especially dealing with their occurrence on cheese and the role in the fermentation process. In current food microbiology the *Penicillium* species which are used as fungal starters for the production of different types of cheese have become of special interest because of their possible toxic metabolites (Gibel, Wegner and Wildner, 1971; Frank, 1973; Anon., 1974).

In their Manual of the Penicillia, Raper and Thom (1949) paid special attention to the cheese-borne species and placed them in two separate series, the *P. roqueforti* and the *P. camemberti* series. The identification of the members

[3] Present address: Bundesanstalt für Fleischforschung, D-8650 Kulmbach, Germany.
[4] Present address: Henkel & Cie GmbH, Dept. of Microbiology, D-4000 Düsseldorf, Germany.

of these two series sometimes proved to be difficult because the species show morphological similarities to other very common Penicillia such as *P. verrucosum* var. *cyclopium* (Samson, Stolk and Hadlok, 1976). Furthermore in the literature and also by cheese manufactures, some old and doubtful names like *P. glaucum* Link and *P. candidum* Link are still infrequently used. This paper deals with a re-investigation of the species belonging to the *P. roqueforti* and *P. camemberti* series. The conidiophore terminology used in this paper is that of Samson et al. (1976).

*Penicillium camemberti* Thom. — Bull. Bur. Anim. Ind. U.S. Dept. Agric. **82**: 33. 1906.

- *Penicillium aromaticum* III Johan-Olsen. — Zentbl. Bakt. ParasitKde, Abt. II. **4**: 161. 1898.
- *Penicillium album* Epstein. — Arch. Hyg. **15**: 360. 1902 (non *P. album* Preuss. — Linnaea **24**: 135. 1851 or *P. album* Riv. — Paras. Véget. p. 452. 1873) = *P. epsteinii* Lindau apud Rabenhorst, Deutschl. Krypt. Flora, Pilze, Bd. 8, 166. 1907.
- *Penicillium rogeri* Wehmer. apud Lafar. — Tech. Mycol. **2**: 226. 1906.
- *Penicillium caseicolum* Bain. — Bull. Soc. Mycol. Fr. **23**: 94. 1907.
- *Penicillium camemberti* Thom var. *rogeri* Thom. — Bull. Bur. Anim. Ind. U.S. Dep. Agric. **118**: 52. 1910.

Colonies on Czapek agar growing slowly, attaining a diameter of 2–3.5 cm within two weeks at 25 C, consisting of a raised floccose aerial mycelium usually up to 1 cm high, at first white, remaining so or changing to yellowish, pinkish

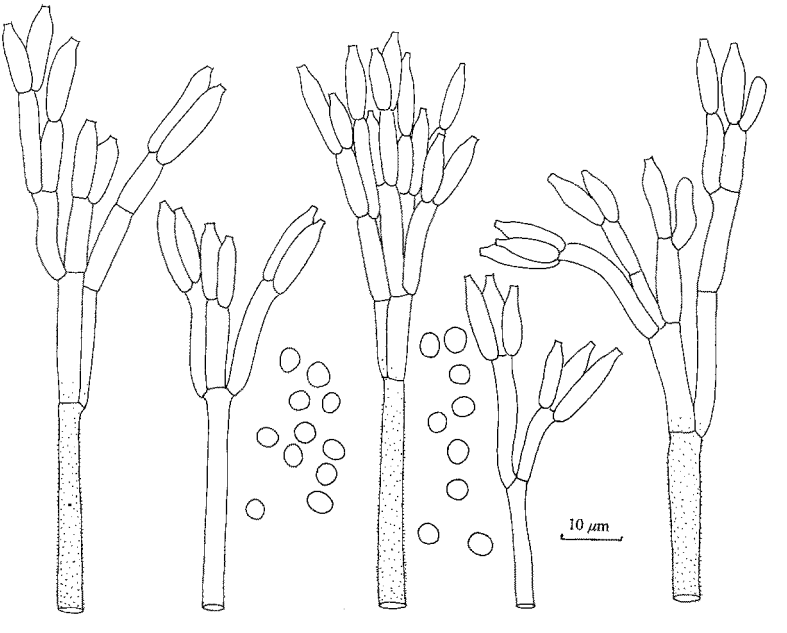


Fig. 1. *Penicillium camemberti*, conidiophores and conidia.

