Peronospora complex on Compositae

O. Constantinescu

The Herbarium, Uppsala University, Box 541, S-751 21 Uppsala, Sweden

Constantinescu, O. (1989). *Peronospora* complex on Compositae. – SYDOWIA 41: 79–107.

Peronospora leptosperma and similar fungi parasitic almost exclusively on plants belonging to the tribe Anthemideae are revised. A new genus, *Paraperonospora,* is introduced to accommodate these fungi. It is mainly characterized by conidiophores having branches broadening upward and by both dicho- and trichotomic branching. Eight new combinations are proposed and lectotypes for 10 taxa are selected. Detailed descriptions and illustrations of seven species of *Paraperonospora* and of *Peronospora radii* are provided, and a key for their identification is added. Five doubtful or excluded taxa are also treated.

Two species of *Peronospora* parasitic on different organs of various Compositae (Asteraceae) were described and illustrated by De Bary (1863). They were placed in the Section Pleuroblastae characterized mainly by the dissemination organs, called conidia, having continuous wall and germination by tube. The first species, *Peronospora radii,* was distinguished by its violaceous colour, and sporulation in the inflorescence of its host. The second, *Peronospora leptosperma,* was characterized by colourless organs and both dichotomous and trichotomous type of conidiophore branching. In addition, De Bary mentioned the upward broadening of branches in *P. leptosperma.*

Two taxa similar to *P. radii,* but parasitic on leaves, were later described under *P. radii* var. *epiphylla* Poirault (1915) and *P. danica* Gäumann (1923). Except for the question if the same fungus may attack both flowers and leaves, *Peronospora radii* generated no taxonomical problems for the subsequent authors.

On the contrary, because of its unusual morphology, *P. leptosperma* was a source of controversial taxonomic decisions.

Gäumann (1923) restricted *P. leptosperma* to the fungus parasitic on *Chamomilla recutita, C. suaveolens* and *Matricaria perforata.* He introduced *P. anthemidis* for the form parasitic on *Anthemis* spp., *P. tanaceti* for the one on *Tanacetum vulgaris,* and added two more species, *P. sulphurea* and *P. artemisiae-biennis.* Six more or less similar taxa were later described by Savulescu & Rayss (1930), Ling & Tai (1946) and Savulescu & Vanky (1956).

Two *P. leptosperma*-like fungi were described in the genus *Plasmopara* by SAWADA (1931) and DUDKA & BURDJUKOVA (1977), and ten such fungi were transferred to *Plasmopara* by SKALICKY (1966) and TAO & QIN (1987).

Rather recently, three *P. leptosperma*-like fungi were placed in the genus *Bremiella,* as one new species and two new combinations (TAO & QIN, 1982).

The difficulty in finding the appropriate generic position of these fungi is illustrated by the fact that each of the epithets *artemisiae-annuae* and *chrysanthemi-coronarii* have been combined into *Peronospora, Plasmopara* and *Bremiella,* during the last decades. Significantly enough, morphologically indistinguishable collections of one and the same fungus were described by SAVULESCU & VANKY (1956) under *Plasmopara halstedii* and four new taxa, *Peronospora achilleae, P. dimorphothecae, P. ursiniae* and *P. buhrii.*

During the preparation of a check list of Romanian Peronosporales (CONSTANTINESCU & NEGREAN, 1983), as well as of a monograph of the genus *Plasmopara,* a number of these fungi parasitic on Compositae were examined. It soon became apparent that, by their morphological characters, they differ not only from typical *Peronospora,* but also from *Plasmopara* and *Bremiella.* Consequently, a revision of all *Peronospora*-like fungi described on Compositae was undertaken.

Material and methods

Some 355 herbarium specimens, including the types of 15 out of the 24 taxa dealt in this paper were examined. Slides were prepared by wetting the specimen with 95% ethyl alcohol and transferring fungal material in lactic acid or lactofucsin. Except for the length of the conidiophores, all other measurements were performed with the aid of a oil-immersion lens and drawing tube at a 2000× final enlargement. The nomenclature of the hosts is mainly in accordance with CRONQUIST (1955), MOORE et al. (1976), SCOGGAN (1979) and SHISHKIN & BOBROV (1961). Herbarium abbreviations are those used by HOLMGREN et al. (1981). In some cases only selected specimens are cited, but complete lists are deposited at the UPS herbarium. Except where abbreviations may cause confusion, *P.* is used for *Peronospora* and *Pp.* for *Paraperonospora.*

Results

Morphology. – With the exception of *Peronospra radii,* all other fungi studied have a number of characters in common. The branches, and in many cases even the trunk, are slightly but consistently broadening toward the growing direction (Fig. 1 A). Although

the general pattern of the branching is dichotomous, the trichotomy occurs at various points of branching (Fig. 1 A), and is present in a number of conidiophores in almost every collection. When branching is dichotomous, the pair branches have appreciable different length. Each branch commonly ends in (1–)2–3(–4) ultimate branchlets (Fig. 1 C). In some cases one ultimate branchlet is longer and terminal, appearing as an extension of the branch, and two are shorter and arise at the base of the terminal one. In other cases three, more or less equally long ultimate branchlets emerge from a common, sometimes swollen, base. The tip of the ultimate branchlets may be blunt, more or less rounded, or swollen in variable degree. The dissemination organs are of conidium-type, i.e. with continuous wall, no dehiscence apparatus and germination by tube. The conidia are rather large, generally over 30 µm long.

In some conidia of *P. leptosperma*-like fungi a membrane-like structure is visible below the conidium apex (Figs 1 D, E, 3 D-F, 4 D). This structure superficially resembles a dehiscence apparatus like the one present in *Plasmopara* or *Bremiella*. However, at a closer examination, the wall of the conidium appears continuous and no papilla is present. Moreover, in a few germinating conidia found in the specimens examined (Fig. 6 C), as well as in one conidium depicted by Tao & Qin (1987: 71), germination does not occur at, and through the apex, but at randomly located points of the conidium wall. Most probably, this membrane-like structure which, significantly enough, is not present in all conidia, is only a vestigial dehiscence apparatus.

Conidium ontogeny. – The determinate growth of the ultimate branchlets and synchronous production of solitary conidia/sporangia are characteristic for Peronosporaceae. *Peronospora-leptosperma*-like fungi fit this pattern. However, in a few herbarium specimens, an apparently indeterminate growth associated with basipetal production of conidia was noticed. This case is now under study.

The relation to other genera of Peronosporales. – The unique character of the conidiophores in *P. leptosperma*-like fungi clearly differentiate them from *Peronospora* in which the branching is consistently dichotomous, the branches have a constant breadth, and each terminates in two ultimate branchlets with truncate tips. By having conidia they are also distinct from *Plasmopara* and *Bremiella,* genera with poroid dissemination organs, i.e. sporangia. *Peronospora leptosperma*-like fungi are sufficiently distinct from other genera of Peronosporales to be placed in a separate genus. Since the introduction of the genus *Peronospora* by Corda (1837), nine genera of plant parasitic Peronosporales s.l. have been erected. As in the case of *P. leptosperma*-like fungi, four of these

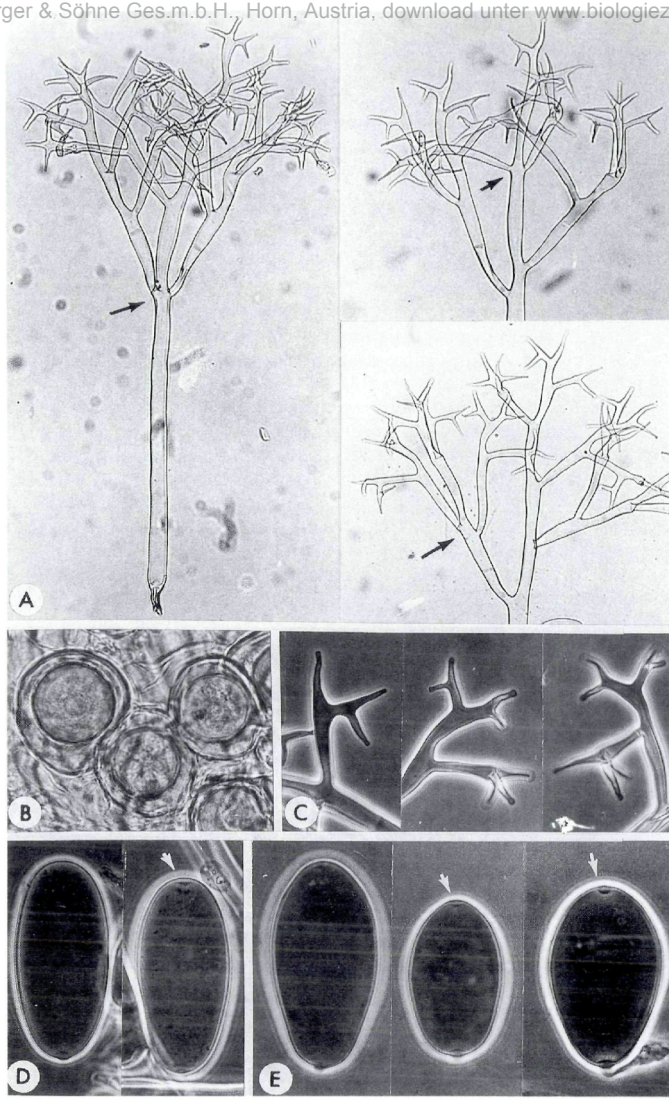

Fig. 1: *Paraperonospora spp.* A–D. *Pp. leptosperma.* – E. *Pp. chrysanthemi-coronarii.* A. conidiophores; arrows show the trifurcate branching. – B. oogonia and oospores. – C. ultimate branchlets. – D & E. conidia; arrows show the vestigial dehiscence apparatus.

show combined characters of different genera and this is also reflected by their names: *Peronosclerospora, Peronophythophthora, Pseudoperonospora, Sclerophthora.*

The value of the branching pattern of the sporangiophore and conidiophore in the classification of Peronosporomycetidae was recently emphasized by DICK et al. (1984). By its branching type and the presence of conidia, *P. leptosperma*-like fungi show relationship to both *Plasmopara* and *Peronospora.* The rudimentary, nonfunctional dehiscence apparatus present in some specimens points out to a possible link with *Bremiella* and, again, *Plasmopara.* In the diagram of the classification of the Peronosporomycetidae presented by DICK et al. (1984), *P. leptosperma*-like fungi should be placed between *Bremiella* and *Bremia,* on the dichotomous lineage of the Peronosporaceae.

Taking into account the above mentioned distinctive characters, a new genus, *Paraperonospora,* is introduced in this paper to accommodate *Peronospora leptosperma* and similar fungi parasitic on Compositae.

Species concept. – The criteria used for delimitation of taxa in *P. leptosperma*-like fungi followed the trend initiated in *Peronospora* by GÄUMANN (1923). It consists of a supposed affinity of a certain fungus to a host or a limited number of hosts, and of biometric studies of conidia, mostly based on a single collection. The limitations of GÄUMANN'S concept have been pointed out, among others, by GUSTAVSSON (1953, 1959b) and YERKES & SHAW (1959).

The species concept adopted in this paper is basically a morphological one. Those specimens which could be placed reasonably safely within a given morphological pattern are grouped under the same species name, irrespective of their host. As a consequence it is accepted that some species, like *Pp. leptosperma, Pp. minor* and *Pp. sulphurea* have more than one host, whereas in other species, like *Pp. artemisiae-biennis, Pp. chrysanthemi-coronarii* and *Pp. tanaceti* the morphological features are consistently associated with one particular host.

