



## A taxonomic guide to the species of *Didymium* (Didymiaceae, Physarales, Myxomycetes) I. The stipitate species

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### Abstract

This guide 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 eighty species have been described, that is defined by the presence of crystalline lime granules occurring on the peridium but not in 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 article is an attempt to provide guidance in the identification of these species.

**Key words** – clonal lines – species complexes – sporangium – sporocarp – stalk types

### Introduction

The genus *Didymium* Schrad., is a Myxomycete taxon having 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 & Keller 1989). Within the family, crystalline lime (as opposed to the granular lime seen in *Diderma* and *Physarina*) is found in *Didymium*, *Mucilago* and *Lepidoderma*. This lime is scattered on the peridium or forms a crust (*Didymium* and *Mucilago*), or is united into distinct scales (*Lepidoderma*). *Didymium* (sporangial or plasmodiocarpic), is separated from *Mucilago* (aethalial) on the basis of sporocarp form. These morphological characters appear to separate valid genera, however, recent rDNA studies (Fiore-Donno et al. 2008, 2012, Nandipati et al. 2012, Wrigley de Basanta et al. 2015) indicate that some adjustments will probably have to be made, since *Mucilago crustacea* and *Protophysarum phloiogenum* (a minute limeless species generally placed in the Physaraceae) were located in a *Didymium* clade, and *Didymium anellus* seems to be either part of a *Diderma* clade (Fiore-Donno et al. 2008) or the *Didymium* clade (Wrigley de Basanta et al. 2015). However, since there is not enough information to sort the large number of species of this genus into coherent phylogenetic grouping within the genus, and some individual DNA determinations appear to be anomalous (possibly due to disagreements concerning the morphological identification of species), we will for this guide, use the standard morphologically determined genera and species.

The species of *Didymium* are often widely distributed and generally form sporocarps on leafy or woody litter in temperate and tropical forest. They are probably living in the soil and litter interface and feeding on the micro-organisms in this habitat (Stephenson & 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 consists of a number of regional (i.e. Eastern US, Central America, etc.) allopatric, and occasionally sympatric, sibling biological species, and numerous clonal lines (believed to be apomictic) that are generally fairly local (Clark 2000), but are 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 intraspecies clades (Winsett & Stephenson 2008, 2011) occur in these species. 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 populations containing distinct variations or morphological aberrations, some of which may be genetic and therefore stable. The separation of these populations into categories such as forms, varieties, biotypes (forms adapted to a particular aspect of the broader species niche) or distinct species without experimental evidence is an arbitrary exercise. 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.

### ***Species Delimitation Criteria***

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 some 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. This is illustrated by the recent

publication of a number of new species from the American deserts. These deserts are large, very arid and the available substrate is scarce and scattered; which combined with their likely colonization by small clonal populations, sets up a situation where selection and genetic drift is likely to produce varieties that may be distinct enough in some cases to be considered new taxa. 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. One possible solution to this problem would be to formally or informally recognize some of the more obvious forms found within a complex, such as the bahiense form of *Didymium iridis*; however, it is probably better not to add more names to the system. Since, there will be situations where the application of even these criteria, become arbitrary, there will be a certain amount of disagreement with our dispositions.

The present taxonomy, especially of the cosmopolitan morphospecies is somewhat confusing. Some of the early taxonomists working with this group described numerous species, on the basis of most of the apparent variations found within the complexes; however, later workers, generally consolidated these names into fewer taxa as synonymies or variations. G. Lister's (Lister 1925) designation of *Didymium elegantissimum*, *D. eximium*, *D. fulvellum*, *D. iridis*, *D. lobatum*, *D. megalosporum*, *D. pertusum*, *D. proximum*, and *D. xanthopus* as synonymies or varieties of *D. nigripes*, is a classic example. However, the present trend has generally been towards the subdivision of these populations back into smaller groups, which has resulted in the restoration of some of the older designations, and the probable renaming of others. Examples from the *D. iridis* complex are the restoration (Nannenga-Bremekamp 1972) of *D. elegantissimum* to species status (considered in this work to be a synonym of *D. megalosporum*), and the description of *D. ovoideum* as a new species (a valid species, but considered in this work to have been earlier described as *D. proximum*). However, since many of the older descriptions were rather brief and general, and type specimens were often not designated, the correlation of specific names with actual taxa is not always obvious, and in many cases, it is more or less a matter of opinion.

In this paper, an attempt will be made to sort the stalked *Didymium* species into distinct groups on the basis of morphology, using our current knowledge of population structure in the Myxomycetes (Clark 2000), and then determine the first valid specific epithet for each distinct group. This separation of the stalked and the sessile species is a matter of convenience and not taxonomic differences since recent studies (Wrigley de Basanta et al. 2015) indicate that the stipitate and non-stipitate species are interspersed within the *Didymium* DNA clade.

### **The genus *Didymium***

Since the genus *Didymium* was established by Schrader (1797), many additional species have been described, and at present, at least eighty species (Lado 2005-18) and two subgenera (Martin & Alexopoulos 1969) are generally recognized: *Didymium* with a membranous peridium and *Lepidodermopsis* with a cartilaginous peridium. Also, Matsumoto (1999) has proposed a number of different tribal subdivisions, the latest of a number of systems. However, in our judgment, the morphological information is not strong enough to subdivide *Didymium* into formal taxonomic categories, and until more convincing evidence, such as DNA studies, is produced, informal groupings based upon morphological similarities will be used.

The morphological observations in Matsumoto's (1999) dissertation "Taxonomic studies in the genus *Didymium* (Physarales, Myxomycetes)" generally based on 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, we will adopt most, but not all, of his terminology and taxonomic observations in this work. Matsumoto used sporophore as a general term for all of the different fruiting body types in the Myxomycetes, and sporocarp for what has generally (Martin & Alexopoulos 1969) been called a sporangium. However, we prefer sporocarp as the general term for the sporophores 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 consists of two parts, the sporotheca and the stipe (see Clark & Haskins 2013) for a discussion of sporocarp morphology and development). 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 components are general regions of the stipe which blend into each other).

### ***Stipe Morphology***

The stipe is secreted by the plasmodium during sporangial development and is separated from the sporotheca by the basal part of the peridium. The hypothallus is the attachment part of the stipe and it usually consists of a membranous outer region (continuous with the tubular region of the stalk in the stipitate species) filled with refuse matter and/or lime. The stalk in most species consists of a fibrous membranous tube which is generally longitudinally folded to produce striations. This tube surrounds a central core region that is either empty or contains refuse matter and/or lime crystals. Lime crystals can also occur on the outside of the stalk tube. The columella, in *Didymium*, is generally a somewhat special structure; in many of the distinctly stalked species, the columella is formed during development by the rolling of the basal part of the sporotheca down over the expanded stalk apex, and the closure of the umbilicus thus created (Weldon 1955). Thus, the columella consists of the stalk apex (generally a flared continuum of the stalk tube), a thickened basal plate composed of refuse matter and/or lime deposits continuous with the core material, and the peridial membrane which covers the basal plate and unites with the stalk. The shape of the columella can vary, depending mainly on the shape and size of the stalk apex, from discoid to globose to clavate. When the stalk apex is wide and the umbilicus does not close, the clavus type of thick basal plate and shallow umbilicus is produced.

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*.

Matsumoto (1999) described three types of stipes: membranous (having a thin semitransparent membranous tube), pellicularous (having a thick opaque non-membranous non-tubular structure), and cartilaginous (having a thick semitransparent cartilaginous tube); that correspond, in the *Didymium* stipitate species, to the three basic types of stalks: tubular, core, and cartilaginous. In the membranous stipe species, a thin fibrous membrane makes up the semitransparent tubular outer region of the hypothallus and stalk (Matsumoto’s semi-translucent peripheral layer), which is generally filled with a core of refuse matter and/or lime. The pellicularous type (typified by *Didymium clavus*) lacks the tubular structure and consists entirely of core material. In the cartilaginous type (typified by *Didymium leoninum*) a thick cartilaginous tube is filled with a spongy material that may contain lime crystals. The membranous stalk types can be divided into subtypes based upon the thickness of the tubular region and the size and material found in the core region. The megalosporum subtype has a thin tube and a core filled with refuse matter and/or lime, the squamulosum subtype has a thin highly folded tube that is covered with lime crystals and contains little core material, and the iridis subtype has a thicker tube and a small core which contains refuse matter only in the lower regions of the stipe. The crustaceum and vaccinum subtypes are similar to the megalosporum subtype, except that the stalks are rudimentary and have little refuse matter in the crustaceum subtype, and the vaccinum subtype has a short wide cup or vase like stalk.