(rare) or grey-greenish, the latter shade usually appearing rather late in the colony development. Odour mouldy or not pronounced. Exudate rarely present as colourless drops. Conidiogenous structures arising from submerged hyphae, occasionally from aerial hyphae. Conidiophores up to 500 μm long, 2.5–4.0 μm wide, two- to three-stage branched; conidiophore stipe rough-walled, rarely smooth-walled, ornamentation sometimes appearing later in the development. Metulae 8–14 × 2.5–3.0 μm, giving rise to 3 to 6 phialides. Philialides flask-shaped with short necks, 10–13 × 2.2–2.5 μm. Conidia in tangled chains, globose to subglobose, or broadly ellipsoidal, hyaline or slightly greenish, 4.0–5.0 × 3.0–4.5 μm (Fig. 1).

Colonies on malt agar similar, but mostly with more conidiophores which are more roughened, than on Czapek agar.

Material examined:
CBS 299.48 = NRRL 877 = ATCC 4845 = IMI 27831, type culture of *P. camemberti*, isolated from camembert cheese by C. Thom, Storrs, Connecticut, USA. CBS 123.08, type culture of *P. camemberti* var. *rogeri*, isolated from camembert cheese by C. Thom.
CBS 303.48 = NRRL 875 = ATCC 10433 = IMI 28810, type culture of *P. caseicolum*, originating from the collection of G. Bainier, Paris.
CBS 249.77 A and B, starter culture "*P. candidum*", used for the production of Camembert in Germany.
CBS 248.77 received as *P. camemberti* var. *candidum* III C3, used by Gibel et al. (1971) in their feeding experiments with rats.
Numerous other strains isolated from German and French Camembert and Brie cheeses and smoked pork. This material also includes the isolates described by Frank (1966).

## Discussion

The species of *P. camemberti* and *P. caseicolum* were considered by Raper and Thom (1949) as two distinct taxa. They were separated on the basis of the colony difference: pale green in *P. camemberti* and white in *P. caseicolum*. According to Raper and Thom (1949) both species differ also in physiological and biochemical characters as revealed in cheese manufacture. In an earlier paper Thom (1910) considered the white form to be a variety of *P. camemberti* and called it *P. camemberti* var. *rogeri*. In 1930, however, Thom placed this white variety in synonymy with *P. caseicolum*.

The status of *P. camemberti* and *P. caseicolum* has been discussed in an extensive study by Leonidse (1930). In that study it was shown that both species do not differ significantly in their morphological or physiological characters. Leonidse (1930) also demonstrated that the grey-green colony colour of *P. camemberti* is unstable. Cultivation of green strains on a sucrose-containing medium (after Bezssonof, 1918) revealed only yellow or uncoloured. A similar comparative study on the morphology and physiology of *P. camemberti* and *P. caseicolum* by Frank (1966) also showed that both species are very similar.

The present study of the type strains and several additional strains of both

species demonstrates that a species delimitation based on colony colour difference is unreliable. Cultures of *P. camemberti* remain white on media with higher sucrose concentrations or change to pale yellow. Some strains of *P. caseicolum* become yellow or even pinkish on normal Czapek agar.

The conidiophore morphology of *P. camemberti* and *P. caseicolum* is very similar. The branching pattern of both species is identical, though the roughness of the wall may vary. In most isolates the conidiophore stipes may become roughened in old cultures. Phialides and conidia are identical in both taxa.

In spite of the small colour difference between *P. camemberti* and *P. caseicolum*, these taxa cannot be separated and are synonymized under the older name *P. camemberti* Thom.

In the literature *P. candidum* Link and *P. album* Preuss have often been cited as used in cheese manufacturing. No type material exists of either species and their descriptions are very inadequate. The two species can therefore best be considered doubtful taxa. The taxonomic status of *P. aromaticum* III Johan-Olsen has been discussed by Thom (1910, 1930) and Raper and Thom (1949) and we accept their suggestion that this species may be identical with *P. camemberti* although no type material exists.

*P. camemberti* resembles *P. verrucosum* Dierckx var. *album* (G. Smith) Samson, Stolk et Hadlok (1976) in its rough-walled conidiophores. The latter species has, however, fasciculate colonies with an earthy odour and uniform globose to subglobose conidia.