Host range. – The hosts of *Paraperonospora,* and of *Peronospora radii,* belong almost exclusively to the tribe Anthemideae. They should be divided into regular or „natural" hosts, i.e. plants frequently attacked in nature by a particular fungus, and accidental or occasional hosts, only rarely attacked. The last are either wild or, more often, cultivated plants, particularly in botanical gardens.

The presence of *Pp. leptosperma* on cultivated *Dimorphotheca,* a member of the tribe Calenduleae, as well as of *Pp. sulphurea* on *Helichrysum* (tribe Inuleae) are in all probability due to accidental infections. Both tribes, but particularly the Inuleae, are not closely related to the Anthemideae (BREMER, 1987). As KUKKONEN (1972)

pointed out in the case of *Anthracoidea* (Ustilaginales), „the exceptional host seems to be a species growing in the very same spot or in the vicinity of a heavy infection". An occasional host may be recognized by the fact that the presence of the parasite is discontinuous. Such a case case is *Plasmopara ammi* CONSTANTINESCU (1968) parasitic on *Ammi majus*, a plant originating from Egypt but cultivated in Romania. Attempts to collect this species again failed, although the host was cultivated in the same place for many years. I am now convinced that *Plasmopara ammi* is only an accidental attack of the widely distributed *Plasmopara umbelliferarum* s.l. on a new host. During this study two specimens of *Achillea clusiana*, an „occasional" host for *Paraperonospora*, were examined. They were collected at the Rostock Botanical Garden, by the same collector, in 1937 and 1939. The first specimens is parasitized by *Pp. leptosperma* (BUCM 3155) and the second by *Pp. sulphurea* (B).

The attack of an unusual host may be due to the presence of a physiological race which may occur even in Peronosporaceae attacking non-crop plants (CRUTE, 1981), or to the favourable environmental and inoculum conditions (PALTI, 1974).

The only experimental study dealing with the host specialization of these fungi was made by DZHANUZAKOV (1962). He showed that the fungus from *Matricaria perforata* can infect the same plant, as well as *M. suaveolens* and *Chamomilla recutita*, but not *Artemisia vulgaris*, *Leucanthemum vulgare* and *Tanacetum vulgare*. This is hardly surprising as the last three plants are natural hosts for different *Paraperonospora* species. Because the fungus from *Matricaria suaveolens* could infect only this host but not *M. perforata* and *Chamomilla recutita* DZHANUZAKOV concluded that the fungus parasitic on *M. suaveolens* represents a different physiological race.

Taxonomy

Paraperonospora O. CONST., gen. nov.

Etym.: from the Greek para = near/similar to.

Oomycotina. A *Peronospora* ramis sursum dilatatis et ramificatione dichotoma vel trichotoma differt.

Specia typica: *Paraperonospora leptosperma* (DE BARY) O. CONST.

Oomycotina. – Plant parasitic. – Conidiophores erect, colourless or slightly yellowish, composed of a trunk and a branched part; branching dichotomous, sometimes trichotomous; all branches more or less broadening towards the distal part; dichotomous branches of different length; each branch ends in (1–)2–3(–4) long-conical ultimate branchlets, having blunt, rounded or inflated tip. – Conidia large, colourless to yellowish, ellipsoidal to broadly ellipsoidal, base round, tip round or slightly apiculate; basal pedicel

short, slightly eccentric. – Oogonia irregular, thin-walled; oospores aplerotic, globose, with smooth, yellowish to brownish wall.

Key to the species treated:

1 Branches of uniform width, conidia brownish ..... *P. radii*
1* Branches broadening upward, conidia colourless, pale yellowish or greyish-brown 2
2 Tip of ultimate branchlets swollen to 3–4 µm 3
2* Tip of ultimate branchlets, blunt, rounded or only slightly enlarged 5
3 Conidia greyish brown ..... *Pp. artemisiae-annuae*
3* Conidia colourless or yellowish 4
4 Most conidia 35–40 µm long *Pp. chrysanthemi-coronarii*
4* Most conidia less than 35 µm long ..... *Pp. multiformis*
5 Broadest part of conidia supramedian ..... *Pp. tanaceti*
5* Broadest part of conidia median. 6
6 Most conidia 35–45 µm long, length/width ratio ca. 2 ..... *Pp. artemisiae-biennis*
6* Conidia shorter, length/width ratio <2 7
7 Most conidia 20–26 µm broad, tip often apiculate ..... *Pp. sulphurea*
7* Most conidia 17–22 µm broad, tip rounded 8
8 Conidia mostly 25–30 µm long ..... *Pp. minor*
8* Conidia mostly 30–40 µm long ..... *Pp. leptosperma*

1. *Paraperonospora artemisiae-annuae* (Lee & M. C. Tai) O. Const., comb. nov.

Bas.: *Peronospora artemisiae-annuae* Ling & M. C. Tai – Lloydia 9: 144. 1946
= *Plasmopara artemisiae-annuae* (Ling & M. C. Tai) Skalicky – Preslia 38: 127. 1966
= *Bremiella artemisiae-annuae* (Ling & M. C. Tai) Tao – Acta mycol. sin. 1: 64. 1982. Type on *Artemisia annua* L., CHINA: Chengtu, 21 April 1943.

No original specimen was available. According to the description and illustration there is no doubt that this is a *Paraperonospora*. The swollen tip of the ultimate branchlets and the size of conidia (24–46 × 14–24 µm, average 37.03 × 20.19) place this species close to *Pp. multiformis* and *Pp. chrysanthemi-coronarii*. The greyish brown colour of the conidia clearly distinguishes it not only from the last two mentioned species but also from all other species of *Paraperonospora*. However, such colour of conidia is quite unusual in *Paraperonospora*.

Host. – *Artemisia annua L.*
Distribution. – CHINA.

2. ***Paraperonospora artemisiae-biennis*** (GÄUM.) O. CONST., comb. nov. – Fig. 2.

BAS.: *Peronospora artemisiae-biennis* GÄUM. – Beitr. KryptogFl. Schweiz 5(4): 131. 1923
= *Plasmopara artemisiae-biennis* (GÄUM.) SKALICKY – Preslia 38: 127. 1966.
Type on *Artemisia biennis* WILLD., USA: Dakota, Kulm, 9 July 1912, BRENCKLE, Fungi dakot. 197 (S – lectotype; S, NY – isolectotypes).

Spots epiphyllous, pale yellowish, margin diffuse. – Down hypophyllous, yellowish, often covering the whole surface. – Conidiophores pale yellowish, erect, 320–600 µm long, trunk 100–280 × 7.5–18 µm; upper part dichotomously, rarely trichotomously branched 3–4(–5) times; ultimate branchlets 2–4 at the tip of

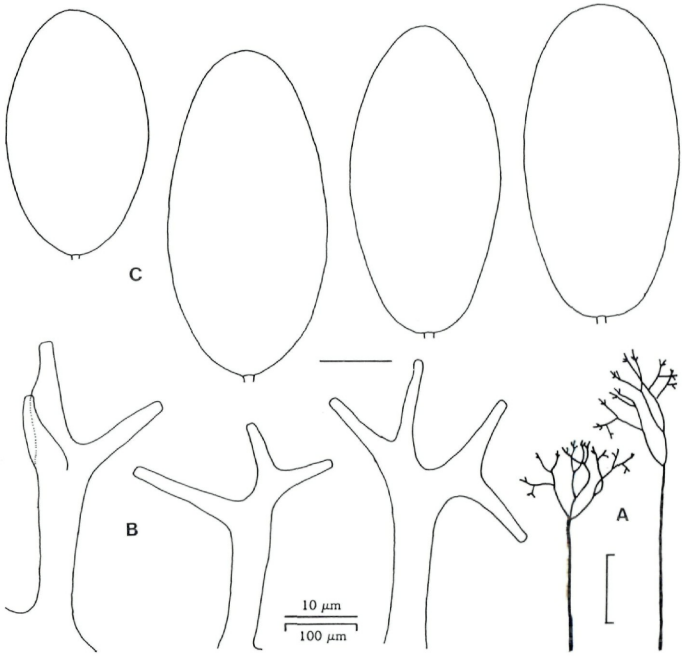

Fig. 2: *Paraperonospora artemisiae-biennis* (lectotype); A. conidiophore. - B. ultimate branchlets. - C. conidia.

each branch, long-conical, 8–16 µm long, base 2.5–5 µm, gradually tapering to 1–2 µm below the truncate or rarely almost rounded tip. – Conidia yellowish, ellipsoidal, (35–)38–45(–48) × (17–)19–21(–24) µm, broadest part median, wall ca 0.5 µm thick; pedicel 1 × 1-1.5 µm. – Sexual organs unknown.

Host. – *Artemisia biennis* WILLD.

Distribution. – NORTH AMERICA.

Additional specimens examined. – On *Artemisia biennis*. CANADA: Alberta, Stettler District, Killan Station, 3 June 1926, coll. A.H. BRINKMAN, det. J. L. CONNERS (FH). U.S.A.: Minn., Lake Minnetonka, Aug. 1883, FARLOW (NY); Iowa, Iowa City, Oct. 1887, T. H. MACBRIDE (NY); S.Dakota, Brookings, 20 June 1895, WILLIAMS & ? (S); Wis., Racine, 23 July 1897, J. J. DAVIS (BPI).

Notes. – *Paraperonospora artemisiae-biennis* is easily recognizable by its ellipsoidal conidia, mostly 40 µm or more long, and the length/width ratio = ca 2.

3. ***Paraperonospora chrysanthemi-coronarii*** (SAWADA) O. CONST., comb. nov. – Figs 1 E, 3.

BAS.: *Plasmopara chrysanthemi coronarii* SAWADA – Rep. Govt. Res. Inst. dep. Agric. Formosa 51: 15. 1931
= *Peronospora chrysanthemi-coronarii* (SAWADA) S. ITO & TOKUNAGA – Trans. Sapporo nat. Hist. Soc. 14: 29. 1935
= *Bremiella chrysanthemi-coronarii* (SAWADA) TAO – Acta mycol. sin. 1: 64. 1982. Type on *Chrysanthemum coronarium* L., CHINA (TAIWAN): Taichung Prov., Yuanlin, 21 March 1930, E. KUROSAWA (TNS F-192975 – holotype).

Spots epiphyllous, yellowish, irregular, up to 15 mm diam, margin diffuse.– Down hypophyllous, greyish to yellowish, felt-like. – Conidiophores colourless, erect, 350–600 µm long, trunk 180–430 × 11–17.5 µm, base not or slightly swollen; upper part dichotomously and often trichotomously branched 4–6 times; ultimate branchlets 2–3 at the tip of each branch, often arising from a slightly swollen, common base, divergent, long-conical, 6–20 µm long, base 2.5–4.5 µm, gradually tapering to 1.5–2 µm below the swollen up to 4 µm diam tip. – Conidia colourless to slightly yellowish, ellipsoidal to broadly ellipsoidal, (31)36–42(–50) × (18–)22–25(–27) µm, broadest part median, tip elongate to round, wall ca 0.3 µm thick; pedicel 1–2 × 2–3 µm; a vestigial, nonfunctional dehiscence apparatus, appearing as a membrane located under the apex is present in many conidia. – Sexual organs unknown.

Host. – *Chrysanthemum coronarium L.*

Distribution. – CHINA (TAIWAN).

Additional specimens examined. – CHINA (TAIWAN): Taipei, 14 Feb. 1931, K. SAWADA (TNS F-234562); ditto (TNS F-234560); ditto, 13 Feb. 1931 (TNS F-234561); ditto, 4 Jan. 1946 (TNS F-234572).