Stipe color is due to the interaction of a number of different factors: the color of the membranous tube, which is partially determined by plasmodial color (the stipe of *D. iridis* varies from light yellow to dark brown depending upon the genetically determined color of its plasmodium (Collins & Clark 1966), the presences or absences of refuse matter (usually dark) or lime (light) in the core region, and the presence or absence of exterior lime, which can obscure the

other factors. Also, the hypothallus is often darker than the stalk due to the uptake or incorporation of substrate materials; and a slow or abnormal sporangial development can cause an increased accumulation of dark pigments and the production of less lime. Thus, stipe color can be a rather variable and sometimes unreliable taxonomic character.

### ***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 also three basic subtypes of peridia: areolate, non-areolate, and cartilaginous, with only the cartilaginous subtype correlating directly with the hypothallus and stalk subtypes (Matsumoto 1999). The areolate subtype consists of a thin, colorless 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, colorless to brownish membrane without areola, and it may display an irregular or circumscissile 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 stalked 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 & 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 (appearing 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 fifty percent 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.

### ***Species Groups***

The stipitate *Didymium* species can be placed in several groups in terms of their basic morphology (Table 1). The cartilaginous peridial (leonium group) species and the cupulate base

(vaccinum group) species are both small groups with distinct morphological features; that separates them from the rest of the genus. The rest of the stipitate species form a large fairly uniform group; that can be divided into a number of smaller clusters by relatively minor morphological variations.

**Table 1** Species groupings based mainly on stipe morphology

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**The cupulate or very short stipe and egg-shell peridial lime group:** a group of species with a stipe consisting of a membranous tube forming a short wide cup-like base (vaccinum type) or a short cylindrical base (peruvianum type); and having peridial lime forming an egg-shell like crust.

**The cartilaginous tube stipe group (leonium type):** a group of species with a stipe consisting of an elongate cartilaginous tube filled with lime and amorphous material.

**The empty tube non-calcareous stipe group (iridis type):** a group of species with a stipe consisting of an elongate membranous tube which lacks any interior core material in its stalk (the middle region of the stipe) and has no lime on the exterior of the stipe

**The empty tube externally calcareous stipe group (squamosum type):** a group of species with a stipe consisting of an elongate membranous tube which lacks any interior core material in its stalk (the middle region of the stipe), however, its stipe has an outer coating of lime that due to the longitudinal pleating of the tube may appear to be internal (the lime is inside the folds of the tube).

**The refuse matter or lime filled tube stipe group:** a group of species with a stipe consisting of an elongate tube which is filled with amorphous material (melanospermum type) or lime (intermedium type), but lacks any exterior lime.

**The refuse matter and lime core non-tube stipe group:** a group of species with a stipe which consists solely of amorphous material (clavus type) or amorphous material and lime (floccoides type), and lacks a membranous or cartilaginous tube structure

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“The Myxomycetes” (Martin & Alexopoulos 1969), which recognized 30 species of *Didymium*, is the starting point for modern Myxomycete taxonomy. However, since its publication, there has been a major increase in taxonomic activity with the description of many new species (Schnittler & Mitchell 2000). In *Didymium* alone, over forty new species, the majority known only from their type collection, have been described, and at least fifteen of Martin and Alexopoulos’ synonymies have been restored to species status by various authors (Lado 2005-18).

In this work all of the stalked species will be sorted, as far as possible, into morphologically similar groups using Matsumoto’s criteria (with some minor modifications), and then discussed in terms of coherent species level units and their correct taxonomic designations. Since the individuals within each species can display considerable variability in terms of their stalk, this discussion will also include those species which are generally considered as sessile but occasionally produce a rudimentary stalk. Also, since it is quite likely that not everyone will agree with our designations, we are including a description (modified to fit a standard format) of all of the taxa recognized by Lado (2005-18).

### **The empty tube non-calcareous stipe group**

This group has fibrous-membranous tubes, which are longitudinally folded to produce striation, and contain little (or no) core material in the tube. They generally have lime in the columella and may have refuse matter in the hypothallus. The long stipe species of this group, which has been extensively studied in culture (Clark 2000), make up the *iridis* super species complex that contains four species complexes: *Didymium iridis* (Ditmar) Fr., *D. nigripes* (Link) Fr.,

*D. megalosporum* Berk. & M. A. Curtis, and *D. proximum* Berk. & M. A. Curtis. *Didymium iridis* is the central type in this group and is quite variable, although it generally has a pale-yellow to pale-reddish-brown stalks, a white columella and a depressed globose sporotheca. However, *D. nigripes* which generally has a dark-reddish-brown to black stalk, a brown columella, and a depressed globose sporotheca, grades into the darker forms of *D. iridis* (a number of collections identified as *D. nigripes* were shown to be *D. iridis* after they were cultured). Also, variant forms of *D. megalosporum*, which generally has a yellow-brown to orange-brown stalk, a dull-yellow to orange-brown columella, and a discoid to saddle-shaped sporotheca, grade into the common *D. iridis* morphology. *D. proximum* is generally more distinct, with a red-brown stalk, pale-yellow to white columella, and a prolate sporotheca and columella; however, it also can merge into the common *D. iridis* form. *D. proximum* which had generally been considered a synonym for *D. iridis* was reinstated as a valid species by Nannenga-Bremekamp (1972) on the basis of its clavate columella and stalk. However, if it is not *D. iridis*, then *D. proximum* is in the *D. ovoideum* Nann.-Bremek. population, and has priority as to name. *D. elegantissimum* Masee, considered a synonym for *D. iridis*, and *D. eximium* Peck, considered a synonym for *D. megalosporum*, have also been restored to species status by Nannenga-Bremekamp (1972), however, we agree with Matsumoto (1999) that they are both variations and thus synonymies of *D. megalosporum*. Nannenga-Bremekamp (1972) also suggested that *D. xanthopus* (Ditmar) Fr. is distinct from *D. iridis*, based on the original descriptions by Ditmar (Sturm 1813, 1816). If this is accepted then *D. xanthopus* would be the correct name for the population now known as *D. iridis*, and *D. iridis* would probably become an uncertain name. While one might read the descriptions in this manner, we do not think such a reading is justified, especially since it would upset a long term consensus concerning these rather marginal descriptions and drawings. Other described species, which can be placed in this group, on the basis of their morphology, are *D. bahiense* Gottsb., *D. verrucisporum* A. L. Welden, *D. carnariense* Ing, and *D. crassicolle* Ing. *Didymium bahiense*, which has unfortunately gained wide acceptance as a valid species, is merely a columella form of *D. iridis* (Clark & Mires 1999), and *D. verrucisporum* is basically a nodding stalk form of *D. iridis*; that disappears when cultured, (nodding forms can be induced by manipulating culture conditions, mainly humidity, during sporulation of other *D. iridis* specimens). *Didymium carnariense* is very similar to *D. megalosporum*, but lacks the distinctive saddle-shaped sporotheca; whether or not this isolated island form qualifies as a separate species is problematic, however, with some reservations, we recognize it as a minimally distinct species. On the other hand, we consider *D. crassicolle*, which is known only from the type collection, to be an aberrant form of *D. megalosporum*; that has failed to form a columella during development (the sporotheca did not roll back over the stalk apex). *Didymium rugulosum* Berk. could be another taxon similar to *D. crassicolle*, in that it lacks a columella, however we believe that its brief description is not sufficient to identify any specimens and is therefore the taxon is an uncertain species. *Didymium chilense* Estrada, Lado & Wrigley, a recently described species from the arid regions of Chile, can also be placed in this group. It is similar to *D. megalosporum*, with the exception that its columella resembles a true columella and thus lacks the closed umbilicus structure normally found in this group.