In many studies the enzyme activities of *P. camemberti* and *P. caseicolum* have been investigated (Raper and Thom, 1949; Jacquet et al., 1957; Prokš and Cingrošová, 1962; Eichler, 1968; Doležálek and Minarik, 1968; Kikuchi and Takafuji, 1971; Lenoir et al., 1971; Lamberet and Lenoir, 1972). At present, camembert cheeses are mostly fermented by the white forms of *P. camemberti* (= P. *caseicolum*) because the white mycelium gives the cheese more aesthetic appearance (Lübenau-Nestle and Mair-Waldburg, 1968). During our studies we also obtained a few isolates with green conidia from cheese. Most isolates, however, were white, yellowish or pinkish.

*Penicillium casei* Staub. — Zentbl. Bakt. ParasitKde, Abt. II. **31**: 454. 1911.

This species has been re-described by Thom (1930) and Raper and Thom (1949), based on a culture (CBS 302.48 = NRRL 844) isolated from Swiss cheese. This culture does not represent the type strain described by Staub (1911). Examination of Thom's strain and the original description of *P. casei* proved that this species can best be considered to be a synonym of *P. verrucosum* var. *cyclopium* (cf. Samson et al., 1976: 37–40).

*Penicillium casei* Staub var. *compactum* Abe. — J. Gen. Appl. Microbiol. (Tokyo) **2**: 101. 1956.

*Penicillium pseudocasei* Abe. — J. Gen. Appl. Microbiol. (Tokyo) **2**: 102. 1956; ex G. Smith – Trans. Br. Mycol. Soc. **46**: 335. 1963.

*Penicillium roqueforti* Thom var. *punctatum* Abe — J. Gen. Appl. Microbiol. (Tokyo) **2**: 99. 1956.

These three taxa were not validly described, because they lacked a Latin diagnosis. After examination of the type cultures Samson et al. (1976) regarded these 3 species as synonyms of *P. verrucosum* var. *cyclopium*.

*Penicillium roqueforti* Thom. — Bull. Bur. Anim. Ind. U.S. Dep. Agric. **82**: 35. 1906.

- *Penicillium aromaticum casei* Johan-Olsen. — Zentbl. Bakt. ParasitKde Abt. II. **4**: 164. 1898.
? - *Penicillium atroviride* Dierckx. — Ann. Soc. Scient. Brux. **25**: 87. 1901.
? - *Penicillium vesiculosum* Bain. — Bull. Soc. Mycol. Fr. **23**: 10. 1907.
- *Penicillium roqueforti* Thom var. *weidemannii* Westling. — Ark. Bot. **11**: 52. 1911.
- *Penicillium atroviride* Sopp. — Vidensk Selsk. Skr. Kristiana, mat.-naturv. Kl. **11**: 149. 1912 (non *P. atroviride* Dierckx).
- *Penicillium aromaticum* Sopp. — ibid. **11**: 155. 1912.
- *Penicillium roquefort* Sopp. — ibid. **11**: 156. 1912.
- *Penicillium gorgonzola* Weidemann apud Biourge. — Cellule **33**: 204. 1923.
- *Penicillium stilton* Biourge. — Cellule **33**: 206. 1923.
- *Penicillium suaveolens* Biourge. — Cellule **33**: 200. 1923.
- *Penicillium biourgei* Arnaudi. — Zentbl. Bakt. ParasitKde, Abt. II. **73**: 321. 1928.

Colonies on Czapek agar growing rapidly, attaining a diameter of 4–5 cm within 14 days at 25 C, consisting of a dense felt of erect conidiophores; in fresh isolates typically velvety without production of aerial mycelium; in older cultures becoming more lanose with production of aerial vegetative mycelium. Colour blue-green near Pois or Leaf green (Ridgway, 1912. pl. 41), later becoming darker. Exudate in fresh isolates often present as hyaline droplets. Odour mostly absent or not pronounced. Reverse greenish, often changing to darker shades of green to black. Conidiophores two- or three-stage branched, 100–200 μm tall and 4–6.5 μm wide, the stipe typically ornamented with conspicuous warts, some strains less roughened at the apex of conidiophore stipes, but usually ornamentated at the base. Metulae 10–15 × 3–4.5 μm, rough-walled, giving rise to clusters of 4–7 phialides. Phialides flask-shaped with short neck, 8–12 × 3.0–3.5 μm. Conidia in loose columns, globose to subglobose, greenish, smooth-walled, mostly 4–6 μm, occasionally up to 8 μm (Fig. 2).