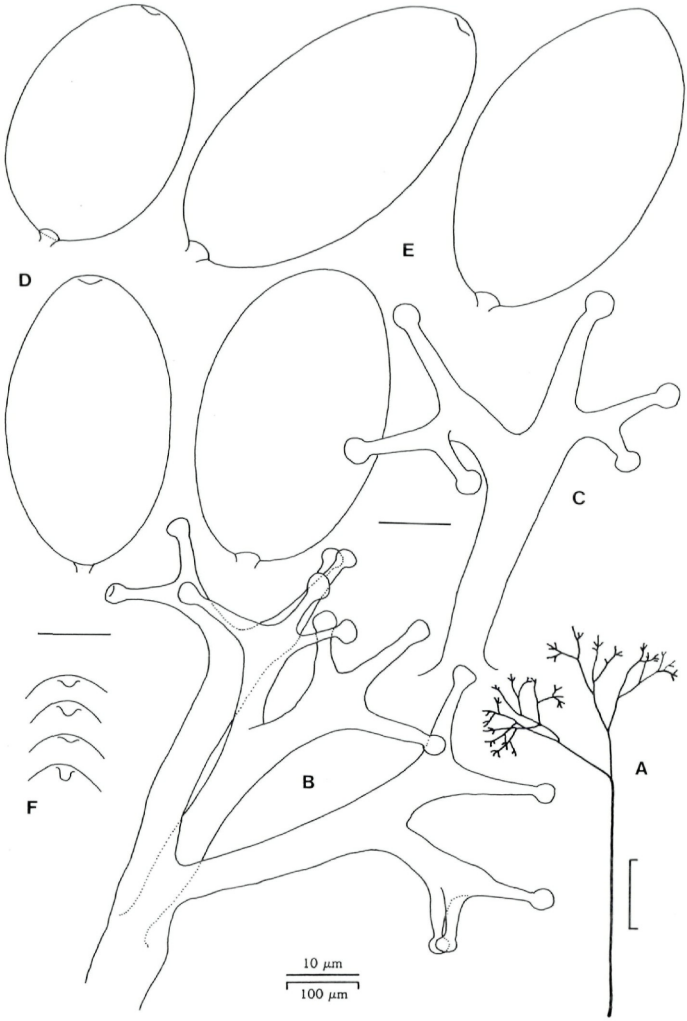

Fig. 3: *Paraperonospora chrysanthemi-coronarii* (A–C, E, F from holotype; D from TNS F-234561); A. conidiophore. – B. branches. – C. ultimate branchlets. – D, E. conidia. – F. tips of conidia showing variation of the vestigial papilla.

4. ***Paraperonospora leptosperma*** (De Bary) O. Const., comb. nov. – Figs 1 A–D, 4.

Bas.: *Peronospora leptosperma* De Bary – Annls Sci. nat., Bot., sér. 4, 20: 48 and 121. 1863
= *Plasmopara leptosperma* (De Bary) Skalicky – Preslia 38: 127. 1966. Type on *Matricaria perforata* Mérat (= *Tripleurospermum inodorum* (L.) Schultz Bip.), GERMANY: Freiburg, Autumn 1862, De Bary in Rabenh., Fungi europ. 574 (BPI – lectotype, L 910.237-1204 – isolectotype).

Syn.: *Peronospora leptosperma* Gäum. – Beitr. KryptogFl. Schweiz 5(4): 129. 1923 as „(De Bary) Gäum." Nom. illegit. (Art. 64 ICBN).
Peronospora anthemidis Gäum. – Beitr. KryptogFl. Schweiz 5(4): 126. 1923 = *Plasmopara anthemidis* (Gäum.) Skalicky – Preslia 38: 127. 1966. Type on *Anthemis austriaca* Jacq., CZECHOSLOVAKIA: Teplitz, Frühling (formerly AUSTRIA), 1872, F. Thümen, Fungi austr. 745 (UPS – lectotype; NY – isolectotype).
Peronospora achilleae Savul. & Vanky – Arch. Freunde Natgesch. Mecklenb. 2: 347. 1956 = *Plasmopara achilleae* (Savul. & Vanky) Skalicky – Preslia 38: 127. 1966. Type on *Achillea atrata* L., GERMANY: Rostock, Neuer Botanischer Garten, 3 Aug. 1940, H. Buhr (BUCM 868 – lectotype); on *Achillea* sp., ditto, 12 Aug. 1940 (BUCM 869 – paratype).
Peronospora dimorphothecae Savul. & Vanky – Arch. Freunde Natgesch. Mecklenb. 2: 350. 1956. Type on *Dimorphotheca aurantiaca* DC, GERMANY: Rostock, Neuer Botanischer Garten, 16 July 1950, H. Buhr (BUCM 1564 – holotype; B – isotype).
Peronospora ursiniae Savul. & Vanky – Arch. Freunde Natgesch. Mecklenb. 2: 352. 1956 = *Plasmopara ursiniae* (Savul. & Vanky) Skalicky – Preslia 38: 127. 1966. Type on *Ursinia calenduliflora* (DC) N. E. Br., GERMANY: Rostock, Neuer Botanischer Garten, 16 July 1950, H. Buhr (BUCM 2885 – lectotype); on *U. anthemoides* (L.) Poiret (= *U. pulchra* N.E. Br.), ditto, 9 July 1940 (BUCM 2884 – paratype).
Peronospora buhrii Savul. & Vanky – Arch. Freunde Natgesch. Mecklenb. 2: 355. 1956 = *Plasmopara buhrii* (Savul. & Vanky) Skalicky – Preslia 38: 127. 1966. Type on *Ursinia anthemoides* (L.) Poir., GERMANY: Rostock, Neuer Botanischer Garten, 27 July 1947, H. Buhr (BUCM 1233 – lectotype; B – isolectotype); on *U. speciosa* DC, ditto, 16 July 1950, H. Buhr (BUCM 1232 – paratype).

Symptoms hardly visible. – Down commonly on leaves but sometimes on involucral bracts or petals, whitish, rarely yellowish, scattered, in patches or covering rather restricted areas. – Conidiophores colourless, erect, 290–800 µm long, trunk 120–500 × 6–15 µm; upper part dichotomously or trichotomously branched 3-5 times; ultimate branchlets 2–4 at the tip of each branch, often arising from a slightly swollen common base, long-conical, 8–17 µm long, base 3–6 µm, gradually tapering to 1–1.5 µm below the truncate, rounded or slightly swollen tip. – Conidia colourless or pale yellowish, cylindrical with rounded ends to broadly ellipsoidal (21–)30–40(–45) × (15–)17–22(–25) µm, broadest part median, rarely supramedian, base round, tip sometimes slightly flattened, wall ca 0.3 µm thick; pedicel 1–2 × 1–1.5 µm; a membrane-like structure, possibly a rudimentary dehiscence apparatus, is rarely visible under

the apex. – Oogonia yellowish, irregular, 33–53 µm diam, wall 1.5–2 µm thick. – Oospores aplerotic, globose, (22–)25–27(–31) µm diam, wall yellowish to pale brown, smooth, 2–4 µm thick.

Hosts. – (Cultivated plants marked with asterisk) *Achillea atrata* L.*, *A. clusiana* TAUSCH.*, *A. millefolium* L., *A. umbellata* SIEB. & SM.*, *Anthemis altissima* L., *A. arvensis* L., *A. austriaca* JACQ. and *A. cotula* L., *Chamomilla aurea* (LOEFL.) GAY ex COSSON & KRALIK, *C. recutita* (L.) RAUSCHERT, *C. suaveolens* (PURSH) RYDB., *Cotula turbinata* L.*, *Dimorphotheca aurantiaca* DC*, *Lasiospermum bipinnatum* (THUNB.) DRUCE.*, *Matricaria caucasica* (WILLD.) POIRET, *M. perforata* MÉRAT, *Ursinia anthemoides* (L.) POIRET.*, *U. calenduliflora* (DC) N. E. BR.* and *U. speciosa* DC*.

Distribution. – EURASIA.

Selected specimens examined other than types. – On *Achillea clusiana*. GERMANY: Rostock, Neuer Botanischer Garten, 31 Aug. 1937, coll. H. BUHR, det. T. SAVULESCU (BUCM 3155).

On *Achillea millefolium*. SWEDEN: Uppland, Lunda, 2 Sept. 1954, A. GUSTAVSSON 4877 (LD); Skåne, Räften. 14 Sept. 1882, coll. E. LJUNGSTRÖM, det. A. GUSTAVSSON (LD).

On *Achillea umbellata*. GERMANY: Rostock, Neuer Botanischer Garten, 12 Aug. 1940, coll. H. BUHR, det. T. SAVULESCU (BUCM 3154); ditto, coll. H. BUHR, det. O. CONSTANTINESCU (B).

On *Anthemis altissima*. FRANCE: l'Hérault, near St. Martin-de-Loudres, 19 June 1953, E. MAYOR (BPI).

On *Anthemis arvensis*. FRANCE: Départ. du Tarn, Espérausses, 15-30 Aug. 1927, E. MAYOR (BPI). GERMANY: Bayern, Bayreuth, July 1879, THÜMEN (NY). ROMANIA: Prahova Dist., Plopeni forest, 19 June 1977, O. CONSTANTINESCU & G. NEGREAN in Herb. mycol. rom. 2699 (UPS). SWEDEN: Skåne, Perstorp, 2 Sept. 1953, A. GUSTAVSSON 3493 (LD); ditto, Matteröd, 2 Sept. 1953, A. GUSTAVSSON 3516 (LD); ditto, Bosjökloster, 8 Sept. 1953, A. GUSTAVSSON 3549 (LD).

On *Anthemis austriaca*. CZECHOSLOVAKIA: Bohemia, Teplitz (formerly AUSTRIA) May 1872, THÜMEN (NY). GERMANY: Bayern, Parsberg Dist., Pielenhofen, 27 May 1937, E. EICHORN in SYDOW, Myc. germ. 3278 (S; UPS); ditto, Riedenburg Dist., Prunn, 12 June 1938, E. EICHORN in SYDOW, Myc. germ. 3279 (S, UPS). ROMANIA: Ilfov Dist., Greci, 25 June 1978, O. CONSTANTINESCU & G. NEGREAN in Herb. mycol. rom. 2923 (UPS).

On *Anthemis cotula*. GERMANY: Rheinprovinz, Altenkirchen Dist., near Mühlenberg, 13 Aug. 1933, A. LUDWIG in SYDOW, Myc. germ. 2661 (BPI; S). ROMANIA: Prahova Dist., Busteni, Valea Cerbului, 10 Oct. 1978, O. CONSTANTINESCU & G. NEGREAN in Herb. mycol. rom. 2924 (BPI; UPS).

On *Chamomilla aurea*. IRAQ: Mosul, 9 Apr. 1977, coll. S. A. KHAN, det. G. LUNN (IMI 223334).

