

Species Diversity in Myxomycetes Based on the Morphological Species Concept – a Critical Examination

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Abstract

Using two databases, a world inventory of validly described taxa and a keyworded bibliography of myxomycete literature, research activities for myxomycetes from the year 1753 up to the present time have been documented by the authors. The numbers of described taxa and publications have both increased sharply during the last 30 years, reaching a total of 1012 described taxa of subgeneric rank, with about 1200 published papers presenting regional species lists and about 400 papers describing new taxa. An increasing number of recently described taxa appears to be very rare and is often known only from the type locality. With the well-known morphological plasticity of myxomycete fructifications

caused by fluctuations in environmental conditions during development, it cannot be ruled out that aberrant fructifications have been described as new taxa under the current morphological species concept. On the other hand, many apomictic biotypes distinguished by only slight morphological differences may remain unrecognised.

In this paper we propose a set of criteria to make descriptions of new taxa more comprehensive. Examples drawn from the authors' experiences illustrate the application of these criteria.

Key Words

Database, myxomycetes, research history, species description, taxonomy.

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Introduction

Myxomycetes (plasmodial slime moulds) are phagotrophic eukaryotes that commonly occur in association with decaying plant material in terrestrial ecosystems. The myxomycete life cycle involves two morphologically distinct trophic stages, one consisting of uninucleate amoebae, with or without flagella, and the other consisting of a distinctive multinucleate structure, the plasmodium (STEPHENSON & STEMPEN 1994). Under favourable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. The spores complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. Two features, the production of fruiting bodies and dispersal by spores, cause myxomycetes to appear similar to fungi, therefore most of the research on this group of organisms has been carried out by mycologists. The scientific careers of G. W. MARTIN and C. J. ALEXOPOULOS illustrate this impressively (LENTZ & BENJAMIN 1971; BLACKWELL 1988).

Due to both their cryptic life style and the almost complete absence of meaningful taxonomic plasmodial characters, field studies of myxomycetes have invariably focused on the reproductive, spore-producing, stage in the life cycle (STEPHENSON et al. 1993). Since plasmodia are often hidden within their substrates, fruiting bodies are usually the only readily observable indication of the presence of myxomycetes and can be stored as dry herbarium specimens. These features, as well as the difficulties to maintain most myxomycete species in culture, are the reason that the morphological species concept dominates myxomycete taxonomy.

Methods

Two databases were used to assess the world-wide species diversity in myxomycetes. The first database includes all original descriptions of myxomycetes, according to the current knowledge of the authors (MITCHELL 2000). Names for taxa were cited according to MARTIN & ALEXOPOULOS (1969) wherever possible. In all other cases a citation of the protologue and its reference is given. Due to the

often very brief Latin diagnoses, the original authors' descriptions were translated into English, if necessary, and standardised using the terminology for myxomycete fructifications proposed by LADO & PANDO (1997). For each taxon described as new from 1753-2000, the publication year of the respective basionym was recorded. Only validly published descriptions, according to the Code of Botanical Nomenclature (GREUTER et al. 1994), were included. Based on a survey of the literature, our own collections and those of our colleagues, the known world-wide collections for each taxon were estimated. Taxa were classified into three groups: those known only from the type locality as one or more collections, those reported from 2 to 20 localities, and those reported from more than 20 localities.

A second database was compiled from all of the available literature relating to myxomycete taxonomy, ecology, reproductive system, floristics and distribution (SCHNITTLER, in preparation). Whereas completeness was attempted in the topics mentioned above, papers dealing exclusively with biochemical or physiological aspects are certainly under-represented. Key words were assigned to all references, allowing the main topics of a paper to be assessed, e.g. the description of a new species or a regional survey of myxomycetes. For regional species lists, all publications recording more than a small set of very conspicuous species and focusing at least partially on myxomycetes were considered. For taxonomic publications, only those papers describing new taxa were included. This excluded a small but important number of publications which dealt with the clarification of species concepts. To document the use of scanning electron microscopy (SEM), all publications containing SEM micrographs were recorded.

Results and Discussion

According to our current data, 1012 subgeneric taxa of myxomycetes have been validly described as valid, including 866 of them at the species level. These figures are considerably higher than those published in standard floras for the group. MARTIN & ALEXOPOULOS (1969) recognised 422 taxa, almost exclusively at the

species level, in their world monograph. NANNENGA-BREMEKAMP (1991) estimated that "about 600 named species" exist world-wide. YAMAMOTO (1998) listed 925 taxa of various rank (species, varieties, and forms) world-wide in his treatment of Japanese myxomycetes (mentioning all names recognised by him as valid).