The short stalked specimens of this group are not often collected, and have traditionally been identified as *D. laxifilum* G. Lister & Ross, however, several other taxa have been described which would belong in this subgroup: *D. aurantipes* T.E. Brooks & Kowalski, *D. rubropus* G. Moreno, A. Castillo & Illana, *D. macquariense* G. Moreno & S.L. Stephenson, *D. marineri* G. Moreno, Illana & Heykoop, *D. aquatile* Gottsb. & Nann.-Brek. And *D. radiaticolumellum* Bellido, G. Moreno, Mar. Mey., & J.F. Moreno in Bellido, Moreno, Meyer & Castillo. *Didymium aurantipes*, which was mainly based on its golden stipe color, was later placed in synonym with *D. laxifilum* by one of its authors (Kowalski 1973). While *D. laxifilum* has been found to be fairly variable (stalk and capillitial color), it's somewhat stout, flattened capillitium is quite distinct (Moreno et al. 1997a, Clark & Landolt 2001). Thus, while *D. rubropus* is generally similar to *D. laxifilum*, it's finer, round and less branched capillitium sets it apart as a separate taxon (Moreno et al. 1997a). *D. macquariense* is an isolated island taxon that is very similar to *D. rubropus* and *D. laxifilum*,

however its variable capillitial nodes and partially reticulate spores set it apart from these species. *Didymium marineri* is not considered a true member of this group, and therefore, it will be considered in the next group. *Didymium aquatile* is a rare taxon known only from the type site (a brook in Brazil), and it is apparently an aberrant/variant form of a *D. rubropus* or *D. proximum*, induced by its habitat. *Didymium radiaticolumellum* is a newly described species, that has large spores and abundant capillitial nodules contain lime inclusion, however, these traits may be abnormalities due to morphological or genetic causes; therefore unless more collections or DNA studies are made we consider this taxon to be a *D. laxifilum* variant. While *D. subreticulosporum* Oltra, G. Moreno & Illana can be placed in this group, it appears to be an atypical species lacking many of the characteristics of other stipitate taxa (Mosquera et al. 2000). Thus, its unique morphology (discontinuous peridium, capillitium replaced by a crystalline structure) would seem to set it apart from all other *Didymium* species.

### **The empty tube externally calcareous stipe group**

This group has fibrous-membranous tubes, which are longitudinally folded to produce striations, and they generally contain little (or no) core material in the central tube part of the stipe. The lime, which is present on the outside of the tube, can appear to be internal, since the tube is highly folded and the lime in these folds is inside the outer edge of the stalk (Matsumoto 1999). The stipe is coated on the exterior with lime, and generally there is lime in the columella, and there also may be refuse matter in the hypothallus and lower region of the stalk.

The intermediate to long stalked species, which have been extensively studied in culture (El Hage et al. 2000), are in the squamulosum super complex, which contains two species complexes: *D. squamulosum* (Alb. & Schwein.) Fr. and *D. dictyopodium* Nann.-Bremek. & Y. Yamam. (It is extremely likely that there is a previous valid name for this taxon in the *D. squamulosum* synonyms, however, the lack of types and the overlapping descriptions, makes such a determination very difficult, if not impossible). *D. squamulosum* is the central type in this group and is a very variable taxon, although it generally has a stout intermediate length white stipe and a globose to depressed-globose white columella. However, *D. dictyopodium*, which generally has a slender long to intermediate whitish-gray stipe and a white to pale-brown basal-plate columella, is also variable, and thus, often grades into the taller less robust forms of *D. squamulosum*. The newly described *Didymium operculatum* D. Wrigley, Lado & Estrada differs from *D. squamulosum* in that it lacks a columella, has circumscissile dehiscence, reticulate spores and is apparently endemic to the Atacama Desert in Chile. *Didymium infundibuliforme* D. Wrigley, Lado & Estrada, also newly described from South American deserts, also lacks a columella, has a funnel-shaped sporotheca with circumscissile dehiscence, and baculate spores. A third, newly described species, from arid regions of Mexico, *Didymium umbilicatum* D. Wrigley, Lado & Estrada has short (often absent) stalks, no columella and spores with cristae of fused bacula.

There are also a number of other described taxa (*D. lenticulare* K.S. Thind & T.N. Lakh., *D. marineri*, *D. projectile* T.N. Lakh. & K.G. Mukerji, *D. balearicum* Ing, *D. applanatum* Nann.-Bremk. and *D. pseudocolumellum* H.Z. Li, Yu LI & Q. Wang), that we consider to be synonymous to *D. squamulosum* or *D. dictyopodium*. We consider *D. lenticulare*, which has very little stalk lime and a dark coloration, to be an aberrant developmental form and thus an uncertain name, however, it is very similar to *D. dictyopodium*, except for the lack of stalk lime, and is therefore probably part of that species complex. Although *D. marineri* is described as lacking stalk lime, it is identical to many *D. squamulosum* isolates when they are grown in culture (which also lack stalk lime), therefore, we consider the *D. marineri* specimens to a limeless stalk forms of *D. squamulosum*. The spirally twisted apical capillitial threads of *D. projectile*, by which it is separated from *D. squamulosum*, is not considered to be a sufficient basis for a separate species, and the yellow coloration of *D. balearicum*, is also considered to be too minor to separate it from *D. squamulosum*. *Didymium applanatum* Nann.-Bremk. would appear to be a unique taxon, but its rarity and substrate indicates that is probably an aberrant developmental form of *D. squamulosum* (Oltra 2003). While *D. pseudocolumellum*, which is known only from its type collection, has a

pseudocolumella that is unique for this group, it is otherwise similar to *D. squamulosum*, and therefore, unless more collections are found, we will consider it to be an aberrant developmental form, where the columella was not formed by the rolling back of the sporotheca over the stalk apex. *Didymium nigrisporum* Nann.-Bremk. K.G. Mukerji & Pastricha was a rare taxon, differentiated from *D. squamulosum* on the basis of spore characteristics (very dark densely warted with polygonal ridges), which has been validated by numerous collections in Peru (Lado et al. 2016).

The shorter stalked to sessile species in this group are often similar to the shorter forms of *D. squamulosum*. *Didymium crustaceum* Fr. differs from *D. squamulosum* mainly in having crowded short-stalk to sessile sporangia, generally covered by a united peridial crust and somewhat larger spores. Also, *D. obducens* is separated from *D. squamulosum*, by its pale-brown short-stalked to sessile pulvinate sporangia and larger, more warted spores. *Didymium fulvum* Sturgis, which was recognized by Martin & Alexopoulos (1969) as a valid species, has been shown by Härkönen (1979), to be a synonym of *D. obducens*. The short-stalked to sessile pulvinate sporangia of *D. nivicolium* Meyl., differs from *D. squamulosum* by its larger and more warted spores, general lack of a columella, and nivicolus habitat (Kowalski 1975). *Didymium muscorum* T.N. Lakh. & K.G. Mukerji, is a rare taxon, very similar to *D. squamulosum*, but it is apparently a valid “spore species” due to its spiny warts, while *Didymium karstensii* Nann.-Bremk., with its non-umbilicate globose sporangium and peridial lime crust separating from the peridial membrane, also appears to be separated from *D. squamulosum*; therefore, while we have some reservations, this taxon is recognized as a valid species, although it is rather similar to *D. muscorum*. *Didymium mexicanum* G. Moreno, Lizárrage & Illana may have short calcareous stipes, which places it in this group, and it also has distinct large spores with reticulate arranged warts

### **The refuse matter or lime filled tube stipe group**

This group has fibrous membranous tubes, which are longitudinally folded, and contain refuse matter and/or lime in the core. *Didymium melanospermum* (Pers.) T. Macbr. and *D. minus* (Lister) Morgan, which have overlapping morphologies, form the center of a subgroup having refuse matter cores; however, they have separate foci, and are considered separate species. *D. melanospermum* is generally more robust and has slightly larger and more warted spores; and *D. minus* often has longer stipes. *Didymium angularisporum* J. Matsumoto belongs in this subgroup, however, this taxon, known only from the type specimen, with its angular spores, may be based upon an aberrant *D. minus* sporangium. *Didymium eremophilum* M. Blackw. & Gilb., which has a minute sporangium with refuse matter in its stalk, is likely to be a biotype miniature; however, since it is so different from everything else, it must be accepted as a separate valid species.