On *Chamomilla recutita*. CZECHOSLOVAKIA: Bohemia, Tabor, 12 June 1909, F. BUBAK in SYDOW, Phycom. et Protom. 254 (S, UPS); ditto,8 May 1903 in SYDOW, Phycom. et Protom. 211 (UPS). ITALY: Catania, Mascalucia, Mar. 1902, G. SCALIA in SACC., Myc. ital. 886 (S). GERMANY: Sachsen, Moritzburg, 11 Aug. 1899, W. KRIEGER, Fungi sax. 1487 in (S). HUNGARY: Ujszasz, May 1927, G. MOESZ in PETRAK, Myc. gen. 340 (S, UPS); ditto in Flora hung. exs. 801 (S). ROMANIA: Craiova dist., near Isalnita, 10 May 1965, M. COSTESCU in Fl. olt. exs. 513 (UPS). SWEDEN: Uppland, Uppsala, 27 Sep. 1884, L. ROMELL (S, UPS); Södermanland, Tuna, July 1915, T. VESTERGREN (S); Skåne, Mölleberga, Önsvala, 16 Sept. 1953, A. GUSTAVSSON 3683 (LD); Svedala, Aggarp, 5

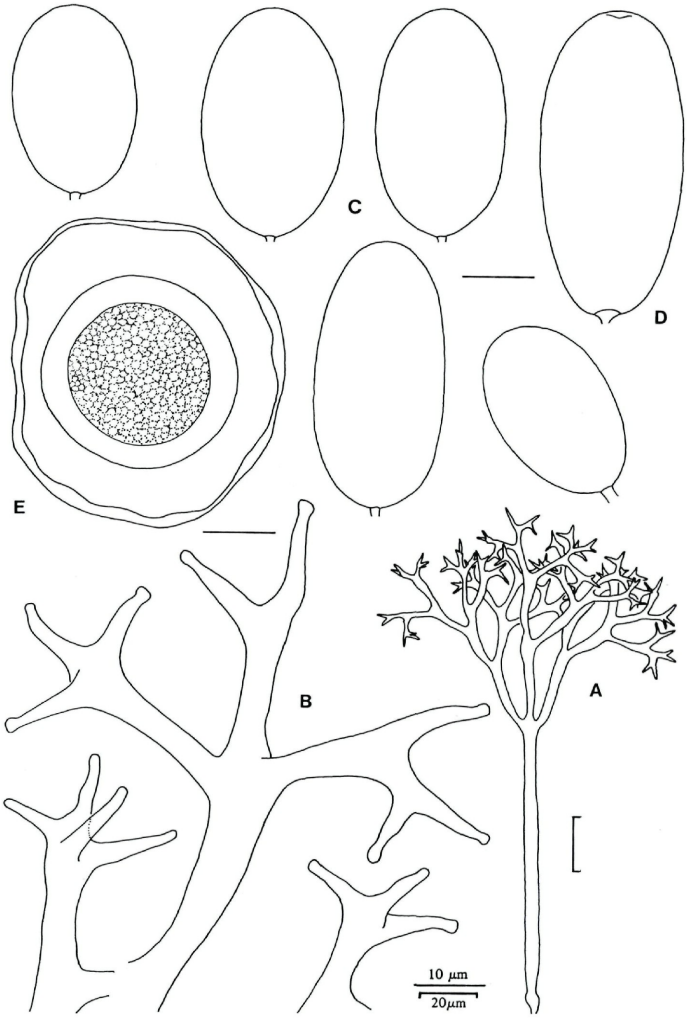

Fig. 4: *Paraperonospora leptosperma* (A–C from lectotype; D from Finland, Reinikainen, 12 Sept. 1963, H. ROIVAINEN in UPS; D from PETRAK, Myc. gen. 340 in UPS); A. conidiophore. – B. branch and ultimate branchlets. – C, D. conidia. – E. oogonium and oospore.

Aug. 1953, A. GUSTAVSSON 3004 (LD); Svalöv, 22 Sept. 1928, coll. C. HAMMARLUND, det. O. CONSTANTINESCU (LD); ditto, 16 Oct. 1929 (LD). U.S.S.R.: Litov SSR, Kaunas, Botanical Garden, 14 June 1934, A. MINKEVICIUS (S).

On *Chamomilla suaveolens*. FINLAND: Alandia, Hammarland, Drygsböle, 1 Aug. 1919, T. PUTKONEN in Myc. fenn. 23 (UPS); Regio aboënsis, Kakskerta, Monnonen, 29 June 1936, L. E. KARI in Fungi exs. fenn. 738 (UPS). GERMANY: Bayern, distr. Regensburg, Mosham, 21 June 1936 and 26 June 1937, E. EICHHORN in SYDOW, Myc. germ. 3079 (S); Sachsen, Moritzburg, 11 Aug. 1899, W. KRIEGER in Fungi sax. 1488 (S). ROMANIA: Harghita Dist., Gheorgheni, 23 July 1977, O. CONSTANTINESCU & G. NEGREAN in Herb. mycol. rom. 2700 (UPS). SWEDEN: Gästrikland, Gävle, Lövudden, 24 Aug. 1942, J. A. NANNFELDT in Fungi exs. suec. 1677 (S, UPS); Skåne, Snårestad, 28 July 1953, A. GUSTAVSSON 2864 (LD). U.S.S.R.: Latvij SSR, Latgale Dist., Vidsmuiza, 12 June 1934, K. STARKS 1621 (S); ditto, Vidzeme Prov., Rizh Dist., Maryupe, 18 July 1955, YU. SMARODS in Griby SSSR 114 (L, UPS).

On *Cotula turbinata*. GERMANY: Rostock, Neuer Botanischer Garten, 14 July 1948, coll. H. BUHR, det. T. SAVULESCU (BUCM 3152); ditto, coll. H. BUHR, det. O. CONSTANTINESCU (B).

On *Lasiospermum bipinnatum*. GERMANY: Rostock, Neuer Botanischer Garten, 16 July 1950, coll. H. BUHR, det. T. SAVULESCU (BUCM 3140).

On *Matricaria caucasica*. GERMANY: Rostock, Neuer Botanischer Garten, 12 Aug. 1940, coll. H. BUHR, det. T. SAVULESCU (BUCM 3153).

On *Matricaria perforata*. ENGLAND: Exeter, Stoke Woods, 4 Sept. 1978, G. M. WATERHOUSE (IMI 232657). FINLAND: Regio aboënsis, Korppoo, Bonäs, 11 July 1948, L. A. KARI in Fungi exs. fenn. 981 (UPS). GERMANY: Bayern, Bayreuth, July 1874, THÜMEN, Myc. univ. 50 (L, UPS); Brandenburg, Lichtenrade near Berlin, 10 May 1918, H. SYDOW, Myc. gen. 1516 (S, UPS); Freiburg, summer 1862, DE BARY in RABENH., Fungi europ. 573 (UPS). POLAND: Schottwitz near Wroclaw (formerly GERMANY: Breslau), SCHRÖTER, Pilze schles. 385 (S). ROMANIA: Ialomita Dist., Fierbinti railway station, 21 May 1982, G. NEGREAN (BUCM 70340); Satu-Mare Dist., Dindesti, 16 Aug. 1974, G. NEGREAN in Herb. mycol. rom. 2425 (UPS). SWEDEN: Södermanland, Sockholm, Oct. 1915, G. LAGERHEIM (S); Skåne, Bösarp, Markiedal, 3 Aug. 1953, A. GUSTAVSSON 2959 (LD). U.S.S.R.: Latvian SSR, prov. Zemgale, distr. Tervete, Uplejas, 30 June 1963, E. VIMBA in SMARODS, Fungi latv. exs. 1357 (UPS).

On *Ursinia speciosa*. GERMANY: Rostock, Neuer Botanischer Garten, 12 July 1947, coll. H. BUHR, det. O. CONSTANTINESCU (B).

Notes. – It seems that the original material of this fungus, distributed in Rabenh. Fungi europ. 574, was not carefully checked. The copies present at S and UPS contain no fungus, whereas of the two specimens preserved at L one (910.237-1221) shows *Pp. leptosperma* and another (910.237-1204) no fungus at all.

The fungus parasitic on *Anthemis* spp. was traditionally treated as a separate species, *P. anthemidis*. Besides the different host, *P. anthemidis* was stated to have yellowish conidia vs. colourless ones in *P. leptosperma*. However, many specimens exhibiting intergrading characters were found during this study. Although the conidia of the fungus on *Anthemis* are slightly broader, no clear distinction could be made on the basis of morphological characters.

The pigmentation of the down and conidia in *Pp. leptosperma* is variable. The down is almost always white in properly dried specimens, but it may be greyish or yellowish, especially when the drying

was poor. The young conidia are commonly colourless but in most specimens they become yellowish with age.

5. ***Paraperonospora minor*** (SAVUL. & RAYSS) O. CONST., comb. nov. – Fig. 5.

BAS.: *Peronospora sulphurea* GÄUM. forma *minor* SAVUL. & RAYSS. in SAVUL. – Herb. mycol. rom. 146. 1930. Type on *Artemisia vulgaris* L., USSR: Distr. Cetatea Alba, Crocmaz (formerly in ROMANIA), 22 June 1926, T. SAVULESCU & T. RAYSS (BUCM 60146 – lectotype; L – isolectotype).

Spots epiphyllous, pale, brown when tissues become necrotic, polyangular. – Down hypophyllous, whitish or yellowish, in patches, sometimes powdery, covering large, vein-limited areas or the entire lower surface, but often obscured by the trichoma. – Conidiophores colourless, erect, 160–730 µm long, trunk 90–400 × 6–15 µm; upper part dichotomously or very rarely trichotomously branched 3–6 times; ultimate branchlets 2–3 at the tip of each branch, long-conical, up to 27 µm long when terminal, 6–15 µm when lateral, base 3–5 µm, gradually tapering to 1.5–2 µm below the truncate or rounded tip. – Conidia yellowish, broadly-ellipsoidal, (21–)25–30(–35) × (15–)19–22(–24) µm, broadest part median or, rarely, submedian, wall ca 0.3 µm thick. Oogonia pale, globose to irregular, 34–45 µm diam, wall 1–3 µm thick. – Oospores aplerotic, globose, 22–26 µm diam, wall yellowish, smooth, 2.5–3 µm thick.

Hosts. – (Cultivated plants marked with asterisk) *Achillea clusiana* TAUSCH.*, *Artemisia sieversiana* WILLD., *A. tilesii* LEDEB., *A. vulgaris* L. and *Leucanthemum nipponicum* FRANCH.* (= *Chrysanthemum nipponicum* MATSUM.).

Distribution. – EURASIA.

Additional specimens examined. – On *Achillea clusiana*. GERMANY: Mecklenburg, Rostock Neuer Botanischer Garten, 20 Sept. 1939, coll. H. BUHR, det. O. CONSTANTINESCU (B).

On *Artemisia sieversiana*. U.S.S.R.: Siberia occid., Omsk Prov., near Omsk, 3 June 1922, MURASHKINSKY (BPI).

On *Artemisia tilesii*. JAPAN: Ishikari Prov., Hokkaido, Nopporo, 8 May 1920, K. TOGASHI (BPI, NY); Shiribeshi Prov., Hariusu, 22 July 1930, K. TOGASHI (NY).

On *Artemisia vulgaris*. DENMARK: Jylland, Skive, 12 July 1909, J. LIND in SYDOW, Phycom. et Protom. 253 (S, UPS). SWEDEN: Skåne, Oppomanna, Bokenäset, 24 June 1954, A. GUSTAVSSON 4272 (LD); Iistorp, 23 Sept. 1953, A. GUSTAVSSON 3777 (LD); Genarp, Häckeberga, 20 Sept. 1953, A. GUSTAVSSON 3724 (LD); Hörröd, Ribbetuaröd, 24 Sept. 1953, A. GUSTAVSSON 3798 (LD); Vanstad, Äsperöd, 22 Sept. 1953, A. GUSTAVSSON 3743 (LD); Eslöv, 15 Sept. 1953, A. GUSTAVSSON 3658 (LD).