Figure 1 shows the increase in numbers of described sub-generic myxomycete taxa (species, varieties and forms) from the nomenclatural starting point. In contrast to almost all fungal groups the nomenclature of the myxomycetes begins with LINNAEUS (1753). PERSON'S initial work (1794) and supplements in subsequent years accounted for the first significant increase in the number of taxa, followed by ROSTAFINSKI'S monographs (1874, 1875, 1876) and the first edition of LISTER'S treatment (1894). The last world-wide monograph of the group by MARTIN & ALEXOPOULOS (1969) marks the beginning of the modern era in myxomycete taxonomy, with an almost continuous and steep increase in the numbers of taxa described since its publication.

The number of published papers focusing on myxomycetes reflects the increasing interest in myxomycete taxonomy and ecology since the publication of the MARTIN & ALEXOPOULOS monograph (Fig. 2). Up to the present time, about 3000 (or probably more, due to under-representation of publications on biochemical aspects) papers focusing on myxomycetes have been published (with 2796 currently recorded in the literature data base). About 1200 of these are local or regional species lists, and about 400 describe new taxa.

Even for a mycologist familiar with the myxomycetes, the number of described taxa for the group is surprisingly high, since regional species surveys seldom yield more than 150 taxa, and many species seem to be widely distributed, although often confined to special microhabitats. By comparison, only about 40 species of myxobacteria "can presently be distinguished more or less reliably" (REICHENBACH 1993). Although being prokaryotic microorganisms, myxobacteria display a similar ecology (forming more or less elevated fructifications, preying on other, non-motile bacteria and dispersal by spore-like cells)

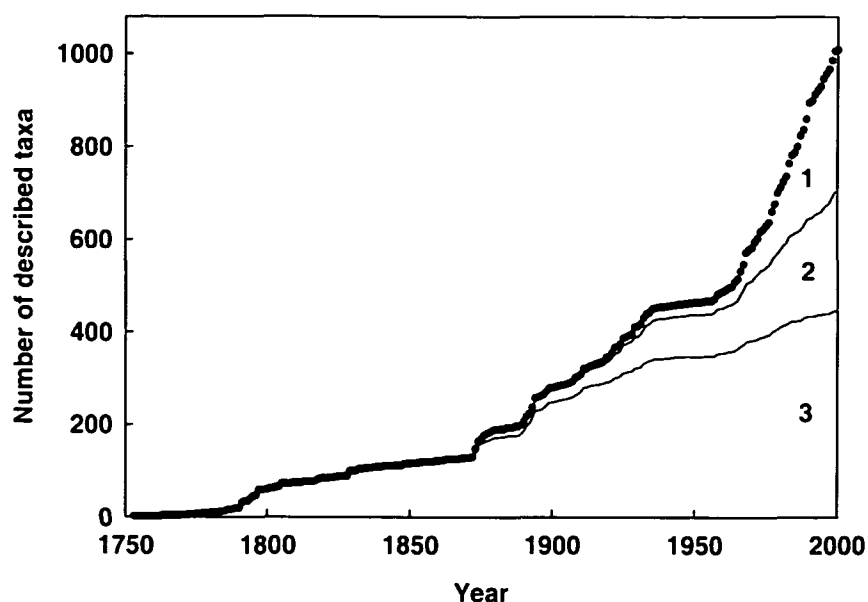


Fig. 1: Numbers of subgeneric myxomycete taxa described as new from the year 1753 (the nomenclatural starting point) up to the present time. The rarity status for all taxa was estimated, by assigning each taxon to one of the three classes, as explained under materials and methods. Numbers from one to three indicate the status of each group as: 1 – taxa known only from the type locality; 2 – taxa known from 2-20 collections; and 3 – more common taxa.

