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A taxonomic guide to the species of *Didymium*. II. The sessile species including *Mucilago*

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Abstract: This paper is an attempt to consolidate all information pertinent to the taxonomy of the genus *Didymium*, including uniform species descriptions and a key for all of the species, and to make this information available to interested persons in an open access journal. *Didymium* is a genus, in which over ninety accepted species have been described, that is defined by the presence of crystalline lime granules occurring on the peridium but not the capillitium. The number of different species and the morphological variability within many of them has produced a situation where it is sometimes difficult to identify a particular specimen. Thus, this paper is an attempt to provide guidance in the identification of the sessile species.

Keywords: identification, sporangia, sporocarps, plasmodiocarps

Introduction

The genus *Didymium* Schrad. has calcareous peridia (order Physarales) and non-calcareous capillitia, which places it in the family *Didymiaceae*. This calcareous material, traditionally designated lime, varies somewhat in composition in the Physarales, but is calcium carbonate in the *Didymiaceae* (Schoknecht and Keller 1989). Within the family crystalline lime (as opposed to the granular lime seen in *Diderma* and *Physarina*) is found in Didymium, *Lepidoderma* and *Mucilago*. This lime is scattered on the peridium or forms a crust (*Didymium* and *Mucilago*), or is united into distinct scales (*Lepidoderma*). These genera also have sporangial or plasmodiocarpous (*Didymium* and *Lepidoderma*) or aethalial (*Mucilago*) sporocarps.

The *Didymium* species are widely distributed and generally form sporocarps on leafy or woody litter in temperate and tropical forest. They are probably living in dead wood or the soil and litter interface and feeding on the micro-organisms in this habitat (Stephenson and Landolt 1996). Some species appear to have more restricted habitats, such as the bark of living trees, animal dung, desert plant litter, or the litter and plants of the snow melt zones of snow packs (Ing 1994).

The general taxonomy of the Myxomycetes, based on the present somewhat artificial system, is in a usable state, although the situation is by no means perfect. However, this may soon become unworkable

due to the current tendency to define new species based on fewer and finer morphological characters, since these characters may not reflect true species gaps (Clark 2000). Culture studies have shown that the cosmopolitan myxomycete morphospecies often consist of a number of regional (i.e. Eastern US, Southern US, Central America) allopatric, and occasionally sympatric, sibling biological species, and numerous clonal lines (generally believed to be apomictic) that are generally fairly local (Clark 2000, 2004), but occasionally quite extensive (Stephenson et al. 2004). Also, extensive DNA diversity studies of *Didymium squamulosum* and *D. difforme* collections indicate long-range geographical dispersal and a number of intra species clades (Winsett and Stephenson 2008, 2011).

These biological species and clones are related genetically and display the full range of the possible combinations of the suite of morphological variations found within the group. This produces an integrated continuum of biological species and clones (species complex) displaying considerable morphological variation; in which individual populations cannot be separated out morphologically, although two collections considered out of this context may appear to be minimally distinct taxa. This makes the identification and naming of the biological species problematical at best, and that of the clonal lines generally impossible.

Further difficulties arise when several of these cosmopolitan species complexes have overlapping morphologies, such as in the *Didymium iridis* super complex (Clark et al. 2001). In this situation, a morphological circumscription of the taxonomic categories, that will place every collection into its correct taxon, is impossible. Also, the clonal lines in these complexes are subject to independent selection, separate from that of the rest of the group; this can lead to the production of small, usually ephemeral, populations containing distinct variations or morphological aberrations, some of which may be genetic and therefore have short term stability. Thus, it will be difficult to find a place for these variant clonal populations in a coherent taxonomy. This complex population structure, and the general lack of other non-morphological characteristics, would seem to indicate that, at this time, the only realistic systematic procedure; that is practicable and consistent for the group, is to identify and name the species complexes and any distinct specialized or local population groups.

Materials and methods

The following criteria will serve as the basis for species delimitation in this work. Populations which display integrative morphologies, without distinct gaps, will be deemed a single species, unless there is some non-morphological evidence for separation. However, if there appears to be several morphological foci with some overlap at the edges (intermediate forms are not common), they will then be deemed separate species. If the proposed species level variations are integrative in a single collection, direct genetic evidence is the only possible way to validate them as separate species. A collection from a single site, that is obviously related to a species complex, but which also displays a distinct morphological variation, cannot serve as the basis for a new species description unless the variation is complex and not likely to be due to a single gene, or there is other non-morphological evidence. Similarly, collections or cultures, which have an apparent morphological aberration (amorphous sporocarps, unusual or poorly formed structures, lack of lime, etc.), will also be rejected as a basis for species delimitation, even if they have been found to be stable in culture.

This procedure will eliminate a number of named taxa, and will also over-represent taxa consisting of isolated populations in harsh environments; since they will more likely be subject to selection for a distinct morphological variation. Also, one should keep in mind that the cosmopolitan species, in general,

are complexes of valid genetic species that cannot be distinguished morphologically, even when they display a fairly broad range of morphological variations. Therefore, in this paper, the species of *Didymium* will be sorted into distinct groups on the basis of morphology, using our new knowledge of population structure in the Myxomycetes (Clark and Haskins 2010), and then the first valid specific epithet for each distinct group will be determined.

Sporocarp Morphology

The morphological observations in Matsumoto's (1999) dissertation "Taxonomic studies in the genus *Didymium* (Physarales, Myxomycetes)" generally covering the Japanese species of *Didymium*, is an excellent starting point for continued studies in this genus. While we have very few disagreements with his observations, we do have some differences with his terminology and a number of his taxonomic conclusions, based on these observations. However, most, but not all, of his terminology and taxonomic observations will be adopted in this work.

Matsumoto used sporophore as a general term for all the different fruiting body types in the Myxomycetes, and sporocarp for what has generally (Martin and Alexopoulos 1969) been called a sporangium. However, we prefer sporocarp as the general term and sporangium as the specific term for the generally small sporocarps, which are constant in size and form for each species. Plasmodiocarps are the only other sporocarp form found in the genus, and they are generally larger and more irregular in size and form than sporangia (in some species sessile sporangia and plasmodiocarps form a continuum).

The sporocarp in the stipitate species consists of two parts, the sporotheca and the stipe. The sporotheca is the spore containing part of the sporocarp and it consists of the peridium, capillitium and spores, while the stipe is the support and attachment part of the sporocarp consisting of the hypothallus, stalk, and columella in the stipitate species (these stalk components are general regions of the stipe which blend into each other). Most of the sessile sporangial and plasmodiocarpous species lack a columella, but generally retain the thick peridial basal plate, which sometimes forms a "columella" such as the folded wall seen in *Didymium flexuosum*.

Peridial Morphology

The peridium is the outer layer of the sporotheca and is usually covered with stellate lime crystals, either in a loose powder or a compact smooth (eggshell) crust. There are three basic subtypes of peridia: areolate, non-areolate, and cartilaginous (Matsumoto 1999). The areolate subtype consists of a thin, colourless to brownish membrane with thinner regions producing a reticulate pattern (generally seen as lighter colored patterns with the light microscope, although they can only be seen with the electron microscope in some species), that produces scale-like fragments upon dehiscence.

The cartilaginous subtype is similar to the areolate subtype, except that it consists of a brownish cartilaginous material (areolate patterns can be seen with the electron microscope). The non-areolate subtype has a thin, colourless to brownish membrane without areola, and it may display an irregular or circumscissle dehiscence.

Capillitial Morphology

The capillitial threads are thin, hyaline to brownish, and run from the peridial basal plate (columella) to the upper peridial surface. Sporadic expansions and inclusions can occur in the capillitial threads, but only the regular and distinct variations, such as the vesicles seen in *Didymium serpula*, are of taxonomic importance. Matsumoto (1999) also divided capillitia into three subtypes: dichotomous (dichotomously branching with sparse cross-bar anastomoses), netted (branching and anastomosing to form a net), and rudimentary (reduced and fragmentary). The dichotomous subtype is generally found in the stipitate species, including those with rudimentary or cupulate stalks, with a few exceptions such as *D. difforme* var. *comatum* which has a netted capillitium. The rest of the netted and rudimentary subtypes are generally correlated with sessile sporangia and plasmodiocarps.

Spore Morphology

The spores are globose (rarely ovoid), brownish, and ornamented, with the variations in size, color and ornamentation within a species varying more than is generally stated (Martin and Alexopoulos 1969). Spore ornamentation has been generally described using the light microscope, according to density (dense, sparse, patchy), size (large, small, minute), and shape (warts, spines, reticulate). However, the scanning electron microscope has revealed considerable more detail and new terms have been introduced (Rammeloo 1974) for ornament shapes: pila (rods with heads), bacula (rods without heads), verruca (wide irregular lumps), spines (long pointed processes), coni (short pointed processes), muri (smooth walled ridges), and cristae (ridges made up of individual processes).

Besides pilate, baculate, verrucose, spinulate and conate spore types, there are a number of compound types in the genus (Matsumoto 1999). There is a broken reticulate type with cristae consisting of branched bacula (not seen with the light microscope, and thus they appear to be minutely warted or nearly smooth), a reticulate type with cristae consisting of connected pila, a broken reticulate type consisting of coalescence bacula (appears verrucose or broken reticulate with the light microscope), and a reticulate type consisting of large murate walls, which also has pila. The pilate spore type is the most common type (approximately one half of determinations) and seems especially common in the stalked species; but the remaining spore types are scattered within all of the groups including the sessile sporangial and plasmodiocarpous species.

Results and Discussion

Since a guide to the stipitate species of *Didymium* has been published (Clark and Haskins 2018), only the non-stipitate species will be dealt with in this paper. The non-stipitate species of *Didymium* are a somewhat amorphous collection with sessile sporangia grading either into short stalked sporangia or plasmodiocarps. Also, the available taxonomic characters of these species are restricted to the peridium, capillitium and spores, with the peridium and capillitium appearing to be quite variable in some collections.

This has resulted in a degree of taxonomic confusion, since various authors have emphasized different characters, and thus the morphological descriptions for a particular taxon are often variable and sometimes contradictory. Although they are not clear cut characters, we will use peridial lime and sporocarp type as a means of designating groups for these species Since some may consider the cupulate

stalked species to be non-stipitate, this group (covered in the stipitate paper (Clark & Haskins 2018) will also be covered here. In addition, a number of the other short stalked species often produce sessile sporangia and they may also be included in the discussions, key and descriptions.

The egg-shell peridial crust group

A group of species having peridial lime that forms an egg-shell like crust, and generally have a pulvinate sporangial sporocarp (difforme type), although some species are more variable and may have plasmodiocarpic sporangia, or a short cup-like stalk (vaccinum type) In general these species have a smooth compact peridial lime crust, which generally separates from the peridial membrane. They also, generally have sessile sporangia that may grade into plasmodiocarps, and some have a cup or plate-like basal region. *Didymium difforme* (Pers.) Gray is a cosmopolitan and variable species; which appears to be the central species in a large cluster of species in this group. It has a cupulate base, no columella, and dark-purplish-brown minutely warted (cristae of branched baculae by electron microscopy) fairly large (11-13 μm diam.) spores.

Nannenga-Bremekamp (1966) has elevated *D. difforme* var. *comatum* Lister to species status as *Didymium comatum* (Lister) Nann.-Bremk., based mainly on its profuse netted capillitium, as opposed to sparsely branching capillitium in *D. difforme*. However, since continuous gradations of capillitial types can be found within a single collection (Martin and Alexopoulos 1969, Ukkola and Rikkinen 2000), we consider *D. comatum* to be a form of *D. difforme*. Nannenga-Bremekamp (1991) also considered *Didymium tubulatum* E. Jahn to be a valid species separate from *D. difforme*, on the basis of a more plasmodiocarpic habit and the presents of pillars. However, this form also integrates into the typical *D. difforme* form (Neubert et al. 1995), and thus, *D. tubulatum* is also a synonym for *D. difforme*.

Didymium quitense (Pat.) Torrend, *D. trachysporum* G. Lister, *D. synsporum* T.E. Brooks & H.W. Keller, *D. rugulosporum* Kowalski, *D. azorellae* D. Wrigley, Lado & Estrada and *D. annulisporum* H.W. Keller & Schokn. are all relatively rare and differ from *D. difforme* basically in terms of their unique spore morphology. *D. quitense* is a generally pulvinate sporangial species with dark-purplish-brown 13-14 μm diam. spores with large warts that form (usually) a partial reticulum; while it has been considered to be a montane form of *D. dubium* by some (Mitchell and Chapman 1980, Kowalski 1971), we consider the egg-shell crust peridium and spore characteristics to be enough to designate it a minimally distinct species closely allied to *D. difforme*. *Didymium trachysporum* is a similar pulvinate species with purplish-brown spores, however, in this case the spores are smaller (9-10 μm diam.) and coarsely and irregularly warted. This taxon basically differs from *D. quitense* by its spore size, and is only accepted as a valid species on the long history of separation of these two taxa in earlier works.

Didymium azorellae is a newly described species from the cold arid regions of South America which occurs on the litter of succulent cushion plants (*Azorellae* spp.); besides this unique habit it has a combination of fairly large (11-5-14.5 μm diam.) spores with small dense warts and scant capillitium which delimits it from the other species. *Didymium synsporum* is a clustered spore taxon, which is also close to *D. difforme*. Spore clustering, which could be caused by a single genetic mutation, is by itself not ground's for species delimitation (Schnittler and Mitchell 2000); however, in this case, there also appears to be a suite of small changes that adapt this taxon to its specialized bark habitat, and thus confirms it as a minimally distinct species. *Didymium rugulosporum* differs from *D. difforme* in its large (18-20 μm diam.) coarsely warted spores and capillitium with connecting transverse bars; while its rarity would indicate that

it could be a local variant form, the morphological differences seem to be more than minor, and we therefore conclude (with some reservations), that this is also a minimally distinct taxon.