The lime core subgroup contains a number of species that are rarely collected. *Didymium intermedium* J. Schröt., with its discoid columella, white to pale-orange-brown stalks, extensive hypothallus (that produces clustered sporangia), and dark spiny spores is a very distinct species. *Didymium floccosum* G.W. Martin, K.S. Thind & Rehill, which has a floccose peridium, dark clavate columella, orange-brown stalk, inconspicuous hypothallus, and yellow-brown densely warted spores, is also distinct, although it is similar in many aspects to *D. floccoides* (in the following group) which lacks a membranous stalk tube. *Didymium melanospermum* var. *bicolor* G. Lister, appears to be a variant of *D. floccosum* where the dark refuse matter in the hypothallus region is extended up into the lower stalk. *Didymium laccatipes* J. Matsumoto is a newly described species, which differs from *D. intermedium* in having pilate spores and separate sporangia not joined by the hypothalli, and from *D. floccosum* in having a white dome-shaped columella, and a white slender stalk. A newly described species, *D. wildpretii* Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado, known only from arid regions in Mexico and the Canary Islands, lacks a columella, has a short stipe and baculate spores. This specialized taxon also appears to be a minimally distinct taxon. *Didymium tehuacanense* Estrada, D. Wrigley & Lado, another distinct taxon from the arid regions of Mexico, has unique calcareous columella projections to which the capillitial threads are attached. *Didymium xerophilum* Lado, Estrada & D. Wrigley, also a new species from arid regions of South America has rhomboidal lime crystals in the stalk, a funnel-

shaped apical invagination and circumscissile dehiscence of the apical region. *Didymium pertusum* Berk., which has been revived by Neubert et al. (1995), appears to be a valid species, which differs from the other species in this subgroup mainly in terms of its red-brown stalk and finely warted spores. The *D. macrospermum* Rostaf. taxon, revived by Nannenga-Bremekamp (1972), also fits into this group, however, the somewhat general description and the lack of any collections make this an uncertain name. *Didymium simlense* T.N. Lakh. & K.G. Mukerji, which is known only from the type collection, may be a non-clustered variant of *D. intermedium*; in any case, it will be considered an uncertain taxon, until further material is discovered. Also, two taxa, known only from their type collections, *D. delhianum* T.H. Lakh. & M.J. Mukerji and *D. chrysosporum* T.H. Lakh. & M.J. Mukerji, are in our opinion, dark aberrant developmental forms of *D. floccosum*.

### **The refuse matter and lime core non-tube stipe group**

This group has stipes consisting solely of core material without a membranous tube. *Didymium clavus* (Alb. & Schwein.) Rabenh., with a refuse matter only stalk, and *D. floccoides* Nann.-Bremek. & Y. Yamam., with a refuse matter and lime stalk, are the only members of this group, since we agree with Matsumoto (1999) that *Didymium columella-cavum* Hochg., Gottsb. & Nann.-Bremek., is a synonym for *D. floccoides*.

### **The cartilaginous tube stipe group**

This group has a cartilaginous, instead of a membranous, stalk tube, which contains a spongy core with lime deposits. *Didymium leoninum* Berk. & Broome and *D. martini* (T.N. Lakh.) H. Neubert, Nowotny & K. Baumann are the only taxa with this type of stipe. However, *D. martini*, known only from the type specimen, is in our opinion an aberrant development form, possibly of *D. nigripes*, and is thus not a valid taxon. *Didymium leoninum* var. *effusum* G. Lister is plasmodiocarpous, and Matsumoto & Deguchi (1999a) could not find any intermediate forms between it and the stipitate form. They therefore, consider this variety to be a separate taxon, and named it *D. panniforme* J. Matsumoto; we therefore accept the species, unless and until intermediate forms are found.

### **The cupulate or very short stipe and egg-shell peridial lime group**

*Didymium vaccinum* (Durieu & Mont.) Buchet is the core of this group. It has turbinate to hemispheric sporangia with a wide stalk-like, cupulate base, a large (usually) hemispheric columella, scanty capillitium, and dark-purplish-brown 12-14 µm spores with large warts (conate by electron microscopy). *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) spores. However, since *D. vaccinum* often produces small columella (and occasionally stalk like bases) when cultured (Clark 2004), we consider *D. disciforme* and *D. haretianum* to be aberrant/variants of *D. vaccinum*. *Didymium peruvianum* Lado, D. Wrigley & SL Stephenson which is also in this group has a very short or absent stalk and lacks a columella, which separates it from *D. vaccinum*.

### **Key to the stalked species**

1. Stipe and peridium cartilaginous ..... 2
1. Stipe and peridium not cartilaginous ..... 3
2. Stipes short, stout and orange-yellow to buff (mostly tropical) ..... *D. leoninum*
2. Stipes long, striate and dark..... *D. martinii*  
(probably an aberrant sporocarp of *D. nigripes*, single collection)
3. Stipe calcareous (exterior and/or interior) .....24
3. Stipe not calcareous ..... 4

4. Stipes long (more than half the total sporangial height) .....	5
4. Stipes short (less than half the total sporangial height) .....	16
5. Stipes pale-yellow, yellowish-brown, orange-brown or pale reddish-brown .....	6
5. Stipes dark reddish-brown to black .....	10
6. Small sporangium lacking a columella and capillitium. (Apparently restricted to arid North American regions) .....	<i>D. eremophilum</i>
6. Sporotheca having a columella and capillitium .....	7
7. A white columella in a depressed globose sporotheca .....	<i>D. iridis</i>
includes <i>D. xanthopus</i> (a synonym), <i>D. verrucisporum</i> (a fairly rare nodding sporangial form), and <i>D. bahiense</i> (a common discoid columella form)	
7. A dull yellow to orange-brown columella .....	8
8. A discoid to saddle shaped sporotheca .....	<i>D. megalosporum</i>
includes <i>D. elegantissimum</i> (a synonym) <i>D. eximium</i> (a synonym), and <i>D. crassicolle</i> (probably an aberrant form that did not form a columella, single collection)	
8. Sporotheca not discoid to saddle shaped .....	9
9. Sporotheca subglobose to oblate (apparently restricted to Chile) .....	<i>D. chilense</i>
9. A depressed globose sporotheca (apparently restricted to the Canary Islands) .....	<i>D. canariense</i>
10. Sporotheca with a basal plate that is not enclosed .....	11
10. Sporotheca with an enclosed columella .....	12
11. Sporotheca with capillitium .....	<i>D. clavus</i>
11. Sporotheca with capillitium replaced by a crystalline structure (apparently restricted to arid regions of Mexico and the Canary Islands) .....	<i>D. subreticulosporum</i>
12. Dark reddish-brown to black stipes and dark brown columella .....	13
12. Red-brown stipes .....	14
13. Angular spores .....	<i>D. angularisporum</i>
(probably an aberrant spore form of <i>D. minus</i> , single collection)	
13. Spores not angular .....	<i>D. nigripes</i>
14. A prolate (generally) sporotheca with a pale-yellow to white columella .....	<i>D. proximum</i>
(includes <i>D. ovoideum</i> a synonym)	
14. Globose to ovoid sporotheca with a white columella .....	15
15. Capillitium with expanded ellipsoid to spiny nodes (apparently restricted to Macquarie Island) .....	<i>D. macquariense</i>
15. Capillitium lacking expanded ellipsoid to spiny nodes .....	<i>D. rubropus</i>
16. Capillitium replaced by a crystalline structure (apparently restricted to arid regions of Mexico and the Canary Islands) .....	<i>D. subreticulosporum</i>
16. Capillitium consisting of amorphous filaments .....	17
17. Capillitium a network of stout flattened filaments .....	<i>D. laxifilum</i>
includes <i>D. aurantipes</i> (a golden stipe form, few collections) and <i>D. radiaticolumellum</i> (a large spore variant with lime filled capillitial nodules)	
17. Capillitium a network of round filamentous threads .....	18
18. Capillitium with expanded ellipsoid to spiny nodes (apparently restricted to Macquarie Island) .....	<i>D. macquariense</i>
18. Capillitium lacking expanded ellipsoid to spiny nodes .....	19
19. Columella absent .....	<i>D. peruvianum</i>
19. Columella present .....	20
20. Columella a basal plate in an open umbilicus .....	<i>D. aquatile</i>
(an aberrant form, possibly of <i>D. rubropus</i> , induced by the aquatic habitat, single collection)	
20. Columella in a closed umbilicus .....	21
21. Columella white .....	22
21. Columella dark-brown to dirty white .....	23
22. Stipes yellowish to reddish-brown .....	<i>D. marineri</i>
(probably a lime-less form of <i>D. squamulosum</i> )	