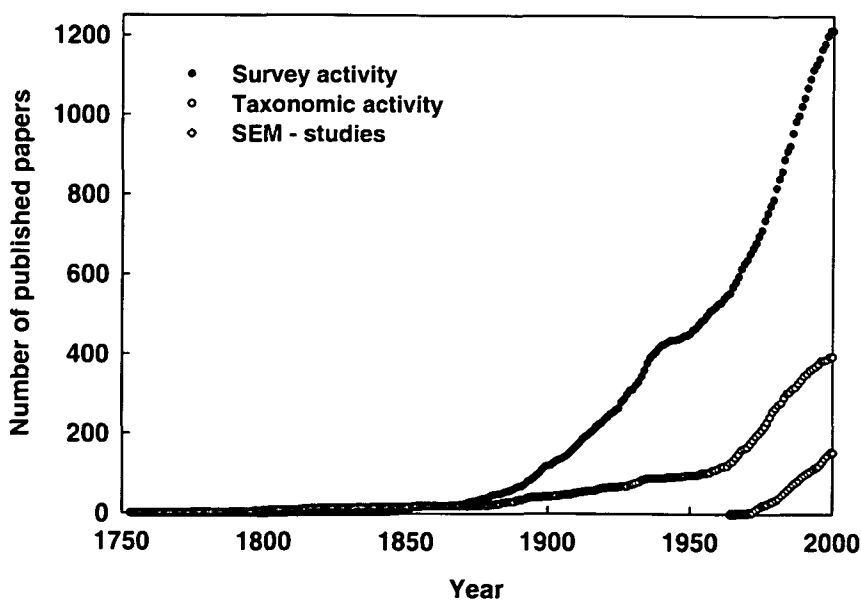


Fig. 2: Numbers of published regional species lists (filled circles – survey activity), publications describing new taxa (open circles – taxonomic activity), and publications using scanning electron microscopy (open diamonds – SEM studies).

and probably inhabit all substrata upon which myxomycetes occur. While myxobacteria have fewer morphological characters, they do have several taxonomic advantages over the myxomycetes since they are easier to culture

and are already accessible to DNA-sequencing studies.

A closer look at the estimations for rarity or abundance of validly described myxomycete taxa may help to elucidate this situation (Fig. 1). From the 1012 taxa recorded in the taxonomic database, 446 were estimated to be at least fairly common (known from more than 20 collections and reported from several localities), 258 to be rare (known from 2-20 collections and more than one locality), and 305 reported only from the type locality (in one or a few collections). As it is impossible to achieve a complete overview of all myxomycete records, these estimations may overweight rarity. Furthermore, numerous taxa are not well documented and a better knowledge of their microhabitat requirements could easily produce many more records, as indicated by the ecology and distribution of *Barbeyella minutissima* MEYL. (SCHNITTNER et al. 2000). Nevertheless, these estimations clearly reveal a rapidly increasing tendency towards the description of rare myxomycete taxa, often based on a single collection.

The use of SEM not only allows for more detailed species descriptions, but also greatly increases the resolution of taxonomic characters far beyond that of ordinary light microscopy. This has led to the description of taxa based entirely or largely on differences that are visible only by SEM. Prominent examples include *Hemitrichia serpula* var. *parviverrucospora* LIZÁRRAGA, ILLANA & MORENO 1999 and *H. pseudoleiocarpa* ILLANA, MORENO, LIZÁRRAGA & CASTILLO 1999. The former deviates from the typical form of this very common species by the presence of small verrucae between the coarse network of ridges on the spores, whereas the latter is in habit looking "alike with *Arcyria leiocarpa*" (COOKE) G.W. MARTIN & ALEXOP., but differing by a less branched capillitium with more numerous free ends (which accounts for its position in *Arcyria*). However, the most notable differences between *Hemitrichia pseudoleiocarpa* and *Arcyria leiocarpa* are found in spore size (8-9 µm, versus 8-10 µm in the new species) and the presence of dendroid warts on the spore surface in the new species (versus simple warts in *A. leiocarpa*). This leaves the spore ornamentation as

the only qualitative character distinguishing the two species.