Reduced conidiogenous structures occur submerged in the agar. The conidiophore is frequently branched (see Fig. 3) in a manner slightly resembling the branching pattern of the Divaricata. The ornamentation is sometimes less pronounced. Phialides are slightly larger and less uniform in shape. Conidia are produced in short chains and are mostly larger than those produced by aerial conidiophores.

Sclerotia are often formed in old cultures which usually also produce some aerial vegetative hyphae. The sclerotia are white, soft, 50–100 μm in diameter, and consist of a loose thin knit of hyphae. The sclerotium centre consists of a pseudoparenchymatic cell mass.

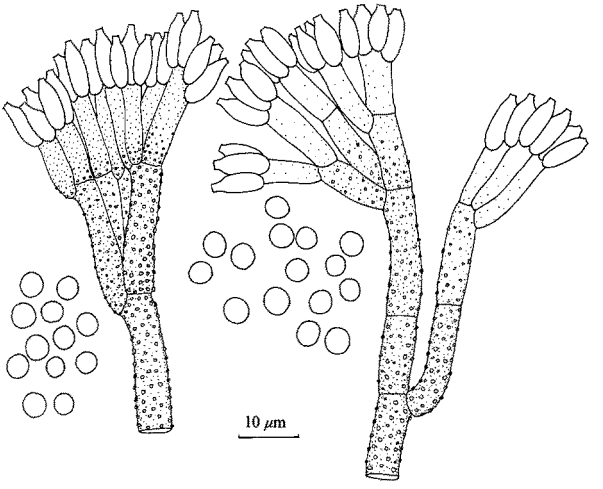


Fig. 2. *Penicillium roqueforti*, conidiophores and conidia.

Colonies on malt agar similar in growth and colour but the texture is thinner. Conidiogenous structures are identical to those on Czapek agar, but the ornamentation of the conidiophore stipe is usually more pronounced.

Material examined:
CBS 221.30 = NRRL 849 = ATCC 10110 = IMI 24313, type culture of *P. roqueforti*, isolated from roquefort cheese by C. Thom.

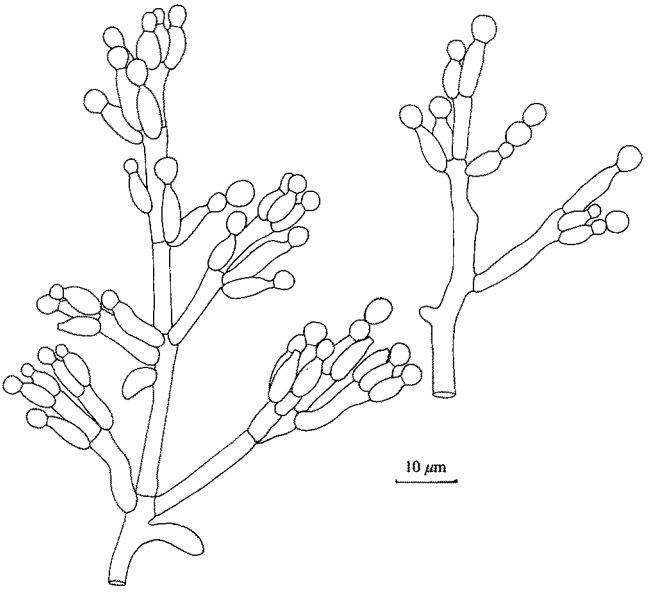


Fig. 3. *Penicillium roqueforti*, conidiogenous structures in submerged agar.

CBS 234.38, isolated from blue Cheshire cheese and sent by S. Dattilo-Rubbo, probably type culture of *P. roqueforti* var. *viride*.
Numerous other isolates from French, Italien, German, English and Danish Blue cheeses but also from meat products, bread, ice cream, and other food products. This material also includes isolates described by Frank (1966).

## Discussion

*P. roqueforti* can be easily recognized by its fast growth, its dark blue-green, velvety colonies and the wide, warted conidiophore stipes. The species has sometimes been confused with velvety forms of *P. verrucosum* var. *cyclopium*, but this fungus usually has smaller conidia and thinner conidiophore stipes with smaller protuberances. In addition, the colonies of *P. verrucosum* var. *cyclopium* typically produce strong earthy or streptomyces-like odours, while colonies of *P. roqueforti* are odourless. Raper and Thom (1949) did not describe sclerotial development in *P. roqueforti* strains, and we were unable to find mention of sclerotium development by this species in the literature. Sclerotia were often found in old colonies (3 weeks and older) and hence they were probably not observed by previous authors.