Didymium annulisporum is another pulvinate taxon, which differs from *D. difforme* in terms of its distinct spores (9-11 μm diam. with dense warts and an annulate separation ridge). Again, this spore morphology would appear to be due to a number of genes; which indicates that this is another minimally distinct species. *Didymium peruvianum* Lado, Wrigley & Stephenson has a small, often stalked sporangium with a number of minor differences (mainly the dark warted spores with pale bands) from the rest of the egg-shell group; this rare species from the Peruvian desert is, in our opinion, a marginal taxon. These "spore species" are assumed to be valid on the basis that such variations require considerable genetic difference; while, this seems to be a reasonable assumption, there is a real need for experimental evidence on this point.

Some collections of the non-egg-shell peridial crust species, *Didymium nivicolum* Meyl. and *Didymium dubium* Rostaf., have been reported to display egg-shell crusts (Mitchell and Chapman 1980); thus, this character is not a completely reliable basis to separate species in all cases. Since *Didymium listeri* Massee is identical to *D. dubium*, except for the peridial lime, we consider this taxon to be included in the *D. dubium* complex. *Didymium saturnas* H.W. Keller can also be included in this egg-shell peridial crust group. This taxon generally has a dull-yellow peridium with non-stellate lime crystals embedded in the peridial matrix, and these characteristics were suggested by the author as indicating that the taxon was somewhat intermediate between *Didymium* and *Diderma*. These characters led Matsumoto (1999a) to move this taxon to *Diderma*; however, since crystalline lime is being used as the defining character of the genus *Didymium*, this species with its distinctive equatorial spore ring will be retained in *Didymium.*

Didymium vaccinum (Durieu & Mont.) Buchet is the core of a second cluster in this group. It has turbinate to hemispheric sporangia with a stalk-like cupulate base, a large (usually) hemispheric columella, scanty capillitium, and dark-purplish-brown 12-14 μm diam. spores with large warts (conate by SEM). *Didymium disciforme* Kowalski & T.N. Lakh. and *D. haretianum* T.N. Lakh & K.G. Mukerji are also in this cluster. *Didymium disciforme* is known only from moist chamber cultures from the type site, and differs from *D. vaccinum* mainly in terms of its small columella and membranous cup base; while *D. haretianum*, also known only from the type collection, differs in having a longer stalk-like region that leaves a membranous cup base and smaller (7-9 μm diam.) spores. However, since *D. vaccinum* often produces small columella (and occasionally stalk like structures) when cultured (Clark 2004); we consider *D. disciforme* and *D. haretianum* to be aberrant/variants of *D. vaccinum.*

The non-egg-shell sessile sporangiate to small plasmodiocarpic group

A group of species having peridial lime which does not form an egg-shell like crust, and generally have a sessile sporangial sporocarp, although some species may have small plasmodiocarpic sporocarps. *Didymium anellus* Morgan, with its white to gray flat-pulvinate sporangia to annulate plasmodiocarps having profuse capillitium forming a somewhat elastic network, and dark-brown 8-10 μm diam. minutely warted spores is the central species in this group. *Didymium ochroideum* G. Lister differs from *D. anellus* in having smaller usually pale-brown sporangia, a loose capillitium network, and small (6-8 μm) pale-purplish-gray, nearly smooth spores; while *D. inconspicuum* Nann.-Bremek. & D.W. Mitch., known only from the type collection, differs from *D. ochroideum* only in having larger (12-14 μm diam.) spores. While this spore size difference is not trivial, we do not consider a single large-spored collection to be an adequate basis for a new species.

Didymium reticulosporum Novozh. & Zeml., *D. clavodecus* K.D. Whitney, *D. mexicanum* G. Moreno, Lizárraga, & Illana, and *D. circumscissile* K.D. Whitney & L.S. Olive are other taxa that can be included in this group. *Didymium reticulosporum* has a snow-white to ash-gray sessile sporangium and is known from only a few sites and collections; however, its lack of a capillitium and distinct 13-16 μm diam., banded-reticulate spores indicates that it is a valid species. *Didymium clavodecus*, a fairly rare species from California and Mexico, has a white sessile sporangium or irregular plasmodiocarp, a profuse rigid capillitium, a columella, and 11-14 μm diam. spores with large pilate warts and a reticulum; which distinguishes it from the rest of the species in the group. *Didymium mexicanum* is another rare taxon from Mexico with morphological similarities to *D. clavodecus*, from which it differs mainly in that its spores have non-pilate laterally fused warts and a less prominent reticulum, and it occasionally has very short calcareous stalks. *Didymium circumscissle*, known only from the type collection, is a minute sporangial taxon lacking capillitium and having 10-12 μm diam. minutely warted spores. Apparently this is a miniature biotype, possibly of *D. anellus*, which we do not consider deserving of a name unless more material is found.

Several other taxa, which can be included in this group, display a number of indications of aberrant development, similar to those which are often seen in culture. They often have small, rather amorphous sporocarps, which often lack peridial lime and have sparse to no capillitia; and in general they appear to be abnormal sporocarps or genetic freaks, that should not be used as a basis for species delimitations. *Didymium atrichum* Henney & Alexop., which is known from the type culture, has peridial lime and no capillitium, and while it is stable in culture, we consider it to be an abnormal specimen of uncertain affinities. *Didymium nullifilum* (Kowalski) M.L. Farr, which is again known only from its type culture, also has no capillitium, little peridial lime (amorphous squamules according to Henney et al. (1980), and is stable in culture. Again, in our opinion, this taxon is an aberrant of unknown affinities. Similarly, *Didymium nigrum* Krzemien., which also has no capillitium, little peridial lime, and is known only from the type, falls into this group of aberrant developmental specimens with unknown affinities.

Three other species—*Didymium tussilaginis* (Berk. & Broome) Masse, *Didymium vernum* Kuhnt, K. Baumann & Nowotny, and *Trabrooksia applanata* Keller—also display indications of aberrant development and occur in a specialized habitat, however, they have been collected a number of times over a period of years and thus appear to have a stable morphology. Therefore, since in our opinion the validity of these taxa is a difficult problem that will only be determined by DNA or other genetic procedures, we provisionally accept them as species. *Didymium tussilaginis* and *D. vernum* are found only on the underside of *Petasites hybridus* leaves, and have sporocarps with sparse patchy peridial lime, irregular capillitia and spinulose spores, with *D. vernum* having slightly smaller and less spiny spores and large ochraceous lime crystals. Farr (Martin, Alexopoulos & Farr 1983) reduced the monotypic genus *Trabrooksia* to a synonym of *Didymium* and considered *T. applanata* H.W. Keller to be a synonym for *D. sturgisii*. This taxon, a small plasmodiocarpous sporocarp lacking lime and having capillitium, has been collected at least thirty-seven times over a number of years from the bark of living trees, and is thus also a candidate for genetic studies.

There are also a number of species with short stipes which often grade into sessile sporangia, such as *Didymium crustaceum* Fr., *Didymium karstensii* Nann.-Bremek., *Didymium muscorum* Mukerji, *Didymium macquariense* G. Moreno & S.L. Stephenson, *Didymium obducens* P. Karst., *Didymium wildpretii* Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado, and *Didymium umbilicatum* D. Wrigley, Lado & Estrada. Besides the presence of short stalks, which are often hidden under the sporotheca or absent, the sessile specimens of these stalked species can be separated from the sessile species as follows: *D. crustaceum* has a calcareous crustose layer which covers a number of sporangia, *D. karstensii* has a

subglobose sporangium with a free lime crust and spores with spinulose processes which form a partial reticulum, *D. muscorum* is similar to *D. karstenii* but lacks the free crustose layer and has less reticulate spores, *D. macquariense* has spores with a partial reticulum of warts, a capillitium with ellipsoid to spiny nodes, and is apparently endemic to Macquarie Island, *D. obducens* has a pale-brown discoid to pulvinate sporangium and black 11-13 μm diam. spores with coarse warts, *D. wildpretii* has a white to pale orange-yellow subglobose to slightly reniform sporangium and brown-black 7.5-9.5 μm diam. spores with dense uniform warts, and *D. umbilicatum* has a yellowish-white sporangium with a deep apical umbilicus, black 11-15μm diam. spores with warts forming a subreticulum and appears to be restricted to arid regions of Mexico**.**

Didymium yulii S-Y. Lieu & F-Y. Zhao, a newly described species that has an aethalial sporocarp and thus would normally be placed in the genus *Mucilage*; however, the authors (Zhao et al. 2021) also conducted a molecular study which found that this species is closer to a *Didymium* DNA clade that it is to the *Mucilago* clade. This conflict between morphology and molecular studies may become increasing more common due to current increase in molecular studies. *D. yulii* can be distinguished from *M. crustacea* by its lack of true capillitia.

The non-egg-shell large plasmodiocarpic group

A group of species having peridial lime which does not form an egg-shell like crust, and generally have a large plasmodiocarpic sporocarp, although some species may also produce small plasmodiocarps or sessile sporangia. *Didymium dubium* Rostaf. is a central species in this group; it has a profuse, rigid pallid to brown capillitium, that branches and anastomoses to form an elastic net, 10-15 μm diam. purplish-brown spores with dense fine warts, and a white to greyish thin flat plasmodiocarp usually accompanied by flat-pulvinate sessile sporangia. We include *D. listerii*, which has egg-shell peridial lime, as a developmental form of *D. dubium* and *Didymium anomalum* (Rostif.) Massee which has a thicker columella. *Didymium decipiens* Meyl. differs from *D. dubium* in having spores with somewhat larger warts, and a capillitium which is less netted and which also bears closely wound spiral bands.

Didymium orthonemata H.W. Keller & T.E. Brooks, is a rare taxon found on red cedar, which has a white to gray plasmodiocarp, scanty coarse capillitia, and 12-15 μm diam. echinulate spores. This rare taxon, which appears to be more than a biotype, meets the minimal criteria needed to be accepted as a valid species. *Didymium sturgisii* Hagelst., which is also fairly rare has a thin white to gray plasmodiocarp, but differs from *D. dubium* in having limy pillars (extending from the base to the upper peridium) and a scanty capillitium. *D. nivicola Meyl.* differs from *D. dubium* in that it may have a short stalk and occurs in the snow melt zone.

Didymium serpula Fr., *D. perforatum* Yamash., and *D. flexuosum* Yamash. are also generally rare taxa in this group. *D. serpula* differs from *D. dubium* mainly in having a generally larger perforated white to gray plasmodiocarp, smaller (8-11 μm diam.) spores and large (30-50 μm diam.) yellow vesicular bodies attached to the capillitium; while *D. perforatum* has a larger labrinthulform ash-gray plasmodiocarp, spores with sparse large spines, and a closely netted (5-15 μm mesh) capillitium. On the other hand, *Didymium flexuosum* has a laterally compressed plasmodiocarp which contains an elongate limy columella, and sparsely spiny spores associated with spore-like (larger, paler and irregular in shape) vesicle bodies.

Didymium panniforme J. Matsumoto somewhat resembles *D. ochroideum*, but its unique glossy cartilaginous peridium separates it from all of the other sessile or plasmodiocarpic species. *Didymium leptotrichum* (Racib.) Massee, which could possibly be placed in this group, is impossible to correctly

characterize, and is thus considered to be an uncertain taxon. *Didymium tubi-crystallium* Nann.-Bremek. & R.L. Critchf. would also fit into this group, however, it appears to be a developmental aberration and is thus considered to be a doubtful species. *Didymium charoae* JF. Moreno, G. Moreno & Lopez-Vill. and *Didyium corticola* Kuhnt are two newly described species, both of them found in a special habitat on moss and moss covered hardwood tree in Europe. *D. charoae* can be identifies from other plasmodiocarpic species by its dark somewhat coarse capillitium which has swelling containing lime grandules and large (12.7-16.1 μm diam.) spinulate spores; while *D. corticola* has a dark coarse capillitium lacking swellings and small (7-8 μm diam.) spores densely covered with warts which do not form a reticulum.

The genus Mucilago

The genus *Mucilago* Battarra is also in the order Physarales (calcareous peridium) and family Didymiaceae (no lime on capillitium), and its crystalline non-scalar lime and aethalial sporocarp separates it from the other genera in the family. The single species in the genus, *Mucilago crustacea* F.H. Wigg, is cosmopolitan and generally forms sporocarps on wood, leaves and the stems of living plants. The genus is separated from *Didymium* on the basis of its aethalioid sporocarp, and the two genera could easily be combined as suggested by DNA studies (Fiore-Donno et al. 2008); however, since this would necessitate a number of name changes, it should be undertaken only if considerably more evidence (such as DNA) is obtained upon which a complete revision of the family can be made.

Martin and Alexopoulos (1969) settled the question as to which was the correct name for this genus—*Mucilago* or *Spumaria*. They also concluded that the genus contained a single variable species (*M. crustacea*) and that the named varieties were not distinct. With the exception of Lizárraga et al. (1999) description of *Mucilago dictyospora* (R.E. Fr.) Lizárraga, G. Moreno & Illana, and Nannenga-Bremekamp's (1974) recognition of *Mucilago crustacea* var. *solida* (Sturgis) G. Lister ex Nann.-Bremk., the Martin and Alexopoulos dispositions have been recognized by other (Lado 2005-2020) and this study. These recent separations were based mainly on spore characteristics, which are highly variable in this widespread morphospecies complex.