22. Stipes reddish-orange .....	<i>D. rubropus</i>
23. Spores 10-14 microns, strongly warted and dull purplish-brown in transmitted light .....	<i>D. melanospermum</i>
(generally more robust than <i>D. minus</i> )	
23. Spores 8-11 microns, minutely and densely warted and purplish-brown in transmitted light .....	<i>D. minus</i>
includes <i>D. angularisporum</i> (probably an aberrant spore form of <i>D. minus</i> , single collection)	
24. Stalks short .....	25
24. Stalks long .....	42
25. Peridial lime having an egg-shell like consistence .....	<i>D. vaccinum</i>
includes <i>D. haretianum</i> (a more stalked form, single collection) and <i>D. disciforme</i> (a reduced form with small columella, single collection)	
25. Peridial lime not egg-shell like .....	26
26. Pseudocolumella present .....	<i>D. pseudocolumellum</i>
(probably an aberrant <i>D. squamulosum</i> which did not form a proper columella, single collection)	
26. Pseudocolumella not presents .....	27
27. Columella absent or consisting of a basal plate in an open umbilicus .....	28
27. Columella enclosed in the sporotheca .....	35
28. Columella consisting of a basal plate in an open umbilicus .....	29
28. Columella absent .....	32
29. Short stipes, scanty capillitium and dark-brown 8-11 micron warted spores .....	<i>D. applanatum</i>
(probably a developmental aberrant, a few collection in sandy areas).	
29. Very short stipes, abundant capillitium and black spores .....	30
30. Black 7-5-9.5 µm spores apparently restricted to arid regions of Mexico and the Canary Islands .....	<i>D. wildpretii</i>
30. Black 10-13 µm spores .....	31
31. Snow-melt species with warted spores .....	<i>D. niviculum</i>
31. Non- snow-melt species with coarsely warted spores .....	<i>D. obducens</i>
(includes <i>D. fulvum</i> (a synonym))	
32. Sporotheca shaped like a funnel or having a umbilicate upper surface .....	33
32. Sporotheca subglobose to pulvinate or oblate with an operculum .....	34
33. Funnel-shaped sporotheca .....	<i>D. infundibuliforme</i>
(apparently restricted to arid regions of South America)	
33. Umbilicate upper sporotheca surface .....	<i>D. umbilicatum</i>
(apparently restricted to arid regions of Mexico)	
34. Sporotheca oblate and having an operculum .....	<i>D. operculatum</i>
(apparently restricted to the Atacama Desert in South America)	
34. Sporotheca subglobose to pulvinate and having large 12-18 µm warted (forming a partial reticulum) dark-purple-brown spores .....	<i>D. mexicanum</i>
(apparently restricted to arid regions in Mexico)	
35. Stipes weak and indistinct .....	36
35. Stipe short but distinct .....	38
36. Clusters of sporangia covered (usually) with a united limy crust, having a white to orange-brown dome shaped columella .....	<i>D. crustaceum</i>
36. Sporangia never covered with a limy crust, having small white to pale columella .....	37
37. Having a free peridial lime crust .....	<i>D. karstenii</i>
37. Lacking a free peridial lime crust .....	<i>D. niviculum</i>
(a snow melt species)	
38. Orange-brown to black stipe, floccose peridium, and small 6-8 µm dark-brown to black warted spores .....	<i>D. floccoides</i>
includes <i>D. chryso sporum</i> (two collections) and <i>D. dehlianum</i> (dark aberrant forms, single collection)	

38. White to dark-brown stipes, peridium not noticeably floccose, and spores 8-12 µm in diameter .....	39
39. White stipe, and a white column-like columella with projections attached to the capillitium .....	<i>D. tehuacanense</i>
(apparently restricted to arid regions of Mexico)	
39. White to orange-brown stipe, and a globose to discoid columella lacking projections .....	40
40. Spiny black 8-10 µm spores (rare, found in India) .....	<i>D. muscorum</i>
40. Warty 8-12 µm spores .....	41
41. Spores very dark, densely warty and having polygonal ridges .....	<i>D. nigrisporum</i>
41. Spores brown and lacking polygonal ridges .....	<i>D. squamulosum</i>
includes <i>D. balearicum</i> (yellow color variant found on Mallorca Island, single collection), <i>D. chryso sporum</i> (probably a developmental aberrant, two collections), and <i>D. projectile</i> (variant with capillitia with spiral ends)	
42. Columella absent or consisting of a basal plate in an open umbilicus .....	43
42. Columella enclosed in the sporotheca .....	44
43. Columella consisting of a basal plate in an open umbilicus .....	<i>D. dictyopodium</i>
( <i>D. lenticulare</i> is probably an aberrant form of this taxon, single collection)	
43. Columella absent, sporotheca opening by a operculum (apparently restricted to the Atacama Desert in Chile) .....	<i>D. operculatum</i>
44. Spores brown to black and spiny .....	45
44. Spores brown to dark-brown and warty .....	47
45. Sporangia clustered and having fused calcareous hypothalli (rare) .....	<i>D. intermedium</i>
45. Hypothalli not fused into a large unit .....	46
46. Brown 9.5-12.5 µm spiny spores, columella clavate and yellow to orange-brown .....	<i>D. simlense</i>
(possibly a developmental aberrant of <i>D. intermedium</i> , single collection)	
46. Dark-brown 12.5-13.5 µm spiny spores, discoid to globose white columella.....	<i>D. macrospermum</i>
(a rare indeterminate taxon)	
47. Peridium floccose and forming small platelets attached to the capillitium .....	48
47. Peridium not distinctly floccose .....	49
48. Brown to dark-brown 7-8 µm minutely warty spores, stipe has a fibrous tube .....	<i>D. floccoides</i>
includes <i>D. columella-cavum</i> (minor columella variant)	
48. Brown 8-10 µm densely warty spores, stipe lacks a fibrous tube .....	<i>D. floccosum</i>
49. Pale purple brown 10-13 µm warty spores, stipe and columella reddish-brown (apparently rare) .....	<i>D. pertusum</i>
49. Dark brown 8-11 µm warty spores, stipe and columella white to orange-brown .....	50
50. Having a funnel-shaped apical invagination, circumscissile dehiscence and rhomboidal lime crystals in the stalk .....	<i>D. xerophilum</i>
50. Not as above .....	51
51. Columella white to pale orange and conical; spores dark-brown strongly warty and 9-11 µm in diameter; stipe lime internal (four collections) .....	<i>D. laccatipes</i>
51. Columella white to grayish-white and discoid to globose; spores dark brown to black finely warty and 8-11 µm in diameter; stipe lime external (very variable) .....	<i>D. squamulosum</i>
includes <i>D. chryso sporum</i> (probably a developmental aberrant, two collections) and <i>D. balearicum</i> (yellow color variant found on Mallorca Island, single collection)	

## Discriptions

The distribution information is not meant to be complete, but to provide a basis understanding of the current state of available information.

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

= *Lepidodermopsis* Höhn., Akad. Wiss. Wien Sitzungsber. 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 angularisporum*** J. Matsumoto, in J. Matsumoto & H. Deguchi Mycotaxon 70: 157. 1999b.

Types: TNS (M-H-3526); HIRO.