Although *P. roqueforti* has normally blue-green colonies, we have encountered one brown strain which agrees exactly in its microscopic characters. This strain (CBS 501.75 = IMI 54229) was isolated from barley grains and probably represents a natural colour mutant. Knight, Mohr and Frazier (1950) and Morris, Jezeski and Combs (1954) reported white mutants of *P. roqueforti* obtained by irradiation with UV light of a normal green strain. These mutants proved to be of value in cheese manufacture, because of the similar enzymatic and growth characters. Knight et al. (1950) also suggested that one gene is probably responsible for the green pigmentation of the conidia.

## Occurrence and toxicology of *P. camemberti* and *P. roqueforti*

In addition to being used for the production of fermented cheeses, *P. camemberti* and *P. roqueforti* also occur on other substrates. Jirkovsky and Galgóczy (1966) reported that 61% of the fungal isolates from Hungarian salami proved to be *P. camemberti*. *P. roqueforti* is one of the common microorganisms in fermented silage (Raper and Thom, 1949; Le Bars and Escoula, 1974), meat products (Leistner and Ayres, 1967; Racovita, Racovita and Constantinescu, 1969; Hadlok, Samson and Schorr, 1975) and other food products. Mycotoxicoses by *P. roqueforti* have been reported by Kanota (1970), Still et al. (1972) and Lafont et al. (1976). Toxic substances have been isolated and incompletely characterized by Kanota (1970). Wei et al. (1973, 1975) isolated a "PR-toxin" from *P. roqueforti* culture media, a sesquiterpenoid metabolite, and Polonelli et al. (1975), Moreau et al. (1976) and Orth (1976) confirmed these findings. Alkaloids have been isolated and characterized by Taber and Vining (1958),

Abe et al. (1967), Bekmakhanova (1974), Ohomo et al. (1975), Scott, Merrien and Polonsky (1976) and Scott and Kennedy (1976), and one of these, roquefortine A, proved to be weakly toxic (Ohomo et al., 1975). Long-term feeding experiments with rainbow trouts (Frank et al., 1975) and rats (Frank et al., 1977) using *P. camemberti* and *P. roqueforti* have, however, not revealed any evidence of carcinogenic or other pathogenic effects.

This work was completed during tenure of a NATO Science Fellowship at the Centraalbureau voor Schimmelcultures, Baarn, awarded to C. Eckardt by the D.A.A.D. (German Academic Exchange Service). We thank Professor Dr. H. K. Frank for the *Penicillium* cultures used in the present study.

*Received* 9 *June* 1977

## REFERENCES

ABE, M., YAMATODANI, S., YAMANO, T., KOZU, Y and YAMADA, S. 1967. Production of alkaloids and related substances by fungi. I. Examination of fungi for their ability of producing ergot alkaloids. — J. Agric. Chem. Soc. Japan. **41**: 68–71.

Anon. 1874. Mikroorganismen für Lebensmitteltechnik. Gemeinsame Mitteilung der Kommission für Ernährungsforschung und der Kommission zur Prüfung fremder Stoffe bei Lebensmitteln. — Deutsche Forschungsgemeinschaft, Bonn-Bad Godesberg.

BEKMAKHANOVA, N. E. 1974. Evaluation of various media for selecting microscopic fungi as potential producers of alkaloids. — Mikol. Fitopatol. **8**: 152–155.

BEZSSONOF, N. 1918. Über die Bildung der Fruchtkörper des *Penicillium glaucum* in konzentrierten Zucker lösungen. — Ber. dtsch. bot Ges. **36**: 225–229.

DIERCKX, R. P. 1901. Un essai de révision du genre *Penicillium* Link. — Ann. Soc. Sci. Brux. **25**: 83–89.

DOLEŽÁLEK, J. and MINARIK, R. 1968. Effect of acidity of the medium and of rennet on the enzymic activity of the mold-strains *Penicillium camemberti* and *Penicillium nalgiovense*. — Sb. Vyz. Sk. Chem. Technol. Proze E**20**: 67–77.

EICHLER, F. 1968. Beurteilung der Auskeimfähigkeit von Blauschimmelsporen. — Milchwissenschaft **23**: 632–635.