Other Didymium and Mucilago names

Many of the *Didymium* and *Mucilago* names that have been proposed have later been found to be illegitimate or doubtful names and are no longer considered valid. Also many valid names are now considered to refer to species in other genera. Anyone interested in the taxonomy of these genera (or any other myxomycete genera) should be aware of these names, which can be found and examined on the on line nomenclature information system of Eumycetozoa (Lado 2005-2022).

The recent report (Fiore-Donno et al. 2010) that the DNA of several amoeboflagellates, named by protozoologists, places them in the genus *Didymium*, has led to their descriptions as *Didymium crytomastigophorum* (R. Michel, Walochnik, & Aspöck) Fiore-Donno, Kamono, & Caval.-Sm. and *Didymium dachnayum* (G. Walker, Siberman, Karpov, Preisfeld, P. Foster, Frolov, Navozh & Sogin) Fiore-Donno, Kamono. & Caval,-Sm. While these names are apparently legitimate (Lado 2005-2022) they do pose a problem to the taxonomy of the genus, since these cultures do not display the rest of the myxomycete life cycle and they can only be delimited from the other valid taxa by means of DNA

differences. However, since not all of the described *Didymium* species have a DNA profile, the utility of these new names is not readily apparent.

Key to the species

1. Sporophore an aethalium – 2.
1. Sporophore a sporangium or plasmodiocarp – 3.

2. Only pseudocapillitia present – *Mucilago crustacea*
2. Both pseudocapillitia and capillitia present – *Didymium yulii*

3. Peridium lacking lime crystals (closely related to *D. sturgisii* either as a biotype or a separate species) –*Trabrooksia applanata*
3. Some peridial lime evident – 4.

4. Sporophore having a shell-like outer crust – 5.
4. Sporophore lacking a shell-like outer crust – 15

5. Sporangia pulvinate, sessile or with a short thick stalk; columella large (usually) and dome-shaped (includes *Didymium disciforme*, two collections) – *Didymium vaccinum*
5. Sporangium sessile (may have a short stalk) to plasmodiocarpic; columella not large and dome shaped – 6.

6. Spores united in clusters – *Didymium synsporum*
6. Spores not united in clusters – 7.

7. Spores with an equatorial ring ridge – 8.
7. Spores lacking an equatorial ring ridge – 9.

8. Sporangium white and lacking a columella – *Didymium annulisporum*
8. Sporangium dull yellow to nut brown and having a hemispheric columella – *Didymium saturnas*

9. Large (18-20 μm) spores with a lax reticulum of warts – *Didymium rugulosporum*
9. Spores smaller (less than 15 μm) – 10.

10. Spores dark with paler bands, small yellowish white discoid sporangium with scanty capillitium (rare taxon from Peru) - *Didymium peruvianum*
10. Spores lacking paler bands - 11.

11. Spores minutely warted to nearly smooth – 12.
11. Spores coarsely warted, the warts often in a subreticulate pattern - 13.

12. Sporocarp small hemispherical sporangium to small plasmodiocarp found only on *Azorellae* spp. (cushion plants) litter, capillitium scanty, spore densely warted 11.5-14.5 μm - *Didymium azorellae*
12. Not as above – 14.

13. Sporocarp pulvinate to thin and broadly effuse; capillitium often rigid; spores 9-11 μm – *Didymium listeri*
13. Sporocarp pulvinate to plasmodiocarpous; capillitium not notably rigid; spores 11-14 μm (includes *Didymium comatum*, a form with profuse elastic capillitia which grades into the normal sparser less elastic form) – *Didymium difforme*

14. Sporocarp large (0.4-1 mm); spores 13-14 μm – *Didymium quitense*
14. Sporocarp small (0.1-0.6 mm); spores 9-10 μm – *Didymium trachysporum*

15. Sporocarp having a distinct plasmodiocarp – 16.
15. Sporocarp having a sporangium or a sporangial-like plasmodiocarp – 29.

16. White plasmodiocarp, capillitial threads marked with spiral bands, lime often only partly crystalline – *Didymium decipiens*
16. Capillitial threads not marked with spiral bands, lime usually entirely crystalline – 17.

17. Peridium cartilaginous and glossy, white to buff to orange-brown – *D. panniforme*
17. Peridium not cartilaginous – 18.

18. Prominent vesicle intermixed with the spores and capillitium - 19.
18. No prominent vesicles intermixed with the spores and capillitium; swollen regions of the capillitium may be present – 20.

19. Yellow granular filled vesicles attached to the capillitium; thin broadly effuse plasmodiocarp lacking a columella – *D. serpula*
19. Pale brown vesicles free from the capillitium; branching and anastomosing, plasmodiocarp with a wall like columella – *D. flexuosum*

20. White to pale-yellow plasmodiocarp intricately labyrinthiform, the strands generally flattened and fused into a nearly continuous perforated layer – *D. perforatum*
20. Plasmodiocarps not intricately labyrinthiform or forming a perforated layer – 21.

21. Trabeculae (lime pillars) connecting the base and upper peridium; peridial lime consisting of white angular crystals; spores 10-12 μm with minute irregular warts – *D. sturgisii*
21. Plasmodiocarps lacking trabeculae – 22.

22. Capillitium with swollen nodes or regions – 23.
22. Capillitium lacking swollen nodes or regions – 26.

23. Capillitium nodes containing lime inclusion – 24.
23. Capillitium nodes not containing lime inclusions – 25

24. Thick coarse capillitium with irregular lime filled nodes; spores 12-13 μm coarsely and irregularity to sub-reticulate warted (single collection from California, we consider this specimen to be a developmental abnormality of an unknown species) – *D. tubi-crystallium*

24. Abundant wavy brown capillitium with spindle-shaped to irregular enlargements which may contain lime; spores 12.7-16.1 µm with spine-like ornamentation, found only on moss on *Quercus* trees – *D. charoae.*

25. Capillitium with darker regions and ellipsoid to spiny nodes; spores 12-15 µm with a partial reticulum of warts (found only on sub-Antarctic Macquarie Island) – *D. macquariense*
25. Capillitium with rounded to funnel-shaped swellings; spores 13-18 µm with a partial reticulum of warts – *D. mexicanum*

26. Capillitium sparse and rather thick – 27.
26. Capillitium profuse and rather fine – 28.

27. Spores 12-15 µm with spiny warts; capillitium somewhat scanty, coarse and somewhat flattened (generally on the bark of Juniper trees) – *D. orthonemata*
27. Spores 12-15µm densely and coarsely warted; capillitium sparse and rather thick (rare, occurs in the snow melt zone, we consider this to be an uncertain species) – *D. leptotrichum*

28. Spores 10-15 µm with dense small warts producing a partial reticulum; capillitium profuse and forming an elastic net (includes *D. listeri* which has smaller lighter spores and a less elastic net which we consider to be a egg-shell peridial form) and *D. anomalum* (has a thicker collumellum) – *D. dubium*
28. Spores 7-8 µm with dense small warts not producing a reticulum, capillitium abundant, smooth, branching and annastomosing – *D. corticola*

29. Capillitium absence or rudimentary; columella usually absence - 30.
29. Capillitium presence – 33.

30. Small sporangium with an operculum (single culture, may be a abnormal development of *D. anellus*) – *D. circumscissle*
30. Sporophore lacking an operculum – 31

31. Spores 13-16 µm with prominent reticulation – Peridial lime consisting of white polygonal crystals; spores 13-16 µm with prominent reticulate bands – *D, reticulosporum*
31. Spores 10-11 µm and are not prominently reticulated – 32.

32. Peridial lime consisting of white flattened disks; spores 10-11 µm and warted (single culture, we consider it to be a developmental abnormality of unknown origin) – *D. atrichum*
32. Peridial lime consisting of minute white to yellow scales; spores 8-10 µm and spinulose (single culture, we consider it to be a developmental abnormality of unknown origin) – *D. nullifilum*

33. Sporangia which may have a weak stalk are globose, densely clustered and usually covered with a free common crust of white lime crystals – *D. crustaceum*
33. Sporocarps not densely clustered and covered with a free common lime crust – 34.

34. Spores spinulose – 35.
34. Spores warted – 37.

35. Columella a thin flat basal plate, scanty peridial lime, and found only on the lower surface of *Petasites hybridus* leaves – 36.
35. Columella pulvinate to discoid, abundant peridial lime - 38.

36. Peridium with patches of large ochraceous lime granules, spores 9-11μm with irregular spines - *D. vernum*
36. Peridium lacking ochraceous lime granules, spores 11-14μm with dense spines - *D. tussilaginis*

37. Spores 10-11 μm with spines and often with ridges that form a faint reticulum; sporangium subglobose with a free lime crust and often with a short stalk – *D. karstensii*
37. Spores 11-14 μ with strong spines forming lines and clusters; sporangium globose with an attached lime crust and often with a short stalk (may be a variant of *D. karstensii*) – *D. muscorum*

38. Capillitium of profuse somewhat flattened threads; spores 11-14 μm with irregularly spaced large warts forming a coarse reticulum; sporocarp a white stalk-less globose sporangium to a elongate plasmodiocarps – *D. clavodecus*
38. Capillitium not having flattened threads, and lacking the above combination of spores and sporocarp features – 39.

39. Sporocarp a pale-brown discoid to pulvinate sporangium which may have a weak stalk; spores 11-13 μm with coarse warts – *D. obducens*
39, Sporocarp and spores not as above – 40.

40. Sporocarp pale orange-brown or yellow-brown sporangium – 41.
40. Sporocarp a gray or white sporangium or a small plasmodiocarp – 42.

41. Sporocarp a pale orange-yellow subglobose to reniform sporangium which may have a short stalk; spores 7.5-9.5 μm with dense uniform warts (report only from arid regions of Mexico and the Canary Islands) – *D. wildpretii*
41. Sporocarp a pale orange-brown pulvinate sporangium; spores 6-8 μm nearly smooth warts (includes *D. inconspicuum* which has larger spores) - *D. ochroideum*

42. Capillitium with swollen nodes or regions – 43.
42. Capillitium lacking swollen nodes or regions – 44.

43. Capillitium with darker regions and ellipsoid to spiny nodes; spores 12-15 μm with a partial reticulum of warts (reported only from sub-Antarctic Macquarie Island) – *D. macquariense*
43. Capillitium with rounded to funnel-shaped swellings; spores 13-18 μm with a partial reticulum of warts (reported only from arid regions of Mexico) – *D. mexicanum*

44. Sporocarp a discoid to irregular (fused) sporangia which may have a short stalk and usually has a deep apical umbilicus (reported only from arid regions of Mexico) – *D. umbilicatum*
44. Sporocarp a depressed globose to pulvinate sporangium to a flat thin plasmodiocarp usually lacking a stalk or apical umbilicus – 45.

45. Sporocarp a depressed globose sporangium which may have a weak stalk to a plasmodiocarp; spores black 10-13 µm with small warts (may be a snow melt variant of *D. dubium*) – *D. nivicolum*
45. Sporocarp a pulvinate sporangium to a plasmodiocarp – 46.

46. Sporocarp a white to gray-white pulvinate sporangium to a plasmodiocarp which is often annulate; capillitium slightly elastic; spores dark brown 7.5-11 µm minutely warted and faintly reticulate - *D. anellus*
46. Sporocarp a white flat-pulvinate sporangium to a flat thin plasmodiocarp; capillitium strongly elastic; spores black 10-15 µm with dense warts arranged in a partial reticulum – *D. dubium*

Descriptions

The distribution information is not meant to be complete, but to serve as an indication of the current state of knowledge.

Didymium Schrad., Nov. Gen. Pl. 20. 1797

= *Lepidodermopsis* Höhn., Akad. Wiss. Wien Sitzungsberr. Math.-Naturwiss, 118: 439. 1909.

= *Squamuloderma* Kowalski, Mycologia 64: 1282. 1972.

= *Trabrooksia* H.W. Keller, Mycologia 72: 369. 1980.

Sporangiate to plasmodiocarpous; dark spored; powdery to crustose crystalline lime on the peridium which is not united into distinct scales; no lime on the hyaline to brown capillitium.

Didymium aggregatum G. Moreno & Lizárraga, in Moreno, Lizárraga and Lopez-Peña Bot. Soc. Micol. Madrid 41: 28. 2017.

Types: AH 39373 (UACJ 1525)

Hypothallus: thin membranous straw-colored attachment to the substrate. Stalk: none. Columella: a whitish, brittle calcareous pseudocolumella arising from the base and occasionally branching at the apex; rarely absent. Sporotheca: grouped to aggregated sessile globose to amorphous sporangia, appearing to be a moriform to cerebriform pseudoaethalium (2-7 x 1-2 mm and 1-2 mm high). Peridium: a floury, thin, very fragile membrane with irregular dehiscence; densely covered with stellate lime crystals. Capillitium: scarce, thin whitish to violaceous threads with globose to fusiform nodules; dichotomously branching with cross-bar connections. Spores: globose to subglobose (10-13 µm) with variable short sinuous crests (appearing sub-reticulate); blackish violaceous (in mass) to dark violaceous (in transmitted light). Plasmodium: unknown.

Habitat: on crop straw.

Distribution: Mexico, rare (two collections).