Myxomycetes as a group have two contrasting features, which make their proper taxonomic treatment a challenge for the biologist. Due primarily to their cryptic vegetative stages and as a result of the paucity of taxonomic characters that these stages display, myxomycete taxonomy rests almost entirely on the morphology of the fruiting body. But, as every student of myxomycetes employing the moist chamber technique knows, the normal development of fruiting bodies is highly dependent upon environmental conditions; unsuitable conditions easily produce aberrant fructifications. Hence, environmental variability during the development of myxomycete fructifications is certainly a major source of variability in taxonomic characters, and the application of SEM provides a resolution well within this range of variability. Secondly, as shown by many experiments with the small percentage of species that are easy to cultivate, the occurrence of apomictic lineages (biotypes) in myxomycetes is a common phenomenon, which probably holds true for many of the species-rich genera. These apomictic strands are probably produced by conversion of sexually reproducing forms (COLLINS et al. 1983). The consequences of this special reproductive behavior are explained in detail in this issue (CLARK 2000). The main consequence of this phenomenon for taxonomy is that these apomictic biotypes are genetically isolated. As such, they can accumulate and conserve new characters inherited from their sexually reproducing parental forms or characters can be acquired by mutation. Instead of a continuum of characters, this process produces a set of character combinations deviating in minor features. With the sophisticated tools of modern taxonomy, such minor differences can be recognised. The taxonomic history of brambles (*Rubus*) in Germany can serve as an example for the taxonomic consequences of apomictic reproduction (WEBER 1996, see CLARK 2000). In this group of vascular plants, which possesses much more and better accessible morphological traits, two sexually reproducing parental species (*R. ulmifolius* and *R. canescens*) gave rise to an agamous complex with about 300 (WEBER 1995) apomictic

biotypes, which occasionally hybridise and form new biotypes.

As a consequence, myxomycete taxonomy must deal with the considerable morphological plasticity of the fructifications that results from environmental influence, adding a lot of "taxonomic noise" to the often minor differences that may result from genetically distinct (perhaps often apomictic) lineages in the group. With insufficient understanding of the causes of such variability, considerable caution is necessary in the description of new taxa. Thus, in this situation, the criteria for evaluating candidates for new taxa should be comprehensive. As a result of this thesis, we suggest the following five criteria.

1. When considering a taxon as being new to science, the body of world-wide published myxomycete literature should be checked to find any possible matching description.

Myxomycete distribution seems to depend much more on the available microhabitat than on geographic location. Two cases experienced by us may illustrate this point. *Lamproderma granulatum* NEUBERT, NOWOTNY & SCHNITTLER (1990), described from several collections growing on liverwort mats on wet and well-sheltered sandstone rocks in eastern Germany, was found again in the same microhabitat in the Great Smoky Mountains, USA (SCHNITTLER, unpubl. results). *Licea erecta* var. *erectoides* (NANN.-BREMEK. & Y. YAMAM.) Y. YAMAM. (YAMAMOTO 1999) was recently found as five perfectly matured sporocarps in a Costa Rican rainforest. Considered at the species level, four collections of this myxomycete are now known: India, Darjeeling, on decaying bamboo twigs (typus of *L. erecta*, THIND & DHILLON 1967); Japan, Kochi Pref., two collections differing somewhat from each other on decaying aerial twigs and on tree bark (originally described as *L. erectoides*, NANNENGA-BREMEKAMP & YAMAMOTO 1983); and Costa Rica, cloud forest at Monteverde, from decaying leaf sheaths of a living *Chamaedorea* palm (perfectly matching the description of *L. erectoides*, SCHNITTLER, unpub. results). Although these localities span the globe, the microhabitat and vegetation type appear to be similar.

2. To exclude the possibility of describing an aberrant form that has resulted from development under adverse conditions, a new taxon should be represented by several specimens from more than one locality.

While checking the Costa Rican myxomycete collections at the University of San Jose herbarium, one specimen was found that did not conform to any known species description. It consisted of one, perfectly mature collection of at least 1000 sporocarps from a high-elevation cloud forest of the Cerra de la Muerte (leg. A. JIMINEZ). The sporocarps occur gregariously, but not crowded, and display the general habit of a large *Cribraria* with a well developed stalk and a network of perforations in the upper half of the peridium. However, the spore size and ornamentation are identical to those of *Tubifera ferruginosa* which, although predominantly temperate in distribution, is known to occur at high elevations in Costa Rica. Even though the description of a new taxon would be formally correct and acceptable, since the material is more than sufficient for a type collection, it is certainly possible that this specimen represents an aberrant form of *T. ferruginosa*. However, the possibility that it represents a new taxon cannot be ruled out at this stage.

3. Since there are often only minor morphological differences in the characters separating apomictic species groups, taxonomic descriptions should be as exact as possible. Therefore, photographs made by light microscopy as well as SEM images of all relevant parts of a fructification should be mandatory for an original description. Colours, especially for the dry spore-mass, should be referred to a colour chart, and the variability of characters for the specimens investigated should be given. Spore-to-spore cultures should be attempted to ascertain the constancy of the main characters upon which the diagnosis of the new taxon is based.