FFANK, H. K. 1966. Ein Beitrag zur Taxonomie der Gattung *Penicillium* Link. — Habilitationsschr. Fak. allg. Wiss., München.

FRANK, H. K. 1973. Starterkulturen in der Lebensmitteltechnik. — Chem. Mikrobiol. Technol. Lebensm. **2**: 52–56.

FRANK, H. K., ORTH, R., FEICHLE, G. und WUNDER, W. 1975. Fütterungsversuche an Forellen mit Camenbert- und Roquefort-Kulturen. — Michwissenschaft **30**: 594–597.

FRANK, H. K., ORTH, R., IVANKOVIC, S., KUHLMANN, M. and SCHMÄHL, D. 1977. Investigations on carcinogenic effects of *Penicillium caseicolum* and *Penicillium roqueforti* in rats. — Experientia **33**: 515–516.

GIBEL, W., WEGNER, K. und WILDNER, G. P. 1971. Experimentelle Untersuchungen zur Frage einer kanzerogenen Wirkung von *Penicillium camemberti* var. *candidum*. — Arch. Geschwulstforsch. **38**: 1–6.

HADLOK, R., SAMSON, R. und SCHNORR, B. 1975. Schimmelpilze und Fleisch: Gattung *Penicillium*. — Fleischwirtschaft **7**: 979–984.

JACQUET, J., VILLETTE, O., DELACROIX, J., GONDOUIN, H. et DESFLEURS, M. 1957. Considérations sur l'action du pH dans la croissance des moisissures utilisées pour la fabrication du camembert – rôle du sel. — Bull. Soc. Linn. Normandie **8**: 115–132.

JIRKOVSKY, M. und GALGÓCZY, J. 1966. Die Untersuchung der Schimmelpilzflora der ungarischen Wintersalami. — Fleischwirtschaft **46**: 128–129.

JOHAN-OLSEN, O. 1898. Die bei der Käsereifung wirksamen Pilze. — Zentbl. Bakteriol. Parasitenk. InfektionsKr. II. Abt. **4**: 161–169.

KANOTA, K. 1970. Studies on toxic metabolites of *Penicillium roqueforti*, p. 129–132. *In* M. Herzberg, (ed.), Proc. 1st U.S. — Japan Conf. Toxic Microorganisms, mycotoxins and botulism. Honolulu, Hawai, 1968. — U.S. Dept. interior, Washington D. C.

KIKUCHI, T. and TAKAFUJI, S. 1971. Microorganisms of Camembert cheese. 11. Protease of Camembert cheese mold. — Nippon Chikusan Gakkai-Ho **42**: 205–209.

KNIGHT, S. C., MOHR, W. H. and FRAZIER, W. C. 1950. White mutants of *Penicillium roqueforti*. — J. Dairy Sci. **33**: 929–933.

LAFONT, P., LAFONT, J., PAYEN, J., CHANY, E., BERTIN, G. and FRAYSSINET, C. 1976. Toxin production by 50 strains of *Penicillium* used in the cheese industry. — Food Cosmet. Toxicol. **14**: 137–139.

LAMBERET, G. and LENOIR, J. 1972. Aptitude de l'espèce *Penicillium caseicolum* à la production d'enzymes lipolytiques. — Lait **52**: 175–192.

LE BARS, J. et ESCOULA, G. 1974. Champignons contaminant les fourrages. Aspects toxicologiques. — Aliment. Vie **62**: 126–142.

LEISTNER, L. und AYRES, J. C. 1967. Schimmelpilze und Fleischwaren. — Fleischwirtschaft **47**: 1320–1326.

LENOIR, J., CHOISY, C., AUBERGER, B., MARRASSE, J. et SCHMIDT, M. 1971. Aptitude de l'espèce *Penicillium caseicolum* à la production d'enzymes protéolytiques. — Lait **51**: 138–157.

LEONIDSE, L. 1930. Über den weissen und blauen Camembert-Schimmel. — Zentbl. Bakteriol. Parasitenk. Infektions II. Abt. **82**: 211–246.

LÜBENAU-NESTLE, R. and MAIR-WALDENBURG, H. 1968. Eigenschaften der Käse III, p. 641–687. *In* L. Acker et al. (eds.) Handbuch der Lebensmittelchemie III. — Springer Berlin – Heidelberg – New York.