Similar species: *Mucilago crustacea* - has a large aethalium and warted or spiny spores; *D. obducens* - spores are coarsely warted; *D. crustaceum* - spores are densely warted.

Remarks: with a variable and rather amorphous morphology; therefore we believe that more material is needed to confirm this taxon as a valid species. A very rare taxon.

Didymium anellus Morgan, J. Cincinnati Soc. Nat. Hist. 16: 148. 1894.

= *Didymium effusum* var. *tenue* Lister, J. Bot. 35: 214. 1897.

Types: BM (1716) (see Lado & Wrigley de Basanta 2018).

Hypothallus: inconspicuous, membranous and hyaline to pale-brown. Stalk: none. Columella: none, but may have brownish deposits and rhombic lime crystals in the basal plate. Sporotheca: gregarious, pulvinate (0.2-0.5 mm wide and 0.1-0.2 mm thick), white to greyish-white (dark-metallic-brown without lime), sessile sporangia grading into plasmodiocarpous; often annulate. Peridium: membranous, hyaline to pale-brown and iridescent (dark-metallic-brown); covered with a sparse layer of lime crystals; circumscissile dehiscence may be present. Capillitium: profuse, dark-brown to purplish-brown threads; sparsely branching and anastomosing to form an elastic net. Spores: globose (7.5-11 μm); minutely warted with very faint reticulation (partial cristae of bacula seen with SEM); dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: white, light-yellow to light-orange-yellow phaneroplasmodium.

Habitat: on litter, occasionally on dung or wood.

Distribution: cosmopolitan and probably common, but inconspicuous;

Similar species: *D. orthonemata* - has scanty capillitium which does not form an elastic net, and echinulate spores; *D. ochroideum* - has a a pale brown pulvinate sporangium, a loose capillitium network, and smaller nearly smooth spores; *D. reticulosporum, D.clavodecus*, and *D. mexicanum* - all have prominently reticulate spores.

Remarks: a complex of biological species and asexual clones (Clark & Landolt 2001).

Didymium annulisporum H.W. Keller & Schokn., Mycologia 81: 249. 1989.

Types: Keller no. 2032 (BPI), ATTC, NY, ILLS. K, GB.

Hypothallus: inconspicuous and membranous. Stalk and Columella: none. Sporotheca: gregarious, subglobose to depre ssed (0.1-0.4 mm wide), white sporangia. Peridium: membranous and hyaline; covered with a smooth white crystalline lime crust (eggshell-like); circumscissile dehiscence as a unit near the base. Capillitium: thin hyaline threads, with white lime bodies trapped within the threads; sparsely branching and anastomosing, often sub-parallel. Spores: subglobose (9-11 μm); evenly covered with warts (pilate by SEM) and having an equatorial ring ridge; black (in mass) or dark-brown (in transmitted light). Plasmodium: colorless to milky-white phaneroplasmodium.

Habitat: on dung.

Distribution: France, Russia, US (Colorado, Illinois, Texas), Argentina, rare.

Similar species: *D. saturnas* - has a brown peridium and a columella; *D. nullifilium* and *D. atrichum* have no capillitium or spore ring; *D. quitense, D. trachysporum, D. synsporum*, and *D. rugulosporum* - have no spore ring.

Remarks: a dung “spore” species which may be abundant in certain situations.

Didymium anomalum (Rostaf.) Massee, Monogr. Myxogastr. 245. 1892.

≡ *Chondrioderma anomalum* Rostaf. Sluzowce Monogr. 169. 1874.

Diderma anomalum (Rostaf.) Kuntze Revis. gen. pl. 3(3):465. 1898.

Types: none designated.

Hypothallus: unknown. Stalk: none. Columella: broad, arched basal mound following the shape of the plasmodiocarp. Sporotheca: a branched, curved or variously contorted convex plasmodiocarp. Peridium: covered with minute lime crystals. Capillitium: thin, delicate, flaccid colorless threads forming a dense net. Spores: globose (11-13 μm), minutely warted (verruca by SEM) and yellow. Plasmodium: unknown.

Habitat: unknown.

Distribution: Russia, France, Peru

Similar species: Nannenga-Bremekamp (1991) says that this taxon can be delimited from *D. dubium* by its prominent laterally flattened columella.

Remarks: Nannenga-Bremekamp (1991) decided that this long dormant description was a valid species; however we do not believe that Massee's (1892) short rather general description is capable of delimiting a valid species, therefore we cannot consider this a valid species unless further collections are made.

Didymium atrichum Henney & Alexop., in Henney, Alexopoulos and Scheetz, Mycotaxon 11:161. 1980.

Types: TEX (UTMC-1681), BPI, NY, K, Univ. Helsinki, Facultad de Sciencias Naturales y Museo La Plata Argentina, Kowalski, Nannenga-Bremekamp, Mitchell.

Hypothallus: conspicuous, sometimes resembling a short stalk; membranous; white. Stalk: none. Columella: mostly absent, sometimes rudimentary and calcareous. Sporotheca: scattered to gregarious globose (0.8-1 mm) sessile sporangia grading into plasmodiocarps (2.5 mm long); white. Peridium: membranous; sprinkled or covered with white lime crystals united into flattened disks. Capillitium: none. Spores: globose (10-11 μm); warted to faintly reticulate (reticulum of muri by SEM); black (in mass) or dark-purple (in transmitted light). Plasmodium: milky-white phaneroplasmodium.

Habitat: moist chamber material.

Distribution: Texas, Namibia.

Similar species: *D. nullifilium* - has amorphous lime and warted spores; *D. trachysporum* - has a capillitium and warted spores.

Remarks: We consider this taxon to be a developmental abnormally of unknown affinities.

Didymium azorellae D. Wrigley, Lado & Estrada. In Wrigley de Basanta, Estrada-Torres, Garcia-Cunchillos, Cano and Lado Mycologia 109: 996-1001. 2018.

Types: MA-Fungi (90715)

Hypothallus: inconspicuous. Stalk: none. Columella: none. Sporotheca: pale gray to white, small (0.1-0.6 mm diameter) hemispherical sporangia on a constricted base, or a reniform to irregular (0.1-0.3 x 0.4-0.8 mm) plasmodiocarp; grouped sporotheca. Peridium: double with an inner purplish, iridescent membrane and an outer compacted lime crystal (egg shell like) layer which separated from the inner membrane and is irregularly dehiscent. Columella: none. Capillitium: scant, thin hyaline branching threads attaching to the peridium. Spores: globose (11.5-14.5 μm) warted (by light microscopy) or densely verrucose (by SEM), black (in mass) or brown (in transmitted light). Plasmodium: small milky white phaneroplasmodium,

Habitat: *Azorellae* spp. (succulent cushion plants) litter in cold arid regions.

Distribution: Argentina and Peru.

Similar species: *D. trachysporum* - smaller spores; *D. Listeri* - smaller spores and abundant capillitium; *D. quitense* - spore more warted and capillitium more abundant.

Remarks: apparently a specialized species living on cushion plants in the cold arid regions of South America.

Didymium charoae Moreno, G. Moreno & López-Vill. In Moreno, Moreno, López-Villaba and de Haan Bol. Soc. Micol. Madrid 45: 14. 2021

Types: AH491

Hypothallus: inconspicuous and irregular, blackish and sometimes lime covered. Stalk: none. Columella: a central basal ridge to a pseudocolumella with yellowish-white lime. Sporotheca: gregarious pulvinate to flattened sporangia (0.1-0.7 mm) to short plasmodiocarps 0.2-0.99 x 14-15 mm). Peridium: hyaline

inner membrane covered with a loose fragile irregularly dehiscence layer of white stellate lime crystals. Capillitium: thin wavy brown filaments attached to the basal plate and peridium, the filaments having spindle-shaped to irregular enlargements which may contain yellowish lime bodies or form flattened sheets. Spores: globose to subglobose (12.7-16.1 μm), spinulose (baculate by SEM) blackish (in mass) or purplish-brown (in transmitted light). Plasmodium: unknown.

Habitat: on mosses and mossy bark of *Quercus ilex* near streams.

Distribution: Spain.

Similar species: *D. corticola* – capillitium do not have swelling with lime granules.

Remarks: a rare species associated with a mossy tree bark habitat.

Didymium circumscissile ["*circumcissile*"] K.D. Whitney & L.S. Olive, Mycologia 75: 629. 1983.

Types: BPI (National fungus collection), LSO RA 81-23, NY, ATCC.

Hypothallus: inconspicuous, membranous and confluent. Stalk: none. Columella: a basal plate is present. Sporotheca: gregarious, globose to turbinate (0.07-0.3 mm), white to gray brownish- sporangia. Peridium: membranous and hyaline to pale-translucent-brown; circumscissile dehiscent, producing a lightly encrusted (angular lime) operculum, and a generally limeless basal cup. Capillitium: scantly, usually lacking. Spores: globose (10-12 μm); minutely and closely warted (verrucose by SEM); dark-brown (in mass) or violaceous-brown (in transmitted light). Plasmodium: very small hyaline phaneroplasmodium.

Habitat: on litter (dead plant parts).

Distribution: Cook Islands (Rarotonga), one collection.

Similar species: D. anellus - has abundant capillitia; sporangia often annulate.

Remarks: a minute form, possibly of *D. anellus*.

Didymium clavodecus K.D. Whitney, Mycologia 71: 1257. 1980 ["1979"]

Types: Whitney 414, BPI, UC, NY.

Hypothallus: inconspicuous, membranous and reddish-brown. Stalk: none; restricted base may grade into the hypothallus in a stalk like manner. Columella: irregular calcareous mound or ridge may be present. Sporotheca: scattered, depressed globose to pulvinate (0.5-1.5 mm) to elongate (10 mm long) sessile sporangia. Peridium: membranous, hyaline and iridescent; covered with a scattered to compact layer of stellate white lime crystals. Capillitium: profuse, rigid brown (with hyaline tips) flattened threads; branching and anastomosing. Spores: globose (11-14 μm); irregularly spaced large warts and a course reticulum (pilate with a reticulum of muri by SEM); dark-purple (in mass) or purple-brown (in transmitted light). Plasmodium: white phaneroplasmodium.

Habitat: on litter (*Quercus* leaves).

Distribution: California and Mexico, rare.

Similar species: *D. squamulosum* - has small minutely warted spores, usually stalked; *D. mexicanum* - has spores with bacula and a less prominent reticulum.

Remarks: we consider this taxon to be an acceptable "spore" species.

Didymium comatum (Lister) Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 69: 361. 1966.

≡ *Didymium difforme* var. *comatum* Lister J. Bot. 38:8. 1901.

?= *Leocarpus calcareous* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 3: 25. 1809.

Chondrioderma calcareum (Link) Rostaf. in Fuckel, Jahrb. Nassauischen Veriens Naturk.

27-28: 74. 1874.

Diderma calcareum (Link) E. Sheld.,Minnesota Bot. Stud. 1: 478. 1885.

?= *Diderma chalybeum* Weinn., Hymen. Gasteromyc. 592. 1836.

Types: Tokyo Bot. Gardens, BM (2462) (see Lado and Wrigley de Basanta 2018).

Hypothallus: generally not visible; membranous and hyaline to pale-brown. Stalk: cupulate; pale-brown and containing lime crystals. Columella: none; a thickened whitish-brown peridial base may be present. Sporotheca: clustered, globose to oblong on a wide base (0.2-1.5 x 10 mm wide, 0.1-0.2 mm thick); white to pale-gray sporangia (may appear to be plasmodiocarpous). Peridium: membranous, hyaline to violaceous-brown; circumscissile dehiscence of the smooth compressed (egg-shell) lime crust. Capillitium: profuse, elastic, hyaline to purplish-brown threads; dichotomously branching and anastomosing to form a net. Spores: globose to ovoid (10-13 μm); densely covered with minute warts which are usually united into sinuous ridges (cristae of branched bacula by SEM); dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodia: unknown.

Habitat: on litter.

Distribution: widespread and not uncommon.

Similar species: *D. difforme* - has scanty non-elastic capillitia.

Remarks: We consider this taxon to be a form of *D. difforme*, since it grades into *D. difforme* in the same collection.

Didymium corticola KA. Kuhnt. Ber. Bayer. Ges. 89: 203. 2019.

Types: M-0304289, M-0304290.

Hypothallus: thin, flat, smooth, transparent membrane without lime. Stalk: none. Columella: a basal plate is present. Sporotheca: gregarious, light gray, flat, irregular sporangia to irregular plasmodiocarps (2-7 mm in diameter), often with moss leaflets embedded in the sporotheca with the tips of the leaflets appearing on the surface. Peridium: thin, colourless membrane lightly covered with small lime crystals. Capillitium: somewhat course, smooth dark brown threads branching and anastomosing, attached to the basal plate and peridium. Spores: globose (7-8 μm), densely covered with warts (baculate by SEM), no reticulation present. Plasmodium: unknown.

Habitat: on moss covered hardwood trees.

Distribution: Germany.

Similar species: *D. anellus* – capillitium not dark brown and somewhat coarse, smaller plasmodiocarps, spores faintly reticulate; *D. dubium* - spores larger and partially reticulate; *D. serpula* – spores with ridges, capillitium pale brown with attached vesicles; *D. perforatum* – spores larger and with sparse warts; *D. charose* – capillitium with swelling having lime grandules.

Remarks: A rare species associated with a mossy tree bark habitat.

Didymium crustaceum Fr., Syst. Mycol. 3: 124. 1829.