The description of *Didymium annulisporum* by KELLER & SCHOKNECHT (1989) provides an excellent example, since it included SEM and LM photographs as well as culture work.

4. The characters distinguishing the new taxon from its closest relatives should be critically evaluated for their constancy, and the

new taxon should deviate from the others in more than one character, to exclude cases where a single gene mutation could have altered the species' appearance.

A possible character that may be affected by mutations in a single gene is that of clustered versus free spores. Evidence for this assumption can be derived from the fact that a number of synsporous taxa have been described throughout many genera of myxomycetes. Except for the genus *Badhamia*, with at least seven taxa having firmly clustered spores, all other species with conglobate spores are unique for their genus and are often very rare (Table 1). Therefore, the possibility cannot be ruled out that clustered spores occur easily but rarely as a mutation in numerous myxomycete species. It is conceivable that this condition is mostly not of evolutionary advantage, due to the reduced probability that the spores become airborne for efficient dispersal.

5. To facilitate the repeated discovery of a suspected new species, not only its localities, but also the habitat of all known specimens of a new taxon should be described. This includes a figure for the elevation, at least a brief description of the vegetation type, and all possible details of the microhabitat.

A case in point is that of the recent discovery of a new corticolous species of *Licea* by the second author which was at first considered to be an aberrant form that lacked peridial pigments. The taxon was originally found as a single sporocarp in a culture of the bark of living elder (*Sambucus nigra*). Further moist chamber cultures of bark of the same phorophyte yielded identical material from numerous localities in the Weald, south-east England. The same taxon later appeared on *Sambucus pubens* bark from the Great Smoky Mountains National Park, USA and on *Quercus ilex* bark from Madrid, Spain. In all cases the species was associated with algae, primarily on bark with a high water-capacity. Many field collections were also made and the taxon was eventually described as *Licea sambucina* D.W. MITCHELL (MITCHELL & MCHUGH 2000).

Obviously, the application of these criteria would not only help prevent the accumulation of doubtful species in myxomycetes and the resulting taxonomic confusion, but they would also lead to an accumulation of "candidate specimens" (which do not yet meet these criteria) in the collections of myxomycetologists. This is not a very satisfactory situation. A possible solution could be an Internet site, where descriptions of such candidates could be posted to be evaluated for their taxonomic value by the scientific community. As an additional effect, this would greatly enhance the possibility that another investigator might find more specimens of the putative new taxon, thereby accumulating further evidence that it represents a true biological entity.

Hopefully, in the near future, myxomycete fructifications will be accessible to DNA sequencing, providing an useful additional tool to support or improve the current morphological species concept, as is already the case for many other groups of organisms.

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Table 1. Described myxomycete taxa with clustered (conglobate) spores. For the rarity status, 1 refers to a taxon known from the type locality only, 2 stands for rare taxa known from 2-20 collections, and 3 for more common taxa. The column headed 'Spore clusters' denotes the number of spores per cluster. In the last column a common and similar species of the same genus is mentioned, which differs mainly by having free spores.