MORRIS, H. A., JEZESKI, J. J. and COMBS, W. B. 1954. The use of white mutants of *Penicillium roqueforti* in cheese making. — J. Dairy Sci. **37**: 711–716.

MOREAU, S., GAUDEMER, A., LABLANCHE-BOMBIER, A. and BIQUET, J. 1976. Métabolites de *Penicillium roqueforti:* PR-toxine et métabolites associés. Tetrahedron Lett. **11**: 833–834.

OHOMO, S., SATO, T., UTAGAWA, T. and ABE, M. 1975. Isolation of festuclavine and three new indole alkaloids, roquefortine A, B and C from the cultures of *Penicillium roqueforti*. — Agric. Biol. Chem. **39**: 1333–1334.

ORTH, R. 1976. PR-Toxinbildung bei *Penicillium roqueforti*-Stämmen. — Z. Lebensm. Unters.-Forsch. **160**: 131–136.

POLONELLI, L., DELLE MONACHE, F., MORACE, G., LAURIOLA, L., SAMSON, R. A. e CHEZZI, C. 1975. Isolamento e caratterizzazione di una micotossina prodotta da *Penicillium roqueforti*, p. 327–330. *In* Atti XVII Congr. Naz. Soc. Ital. Microbiol., Padova.

PROKŠ, J. and CINGROŠOVÁ, K. 1962. The influence of *Penicillium camemberti* and *Penicillium caseicolum* on proteolytic and lipolytic changes in the ripening of Camembert cheese. — Proc. 16th Int. Dairy Congr. Copenhagen 1962, Sect. B, p. 442–448.

RACOVITA, A., RACOVITA, A. und CONSTANTINESCU, T. 1969. Die Bedeutung von Schimmelpilzüberzügen auf Dauerwürsten. — Fleischwirtschaft **49**: 461–466.

RAPER, K. B. and THOM, C. 1949. A Manual of the Penicillia. — Williams & Wilkins Co., Baltimore.

RIDGWAY, R. 1912. Color Standards and Color Nomenclature. — Washington, D.C.

SAMSON, R. A., STOLK, A. C. and HADLOK, R. 1976. Revision of the subsection Fasciculata of *Penicillium* and some allied species. — Stud. Mycol., Baarn **11**: 1–47.

SCOTT, P. M. and KENNEDY, B. P. C. 1976. Analysis of blue cheese for roquefortine and other alkaloids from *Penicillium roqueforti*. — J. Agric. Food Chem. **24**: 865–868.

SCOTT, P. M., MERRIEN, M. A. and POLONSKY, J. 1976. Roquefortine and isofumigaclavine

A, metabolites from *Penicillium roqueforti*. — Experientia **32**: 140–141.

STAUB, W. 1911. *Penicillium casei* n. sp. als Ursache der rotbraunen Rindenfärbung bei Emmentaler Käsen. — Zentbl. Bakteriol. Parasitenk. Infektionskr. II. Abt. **31**: 454. 466.

STILL, P. E., WEI, R. D., SMALLEY, E. B. and STRONG, F. M. 1972. A mycotoxin from *Penicillium roqueforti* isolated from toxic cattle feed. — Fed. Proc. Fed. Am. Soc. Exp. Biol. **31**: 733.

TABER, W. A. and VINING, L. C. 1958. The influence of certain factors on the in vitro production of ergot alkaloids by *Claviceps purpurea* (Fr.) Tul. — Can. J. Microbiol. **4**: 611–626.

THOM, C. 1906. Fungi in cheese ripening: Camembert and Roquefort. — Bull. Bur. Anim. Ind. U.S. Dept. Agric. **82**: 1–39.

THOM, C. 1910. Cultural studies of species of *Penicillium*. — Bull. Bur. Anim. Ind. U.S. Dep. Agric. **118**: 1–109.

THOM, C. 1930. The Penicillia. — Williams & Wilkins Co., Baltimore.

WEI, R.-D., STILL, P. E., SMALLEY, E. B., SCHNOES, H. K. and STRONG, F. M. 1973. Isolation and partial characterization of a mycotoxin from *Penicillium roqueforti*. — Appl. Microbiol. **25**: 111–114.

WEI, R.-D., SCHNOES, H. K., HART, P. A. and STRONG, F. M. 1975. The structure of PR-toxin, a mycotoxin from *Penicillium roqueforti*. — Tetrahedron **31**: 109–114.