= *Didymium confluens* var. *crustaceum* (Fr.) Rostaf., Sluzowce Monogr. 165. 1874.

?= *Physarum confluens* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 43. 1815.

Types: Russia (Weinmann), UPS

Hypothallus: inconspicuous; membranous and hyaline. Stalk: short and weak; pale-white to buff (often calcareous). Columella: dome-shaped to a thickened base; white to orange-brown; containing lime crystals. Sporotheca: crowded, globose (0.5-1 mm, may be deformed by pressure), white sporangia. Peridium: membranous and hyaline; covered with a fragile free, smooth to rough crust of large white

crystals, that may form a cover over a cluster of sporangia. Capillitium: profuse, rigid hyaline to pale-purplish-brown threads; sparsely dichotomously branching and anastomosing. Spores: globose (10-15 μm); densely warted (pilate by SEM); black (in mass) or purplish-brown (in transmitted light). Plasmodium: white phaneroplasmodium.

Habitat: on wood and litter.

Distribution: cosmopolitan and moderately common.

Similar species: *Diderma spumarioides* - does not have crystalline lime; *Mucilago crustacean* - has an aethalium sporocarp.

Remarks: the multiple sporangial crust is unique in the genus.

Didymium decipiens Meyl., Bull. Soc. Vaud. Sci. Nat. 58: 319. 1935.

Types: LAU.

Hypothallus: inconspicuous and membranous. Stalk and Columella: none. Sporotheca: flat (1.5-30 mm long, 1.6-15 mm wide), thin (0.1-0.6 mm thick); white plasmodiocarp. Peridium: membranous and yellowish-brown; covered with white lime granules and crystals. Capillitium: profuse, pale-yellowish-brown threads, with 3-4 close spiral bands except at the expanded tips; sparsely branching and anastomosing. Spores: globose (13-17 μm); densely and strongly warted; black (in mass) or deep-purplish-brown (in transmitted light). Plasmodium: unknown.

Habitat: litter and plants in the snow melt zone.

Distribution: France, Switzerland, and Colorado, not common.

Similar species: *D. dubium* - has no capillitial bands, and small warts on spores.

Remarks: closely related to *D. dubium*.

Didymium difforme (Pers.) Gray, Nat. Arr. Brit. Pl. 1: 571. 1821.

≡ *Diderma difforme* Pers., Tent. Disp. Meth. Fung. 9. 1797.

Didymium difforme (Pers.) Duby, Bot. Gall. Ed. 2. 858. 1830.

Chondrioderma difforme (Pers.) Rosaf., in Fuckel, Jahrb. Nassauischen Verins Naturk. 276-28: 74. 1873.

= *Licea caesia* Schumach., Enum. Pl. 2: 219. 1803.

= *Amphisporium versicolor* Link, Ges. Naturf. Fruende Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 41. 1815.

?= *Didymium cyanescens* Fr., Symb. Gastromyc. 19. 1818.

Diderma cyanescens (Fr.) Fr., Syst. Mycol. 3: 109.1829.

= *Licea alba* Nees, in Kunze & Schmidt, Mykol. Heffe 2: 66. 1823.

Physarum album (Nees) Fr., Syst. Mycol. 3: 147. 1829.

= *Lycogala minutum* Grev, Scott. Crypt. Fl. 40. 1823.

= *Reticularia pusilla* Fr., Syst. Orb. Veg. 147. 1825.

= *Licea macrospora* Schwein., Trans. Amer. Philos. Soc. 4: 258. 1832.

?= *Diderma neesii* Corda, Icon Fung. 2: 23. 1838.

= *Diderma liceoides* Fr., Summa Veg. Scand. 450. 1849.

= *Diderma libertianum* Fresen., Beitr. Mykol. 28. 1850.

Didymium libertianum (Fresen.) deBary, Mycotozoen 124. 1864.

= *Chondrioderma liceoides* Rostaf., Sluzowce Monogr. Suppl. 17. 1876.

= *Chondrioderma micraspis* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 6: 200. 1899.

= *Diderma persoonii* T. Macbr., N. Amer. Slime-Moulds 96. 1899.
= *Didymium difforme* var. *comatum* Lister, J. Bot. 39: 8. 1901.
= *Didymium tubulatum* E. Jahn, Ber. Deutsch. Bot. Ges. 36: 663. 1919.
= *Didymium difforme* var. *repandum* G. Lister, J. Bot. 59: 91. 1921.
= *Didymium comatum* (Lister) Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 69: 361. 1966.

Types: none designated.

Hypothallus: inconspicuous; membranous and hyaline to pale-brown. Stalk: cupulate; orange-brown to reddish-brown; containing lime crystals. Columella: thick reddish-brown peridial base. Sporotheca: gregarious, dome-shaped (0.3-1.5 mm wide, 0.3-0.4 mm thick) whitest sporangia. Peridium: membranous, fragile, hyaline to violaceous-brown; covered with a free smooth crust (egg-shell) of white lime crystals. Capillitium: generally scanty, hyaline to purplish-brown threads; sparsely dichotomously branching and anastomosing (some specimens have a profuse elastic network). Spores: globose (11-14 μm); smooth to minutely warted (incomplete cristae of branched bacula by SEM); dark-brown to black (in mass) or dark-purple-brown (in transmitted light). Plasmodium: colourless (white) or yellow phaneroplasmodium.

Habitat: on litter, wood, and the bark of living trees.

Distribution: cosmopolitan and moderately common.

Similar species: *Diderma testaceum* - has non-stellate lime, and smaller lighter spores; a number of sessile to cupulate egg-shell taxa are also similar.

Remarks: a complex of variable forms; Winsett and Stephenson (2011) found three distinct DNA clades in 56 collections and also indications of long distance geographical dispersal; also, *D. comatum* (Lister) Nann.-Bremek., a named variation can be found in the same collection as the standard form.

Didymium disciforme ["*disciformis*"] Kowalski & T.N. Lakh., Mycologia 65: 474. 1973.

Types: Kowalski, Lakhanpal (TNL 171), UC.

Hypothallus: inconspicuous, membranous and hyaline. Stalk: short (0.3 mm) to sessile; stout and striate; white to gray. Columella: generally absent, may have a small irregular columella in a slight umbilicus; light-orange, hollow or containing a few lime crystals. Sporotheca: scattered, discoid (0.3-0.8 mm), white to cream sporangium. Peridium: membranous and iridescent; persistent below as a circular disk; covered with a dense smooth lime crust (egg-shell) that is free from the membrane, dehiscing as large fragments. Capillitium: flattened pale-brown threads; sparsely branching and anastomosing to form a relatively rigid net. Spores: globose (11-13 μm); minutely warted (may form an indistinct reticulum); purple-brown (in mass) or violet-brown (in transmitted light). Plasmodium: earthy-brown phaneroplasmodium.

Habitat: on litter.

Distribution: India (Delhi), two collections.

Similar species: *D. vaccinum* - has a large columella, a larger sporangium, and black sparsely warted spores.

Remarks: unless more material is found, we will consider this taxon to be a developmental aberration of *D. vaccinum*.

Didymium dubium Rostaf., Sluzowce Monogr. 152. 1874.

?= *Physarum tussilaginis* Berk. & Broome. Ann. Mag. Nat. Hist. Ser. 4, 17. 1876.

Didymium tussilaginis (Berk. & Broome) Massee. Monogr. Myxogastr. 244. 1892.

= *Didymium listeri* Massee. Monogr. Myxogatr. 244. 1892.

=*Didymium wilczekii* Meyl. Bull. Soc. Vaud. Sci. Nat. 44: 290. 1908.

Types: LAU (Meylan).

Hypothallus: inconspicuous, membranous and hyaline. Stalk: none. Columella: thickened peridial base; hyaline to pale-brown. Sporotheca: solitary to gregarious, white, flat-pulvinate sporangia to flat thin plasmodiocarps (1.5-30 mm long, 1.6-15 mm wide, 0.10.6 mm thick). Peridium: membranous, firm, hyaline to pale-brown; covered with small stellate to nodular white to greyish-white lime crystals (may be floccose or form scales or a crust). Capillitium: profuse, rigid, purplish-brown threads; sparsely branching and anastomosing to form an elastic net. Spores: globose (10-15 μm); dense small warts forming a partial reticulum (incomplete cristae of bacula by SEM); black (in mass) or purplish-brown (in transmitted light). Plasmodium: grey phaneroplasmodium.

Habitat: on coniferous litter, often in the snow melt zone.

Distribution: cosmopolitan and moderately common.

Similar species: *D. decipiens* - has spiral bands on capillitium.

Remarks: a central species in the sessile sporangial/plasmodiocarp group; we include *D. listeri* which has smaller, smoother spores, and a less elastic capillitium in this complex.

Didymium flexuosum Yamash., J. Sci. Hiroshima Univ. Ser. B, Div. 2, Bot. 3: 31. 1936.

= *Didymium parietale* G.W. Martin & T.E. Brooks, Trans. Amer. Microscop. Soc. 57: 320. 1938.

Types: Yamashiro, TNS (M-542).

Hypothallus: inconspicuous; membranous and hyaline. Stalk: none. Columella: wall-like extensions along the entire sporocarp derived from basal invaginations. Sporotheca: gregarious, laterally compressed, branched to reticulate (0.2-0.4 mm wide, up to 2 cm long, 0.2-0.3 mm thick), white to greyish-white plasmodiocarps. Peridium: membranous, fragile and iridescent hyaline; sparsely to densely covered with white to greyish-white lime crystals (sometimes aggregated into small discoid platelets). Capillitium: profuse, rigid, brown threads with hyaline tips; branching and anastomosing to form a net. Spores: globose (10-13 μm); sparsely and irregularly spiny to sub-reticulate (incomplete cristae of pila by SEM); black (in mass) or purplish-brown (in transmitted light); numerous irregular vesicle bodies (larger and paler) interspersed with the spores. Plasmodium: white (colourless) phaneroplasmodium.

Habitat: on litter

Distribution: France, India, Japan, Taiwan and US, rare.

Similar species: *D. serpula* - has yellow vesicle bodies connected to the capillitium, no columella, and smaller paler minutely warted spores.

Remarks: a rare, but distinct species.

Didymium inconspicuum Nann.-Bremek. & D.W. Mitch., in Nann.-Bremk., Proc. Kon. Ned. Akad. Wetensch. C 92: 508. 1989.

Types: Mitchell 4430, Nannenga-Bremekamp 15.603 (BR).

Hypothallus: inconspicuous and membranous. Stalk: none. Columella: a limy basal plate may be present. Sporotheca: scattered, depressed pulvinate (0.4-0.7 mm wide, 0.05 mm thick), fawn to greyish-white sporangia. Peridium: membranous, rough with small white to fawn-colored lime crystals and refuse matter; irregular to circumscissle dehiscence. Capillitium: profuse, flexuous brown threads with pale tips; branching and rarely anastomosing. Spores: globose (12-15 μm), densely and minutely warted; medium-dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: unknown.

Habitat: on litter.

Distribution: Arizona, single collection.

Similar species: *D. obducens* - has course tuberculate spores; *D. ochroideum* - has smaller spores.

Remarks: unless further material is found, we will consider this a large spore variant of *D. ochroideum.*

Didymium karstensii Nann.-Bremek., Acta Bot. Neerl. 13: 247. 1964.

Types: Karstens 387.

Hypothallus: inconspicuous and membranous. Stalk: if present, short, slender, calcareous, and white to yellowish-white. Columella: small pulvinate and often spiny, in a shallow umbilicus. Sporotheca: gregarious, subglobose to depressed (0.5-0.7 mm, rarely up to 1.2 mm), white to pale-yellow sporangia. Peridium: membranous; hyaline (somewhat iridescent) with brownish aerolae; covered with a free smooth to wrinkled crust of densely compacted small white to yellowish lime crystals. Capillitium: hyaline to pale-brown threads; branching and anastomosing. Spores: globose (10-12 µm), spinulose with ridges that may form a lax reticulum; dark-purple-brown (in mass) or purplish-brown (in transmitted light). Plasmodium: unknown.

Habitat: on litter.

Distribution: Galapagos Islands, India, Netherlands, Spain, western US, rare.

Similar species: *D. muscorum* - lacks the free peridial crust and the spores are less reticulate; *D. squamulosum* - no separate lime crust, and has minutely warted spores.

Remarks: we have some reservations concerning this taxon, since the unique characters could easily be due to developmental problems.

Didymium leptotrichum (Racib.) Massee, Monogr. Myxogastr. 242. 1892.

≡ *Chondrioderma leptotrichum* Racib., Rozpr. Spraw. Possiedzen Wydz. Mat.-Przyr. Akad. Umiejetn 12: 75. 1884.

Types: none designated.

Hypothallus: inconspicuous. Stalk: none. Columella: absent, may have a thickened base covered with yellowish to white lime. Sporotheca: gregarious, subglobose, oblate oblong (1-1.5 mm) to oblong (sometimes branching or ring-shaped), with a rough white to pale-gray surface; sessile sporangiate to plasmodiocarpous. Peridium: membranous and hyaline; covered with a crumbly layer of white lime crystals (usually packed into small scales). Capillitium: rather thick dark-purplish-brown threads; sparsely branching and rarely anastomosing. Spores: globose (12-15 µm); densely and coarsely warted; very dark-brown (in mass) or dark-purple-brown (in transmitted light). Plasmodium: unknown.

Habitat: on litter (near snow melt banks).

Distribution: Europe, Japan, Argentina, rare.