On *Leucanthemum nipponicum*. ROMANIA: Bucuresti, Botanical Garden, Oct. – Nov. 1970, E. ELIADE (BUCM 1487).

Notes. – The size of conidia in *Pp. minor* is remarkably uniform. Besides SAVULESCU & RAYSS (1930), GUSTAVSSON (1953, 1959a) also noticed that the fungus on *A. vulgaris* has smaller conidia.

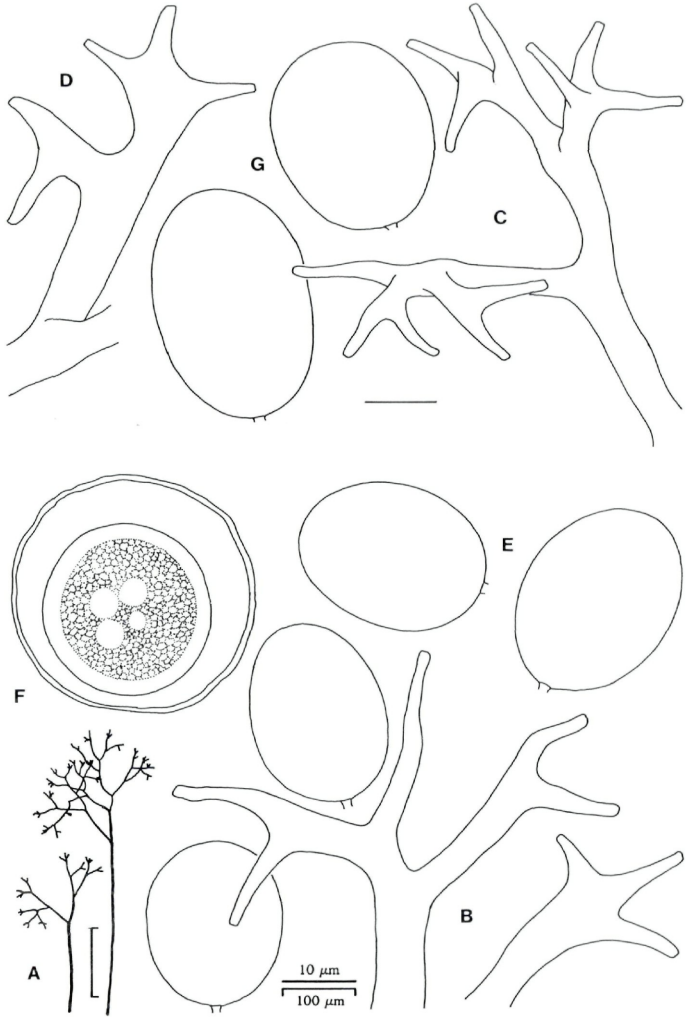

Fig. 5: *Paraperonospora minor* (A, B, E & F from lectotype; C, D, G from various specimens); A. conidiophores. – B, C & D. branches and ultimate branchlets. – E, G. conidia. – F. oogonium and oospore.

6. ***Paraperonospora multiformis*** (TAO & Y. QIN) O. CONST., comb. nov. – Fig. 6.

BAS.: *Bremiella multiformis* TAO & Y. QIN – Acta mycol. sin. 1: 62. 1982. Type on *Chrysanthemum coronarium* L. var. *spatiosum* BAILEY, CHINA: Tian-quan Region, Sichuan Prov., 12 May 1980, Y. QIN & J. Z. QIN 0666 (Herb. Sichuan Agric. College – holotype).

SYN.: *Peronospora crossostephii* SAWADA – Trans. nat. Hist. Soc. Formosa 31: 266. 1941. Nom. invalid. (Art. 35.1 ICBN). Type on *Crossostephium artemisioides* LEES (= *C. chinense* (MAXIM.) MAKINO, CHINA (TAIWAN): Taipeh, 8 May 1936, K. SAWADA (BPI – holotype).

Spots epiphyllous pale, irregular with diffuse margin. – Down hypophyllous, whitish to yellowish, scattered. – Conidiophores colourless, erect 250–700 µm long, trunk 180–460 × 7.5–15 µm, base bulbous, swollen up to 18 µm; upper part dichotomously, rarely trichotomously branched 3–6 times; ultimate branchlets 2–5 at the tip of each branch, sometimes arising from a slightly swollen common base, divergent, long-conical, 15–20 µm long when terminal, 7–13 µm when lateral, base 3–5 µm, gradually tapering to 2 µm below the swollen, up to c. 3 µm tip. – Conidia colourless or slightly yellowish, broadly ellipsoidal to ovoidal rarely ellipsoidal, 26–31(–39) × (19–)20–23(–25) µm, broadest part median, wall c. 0.25 µm thick; pedicel 0.5–1 × 2–2.5µm. – Sexual organs unknown.

Hosts. – *Artemisia annua* L., *Crossostephium artemisioides* LESS. and *Chrysanthemum coronarium* L.

Distribution. – CHINA.

Additional specimen examined. – On *Artemisia annua*. CHINA: Sichuan, Yaan, 19 Apr. 1982, coll. Y. QIN, det. TAO (Herb. Sichuan Agric. Coll.).

7. ***Paraperonospora sulphurea*** (GÄUM.) O. CONST., comb. nov. – Fig. 7.

BAS.: *Peronospora sulphurea* GÄUM. – Beitr. KryptogFl. Schweiz 5(4): 128. 1923 = *Plasmopara sulphurea* (GÄUM.) SKALICKY – Preslia 38: 127. 1966. Type on *Artemisia absinthium* L., USSR: near Nowotserkassk, 27 Apr. 1911, O. TREBOUX in SYDOW, Phycom. et Protom. 280 (UPS – lectotype; BPI, S – isolectotypes).

SYN.: *Peronospora helichrysi* TOGASHI & EGAMI in S. ITO & TOKUNAGA – Trans. Sapporo nat. Hist. Soc. 14: 30. 1935 = *Plasmopara helichrysi* (TOGASHI & EGAMI) TAO – Acta mycol. sin. 6: 72. 1987. Type on *Helichrysum bracteatum* (WENT) ANDREWS, JAPAN: Hokkaido, Ishikari Prov., Sapporo, 26 July 1932, Y. IMAI (n.v.).

Plasmopara pyrethri DUDKA & BURDYUKOVA – Novit. syst. Pl. vasc. & non vasc. (Kiev) 1976: 240. 1977. Type on *Tanacetum corymbosum* (L.) SCHULTZ BIP., U.S.S.R.: Ukr. SSR, Odessa, distr. Baltuanus, Pesniczovka, 24 June 1974 (KW – holotype).

Spots epiphyllous, pale, vein limited or with diffuse margin; attacked tissues become necrotic. – Down hypophyllous, sometimes also epiphyllous, whitish to yellowish to golden-yellow, scattered

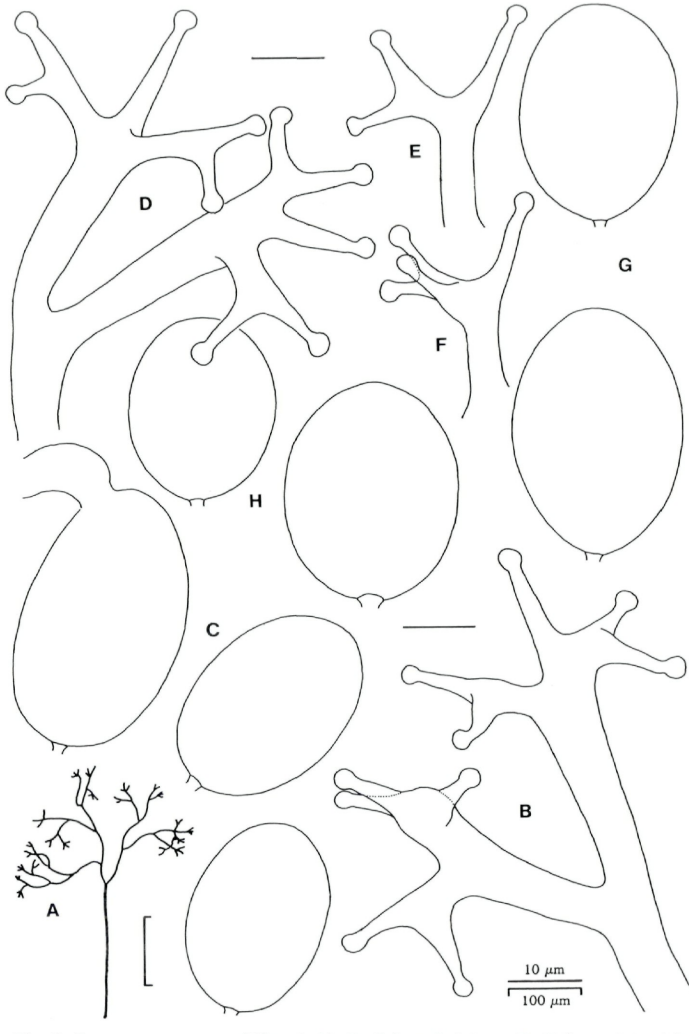

Fig. 6: *Paraperonospora multiformis* (A, B, C from holotype; D, H from *Artemisia annua* 19 Apr. 1982, QIN & TAO in Sichuan Agric. Coll.; E, F, G from the holotype of *Peronospora crossostephi*); A. conidiophore. – B, D. branches. – E, F. ultimate branchlets. – C, G, H. conidia.

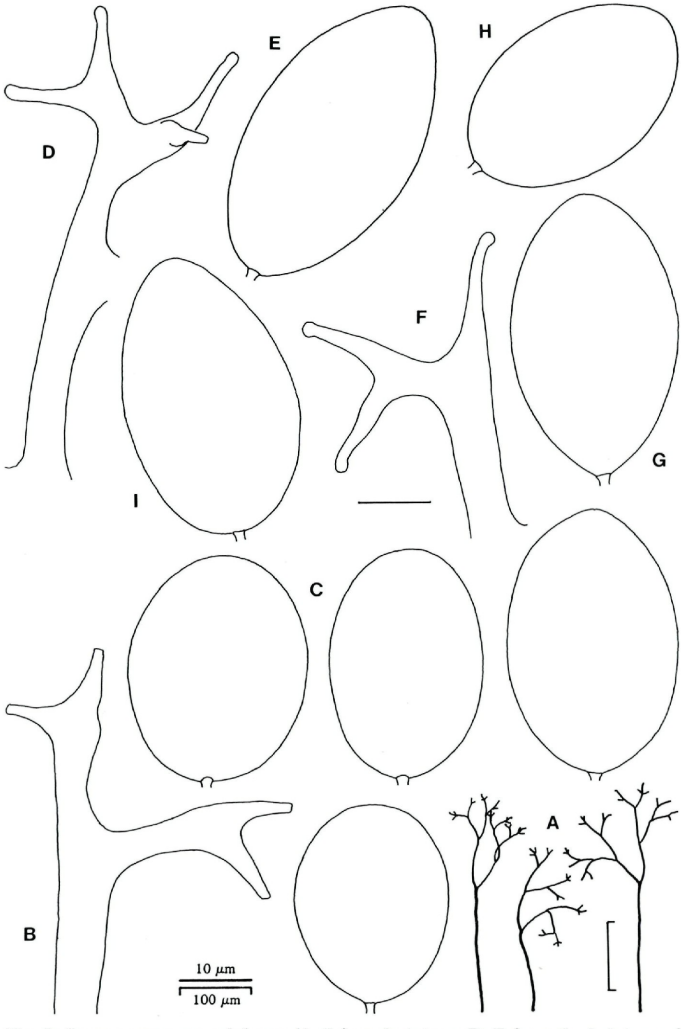

Fig. 7: *Paraperonospora sulphurea* (A–C from lectotype; D, E from the holotype of *Plasmopara pyrethri;* F, G & I from Herb. Mycol. Rom. no. 347 in BPI; H from *Helichrysum orientale* in VLA). A. conidiophores. – B, D, F. branches and ultimate branchlets. – C, E, G–I. conidia.

and obscured by trichoma, to dense, felt-like and above trichoma, often covering large areas. – Conidiophores colourless, erect 240–450 µm long, trunk 110–320 × 5–15 µm; upper part dichotomously or very rarely trichotomously branched 2–3 times; ultimate branchlets 2–3 at the tip of each branch, long-conical up to 22 µm long when terminal, 7–13 µm when lateral, base 3.5-6 µm, gradually tapering to 1–1.5 µm below the truncate or rarely rounded tip. – Conidia yellowish, broadly ellipsoidal when young but ellipsoidal when mature, (26–)32–37(–44) × (18–)20–26(–29) µm, broadest part median tip round in young conidia but slightly apiculate in mature ones, wall ca 0.3 µm thick; pedicel 1.2–2 × 1.5 µm. – Sexual organs unknown.