Hypothallus: discoid; membranous and brown; basal region containing refuse matter. Stalk: intermediate (0.4-0.6 mm); striate; non-calcareous, brown to dark-brown, filled with refuse matter. Columella: discoid in a closed umbilicus; dark-brown to black; containing lime crystals. Sporotheca: grayish-white, gregarious, subglobose to depressed sporangia (0.4-0.5 mm wide, 0.3-0.4 mm thick). Peridium: membranous; purplish-brown (colorless reticulations on upper region); covered with small white lime crystals. Capillitium: relatively thick and rigid brown threads; dichotomously branching at the extremities with little anastomosing. Spores: angular polyhedral (9-10 µm); nearly smooth (faintly verrucose by SEM); brown (in mass) or purplish-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Japan; one collection.

Similar species – *D. minus* – has globose warted spores, delicate pale capillitium, and subglobose columella; *D. melanosporum* – has globose warted spores, abundant capillitium and a short stalk.

Remarks – possibly a developmental aberration of *D. minus*.

***Didymium applanatum*** Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 75: 352. 1972.

Types – Nannega-Bremkamp 7113.

Hypothallus – discoid, membranous and hyaline. Stalk: short (0.2-0.5 mm, rarely up to 1 mm); striate; calcareous and white. Columella: wide basal plate in a shallow open umbilicus. Sporotheca: white, gregarious, discoid sporangia (1 mm wide, 0.1-0.2 mm thick). Peridium: membranous and hyaline; covered with white to pale-gray lime crystals; poorly defined circumscissile dehiscence. Capillitium: scanty hyaline threads, branching and rarely anastomosing. Spores: globose (8-11 µm); covered with small warts, with patches of larger warts; dark-brown (in mass) or pale-grayish-brown (in transmitted light). Plasmodium: unknown. Habitat: on sand.

Distribution – France, Netherlands, Mexico, Ecuador, rare.

Similar species – *D. clavus* – has a dark non-calcareous stalk and columella (basal plate); *D. squamulosum* – has a narrow umbilicus and a globose columella; *D. lenticulare* – has a dark, non-calcareous long stalk and profuse capillitium.

Remarks – a developmental aberration of *D. squamulosum* (Oltra 2003).

***Didymium aquatile*** Gottsb. & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 74: 264. 1971.

Types – Gottsberger 11-7820, Nannega-Bremekamp, Martin, Sp, BM.

Hypothallus – large discoid; brown. Stalk: short (0.5-0.7 mm), thick and tapering; brown with a black base. Columella: basal plate in an open wide umbilicus; packed with crystalline lime bodies. Sporotheca: white, scattered hemispherical sporangia (0.7 mm). Peridium: membranous and hyaline (pale-rosy-brown persistent basal region); covered with powdery lime crystals. Capillitium: scanty, thin hyaline to purple-brown threads (having irregular long dark thickened regions). Spores: spherical (8-11 µm); distinctly, but irregularly warted; dark-brown (in mass) or pale-lilac (in transmitted light). Plasmodium: greenish-yellow aquatic phaneroplasmodium. Habitat: aquatic.

Distribution – Brazil (San Paulo state), one collection.

Similar species – *D. clavus* – has granular matter in the stalk, abundant capillitia, and is not aquatic; *D. lenticulare* – has lime crystals on the stalk, abundant capillitia, and is not aquatic.

Remarks – this taxon was probably based on poorly developed sporangia, which is not acceptable as a basis for a new species description.

***Didymium bahiense*** Gottsb., Nova Hedwigia 55: 365. 1968.

Types – B, GZU, NY, Nann.-Bremek., Alexopoulos.

Hypothallus – discoid and membranous, brown to dark-brown. Stalk: long (0.7-0.9 mm), slender and tapering (sometimes bent); striate; orange-brown to brown. Columella: discoid in a closed umbilicus; white to rarely brown; containing angular lime crystals. Sporotheca: white, gregarious, depressed globose to somewhat lenticular sporangia (0.3-0.6 mm). Peridium: membranous and hyaline to very pale-yellowish-brown (thickened areolae seen with a stain); covered with pale-gray to white stellate lime crystals. Capillitium: profuse, flexuous pale-brown to purplish-brown (with pale tips) threads; dichotomously branching and anastomosing. Spores: globose to subglobose (8-14  $\mu\text{m}$ ); covered with small warts with patches of larger warts (pilate by SEM); dark-brown (in mass) or pale-brown (in transmitted light). Plasmodium: brown phaneroplasmodium. Habitat: on litter and wood.

Distribution – cosmopolitan and common.

Similar species – *D. iridis* - generally has a globose columella.

Remarks – this is a common morphological variant in the *D. iridis* species complex; DNA studies (Wrigley de Basanta et al. 2015) place specimens of this taxon either very close to *D. iridis* or *D. nigripes*.

***Didymium balearicum*** Ing, Stapfia 73: 94. 2000.

Types – Ing 92092.

Hypothallus – discoid and membranous; covered with pale-lemon to white lime. Stalk: short (up to 0.6 mm); thick and furrowed; encrusted with lemon to pale-orange-brown lime. Columella: subglobose in a closed umbilicus; calcareous and lemon-yellow. Sporotheca: lemon-yellow, gregarious, subglobose sporangia (0.8-1 mm). Peridium: membranous, brown and transparent; covered with stellate yellow lime crystals. Capillitium: hyaline threads, sparsely dichotomously branching and anastomosing. Spores: globose (10-11  $\mu\text{m}$ ), evenly covered with small warts; blackish-brown (in mass) or dark-yellow-brown (in transmitted light).

Plasmodium: unknown. Habitat: on leaf litter.

Distribution – Mallorca, one collection.

Similar species – *D. squamulosum* - has white lime.

Remarks – an isolated island variant of *D. squamulosum*.

***Didymium carnariense*** Ing, Stapfia 73: 95. 2000.

Types – Ing 90017.

Hypothallus – discoid, membranous and inconspicuous; brown. Stalk: intermediate (up to 0.8 mm); striate; bright-reddish-brown (darker below). Columella: discoid basal plate in a closed umbilicus; bright-canary-yellow fading to pale-orange-brown. Sporotheca: white, gregarious, globose to slightly flattened sporangia (0.7-0.9 mm). Peridium: membranous, shining, translucent, and pale-red-brown; covered with a thin powder of white stellate lime crystals. Capillitium: hyaline (darker bases) flexuous threads, dichotomously branching and anastomosing. Spores: globose (8-9  $\mu\text{m}$ ); covered with small evenly spaced warts; black (in mass) or dull-brown (in transmitted light). Plasmodium: pale-brown phaneroplasmodium. Habitat: on sclerophyllous litter.

Distribution – Canary Islands, seven collections.

Similar species – *D. melanosporum* - peridium is not pale-red-brown.

Remarks – part of the *D. melanosporum* complex, but it can be considered an island form that has reached the level of a minimum species.

***Didymium chilense*** Estrada, Lado & D. Wrigley, in Lado C, Wrigley de Basanta D, Estrada-Torres A, Stephenson SL. Fungal Diversity 59: 16. 1013

Types – MA-Fungi 80549 (Lado 17514).

Hypothallus – discoid to irregular and membranous; hyaline to yellowish brown. Stalk: intermediate to long (0.55 to 1.2 mm); cylindrical and striate; yellowish-brown. Columella: cylindrical to conical (occasionally dome shaped); hyaline to yellowish-brown membrane filled with lime (tips are occasionally empty); having a closed umbilicus. Sporotheca: white, gregarious, subglobose to oblate sporangia (0.4-1 x 0.2-0.6 mm); a limeless reddish base area often remains after dehiscence. Peridium: colorless membrane with yellowish-brown areolae; covered with stellate lime crystals; dehiscing at maturity with some fragments remaining attached to the capillitium. Capillitium: smooth amorphous threads arising from spike like processes of the columella; dark brown to grayish-brown with hyaline tips; branching and anastomosing with cross bars. Spores: subglobose (9-12 µm); densely and uniformly warted (pilate by SEM); black (in mass) or grayish to yellow-brown with a lighter equatorial band (in transmitted light). Plasmodium: unknown. Habitat: on leaves of sclerophyllous trees.