Similar species: *D. orthonemata* - spores are spinulose, does not occur in snow melt zone.

Remarks: may be a snow melt species, but until more material is found and studies, we will consider this taxon to be uncertain.

Didymium listeri Massee, Mongr. Myxogastr. 244. 1892.

Types: none designated.

Hypothallus: inconspicuous and membranous. Stalk: none. Columella: a thickened basal plate is present. Sporotheca: gregarious, pulvinate (up to 11 mm wide, 0.3-0.5 mm thick) white plasmodiocarps. Peridium: membranous, delicate, and dark-brown; covered with a free (or attached) compacted lime crust

(egg-shell) with loose lime crystals. Capillitium: profuse, rigid, hyaline to dark-brown with pale tips; dichotomously branching and anastomosing. Spores: globose (9-11 μm); minutely warted; black (in mass) or violaceous-brown (in transmitted light). Plasmodium: watery white phaneroplasmodium.

Habitat: on litter.

Distribution: cosmopolitan, but uncommon.

Similar species: *D. dubium* - has a firm peridium, and smaller, paler, less distinctly warted spores.

Remarks: we consider this taxon to be an egg-shell crust form of *D. dubium*.

Didymium macquariense G. Moreno & S.L. Stephenson, in Stephenson and Moreno, Mycol. Progress 5: 255-258. 2006.

Types: BPI (Stephenson 7212)

Hypothallus: discoid, membranous and reddish. Stalk: sessile to intermediate (up to 0.5 mm), reddish and fibrous. Columella: hemispheric and white, in a closed umbilicus. Sporotheca: scattered to gregarious, globose to ovoid sporangia (0.4-0.8 mm) to plasmodiocarpous (up to 2.5 mm long); white. Peridium: membranous and iridescent; covered with white to yellow lime crystals. Capillitium: hyaline to pale-yellow threads with darker violaceous-brown zones and dark violaceous-brown nodes of variable morphology (ellipsoid to spiny); sparsely branching and anastomosing. Spores: globose to subglobose (13-15 μm); partial reticulum of warts (partial cristae of bacula by SEM); black (in mass) or dark-violaceous-brown with darker areas (in transmitted light). Plasmodium: unknown.

Habitat: on litter (sub Antarctic).

Distribution: Macquarie Island (Australia).

Similar species: *D. rubropus* - capillitium has only minor expansions at the nodes, and the spores are pilate-spiny; *D. laxifilum* - capillitium is a network of flattened filaments.

Remarks: clearly related to the laxifilum-rubropus group, but the spores and capillitium differences make this an acceptable specialized taxon.

Didymium mexicanum G. Moreno, Lizárraga & Illana, in Lizárraga, Moreno, Illana and Castillo, II Int. Congr. Syst. Ecol. Myxomycetes 56. 1996.

Types: Alcala de Henares (AH 18481), Nannenga-Bremekamp 17311 (BR).

Hypothallus: inconspicuous, membranous and pale-violet. Stalk: generally absent; if present, short, calcareous and white. Columella: none. Sporotheca: scattered, subglobose, pulvinate to elongate depressed (0.2-1.5 mm sporangia; 1 by 20 mm plasmodiocarps). Peridium: membranous, iridescent and hyaline; sprinkled with white lime crystals. Capillitium: profuse, delicate, pale-brown threads with dark rounded to funnel-shaped swelling; sparingly dichotomously branching and rarely anastomosing; ends forked. Spores: globose (13-18 μm); warted and somewhat reticulate (cristae of branched bacula by SEM); dark-purple-brown (in mass) or purple-brown (in transmitted light). Plasmodium: unknown. Habitat: on desert litter (agave and yucca).

Distribution: Mexico, Argentina, rare

Similar species: *D. dubium* - the capillitium is more elastic; *D. clavodecus* - spores have reticulate ridges, but the warts are large and are not reticulate.

Remarks: a rare desert “spore” species.

Didymium muscorum T.N. Lakh. & K.G. Mukerji, Trans. Mycol. Soc. Japan 17: 123. 1976.

Types: Univ. Delhi TNL/300, Alexopoulos.

Hypothallus: discoid, membranous, white and calcareous. Stalk: short (may be absent), stout, striate, white and calcareous. Columella: large clavate to discoid, in a wide open umbilicus; orange-brown. Sporotheca: gregarious, globose (0.4-0.6 mm), white sporangia. Peridium: membranous and hyaline; densely covered with white lime crystals that form a crust. Capillitium: profuse, slender to stout, pale-violaceous to orange-brown threads; sparingly dichotomously branching and anastomosing. Spores: globose (11-14 μm); strongly warted with long spine-like warts, arranged in lines and clusters; dark-brown (in mass) or deep-purple-brown (in transmitted light). Plasmodium: dirty-white phaneroplasmodium.

Habitat: on litter and living herbs.

Distribution:: India (Dehli), Spain, very rare.

Similar species - *D. karstensii* - has a double peridium, and reticulate ridged spores; *D. squamulosum* - has smaller minutely warted spores, and hyaline or pallid capillitia.

Remarks: we have some reservations about this taxon, but it appears to be a valid "spore" species.

Didymium nivicolum Meyl., Bull. Soc. Vaud. Sci. Nat. 57: 40. 1929.

= *Didymium wilczekii* f. *pulverulentum* Meyl., Bull. Soc. Vaud. Sci. Nat. 53: 454. 1921.

= *Didymium wilczekii* var. *pulverulentum* (Meyl.) Meyl., in Schinz, Ber. Schweiz. Bot.Ges. 30-31: 3. 1922.

Types: LAU.

Hypothallus: inconspicuous, membranous and hyaline to pale-yellow. Stalk: short, usually hidden by the sporotheca; covered with lime crystals. Columella: conical, often absent; white and containing lime crystals. Sporotheca: gregarious, depressed-globose sporangia to plasmodiocarpous (1-2 mm); white. Peridium: membranous and hyaline; covered with aggregations of lime crystals; dehiscing by scale-like fragments. Capillitium: profuse, slender, hyaline threads; dichotomously branching and rarely anastomosing. Spores: globose (10-13 μm) and warted (pilate by SEM); black (in mass) or brown (in transmitted light). Plasmodium: unknown.

Habitat: on litter (snowmelt zone).

Distribution: Japan, Europe, western US, Chile, rare.

Similar species: *D. dubium* - plasmodiocarpous without a stipe; *D. squamulosum* - has smaller spores with less distinct warts, has a columella, and is not a snowmelt species.

Remarks: separated from *D. dubium* by Kowalski (1975).

Didymium nullifilum [*nullifila*] (Kowalski) M.L. Farr, Mycologia 74: 341. 1982.

≡ *Squamuloderma nullifilum* Kowalski, Mycologia 64: 1284. 1972.

Types: Kowalski DTK 11182, UC (Berkeley).

Hypothallus: none to small and inconspicuous. Stalk and Columella: none. Sporotheca: scattered, hemispherical to pulvinate, or slightly elongate (0.1-0.5 mm) brownish sporangia. Peridium: membranous, very thin and hyaline; covered with a compacted layer of yellow, grey or white minute (5-15 μm) circular to angular lime scales. Capillitium: usually absent, a few rudimentary threads may be present. Spores: globose (8-10 μm), with widely scattered spines (spinulose to baculate by SEM); dark-brown (in mass) or violet-brown (in transmitted light). Plasmodium: cream phaneroplasmodium.

Habitat: on dung.

Distribution: California, single collection.

Similar species: *D. saturnas* - has a capillitium and ringed spores.

Remarks: we consider this taxon to be based on an abnormal culture development of an uncertain species.

Didymium obducens P. Karst., Not. Sällsk. Fauna Fl. Fenn. Förh. 9: 356. 1868.

≡ *Didymium crustaceum* var. *obducens* (Karst.) Karst., Bidrg Kännedom Finlands Natur Folk 31: 115. 1879.

= *Didymium fulvum* Sturgis, Mycologia 9: 327. 1917.

Types: H (Karsten 2035).

Hypothallus: inconspicuous and membranous; containing little refuse matter. Stalk: sessile to rudimentary; membranous; no refuse matter; covered with lime crystals. Columella: a thick concave basal plate is present. Sporotheca: gregarious, discoid to pulvinate (0.6-1 mm); pale-brown sporangia. Peridium: membranous; slightly iridescent and pale-yellow; partially covered with large white to pale-yellow lime crystals. Capillitium: profuse; hyaline to pale-purplish-brown threads; dichotomously branching and rarely anastomosing. Spores: globose (10-13 μm); coarsely warted (pilate by SEM); black (in mass) or purplish-brown (in transmitted light). Plasmodium: brownish-yellow phaneroplasmodium.

Habitat: on litter.

Distribution: India, Pakistan, Japan, Europe, Mexico, US, Argentina, rare.

Similar species: *D. crustaceum* - has globose heaped sporangia.

Remarks: Harkonen in: Additions and corrections to the Finnish flora of Myxomycetes. Karsenia 19: 3 (1973); found that *D. fulvum* was the same as *D. obducens*.

Didymium ochroideum G. Lister, J. Bot. 69: 297. 1931.

= *Didymium inconspicuum* Nann.-Bremk. & D.W. Mitch., In Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 92: 508. 1889.

Types: Emperor Showa, BM (4780) (see Lado and Wrigley de Basanta 2018).

Hypothallus: inconspicuous and membranous. Stalk: none Columella: thickened basal plate present. Sporotheca: scattered, pulvinate (0.2-0.5 mm wide, 0.2 m thick), orange-brown small plasmodiocarps which resemble sessile sporangia. Peridium: membranous and pale-orange brown (areoles are sometimes evident), with small projections on outer surface; covered with pale-yellow stellate lime crystals. Capillitium: slender, yellow-brown threads; sparsely branching and rarely anastomosing. Spores: globose or elliptical (6-8 μm), minutely warted (verrucose by SEM); dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: white phaneroplasmodium.

Habitat: on litter, moss and dung.

Distribution: widespread (Canada, Costa Rica, Ecuador, Italy, Japan, India, Madagascar, Mexico, Peru, Norway, US), but inconspicuous and rarely collected.

Similar species: *D. obducens* - has course tuberculate spores.

Remarks: we consider *D. inconspicuum* to be a large abnormal spore variant of this species.

Didymium orthonemata H.W. Keller & T.E. Brooks, Mycologia 65: 290. 1973.

Types: Univ. Iowa, Univ. Texas, Univ. Florida, NY Bot. Garden, NFC, Kew, Kowalski, Keller 838, Brooks.

Hypothallus: membranous and brown to dark-brown; containing refuse matter. Stalk: none. Columella: none; a dark-brown somewhat thickened base is present. Sporotheca: gregarious to scattered flat-pulvinate, linear to branched (0.5-5 mm wide, up to 2 cm long, 0.2 mm thick) white to greyish-white plasmodiocarps. Peridium: membranous and hyaline to pale-brown; densely encrusted with a layer of white lime crystals, or sparsely sprinkled with lime clumps; often showing circumscissile dehiscence. Capillitium: somewhat scanty, coarse, somewhat flattened, hyaline to dark-brown thread; sparsely dichotomously branching and anastomosing. Spores: globose (12-15 μm), uniformly and conspicuously

spiny warted (spinulose by SEM); dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: whitish to sordid-brown phaneroplasmodium.

Habitat: on the bark of living trees (Juniper).

Distribution: Japan, Mexico, Argentina and US (Florida, Missouri), rare.

Similar species: *D. sturgisii* - has trabecular perforations; *D. dubium* - has abundant capillitia, and paler and smoother non-spinulose spores.

Remarks: this taxon appears to be a special habitat species.

Didymium panniforme J. Matsumoto, in Matsumoti and Duguchi, Hikobia 13: 61. 1999.

≡ *Didymium leoninum* var, *effusum* G. Lister, J. Bot. 71: 220. 1933.

Types: The Emperor Showa M-R-1226, BM (4171) (see Lado & Wrigley de Basanta 2018).

Hypothallus: inconspicuous, cartilaginous and buff to orange-yellow; with lime crystals. Stalk: none. Columella: none; a thick brown base is present. Sporotheca: flat, effuse to labyrinthuliform (0.2-0.3 mm thick, up to 2 cm in extent) white, buff to orange plasmodiocarps. Peridium: cartilaginous, glossy, dark-purplish-brown to chestnut brown (with pale-yellow aerolae); covered with large orange, buff or white stellate lime crystals. Capillitium: profuse, dark-purplish-brown threads; branching and anastomosing to form a dense net. Spores: globose (8-11 μm); incomplete reticulate (cristae of fused bacula by SEM); dark-brown (in mass) or dark-purplish-brown (in transmitted light). Plasmodium: red-orange phaneroplasmodium.

Habitat: on litter.

Distribution: Japan, rare.

Similar species: *D. leoninum* - sporangiate; *D. obducens* and *D. ochroideum* - not cartilaginous.

Remarks: Matsumoto and Duguchi (1999) found no intermediate forms connecting this taxon to *D. leoninum*, therefore we accept it as a valid species unless intermediate are discovered.

Didymium perforatum Yamash., J. Sci. Hiroshima Univ. Ser. B, Div. 2. Bot. 3: 33. 1936.

= *Didymium labyrinthuliform* G.W. Martin, Lodhi & N.A. Khan., Sydowia 14: 283. 1961.

Types: TNS (M-564).