Hosts. – *Artemisia absinthium* L., *A. annua* L., *A. ludoviciana* NUTT., *A. serrata* NUTT., *A. suksdorfii* PIPER, *Helichrysum bracteatum* (WENT.) ANDREWS, *H. orientale* (L.) GAERTNER and *Tanacetum corymbosum* (L.) SCHULTZ BIP. (= *Pyrethrum corymbosum* (L.) SCOP.).

Distribution. – EURASIA and NORTH AMERICA.

Selected specimens examined other than types. - On *Artemisia absinthium*. ROMANIA: Ilfov Dist., Moldoveni, 8 May 1977, G. NEGREAN (BUCM 48784); Ialomita Dist., Lehliu, 18 June 1933, T. SAVULESCU & T. RAYSS (LD). U.S.S.R.: Moldav SSR, Lapusna dist., Cornesti (formerly in ROMANIA), 18 June 1931, T. SAVULESCU & T. RAYSS – Herb. mycol. rom. 347 (BPI, L).

On *Artemisia annua*. ROMANIA: Ialomita Dist., Fierbinti Railway Station, 21 May 1982, G. NEGREAN (BUCM 70338); Ilfov Dist., Gradistea, Sitaru, 21 May 1982, G. NEGREAN (BUCM 70334); Constanta dist., Deleni, 25 May 1971, O. CONSTANTINESCU & G. NEGREAN – Herb. mycol. rom. 1980 (UPS).

On *Artemisia ludoviciana*. U.S.A.: Cal., Santa Barbara, Apr. 1895, W. G. FARLOW (BPI); ditto, Santa Cruz, May 1885, W. G. FARLOW (BPI); Dakota, Dickey Co., Hollans' farm, 4 July 1915, J. F. BRENCKLE, Fungi Dakot. 336 (BERN; BPI; IMI 26460; NY); Kansas, Riley Co., Manhattan, 20 June 1889, KELLERMAN & SWINGLE 1644 (NY); Wisconsin, Taylor, 11 July 1916, J. J. DAVIS in Fungi Wisc. exs. 30 (BPI, K, NY).

On *Artemisia serrata*. U.S.A.: Iowa, Decorah, July 1885, E. W. D. HOLWAY in ELL. & EV., N. Am. Fungi 1804 (BPI; NY, UPS).

On *Artemisia suksdorfii*. U.S.A.: Cal., Oxnard, 10 May 1939, Coll. C. L. SHEAR, det. J. A. STEVENSON (BPI 187922).

On *Helichrysum bracteatum*. CHINA: Sichuan Prov., Yaan, 6 June 1988, TAO JIAFENG 1387 (Herb. Sichuan Agric. Univ.); U.S.S.R.: near Vladivostok, 13 Sept. 1968, E. S. NELEN (VLA).

On *Helichrysum orientale*. U.S.S.R.: Sakhalin, Novo-Alexandrovskoe, 16 Aug. 1960, E. S. NELEN (VLA).

Notes. – The holotype of *Peronospora helichrysi* was not available. Nevertheless, both the trichotomic condition in same ramifications and the size of conidia mentioned in the description are relevant for *Paraperonospora*. *Helichrysum* is also parasitized by a *Plasmopara* in North America.

8. ***Paraperonospora tanaceti*** (GÄUM.) O. CONST., comb. nov. – Fig. 8.

BAS.: *Peronospora tanaceti* GÄUM. – Beitr. KryptogFl. Schweiz 5 (4): 130. 1923 = *Plasmopara tanaceti* (GÄUM.) SKALICKY – Preslia 38: 127. 1966. Type on *Tanacetum vulgare* L., CZECHOSLOVAKIA: Bohemia, near Teplitz (formerly in AUSTRIA), summer 1873, THÜMEN in Fungi austr. 1235 (UPS – lectotype).

Symptoms hardly visible on the upper leaf surface. – Down hypophyllous, yellowish, rarely whitish, dense, felt-like, often covering the whole leaf. – Conidiophores colourless, erect, 350–800 µm long, trunk 160–400 × 7–15 µm; upper part dichotomously, rarely trichotomously branched 3–5 times; ultimate branchlets 2–3 at the tip of each branch, when three often arising from a slightly swollen common base, long-conical, 8–22 µm long, base 3–5 µm, gradually tapering to 1–2 µm below the rounded or rarely slightly swollen tip. – Conidia colourless when young, pale yellowish when mature, broadly ellipsoidal, (33–)37–40(–52) × (21–)23–28 (–29) µm, broadest part median or supramedian, base round or gradually narrowing, tip round to slightly flattened, wall ca 0.3 µm thick; pedicel 1–1.5 × 1–2 µm, longer in young conidia. – Oogonia irregular, 34–55 µm diam, wall colourless or pale yellowish, 1–3 µm thick. – Oospore aplerotic, (22–)27–36(–42) µm diam, yellowish, globose, wall smooth, 3–7 µm thick.

Host. – *Tanacetum vulgare* L.

Distribution. – EUROPE.

Selected specimens examined other than type. – CZECHOSLOVAKIA: Sternberg, June 1923, PETRAK, Flora Bohem. et Morav. exs. 1514 (S); Moravia, Rüdersdorf (formerly GERMANY), June 1889, P. SYDOW, Myc. march. 2654 (S; UPS). DENMARK: Fyn, Skårup, 7 June 1874, E. ROSTRUP (UPS); ditto, 11 June 1883 (S). FINLAND: Nyl., Helsinki, Munkkiniemi, 27 July 1935, V. LETHOLA in Myc. fenn. 327 (UPS); Regio aboënsis, Turku, Ruissalo, 19 July 1959, L. A. KARI, in Fungi exs. fenn. 994 (UPS); Karelia australis, Haapasaari, 8 July 1953, L. E. KARI in Fungi exs. fenn. 996 (UPS). FRANCE: Seine-et-Marne, Fontainbleau, May 1896, FEUILLEAUBOIS (S); sine loc. & dat., FAUTREY (herb. Fries in UPS). GERMANY: Bayern, Bayreuth, June 1879, THÜMEN (UPS); ditto, June 1875, A. WALTHER (S); ditto, 1880 (UPS); ditto, summer 1875, THÜMEN Myc. univ. 424 (UPS); Bayern, Hassfurt, June 1898, ALLESCHER & SCHNABLI, Fungi bavarici 646 (S); Brandenburg, Hönow near Berlin, 5 June 1910, H. SYDOW, Myc. germ. 884 (S; UPS); Hessen, Östrich, FUCKEL, Fungi rhen. 1606 (S). NORWAY: Dovrefjeld, N. Knutshö, 9 July 1925, A. G. ELIASSON (S, UPS). POLAND: Wroclaw (formerly Breslau, GERMANY), sine dat, J. SCHRÖTER, Pilze schles. 385 (S). SWEDEN: Helsingland, Söderhamn, 7 Aug. 1926, T. VESTERGREN (S); Jämtland, Ås, 17 July 1920, K. FALCK (LD); Norrbotten, Luleå, Aug. 1915, J. VLEUGEL (S); ditto, Aug. 1913 (S, UPS); Södermanland, Fjäderholmen, spring 1907, T. VESTERGREN (S). Öland, Vickleby, 2 Aug. 1957, A. GUSTAVSSON 5727 (LD). USSR: Akmolensk prov., Albasarsk dist. sine dat., coll. S. GANESEININ, det. A. JACZEWSKI (S).

9. *Peronospora radii* DE BARY. – Fig. 9.

Annls Sci. nat., Bot., sér. 4, 20: 48–49 and 121. 1863. Type on *Matricaria perforata* MÉRAT (= *Tripleurospermum inodorum* SCHULTZ BIP.), GERMANY: Freiburg, Summer 1862 in RABENH., Fungi europ. 573 (see notes).

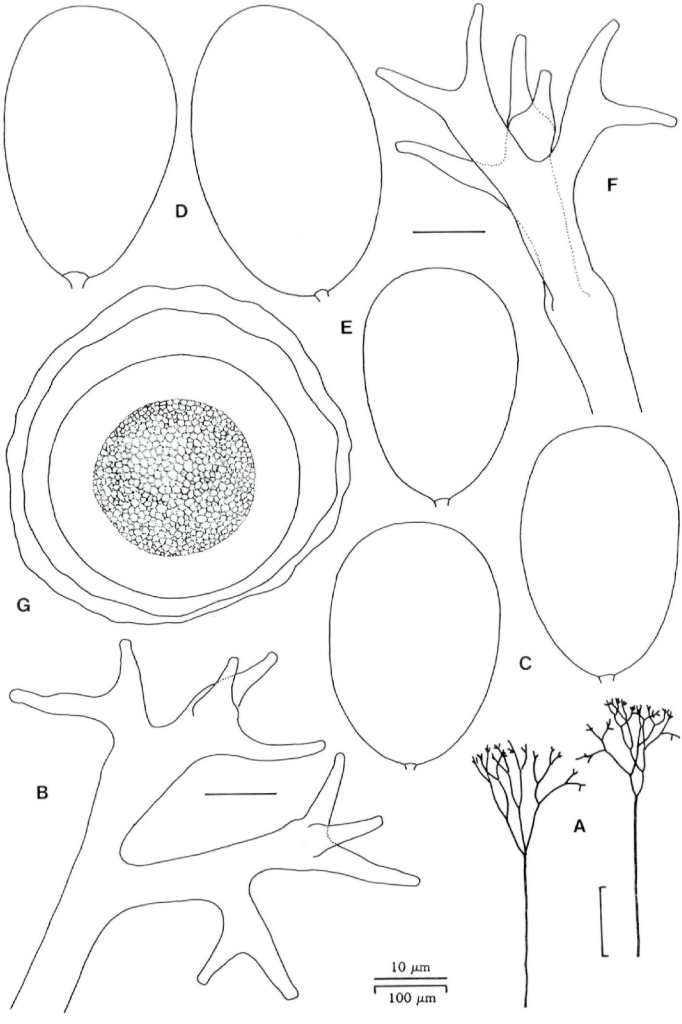

Fig. 8: *Paraperonospora tanaceti* (A–D from the lectotype; E from Fungi exs. fenn. 994 in UPS; F from Fungi exs. fenn. 997 in UPS; G from Fungi exs. fenn. 996 in UPS); A. conidiophores. – B, F. branches and ultimate branchlets. – C–E. conidia. – G. oogonium and oospore.