Distribution – central Chile (22 collections).

Similar species – *D. megalosporum* - columella is subglobose with an invaginated umbilicus, not a cylindrical structure resembling a true columella, spores general have smaller less dense warts. *D. rubropus* – stalks are usually shorter and more reddish; columella is not cylindrical and spiky.

Remarks – Probably derived from the *D. megalosporum* group by modification of the columella apparatus (lost of the umbilicus invaginated structure).

***Didymium chryso sporum*** T.N. Lakh. & K.G. Mukerji, Acta Bot. Indica 6(Suppl):16. 1978.

Types – Univ. Delhi (NA), Nann.-Bremek.

Hypothallus – discoid, membranous and dark-brown. Stalk: intermediate (0.5-0.8 mm); striate; dark at base and filed with lime and refuse matter. Columella: globose to hemispheric in a closed umbilicus; calcareous white to orange-brown. Sporotheca: grayish-white, gregarious, globose to hemispheric sporangia (0.5-0.7 mm). Peridium: membranous and hyaline; covered with compact grayish-white lime crystals; floccose at maturity. Capillitium: profuse, violaceous-brown threads; dichotomously branching and anastomosing. Spores: globose (7-8 µm); warted with prominent clusters; black (in mass) or deep-violaceous- brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – India, Japan, two collections.

Similar species – *D. clavus* - has a dark peridium, no distinct columella, and the spores are not warted; *D. lenticulare* – has long stalks, larger spores, and no distinct columella.

Remarks – we consider this to be an aberrant form of *D. floccosum*.

***Didymium clavus*** (Alb. & Schwein.) Rabenh., Deutschl. Krtpt.-Fl. 1: 220. 1844.

≡ *Physarum clavus* Alb. & Schwein. Comsp. Fung. Lusat. 96. 1805.

*Didymium melanopus* var. *clavus* (Alb. & Schwein.) Fr. Syst. Mycol. 3: 114. 1829.

*Didymium melanopus* var. *clavus* (Alb. & Schwein.) Wallr. Fl. Crypt. Germ. 4: 370. 1833.

= *Didymium commutabile* Berkeley & Broome J. Linn. Soc. Bot. 14: 83. 1873.

= *Didymium neglectum* Masee Monogr. Myxogastr. 231. 1892.

= *Didymium masseeanum* Sacc. & Syd. in Sacc., Syll. Fung. 14: 836. 1899.

Types – none known.

Hypothallus – discoid, membranous and dark-brown to black. Stalk: generally long (up to 1 mm) and tapering; striate; brown to black (containing refuse material). Columella: thickened basal plate present in a wide shallow umbilicus; brown and containing lime. Sporotheca: white to grayish-white, gregarious, discoid sporangia (0.4-1 mm wide, 0.2-0.3 mm thick). Peridium: membranous and purple-brown with colorless reticulations; generally covered with grayish-white lime crystals. Capillitium: profuse purplish-brown threads; sparsely dichotomously branching and anastomosing. Spores: globose (6-8 µm) and minutely warted (baculate by SEM); blackish-brown

(in mass) or pale-brown (in transmitted light). Plasmodium: gray or colorless (white) phaneroplasmodium. Habitat: on wood.

Distribution – cosmopolitan and fairly rare, but may be overlooked.

Similar species – *Diderma hemisphaericum* - has non-stellate lime and smaller spores; *D. floccoides* – has a calcareous stalk and a subglobose columella.

Remarks: a core (no tube) stipe species.

***Didymium columella-cavum*** Hochg., Gottsb. & Nann,-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 92: 73. 1989.

Types – Gottsberger (11-121166), SP, GI, Nannenga-Bremekamp (15.972).

Hypothallus – discoid, membranous and orange-brown to dark-brown; containing refuse matter. Stalk: short to intermediate (0.3-0.5 mm), rugulose; orange-brown and dark below; filled with refuse matter below and obscured crystalline lime throughout. Columella: subglobose to clavate, in a closed umbilicus; white to dark-brown, and hollow (containing lime crystals). Sporotheca: white to grayish-white, gregarious, conical to subglobose sporangia (0.3-0.6 mm wide, 0.3-0.4 mm thick). Peridium: membranous and hyaline to purplish-brown with colorless reticulations; covered with white stellate lime crystals. Capillitium: profuse, delicate, hyaline to pale-purplish-brown (with hyaline tips) threads; sparingly dichotomously branching and anastomosing. Spores: globose (7-9  $\mu\text{m}$ ) minutely warted to nearly smooth with scattered dark patches (baculate by SEM); brown to dark-brown (in mass) or pale-violet-gray (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Brazil (San Paulo State), Peru; rare.

Similar species – *D. chryso sporum* - does not have peridial areolae, spores more warted; *D. floccoides* – peridium dehiscing into small floccose platelets.

Remarks – Matsumoto (1999) has shown that this taxon is synonymous with *D. floccoides*.

***Didymium crassicolle*** Ing, Trans. Brit. Mycol. Soc. 78: 443. 1982.

Types – Kew, Ing.

Hypothallus – discoid, membranous and orange. Stalk: long (0.6-0.8 mm); cylindrical and bright-orange. Columella: none; has a widened stalk apex that forms a base. Sporotheca: white, gregarious, depressed globose sporangia (0.4-0.6 mm). Peridium: membranous and pale-yellow; densely covered with white stellate lime crystals. Capillitium: delicate, hyaline threads; sparsely branching and anastomosing. Spores: globose (7.5-10  $\mu\text{m}$ ); uniformly and strongly covered with warts; black (in mass) or pale-purple-brown (in transmitted light). Plasmodium: orange-yellow phaneroplasmodium. Habitat: on pine and fern litter.

Distribution – England, one collection.

Similar species – *D. lenticulare* - has a deep-brown stalk and capillitium; *D. megalosporum* and *D. eximium* – have columella.

Remarks – we consider this to be a developmental aberration of *D. megalosporum*.

***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 – Peptopoli, Russia (Weinman.), 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: white, crowded, globose sporangia (0.5-1 mm, may be deformed by pressure). 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  $\mu\text{m}$ ); densely warted (pilate by SEM); black (in mass) or

purplish-brown (in transmitted light). Plasmodium: white phanero-plasmodium. 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 dehlianum*** T.N. Lakh. & M.G. Mukerji, Acta Bot. Indica 6(Suppl.): 18. 1978.

Types – Univ. Delhi (NA), Nannenga-Bremekamp.

Hypothallus – small, membranous and dark-brown. Stalk: short to intermediate (< 0.6 mm); tapered, striate and black (partial filled with refuse matter and lime). Columella: small and dome-like, in an umbilicus; brownish. Sporotheca: grayish-white, scattered to gregarious, globose to depressed sporangia (0.3-0.4 mm). Peridium: membranous and grayish-white; covered with compact grayish-white lime crystals; floccose at maturity. Capillitium: profuse, slender subhyaline threads; sparsely branching and anastomosing. Spores: globose (6-7 µm); minutely warted with clustered patches; black (in mass) or violaceous (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – India (Delhi), one collection.

Similar species – *D. clavus* - has a large discoid sporangium, no columella, a dark peridium, and nearly smooth spores; *D. lenticulare* - has a longer stalk, no columella, and larger spores; *D. chryso sporum* – has a larger sporangium, whitish columella, larger spores, and a non-striate stalk.

Remarks – this taxon appears to be based on a developmental aberrant of an uncertain species; most likely *D. floccosum*.

***Didymium dictyopodium*** Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch. C 89: 230. 1986.

Types – Yamamoto (1617), Nannenga-Bremekamp, TNS

Hypothallus – discoid; membranous and dark-brown (containing refuse matter). Stalk: long (up to 1 mm); slender, striate and tapering; grayish-white and covered with lime crystals. Columella: thickened basal plate in a shallow open umbilicus. Sporotheca: white to grayish-white, gregarious, discoid sporangia (0.6-0.8 mm wide, 0.1-0.3 mm thick). Peridium: membranous and hyaline (areolate can be seen with the scanning electron microscope); covered with white stellate lime crystals which often form a wrinkled scale-like crust; often floccose at maturity. Capillitium: profuse, slender, hyaline to pale-brown threads; branching and anastomosing. Spores: globose (9-11 µm); densely and minutely warted with small clusters of large darker warts (pilate by SEM); nearly black (in mass) or pale-purple-brown (in transmitted light).