Species name ^a	Rarity status	Spore clusters	Possible counterpart species
<i>Badhamia bispore</i> WHITNEY	2	2	<i>B. nitens</i> BERK. (see below)
<i>B. calcaripes</i> GOTTSB.	1	6-20	–
<i>B. capsulifera</i> (BULL.) BERK.	2	6-20	–
<i>B. crassipella</i> WHITNEY & H.W. KELLER	3	4-40	–
<i>B. dubia</i> NANN.-BREMKE.	2	7-12	–
<i>B. nitens</i> BERK.	3	6-12	–
<i>B. papaveracea</i> BERK. & RAV.	3	6-20	–
<i>B. populina</i> LISTER & G. LISTER	2	10-20	–
<i>B. versicolor</i> LISTER	3	10-40	–
<i>Calomyxa synspora</i> M.L. FARR & KOWALSKI	1	5-30	<i>C. metallica</i> (BERK.) NIEUWL.
<i>Diachea koazei</i> Y. YAMAM.	2	10-20	<i>D. leucopodia</i> (BULL.) ROSTAF.
<i>Diacheopsis synspora</i> NANN.-BREMKE. & Y. YAMAM.	1	4-8	<i>D. metallica</i> MEYL.
<i>Dianema corticatum</i> LISTER	3	2-6	–
<i>Didymium synsporon</i> T.E. BROOKS & H.W. KELLER	2	4-25	<i>D. difforme</i> (PERS.) S.F. GRAY
<i>Enerthenema berkeleyanum</i> ROSTAF.	2	4-12	<i>E. papillatum</i> (PERS.) ROSTAF.
<i>Licea synsporos</i> NANN.-BREMKE.	2	c. 14	<i>L. tenera</i> JAHN
<i>Leocarpus bisporus</i> NANN.-BREMKE. & D.W. MITCHELL	2	2	<i>L. fragilis</i> (DICKS.) ROSTAF.
<i>Macbrideola synsporus</i> (ALEXOP.) ALEXOP.	3	7-15	<i>M. oblonga</i> PANDO & LADO
<i>Minakatella longifila</i> G. LISTER	2	8-14	–
<i>Perichaena syncarpon</i> T.E. BROOKS	2	4-16	<i>P. depressa</i> LIBERT
<i>Physarum bitunicatum</i> S. CARTER & NANN.-BREMKE.	1	4-12	<i>P. rubiginosum</i> FR. ?
<i>P. lakhanpalii</i> NANN.-BREMKE. & Y. YAMAM.	2	4-6	<i>P. decipiens</i> CURTIS
<i>P. miniatum</i> NANN.-BREMKE.	1	2-6	<i>P. nasuense</i> EMOTO
<i>P. synsporum</i> STEPHENSON & NANN.-BREMKE.	1	3-8	<i>P. decipiens</i> CURTIS ?
<i>Reticularia olivacea</i> (EHRENB.) FR.	3	0-20	spores can be free or clustered
<i>Trichia conglobata</i> M.L. FARR	1	2-12	<i>T. lutescens</i> (LISTER) LISTER
<i>T. synsporum</i> KOWALSKI & MCNICHOLS	1	2-3	<i>T. varia</i> (PERS.) PERS.
<i>Symphytocarpus syncarpus</i> (YAMASHIRO) Y. YAMAM.	1	5-8	<i>S. confluens</i> (COOKE & ELLIS) ING & NANN.-BREMKE.

^a For the following species not mentioned in MARTIN & ALEXOPOULOS (1969) a citation of the protologue is given: *Badhamia bispore* WHITNEY Mycologia 70: 672.1978; *B. calcaripes* GOTTSB. Nova Hedwigia 22: 491.1972; *B. crassipella* WHITNEY & H.W. KELLER Mycologia 74: 620.1982; *B. dubia* NANN.-BREMKE. Proc. K. Ned. Akad. Wet. C 71: 49.1968; *Calomyxa synspora* M. L. FARR & KOWALSKI Mycologia 66: 886.1974; *Diachea koazei* Y. YAMAM. J. Jap. Bot. 62: 346.1987 (syn: *D. synspora* H. Z. LI Acta Mycol. Sinica 7: 99.1988); *Diacheopsis synspora* NANN.-BREMKE. & Y. YAMAM. Proc. K. Ned. Akad. Wet. C 89: 223.1986; *Didymium synsporon* T. E. BROOKS & H. W. KELLER Mycologia 65: 287.1973; *Licea synsporos* NANN.-BREMKE. Proc. K. Ned. Akad. Wet. C 71: 42.1968; *Leocarpus bisporus* NANN.-BREMKE. & D. W. MITCHELL, in NANN.-BREMKE. Proc. K. Ned. Akad. Wet. C 92: 512.1989; *Macbrideola oblonga* PANDO & LADO Mycotaxon 31: 302. 1988; *Physarum bitunicatum* S. CARTER & NANN.-BREMKE. Proc. K. Ned. Akad. Wet. C 75: 328.1972; *P. synsporum* STEPHENSON & NANN.-BREMKE. Proc. K. Ned. Akad. Wet. C 93: 193.1990; *Trichia conglobata* M. L. FARR Mycologia 66: 882.1974; *Trichia synspora* KOWALSKI & MCNICHOLS Mycologia 66: 372.1974; *Symphytocarpus syncarpus* (YAMASHIRO) Y. YAMAM. J. Jap. Bot. 59: 256.1984.

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