SYN.: *Peronospora radii* DE BARY var. *epiphylla* POIRAULT – Bull. Assoc. Nat. Nice. 2(3): 9. 1915. Type on *Coleostephus myconis* (L.) REICHENB. fil. (= *Chrysanthemum myconis* L.), FRANCE: Cap d'Antibes. Collection not indicated.

Peronospora danica GÄUM. – Beitr. KryptogFl. Schweiz 5(4): 128. 1923. Type on *Chrysanthemum segetum* L., DENMARK: near Lingby, 7 Oct. 1913, J. LIND in SYDOW, Phycom. et Protom. 309 (UPS – lectotype; BPI, S – isolectotypes).

Down commonly on florets, rarely on leaves and more rarely on stems, greyish, ochreous, greyish-brown to greyish-violaceous, scattered or densely agglomerated, sometimes completely covering all the florets within the inflorescence or large areas of the leaves. – Conidiophores colourless, the branched part rarely yellowish, erect, rarely flexuous, 280–650 µm long, trunk 120–450 × 8–18 µm, base swollen up to 25 µm; upper part dichotomously branched 4–6 times, very rarely three branches may arise from the trunk, branches straight or rarely flexuous; ultimate branchlets 1–3 at the tip of each branch, long-conical to almost cylindric, up to 20 µm long when terminal, 5–12 µm when lateral, base 2.5–4 µm, gradually tapering to c. 1.5–2 µm below the truncate tip. – Conidia brownish, obovoidal to broadly ellipsoidal or ellipsoidal, (24–)30–35(–42) × (18–)20–23(–32) µm, broadest part median or slightly supramedian, base gradually narrowing, tip rounded, elongate or variously apiculate, wall ca 0.5 µm thick, smooth to finely verruculose; pedicel 1–2 × 1.5–2 µm or only slightly protruding. – Oogonia in florets, yellowish, globose to irregular, 38–58 µm diam, wall 1–2 µm thick. – Oospores aplerotic, golden-yellowish, globose, 24–34 µm diam, wall smooth 1–4 µm thick.

Hosts. – *Achillea ptarmica* L., *Anthemis arvensis* L., *A. ruthenica* BIEB., *Artemisia mexicana* WILLD. ex SPRENG., *Chamomilla recutita* (L.) RAUSCHERT, *Chrysanthemum segetum* L., *Leucanthemum vulgare* LAM. (= *Chrysanthemum leucanthemum* L.), *Matricaria maritima* L. (= *Tripleurospermum maritimum* (L.) KOCH), *M. perforata* MÉRAT.

Distribution. – EUROPE, ISRAEL, MEXICO.

Selected specimens examined other than types. - On *Achillea ptarmica*. SWEDEN: Södermanland, Strengnäs, July 1913, G. LAGERHEIM in Vesterg,, Microm. rar. sel. 1669 (S, UPS).

On *Anthemis arvensis*. GERMANY: Hessen-Nassau, Manderbach, 24 June 1934, A. LUDWIG (BPI, S); Zahlendorf near Berlin, Aug. 1895, P. SYDOW, Myc. march. 4329 (S, UPS); Bayern, Unterfranken, Brünnstadt, Aug. 1904, A. VILL, Fungi bavarici 767 (S); ditto, July 1912 in SYDOW, Myc. march. 1084 (S, UPS). POLAND: Zedlitz near Wroclaw (formerly GERMANY, Breslau), June, July 1866, SCHNEIDER in RABENH., Fungi eur. 1369 (S, UPS); Wilanów near Warszawa, 1 June 1958, J. KOCHMAN, Myc. pol. 14 (UPS). SWEDEN: Öland, Stora Rör, 15 May 1929, A. G. ELIASSON (S);

On *Anthemis ruthenica*. ROMANIA: Satu-Mare Dist., Sanislau, 30 May 1983, G. NEGREAN (BUCM 76638; UPS); Dolj Dist., Cernele, 18 May 1977, O. CONSTANTINESCU & G. NEGREAN in Herb. mycol. rom. 2690 (UPS).

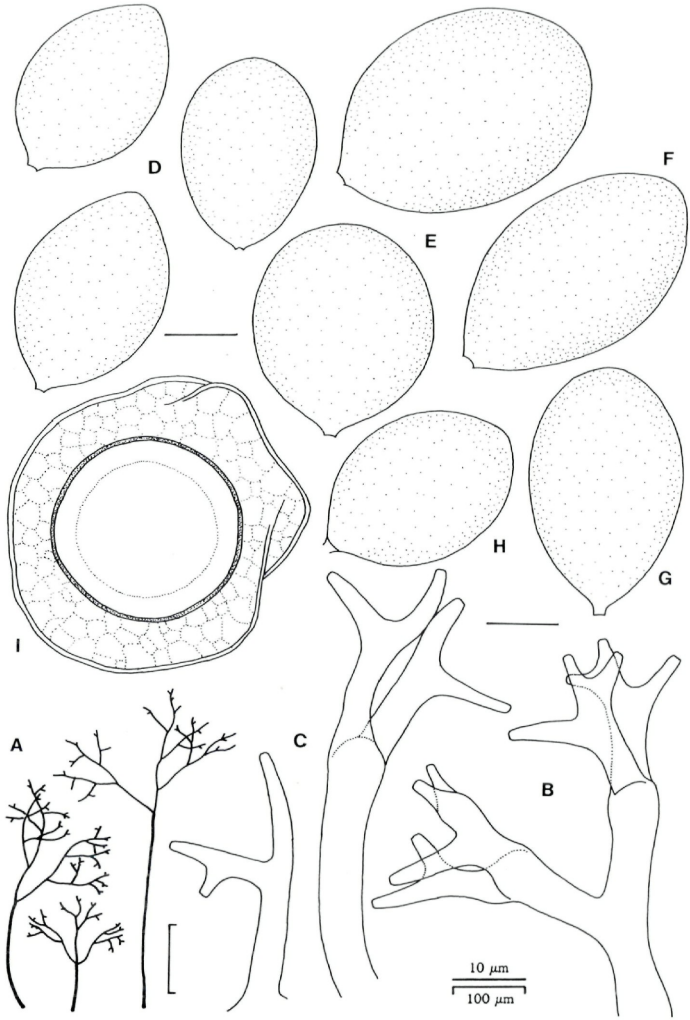

Fig. 9. *Peronospora radii* (from various specimens); A. conidiophores. – B & C. branches and ultimate branchlets; D–H. conidia. – I. oogonium and oospore.

On *Artemisia mexicana*. MEXICO: Chihuahua, 17 Aug. 1980, coll. R. M. ALVAREZ, det. D. WEAST (BPI).

On *Chamomilla recutita*. BELGIUM: Groenendael, 1 June 1890, E. BOMMER & M. ROUSSEAU in ROUMEG, Fungi sel. exs. 5615 (UPS). FRANCE: Lille, 4 June 1918, A. LUDWIG (S). POLAND: West Beskiden Mt, Wsetin, June 1923, F. PETRAK, Myc. carpat. 319 (S). SWEDEN: Skåne, Svalöv, 21 Sept. 1928; Oct. 1928; 16 Oct. 1929, C. HAMMARLUND (LD);

On *Chrysanthemum segetum*. DENMARK: Lyngby, 7 Oct. 1913, J. LIND (S); ditto, 30 Sept. 1913 (BPI, LD). SWEDEN: Hallan, Åled, Enslöv, 4 Sept. 1952, H. ANDERSON 1068 (LD).

On *Leucanthemum vulgare*. CZECHOSLOVAKIA: Bohemia, Kamárover Teich at Dymokur, 7 June 1900, F. BUBÁK in VESTERG., Microm. rar. sel. 347 (UPS). FINLAND: Nylandia, Kerava, Alikerava, 11 July 1965, H. ROIVAINEN (LD). SWEDEN: Södermanland, Strengnäs, July 1913, G. LAGERHEIM in VESTERG., Microm. rar. sel. 1670 (S, UPS); Stockholm, Frescati, 1923, H. DAHLSTEDT (S); Uppland, Norrtälje, Aug. 1915, G. LAGERHEIM in Fungi exs. suec. 1684 (S, UPS); Ljusterö, Äpplerö Isl., 5 July 1927, T. VESTERGREN (S).

On *Matricaria maritima*. ISLAND: Reykjavik, 16 July 1962, J. A. NANNFELDT (UPS). SWEDEN: Gotland, Västerhejde, 30 June 1972, M. THULIN 2010 (UPS); Uppland, Storvreta, Vretalund, 11 July 1981, N. LUNDQVIST 13260 (UPS); ditto, 2 July 1967, N. LUNDQVIST 5325 (UPS); Uppsala, 29 June 1959, R. SANTESSON 12832 (UPS).

On *Matricaria perforata*. CZECHOSLOVAKIA: Bohemia, Laschin, Schlössles, June 1917, R. STEPPAN in PETRAK, Flora Boeh. & Morav. exs. 1345 (S). DENMARK: Jylland, Frijsenborg, 26 June 1915, J. LIND (UPS); Nebsager, 16 July 1892, O. ROSTRUP (S); Fölle, 25 July 1874, E. ROSTRUP (UPS); Fyn, Hindsgavl, 7 Aug. 1928, R. SERNANDER (UPS); Falster, Stubbeköbing, 1 Aug. 1876, E. ROSTRUP (UPS). ENGLAND: Herts., Sandridge, Aug. 1941, A. SMITH (S). FINLAND: Alandia, Saltvik, Hjortö, 8 July 1919, T. PUTKONEN in Myc. fenn. 22 (UPS); Regio aboënsis, Lohja, Karkalinniemi, Linnaniemi, 29 July 1955, L. E. KARI in Fungi exs. fenn. 986 (UPS); Masku, Taipale, 8 July 1956, L. E. KARI in Fungi exs. fenn. 987 (UPS); Turku, Ravattula, 5 July 1937, L. E. KARI in Fungi exs. fenn. 988 (UPS). GERMANY: Bayern, Bayreuth, Summer 1877, WALTHER (UPS); ditto in THÜMEN, Myc. univ. 135 (UPS); Hessen-Nassau, near Langenaubach, 14 July 1935, A. LUDWIG in SYDOW, Myc. germ. 2898 (S, UPS). NORWAY: Hordaland, Hardanger, Jondal, Herandsbygden, 10 July 1908, S. K. SELLAND (S). SWEDEN: Västmanland, Hamre, 19 July 1924, J. A. NANNFELDT in Fungi exs. suec. 697 (S, UPS); Södermanland, Strengnäs, July 1913, G. LAGERHEIM in VESTERG., Microm. rar. sel. 1671 (S, UPS); Uppland; Nortälje, Aug. 1915, G. LAGERHEIM (S); ditto, in Fungi exs. suec. 1684 (UPS); Vaksala par., Skölsta, 11 July 1931, H. SMITH (UPS); ditto in Fungi exs. suec. 199 (S); Uppsala, Norbyskogen, 4 July 1926, J. A. NANNFELDT (UPS); Norrbotten, Rokliden, Aug. 1908, N. SYLVÉN in VESTERG., Microm. rar. sel. 1418 (UPS). U.S.S.R.: Latvij SSR, Zemgale Prov., Dobele Dist., Tervete, 30 June 1963, E. VIMBA in Fungi latv. exs. 1357 (UPS).