Hypothallus: inconspicuous, membranous and hyaline. Stalk and Columella: none. Sporotheca: flat, effuse, often closely reticulate or labyrinthuliform (0.2-0.3 mm thick, up to 2 cm in extent), pale-yellow plasmodiocarps. Peridium: membranous, delicate and smoky-hyaline; covered with pale-yellow lime crystals. Capillitium: profuse, dark-purplish brown threads; branching and anastomosing to form a net. Spores: globose (9-12 μm sparsely and distinctly warted (baculate by SEM); blackish-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: unknown.

Habitat: on litter.

Distribution: widespread (Argentina, Japan, West Pakistan, Taiwan, US), but rare.

Similar species: *D. flexuosum* - has a columella, vesicular bodies associated with the capillitium, and larger spores.

Remarks: a large fairly distinct plasmodiocarpous species, which seems to be widely distributed, but rare.

Didymium peruvianum Lado, D. Wrigley & Stephenson. in Lado, D. Wrigley de Basanta, Estrada-Torres and Stephenson Anales Jard. Bot. Madrid 73: 447. 2016.

Types: MA-Fungi 88473; Stephenson 28943

Hypothallus: inconspicuous. Stalk: sessile to very short (0.02-0.05 mm), brownish. Columella: none. Sporotheca: dispersed yellow-gray to near-white with a darker lower region, discoid (0.25-0.5 x 0.07-0.17 mm) sporangium. Peridium: a smooth outer crust of compacted lime crystals (egg-shell like) with circumscissile dehiscence and an inner colorless separating membrane. Capillitium: scanty brown threads with minor branching and few anastomosing cross-connections. Spores: subglobose (12-14 μm), with warts; black (in mass) or brown with a paler band (in transmitted light). Plasmodium: unknown.

Habitat: on desert plant litter.

Distribution: Peru; newly described from the arid coastal desert; rare, four collections.

Similar species: *D. annulisporum*, *D. trachysporum*, and *D. listeri* have smaller spores without the lighter bands; *D. rugulosporum* has larger spores and a dense rigid capillitium; *D. quitense* has larger spores with warts forming muri; *D. difforme* has smooth to finely warted spores.

Remarks: a small rare egg-shell peridium taxon from South America, which has few distinctive aspects.

Didymium quitense (Pat.) Torrend, Brotèria Sér. Bot. 7: 90. 1908.

≡ *Chondrioderma quitense* Pat., in Patouillard & Lagerheim, Bull. Soc. Mycol. France 11: 212. 1895.

Types: none designated.

Hypothallus: inconspicuous. Stalk and Columella: none. Sporotheca: gregarious, pulvinate (0.4-1 mm) sporangia to plasmodiocarpous (up to 5 mm long). Peridium: membranous, thin and bluish-iridescent; with a free crust of compacted small white lime crystals (egg-shell). Capillitium: rather sparse, yellowish-brown threads; branching and anastomosing profusely to form a net. Spores: globose (12-15 μm); strongly warted (pilate by SEM); black (in mass) or very-dark-purplish-brown (in transmitted light). Plasmodium: unknown.

Habitat: litter and wood.

Distribution: widespread (Argentina, Brazil, Chile, Peru, Canary Islands, Ecuador, Finland, Malta, Turkey, US) but rare (fairly common in western montane US).

Similar species: *D. difforme* - has smaller lighter spores, a less netted capillitium, and a more crustose peridium; *D. trachysporum* - has smaller spores

Remarks: considered, by some, to be a montane from of *D. dubium*.

Didymium reticulosporum Novozh. & Zeml., Mycotaxon 96: 148. 2006.

Types: Zemlyanskaya 204007, NFC(BPI), Lado, Schnitter.

Hypothallus: inconspicuous. Stalk and Columella: none. Sporotheca: gregarious, subglobose to pulvinate (0.5-1.5 mm) snow-white sporangia to short plasmodiocarps. Peridium: membranous, thin and hyaline; covered with polygonal white lime crystals (sometimes nearly limeless). Capillitium: none. Spores: globose (13-16 μm); prominently reticulate banded (small muri reticulum inside a larger muri reticulum by SEM); dark-purplish-brown (in mass) or violet-brown (in transmitted light). Plasmodium: colorless to milky-white phaneroplasmodium.

Habitat: on litter and bark.

Distribution: Russia (Volgograd province).

Similar species; *D. mexicanum* - has capillitium, and the banded reticulate spores are also warted.

Remarks: the distinct banded reticulate spores, and the lack of a columella, makes this a distinct species.

Didymium rugulosporum Kowalski, Mycologia 61: 636. 1969.

Types: Kowalski (DTK 5390), University of Iowa.

Hypothallus: inconspicuous. Stalk and Columella: none. Sporotheca: scattered, hemispheric to pulvinate (1-3 mm) white sporangia. Peridium: membranous and hyaline (slightly iridescent); free, thick, smooth, brittle white lime crust (egg-shell). Capillitium: profuse, rigid, brown threads; branching and anastomosing to form a net (weakly attached to the base and peridium). Spores: globose (18-20 μm), large distinct warts forming a lax reticulum; black (in mass) or purple-brown (in transmitted light). Plasmodium: unknown.

Habitat: on dung.

Distribution: California (Sutter Buttes), France, Peru; several collections.

Similar species: *D. dubium* - has smaller spores, and does not have an egg-shell peridium; *D. difforme* - has smaller nearly smooth spores; *D. quitense* - has smaller spores lacking a reticulum, and sparse capillitium.

Remarks: a distinctive "spore" species.

Didymium saturnus H.W. Keller, Mycologia 62: 1061. 1970.

Types: Keller (#132), NY, BPI, Univ. Iowa, Kew, Univ. Texas.

Hypothallus: inconspicuous, membranous and hyaline to pale-brown. Stalk: none. Columella: a basal peridial plate that is hemispheric and filled with crystalline lime; dull-white to yellowish. Sporotheca: gregarious to scattered, globose to hemispheric (0.2-0.8 mm), dull-brown sporangia. Peridium: membranous and adhering to an outer hard crust, containing yellow to nut-brown cuboid lime crystals and refuse matter. Capillitium: profuse to scanty, hyaline to purplish-brown threads, with some enlargements containing lime crystals and having membranous expansions near the base; branching and anastomosing to form a loose net, attached to columella and the peridium. Spores: subglobose (11-15 μm), minutely and densely warted (pilate by SEM), and having an equatorial ring; black (in mass) or dark-brown (in transmitted light). Plasmodium: watery-white phaneroplasmodium.

Habitat: on litter.

Distribution: Chile, India, Japan, US (Iowa, Kansas), rare.

Similar species: *D. annulisporum* - has no columella and is white; *D. karstensii* - peridium not a hard crust, and spore ring not continuous; *D. vaccinum* - has a large columella, and no spore ring.

Remarks: intermediate between *Didymium* and *Diderma*; Matsumoto (1999) considers it to be a *Diderma*, but we retain it in *Didymium*, due to the presence of crystalline lime.

Didymium serpula Fr., Syst. Mycol. 3: 126. 1929.

= *Lycoperdon complanatum* Batsch, Elench. Fung. Continuatio I: 251. 1786.

= *Didymium complanatum* (Batsch) Rosaf., Sluzowcw Monogr. 151.1874. = Nom. illeg.

Types: none designated.

Hypothallus: inconspicuous, membranous and hyaline. Stalk and Columella: none. Sporotheca: scattered, flattened, effuse, perforated, or nearly continuous (0.1-0.3 mm thick, usually 2-8 mm in extent), white to greyish-white plasmodiocarps. Peridium: membranous, iridescent, hyaline to grey; covered (sometimes sparsely) with white stellate or irregular lime crystals. Capillitium: profuse, pale-brown threads; branching and anastomosing to form a loose net; connected to numerous subglobose vesicles (30-50 micron) filed with yellow granular material. Spores: globose (8-11 μm), minute warts forming ridges (incomplete cristae of bacula by SEM); dull-brown (in mass) or pale-purple-brown (in transmitted light). Plasmodium: yellow phaneroplasmodium.

Habitat: on litter.

Distribution: widespread (Europe, Belize, Costa Rica, Mexico, Japan, Pakistan, US), but rare.

Similar species: *D. flexuosum* - has a wall-like columella, and no vesicles attached to the capillitium.

Remarks: The capillitial vesicles make this a distinct taxon.

Didymium sturgisii Hagelst., Mycologia 29: 397. 1937.

≡ *Didymium anomalum* Sturgis, Colorado Coll. Stud. Sci. Ser. 12: 444. 1913. Nom. Illeg.

= *Trabrooksia applanata* H.W. Keller, Mycologia 72: 396. 1980.

= *Trabrooksia applanata* var. *microspora* Y. Yamam., Hikobia 11: 529. 1994.

Types: none designated

Hypothallus: inconspicuous. Stalk: none Columella: none; but the thickened base produces numerous trabeculae (7-22 microns thick lime pillars) which penetrate the plasmodiocarp and attach to the upper surface. Sporotheca: scattered, thin (0.1-0.2 mm thick), rounded to irregular white to gray plasmodiocarp (1-10 mm long). Peridium: membranous and white to yellowish; scantily (usually) sprinkled with white angular to stellate lime crystals. Capillitium: scanty (often lacking), slender, dark-brown threads; branching and anastomosing. Spores: globose (10-12 μm); minutely and irregularly warted; black (in mass) or bright-violet-brown (in transmitted light) Plasmodium: unknown.

Habitat: on wood (especially bark) and living trees.

Distribution: US, Mexico, England, Spain, France, Costa Rica, Argentina, rare.

Similar species: *D. dubium* - has abundant capillitium and lacks lime pillars.

Remarks: a large, distinctive, but rare plasmodiocarpous species; *T. applanata* is considered as a limeless form by Farr (1982).

Didymium synsporum T.E. Brooks & H.W. Keller, in Keller and Brooks Mycologia 65: 287. 1973.

Types: Univ. Iowa (TEB 2743), Keller.

Hypothallus: inconspicuous and membranous. Stalk: none. Columella: slightly thickened base. Sporotheca: scattered, spherical, linear, branched or pulvinate (up to 3.1 mm wide and 6.3 mm long; 0.1 mm thick) white to buff plasmodiocarps. Peridium: membranous, fragile and pale-buff; covered with an adherent smooth crust of white angular lime crystals (egg-shell). Capillitium: sparse, somewhat rigid, pallid to purple brown (tips hyaline) threads with nodular thickenings; rarely branching and anastomosing; attached to the peridium with an expanded tip. Spores: globose to ovate (11-12 x 12-14 μm); irregularly distributed spines (smooth and paler elsewhere); adhering in clusters of 4-25 spores; dark-brown (in mass) or violaceous-brown (in transmitted light). Plasmodium: unknown.

Habitat: on the bark of living trees (*Juniper*).

Distribution: eastern US, Chile, rare.

Similar species: *D. difforme* - spores are not clustered.

Remarks: probably derived from *D. difforme*.

Didymium trachysporum G. Lister, Essex Naturalist 20: 113. 1923.

Types: BM (2251A) (see Lado and Wrigley de Basanta 2018).

Hypothallus: inconspicuous. Stalk: none. Columella: thickened pale-yellow base. Sporotheca: scattered, hemispheric or pulvinate (0.1-0.6 mm) sporangia to annulated plasmodiocarps; white to cream. Peridium: membranous and hyaline and somewhat iridescent; covered with a free smooth to wrinkled crust of compacted white lime crystals (egg-shell). Capillitium: usually scanty, stout to slender, hyaline to

purple-brown threads; sometimes bearing vesicular swelling enclosing lime crystals; branching and anastomosing to form a net. Spores: globose (9-10 μm), strongly and coarsely warted with the warts sometimes forming an imperfect reticulum; black (in mass) or dark-purplish-brown (in transmitted light). Plasmodium: white phaneroplasmodium.

Habitat: on litter, wood, dung, soil, and the bark of living trees.

Distribution: widespread (Canary Islands, Europe, Greenland, Israel, Peru, Madagascar, US), but fairly rare.

Similar species: *D. quitense* - has larger spores.

Remarks: closely related to *D. quitense*.

Didymium tubi-crystallium Nann.-Bremk. & R.L. Critchf., Proc. Kon. Ned. Akad. Wetensch. C 91: 416. 1988.

Types: Critchfield 342, Nannenga-Bremekamp 15.916, TNS.

Hypothallus: generally inconspicuous, but sometime connecting sporocarps; dark-brown. Stalks: none. Columella: a dirty-white rough ridge filled with crystalline lime. Sporotheca: scattered, pulvinate (1 mm) to elongate (up to 20 mm long), white sporangiate to plasmodiocarpic. Peridium: membranous and hyaline; covered with angular white lime crystals. Capillitium: coarse, thick threads with large swellings (10-25 μm wide) generally filled with white crystalline lumps of lime; branching and anastomosing. Spores: globose (12-13 μm); coarsely irregularly to sub-articulately warted; dark-brown (in mass) or reddish-brown (in transmitted light). Plasmodium: unknown.

Habitat: on wood.

Distribution: California (Butte County), single collection.

Similar species: *D. squamulosum* - usually stalked, and does not have lime filled capillitia.

Remarks: we consider this uncertain taxon to be a developmental aberration of an unknown species.

Didymium tussilaginis (Berk. & Broome) Massee, Monogr. Myxogastr. 244. 1872.

≡ *Physarum tussilaginis* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 4, 17: 139. 1872.

Types: Kew M-0048756

Hypothallus: conspicuous white to beige chalky membrane generally common to a number of sporocarps. Stalk: absent. Columella: thin, occasionally irregular, white to beige chalky basal plate. Sporotheca: gregarious to grouped, irregularly rounded to oblong (0.4 - 2.5 mm wide and 0.2 -0.4 mm tall) light gray sessile sporangia. Peridium: hyaline to pale brown (often metallic to iridescent) membrane sparsely covered with crystalline and amorphous patchy lime. Capillitium: hyaline to pale brown irregularly branching (sometimes forming a reticulum) threads which often contain small irregular line inclusions. Spores: globose to somewhat ovoid (11-14 μm) densely and irregularly spinulose; dark brown (in mass) or light brown (in transmitted light). Plasmodium: dark lilac to grey phaneroplasmodium.

Habitat: found only on the underside of living *Petasites hybridus* leaves.

Distribution: Austria, Germany, Denmark and England.

Similar species: *D. dubium* - ha a more regular sporocarp and spores with small warts.

Remarks: Kuhnt et al. (2014) discuss their revival of this rather amorphous taxon which appears to be relatively common in its specialized habitat; however in our opinion the final say concerning this difficult taxon will require DNA or other genetic evidence.

Didymium umbilicatum D. Wrigley, Lado & Estrada, Mycologia 100: 922. 2008.

Types: MA-fungi 73566

Hypothallus: inconspicuous and membranous. Stalk: short (0.1-0.2 mm) to absent; light-yellow-brown to brownish-pink, with lime crystals on the surface. Columella: absent to a thickened basal funnel. Sporotheca: gregarious to grouped, discoid (0.2-0.7 mm) to irregular (fused sporocarps 0.6-1.3 mm long); pale-gray to white sporangia often with an umbilicate top. Peridium: membranous, iridescent, and light-yellow-brown to brownish-pink; covered with white elongate lime crystals forming a roughened crust. Capillitium: profuse, undulating, slender, light-greyish-brown threads; sparsely dichotomously branching with a few cross connections. Spores: subglobose (11-15 μm); warts forming an irregular subreticulum (cristae of fused branched bacula by SEM); black (in mass) or greyish-brown to brown (in transmitted light). Plasmodium: hyaline to pinkish-white phaneroplasmodium.

Habitat: on Yucca and Agave litter.

Distribution: Mexico Peru

Similar species: *D. mexicanum* - has sessile sporocarps, and larger spores with a strong reticulum; *D. subreticulosporum* - has no true capillitia (replaced by filiform lime); *D. reticulosporum* - has no capillitium, and banded reticulate spores; *D. anellus* - has sessile sporangia and smaller spores.

Remarks: apparently a specialized arid region species.

Didymium vaccinum (Durieu & Mont.) Buchet, in Buchet, Chermezon and Evrard. Bull. Soc. Mycol. France 36: 110. 1920.

≡ *Diderma vaccinum* Durieu & Mont., in Bory de St.-Vincent & Durieu de Msidonneuve, Exp. Sci. Algére 1: 407. 1846-69.

Chondrioderma vaccinum (Durieu & Mont.) Rostaf., Sluzowce Monogr. 180. 1874.

= *Didymium trocus* Lister, J. Bot. 36: 164. 1898.

= *Didymium diciforme* Kolwalski & T.N. Lakh., Mycologia 65: 474. 1973.

= *Didymium haretianum* T.N. Lakh. & M.G. Mukerji, Acta Bot. Indica (suppl.): 18.1978.

Types: P or PC.

Hypothallus: inconspicuous and membranous. Stalk: short, cupulate, furrowed, and with internal lime; white to pale-yellowish-brown. Columella: large (usually), hemispheric and reddish-brown to orange-brown. Sporotheca: scattered to gregarious, hemispheric to turbinate (0.6-1.4 mm wide, 0.5-1.5 mm thick), white to brownish-white sporangia. Peridium: membranous and hyaline to yellowish-brown; covered with a free smooth crust of compacted white to pale-orange-brown lime crystals (egg-shell), which may break off as a whole unit. Capillitium: scanty, hyaline to pale-yellowish-brown threads; sparsely dichotomously branching and anastomosing. Spores: globose (7.5-12 μm); prominently, but sparsely warted (conate by SEM); black (in mass) or dark-brown (in transmitted light). Plasmodium: bright-yellow phaneroplasmodium.

Habitat: on litter and succulent plants.

Distribution: widespread (Algeria, Canary Islands, Europe, Israel, Japan, Mexico, US, Uruguay, Chile); but rare.

Similar species: *Diderma* spp. - they do not have crystalline lime.

Remarks: we consider *D. diciforme* and *D. haretianum* to be variants of this species.

Didymium vernum Kuhnt, K. Baumann & Nowotny, Z. Mycol. 80: 152. 2014.

Types: M (M-0046301), Baumann, Nowotny.

Hypothallus: conspicuous light-orange brown membrane often common to a group of sporocarps. Stalk: none. Columella: flat, thin bright orange to orange-brown calcareous basal plate (often with a rough surface). Sporotheca: scattered to gregarious, irregularly rounded to ovoid (0.3 - 2.3 mm wide, 0.3-0.8 mm tall), light brown to orange-brown sporangium. Peridium: hyaline to pale yellow (often iridescent) membrane often with mottled yellowish patches of large oraceous stellate to amorphous lime crystals. Capillitium: sparse hyaline to light brown threads with occasional large swellings; irregularly dichotomously branching and anastomosing with transverse bars. Spores: globose to ovoid (9.0-11 μm) dark brown (in mass) or light brown (in transmitted light); covered irregularly with short spines. Plasmodium: unknown (dark yellow orange during sporulation).

Habitat: on the underside of living *Petasites hybridus* leaves.

Distribution: Europe (Germany, France, Denmark, Netherlands), rarely collected (may be due to the unusual habitat).

Similar species: *D. tussilaginis* - rather similar amorphous sporocarps in the same unique habitat, but lacking the patches of oraceous lime on the peridium.

Remarks: Kuhnt et al. (2014) described this rather amorphous taxon which appears to be relatively rare in its specialized habitat; however in our opinion the final say concerning this difficult taxon will require DNA or other genetic evidence.

Didymium wildpretii Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado, in Lado, Mosquera, Estrada-Torres, Beltrán-Tejera and Wrigley de Basanta Mycology 99: 603. 2007.

Types: Lado (MA-fungi 61104), TLXM (ET 8404).

Hypothallus: discoid, inconspicuous, membranous and brownish-orange; occasionally calcareous and white. Stalk: short (0.1-0.3 mm) to absent, cylindrical and sometimes slightly striate; filled with lime crystals and refuse matter; pale to dark orange-brown. Columella: basal plate in a wide shallow umbilicus; concolorous with the stalk. Sporotheca: gregarious, subglobose to slightly reniform (0.1-0.5 mm wide, can be 1-2.5 mm long), whitish to pale-orange-yellow sporangia. Peridium: membranous and iridescent; covered (usually) with pale-yellow stellate lime crystals forming a roughened layer. Capillitium: slender, rigid dark-yellowish-brown threads with pale tips; sparingly dichotomously branching and anastomosing. Spores: subglobose (7.5-9.5 μm); densely and uniformly warted (baculate by SEM); brown-black (in mass) or greyish-brown (in transmitted light). Plasmodium: orange-yellow to reddish-orange phaneroplasmodium.

Habitat: on decaying cacti.

Distribution: Mexico and the Canary Islands, Peru, Argentina, rare.

Similar species: *D. vaccinum* - has an egg-shell peridium, and more dispersed warts on its spores; *D. obducens* - has a larger more confluent sporangium, and larger spores with a partial reticulum; *D. squamulosum* - has a columella, longer stalks (usually), and pilate warted spores; *D. mexicanum* - has larger reticulate spores.

Remarks: apparently this species is not uncommon in its restricted habitat.

Didymium yulii S-Y Liu, F-Y Zhao in Zhao, Liu, Stephenson, Hsiang and Qi. Mycologia 113:930. 2021.

Types: IIMS255226

Hypothallus: not apparent or a transparent membrane. Stalk: none. Columella: a pseudocolumella of firm semi-transparent membranous material which often is fractured into erect plates with reticulate veins on the surface when strongly calcareous, thin and fragile if not calcareous. Sporotheca: white to milky-white aethalia (1=2.5 x 0.5 -2 mm) with a dense, rough, spongy or pulverulent cortex composed of

white stellate crystals. Capillitium: none, psedocapillitium present. Spores: globose (10 – 12.5 μm) densely warted (pilate by SEM), blackish (in mass) to dark brown (in transmitted light). Plasmodium: not known. Habitat: on dry bark (4 collections)

Distribution: Inner Mongolia, Jilin province China.

Similar species: *Mucilago crustacea* – has true capillium.

Remarks: DNA studies show that this species is a separate clade in *Didymium* not related to *Mucilago* where it would be placed by its morphology.

Trabrooksia applanata H.W. Keller, Mycologia 72: 369. 1980.

Types: Keller, Beltsville (NFC), Kowalski (Chico), Mitchell, NY Botanical Garden.

Hypothallus: inconspicuous. Stalk and Columella: none. Sporotheca: scattered to gregarious, silvery to brownish pulvinate to effused (up to 5 mm x 2 mm) plasmodiocarps, or rarely subglobose to depressed (0.2-0.4 mm) sporangia. Peridium: membranous, thin, hyaline, and glossy to iridescent; no lime present. Capillitium: profuse, hyaline, simple (occasionally branched), parallel arranged threads; thin walled tubular invaginations of the peridium attenuating to the threads, which are also attached to the base. Spores: globose (11-13 μm); minutely spinulose; brown (in mass) or light-violaceous-brown (in transmitted light). Plasmodium: watery-white phaneroplasmodium.

Habitat: on the bark of living trees.

Distribution: Eastern US, California, and England, rare.

Similar species: *D. sturgisii* - has lime on the peridium.

Remarks: considered to be a synonym for *D. sturgisii*; possibly an ecotype form or a separate limeless *Didymium*; DNA or other genetic studies will be needed to determine the correct position of this taxon.

Mucilago Battarra, Fungi Arimin. 76. 1755.

= *Spumaria* Pers., in Gmelin, Syst. Nat. 2: 1466. 1791.

Aethaloid sporocarp; dark spored; densely powdery lime on the peridium (not united into small scales) but no lime on the capillitium (limy pseudocapillitium present).

Mucilago crustacea F.H. Wigg., Prim. Fl. Holsat. 112. 1780.

= *Mucor spongiosus* Leyss., Fl. Halens. Ed. 2. 305. 1783.

Mucilago spongiosa (Leyss.) Morgan, Bot. Gaz. (London) 24: 56. 1897.

= *Reticularia alba* Bull., Herb. France pl. 326. 1787-88.

Spumaria alba (Bull.) DC., in Lamarck & de Candolle, Fl Franç. Ed. 3. 261. 1805.

= *Spumaria mucilaga* Pers., in Gmelin, Syst. Nat. 2: 1466. 1791.

=*Spumaria alba* var. *mucilago* (Pers. [“Nees”]) Morgan, J. Cincinnati Soc. Nat. Hist. 16: 150. 1894.

=*Spumaria cornuta* Schumach., Enum. Pl. 2. 1803.

= *Spumaria alba* var. *cornuta* (Schumach.) Fr., Syst. Mycol. 3: 95. 1829.

= *Didymium spumarioides* Fr., Syst. Mycol. 3: 121.1829.

= *Spumaria alba* var. *laminosa* Fr., Syst. Mycol. 3: 95. 1829.

= *Diderma spumariiforme* Wallr., Fl. Crypt. Germ. 2: 374. 1833.

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Mucilago dictyospora (R.E. Fr.) Lizárraga, G. Moreno & Illana, in Lizárraga, Illana & G. Moreno, Ann. Bot. Fennici 36: 197. 1999.
=*Spumaria alba* var. *solida* Sturgis, Colorado Coll. Stud. Sci. ser. 12: 29. 1907.
Mucilago spongiosa var. *solida* (Sturgis) G. Lister, in Lister, Monogr. Mycetozoa ed. 2. 138. 1911.
Mucilago solida (Sturgis) E. Jahn, Ber. Deutsch. Bot. Ges. 41: 391. 1923.
= *Mucilago crustacean* var. *solida* (Sturgis) G. Lister ex. Nann.-Bremk., Nederlande Myxomyceten 390. 1974.
Types: none designated.

Hypothallus: conspicuous, membranous to horny; hyaline to white, often containing masses of crystalline lime. Stalk and Columella: none Sporotheca: solitary, large (1-7 cm long, 1-5 cm wide, 1-2 cm thick) pulvinate white aethalium. Peridium: delicate hyaline membrane; covered with a dense spongy to pulverulent, calcareous crystalline cortex. Capillitium: profuse to scanty, dark to light-brown threads; branching and anastomosing to form a net; pseudocapillium present (thin hyaline walls fragments derived from the tubes making up the aethalium). Spores: globose (11-13 μm) densely warted or spiny, rarely reticulate (baculate to reticulate by SEM); blackish-brown (in mass) or purple-brown (in transmitted light). Plasmodium: creamy-white to pale-yellowish phaneroplasmodium.

Habitat: on wood, leaves, and the stems of living plants.
Distribution: cosmopolitan and fairly common.
Similar species: *Didymium crustaceum* - fruiting consist of closely packed sporangia.
Remarks: closely related to *Didymium*.

Acknowledgement

This guide is an attempt to distil the work and ideas of many researchers; however, such an attempt can never do justice to everyone's contributions, and we can only say that we tried to do our best, and hope that we have not committed too many major omissions.

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