Notes. – Original specimens of *P. radii* have been distributed in RABENH., Fungi europ. 573. As in the case of *P. leptosperma*, no. 574 of the same exsiccatum, it seems that the material was carelessly selected. The copies in S and UPS contain no *P. radii* but few conidiophores and conidia of *Pp. leptosperma* on the involucral bracts and/or the leaves. Although no original specimens was examined, there is little doubt about the identity of this rather common species. A lectotytpe should be selected from among the copies of this exsiccatum, if a representative such specimen exists.

Peronospora radii is a variable species. When a limited number

of specimens are examined, it appears that the form on the leaves has more slender conidiophores and branches, longer ultimate branchlets and larger conidia, compared to the form on florets. However, intermediates or forms contradicting this pattern are found when more specimens are seen.

Peronospora radii is commonly found on the ligulate florets of its host. Following the description of *P. danica* by GÄUMANN (1923), on materials collected by J. LIND and distributed in SYDOW'S Phycom. et Protom. no. 309, it was considered that the morphologically similar fungus attacking the leaves is a different species. However, GUSTAVSSON (1959: 214) found among the original specimens of LIND preserved at C and CP one specimen with the fungus present on both florets and leaves. Actually it was POIRAULT (1915) who first mentioned an attack on the leaves of *Chrysanthemum myconis* L., now known as *Coleostephus myconis* (L.) REICHENB. fil., in South of France. He even found plants showing the fungus on both leaves and corolla, but his paper, as well as the new variety *epiphylla* introduced for the form attacking the leaves, have been overlooked by subsequent authors. Recently BEN-ZE'EV et al. (1987) found plants of cultivated *Argyranthemum frutescens* SCHULTZ BIP. (= *Chrysanthemum frutescens* L.) and wild *Chrysanthemum coronarium* L. showing attack of *P. radii* on both leaves and petals. By isozyme analysis they demonstated that the same fungus is responsible for these two forms of attack. During this study additional specimens showing attack on flowers and leaves were found, particularly on *Anthemis*. In one specimen (KOCHMAN, Myc. pol. 14 in UPS) the fungus was present on florets, leaves and stems.

Peronospora radii is sometimes associated with *Pp. leptosperma*. Several specimens of *Anthemis* spp., *Chamomilla recutita* and *Matricaria perforata* having florets attacked by *P. radii* and the involucral bracts and/or leaves attacked by *Pp. leptosperma* were found during this study.

Important damages produced by *Peronospora radii* to cultivated *Chrysanthemum* spp. and/or *Argyranthemum frutescens*, were reported from England (WILCOX, 1961), Yugoslavia (MIJUSKOVIC, 1968) and Israel (KENNETH & BEN-ZE'EV, 1985; BEN-ZE'EV & al., 1987).

Doubtful and excluded taxa

Peronospora brachycomes ENKINA – Mikol. i Fitopatol. 3: 482. 1969. Holotype on *Brachycome iberidifolia* BENTH., U.S.S.R.: Novosibirsk, Botanical Garden, 3 Aug. 1966, T. V. ENKINA. The holotype is preserved at LE, but was not sent upon request. The morphological characters are reminiscent of *Paraperonospora leptosperma* or *Pp. sulphurea*. *Brachycome* belongs to the tribe

Astereae and is a very improbable host for a *Peronospora*. This species was not included in the monograph of U.S.S.R. Peronosporales (Novotel'nova & Pystina, 1985).

Peronospora leptosperma De Bary var. *siegesbeckiae* Lagerh. – Bull. Herb. Boissier 3: 61. 1895 = *Plasmopara siegesbeckiae* (Lagerh.) Tao – Acta mycol. sin. 6: 69. 1987 as ‚(Lagerh. in Sacc.)'. Type on *Siegesbeckia,* ECUADOR: Pichincha. The authentic material was not available but specimens of *Siegesbeckia* collected from Peru, China and Taiwan contain *Plasmopara*.

Peronospora pospelovii Gaponenko – Semejstvo Peronosporaceae Srednej Azii i Yuzhnogo Kazakhstana p. 316. 1972. Holotype on *Aster dahuricus* Benth. ex Baker (= *Galatella dahurica* Dc), U.S.S.R.: Kirgiz SSRN, Tianshan region, Koczar distr., Czapyldyk, 26 July 1946, A. G. Pospelov. The holotype is preserved at TASM, but was not sent upon request. This taxon is apparently based on conidia of a Peronosporaceous fungus attached to the leaves of *Galatella*. It is very unlikely that the host, a member of the tribe Astereae, may bear a *Peronospora*.

Peronospora senecionis Fuckel – Symb. mycol. p. 69. 1870. Type on *Senecio cordatus* Koch, GERMANY: Oberbayern, near Hohenschwangau, summer. No authentic material is available. The host belong to the tribe Senecioneae on which the occurrence of *Peronospora* is highly improbable. According to Gäumann (1923) this is *Bremia lactucae* Regel.

Peronospora sonchi Gaponenko – Not. syst. Sect. crypt. Inst. bot. Acad. Sci. U.S.S.R. 8: 87. 1952 (as ‚Napon.'). Holotype on *Sonchus oleraceus* L., U.S.S.R.: Uzbekistan SSR, Margelan distr., Frunze Collectiv Farm, 25 May 1949. Authentic material was requested from TASM but not received. Judging from the description and illustration it may be *Paraperonospora leptosperma*. However, the host is a member of the tribe Lactuceae and thus very improbable of being parasitized by this fungus.

Acknowledgments

I am indebted to the directors and curators of the herbaria B, BERN, BPI, FH, IMI, KW, L, LD, NY, PC, S, TNS, UPS, VLA and Sichuan Agric. College for loan of material, to Dr. Kåre Bremer for informations concerning the taxonomy of the hosts and to Mrs Ulla-Britt Sahlström for photography. This work was supported by grants from the Swedish Natural Science Research Council and Swedish Council for Forestry and Agricultural Research.

Literature cited

Bary, A. De (1863). Recherches sur le développement de quelques champignons parasites. – Annls Sci. Nat., Bot., sér. 4, 20: 5-148.

Ben-Ze'ev, I. S., R. G. Kenneth & M. R. Bonde (1987). *Peronospora radii* De By., a

causal agent of downy mildew of Anthemideae: complementary description and new hosts recorded in Israel. – Phytoparasitica 15: 51–67.

BREMER, K. (1987). Tribal interrelationships of the Asteraceae. – Cladistics 3: 210–253.

CONSTANTINESCU, O. (1968). *Plasmopara ammii* sp. nov. – Sydowia 20: 268–270.

— & G. NEGREAN (1983). Check-list of Romanian Peronosporales. – Mycotaxon 16: 537–556.

CORDA, A. C. I. (1837). Icones Fungorum hucusque cognitorum. 1. – Pragae.

CRONQUIST, A. (1955). Compositae. In: HITCHCOCK C. L. et al. (eds). Vascular Plants of the Pacific Northwest. Part 5. – University of Washington Press, Seattle.

CRUTE, I. R. (1981). The host specificity of peronosporaceous fungi and the genetics of the relationship between host and parasite. In: SPENCER, D. M. (ed.). The Downy Mildews. Pp. 237–253. – Academic Press, New York & London.

DICK, M. W., P. T. W. WONG & G. CLARK (1984). The identity of the oomycete causing ‚Kikuyu Yellows', with a reclassification of the downy mildews. – Bot. J. Linn. Soc. 89: 171–197.

DUDKA, I. & L. BURDYUKOVA (1977). A new species of the genus *Plasmopara* SCHROETER from USSR. – Novit. syst. Pl. vasc. & non. vasc. (Kiev) 1967: 240–241. (In Russian).

DZHANUZAKOV, A. (1962). The specialization and variability of Peronosporaceous fungi. – Bot. Zh. SSSR 47: 862–866. (In Russian).

GÄUMANN, E. (1923). Beiträge zu einer Monographie der Gattung *Peronospora* CORDA. – Beitr. KryptogFl. Schweiz 5(4): 1–360.

GUSTAVSSON, A. (1953). Some species of the genera *Peronospora* and *Pseudoperonospora* new to Sweden. – Bot. Notiser 1953: 48–64.

— (1959 a). Studies on Nordic Peronosporas. I. Taxonomic part. – Opera bot. 3(1) 1–271.

— (1959 b). Studies on Nordic Peronosporas. II. General account. – Opera bot. 3(2) 1–61.

HOLMGREN, P. K., W. KEUKEN & E. K. SCHOFIELD (1981). Index Herbariorum. Part I. The Herbaria of the World, 7th ed. – Regnum veg. 106: 1–452.

KENNETH, R. G. & I. S. BEN-ZE'EV (1985). *Peronospora radii*, the cause of an unusual downy mildew of marguerite daisy in Israel. – Phytoparasitica 13: 151–152.

KUKKONEN, I. (1972). Micro- and macro-ecological factors in the speciation of obligate parasites. – Ann. Bot. 36: 1029–1040.

MIJUSKOVIC, M. (1968). *Peronospora radii* de Bary kao parasit Buvaca *(Chrysanthemum cinerariaefolium)*. Prethodno saopstenje. – Zast. Bilja 99: 197–200.

LING, L. & M. C. TAI (1946). New Peronosporaceae from China. – Lloydia 9: 144–145.

MOORE, D. M., T. G. TUTIN & S. M. WALTERS (1976). Compositae. In: TUTIN, T. G. et al. (eds). Flora Europaea 4: 103–410. – Cambridge University Press, Cambridge.

NOVOTEL'NOVA, N. S. & K. A. PYSTINA (1985). Flora Sporovykh Rastenij SSSR. Tom XI. Griby (3). Ord. Peronosporales. – Nauka, Leningrad.

PALTI, J. (1974). The significance of pronounced divergences in the distribution of *Pseudoperonospora cubensis* on its crop hosts. – Phytoparasitica 2: 109–115.

POIRAULT, G. (1915). Sur quelques champignons parasites. – Bull. Ass. Nat. Nice 2 (3): 7–19.

SAVULESCU, T. & T. RAYSS (1930). *Peronospora sulphurea* var. *minor*. – In: SAVULESCU, T. Herbarium Mycologicum Romanicum Fasc. 3, no. 146.

— & L. VANKY (1956). Beitrag zur Kenntnis der Peronosporaceae. – Arch. Freunde Natgesch. Mecklenb. 2: 336–365.

SAWADA, K. (1931). Descriptive Catalogue of the Formosan Fungi, V. – Rep. Govt. Res. Inst. Dep. Agric. Formosa 51. (In Japanese).

SCOGGAN, H. J. (1979). The Flora of Canada. Part 4 – Dicotyledoneae (Loasaceae to Compositae). – National Museum of Natural Sciences, Ottawa.

SHISHKIN, B. K. & E. G. BOBROV, Eds. (1961). Flora U.R.S.S. Vol. 26. – Acad. Sci. URSS. Moskva & Leningrad.

Skalicky, V. (1966). Taxonomie der Gattungen der Familie Peronosporaceae. – Preslia 38: 117–129.

Tao, J-F & Y. Qin (1982). New species and new combinations of the genus *Bremiella* on Compositae of China. – Acta mycol. sin. 1: 61–67. (In Chinese).

— & — (1987). Taxonomic studies on the genus *Plasmopara* of China. III. New species, new combination and new record of *Plasmopara* on family Compositae. – Acta mycol. sin. 6: 65–73. (In Chinese).

Wilcox, H. J. (1961). Downy mildew of *Chrysanthemum*. – Pl. Path. 10: 40–41.

Yerkes, W. D. & C. G. Shaw (1959). Taxonomy of *Peronospora* species on Cruciferae and Chenopodiaceae. – Phytopathology 49: 499–507.