Plasmodium: white phanero-plasmodium. Habitat: on litter.

Distribution – Asia, South America (may be tropical), fairly common.

Similar species – *D. lenticulare* - has a coarser capillitium and no stalk reticulations; *D. squamulosum* – has shorter thicker stalks and a globose columella.

Remarks – part of the *D. squamulosum* complex; probably has a prior name, but the large number of synonymies in this complex makes it extremely difficult to decide what the valid name would be.

***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: white to cream colored, scattered, discoid sporangia (0.3-0.8 mm). 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  $\mu\text{m}$ ); 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, this taxon will be considered a developmental aberration, possibly of *D. vaccinum*.

***Didymium eremophilum*** M. Blackw. & Gilb., Mycologia 72: 791. 1980.

Types – BPI (Blackwell 79-017), NY, TX, K.

Hypothallus – discoid, membranous and hyaline. Stalk: proportionally long (0.03 mm); tapering; tan to reddish-brown. Columella: none; stalk attached to a thickened basal plate; no umbilicus. Sporotheca: small, tan, scattered globose sporangia (0.06-0.07 mm). Peridium: membranous and hyaline; covered with oval crystalline scales consisting of rectangular lime crystals. Capillitium: none. Spores: globose (9-11  $\mu\text{m}$ ); echinulate on one hemisphere and darker spiny-reticulate on the other; dark-brown (in mass) or violet-brown (in transmitted light). Plasmodium: minute, colorless to tan phaneroplasmodium producing a single sporangium. Habitat: on dead cacti.

Distribution – Arizona and Mexico, two collections.

Similar species – none.

Remarks – possibly a dwarf biotype; but its distinct morphology makes it an acceptable species.

***Didymium eximium*** Peck, Annual Rep. New York State Museum 31: 41. 1879.

= *Didymium nigripes* var. *eximium* (Peck) Lister, Monogr. Mycetozoa 98. 1894.

Types – none known.

Hypothallus – discoid, membranous and brown. Stalk: long (0.8-1 mm); striate; light-red-brown (black at base from dirt). Columella: yellow basal plate usually covered with a layer of orange-brown lime (may form a pseudocolumella) in a closed umbilicus. Sporotheca: pale-gray to pale orange-brown, gregarious, depressed to saddle-shaped sporangia (0.3-0.8 mm). Peridium: membranous and hyaline to pale-orange-brown; covered with small white to orange-brown stellate lime crystals. Capillitium: sparse, hyaline to lilac-brown threads; rarely dichotomously branching with a few cross bars. Spores: globose (9-10  $\mu\text{m}$ ); densely and evenly covered with very small warts (almost smooth); dark-brown (in mass) or pale-lilac-brown (in transmitted light). Plasmodium: brown to yellow phaneroplasmodium. Habitat: on litter and soil.

Distribution – cosmopolitan, but not common.

Similar species – *D. megalosporum* - has larger lime crystals.

Remarks – this taxon is part of the *D. megalosporum* species complex.

***Didymium floccoides*** Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch. C 90: 323. 1987.

= *Didymium columella-cavum* Hochg., Gottsb. & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 92: 73. 1989.

Types – TNS, Yamamota (3422), Nannenga-Bremekamp (14.833).

Hypothallus – discoid, membranous and orange-brown to dark-brown; containing refuse matter. Stalk: short to intermediate (0.1-0.4 mm); slender, rugulose; orange-brown and consisting of somewhat rounded crystalline lime and refuse matter, darker at the base. Columella: conical to clavate in a closed umbilicus; white to dark-brown, filled with lime and air. Sporotheca: white to gray, gregarious, conical to depressed globose sporangia (0.3-0.6 mm wide, 0.3-0.4 mm thick).

Peridium: membranous and hyaline to purplish-brown with a colorless reticulum; covered with white stellate lime crystals; dehiscing into platelets. Capillitium: profuse and delicate threads; hyaline to pale-purplish-brown with pale attenuated tips; sparsely dichotomously branching and anastomosing. Spores: globose (7-8  $\mu\text{m}$ ); minutely warted with some small dark groups of warts (baculate by SEM); brown to dark-brown (in mass) or pale-brown (in transmitted light).

Plasmodium: unknown. Habitat: on litter.

Distribution – Japan and Brazil, rare.

Similar species – *D. floccosum* - has a larger floccose sporangium, darker capillitium, a tube stalk, and darker warted spores.

Remarks – a core stipe species lacking a stipe tube.

***Didymium floccosum*** G.W. Martin, K.S. Thind & Rehill, Mycologia 51: 160. 1959.

= *Didymium chryso sporum* T.N. Lankh. & K.G. Mukerji, Acta Bot. Indica 6(Suppl.):16. 1978.

= *Didymium dehlianum* T.N. Lankh. & K.G. Mukerji, Acta Bot. Indica 6(Suppl.): 18. 1978.

Types – BPI (Thind 250).

Hypothallus – discoid, inconspicuous and membranous; containing refuse matter. Stalk: long (0.5-0.7 mm); white, smooth and tapering; consisting of lime inside a stalk tube. Columella: rather small and clavate; dark-brown to black; containing lime. Sporotheca: white gregarious, globose to depressed globose sporangia (0.4-0.6 mm wide, 0.3-0.4 mm thick). Peridium: membranous and purplish-brown with colorless reticula; covered with grayish-white crystals; dehiscing at maturity into small minute scales attached to the capillitium. Capillitium: profuse and delicate, hyaline to purplish-brown threads with pale tips; sparingly dichotomously branching and anastomosing. Spores: globose to broadly oval (8-10  $\mu\text{m}$ ); densely (often clustered) warted (pilate by SEM); black to dark-brown (in mass) or purplish-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Galapagos Islands, India, Japan, Mexico, and Venezuela, rare.

Similar species – *D. squamulosum* – has no internal stalk lime (external white lime), lacks peridial scales, and has smaller warts on the spores; *D. floccoides* – lighter capillitium and spores, does not have a stalk tube.

Remarks – may be a subtropical to tropical species.

***Didymium haretianum*** T.N. Lakh. & K.G. Mukerji, Acta Bot. Indica 6(Suppl.): 18. 1979.

Types – Univ. Delhi (TNL 453) (NA), Nannenga-Bremekamp.

Hypothallus – small to large; yellowish-brown and calcareous. Stalk: long (0.7-0.8 mm) to short; fluted and calcareous; yellow-orange to yellowish-brown. Columella: discoid to globular to irregular, small to large, rough, and yellowish-brown. Sporotheca: white, gregarious to clustered, globose to irregular sporangia (0.5-0.6 mm). Peridium: membranous, adhering to a thick shining white to cream-colored layer (egg-shell) of lime crystals (sometimes floccose). Capillitium: profuse, stout, hyaline flattened thread; sparingly branching and anastomosing. Spores: globose (7.5-9.3  $\mu\text{m}$ ); large dense sub-reticulum of warts; black (in mass) or dark-purple-brown (in transmitted light). Plasmodium: unknown. Habitat: on wood.

Distribution – India (H.P.), one collection.

Similar species – *D. vaccinum* – has shorter stalks, no duplex peridium, partly calcareous capillitium, no peridial collar, and the spores are not-sub-reticulate.

Remarks – until further collections are made we will consider this to be a developmental aberrant of *D. vaccinum*.

***Didymium infundibuliforme*** D. Wrigley, Lado & Estrada, in Wrigley de Basanta D, Estrada-Torres A, & Stephenson SL. Mycologia 708. 2009.

Types – Lado 18374 (MA-Fungi 78320)

Hypothallus – inconspicuous and membranous. Stalk: short (0.04-0.05 mm) stout and yellowish-white; calcareous with both external and internal lime. Columella: none, but a thickened

base is present where the stalk flares to form the funnel shaped sporotheca. Sporotheca: white to grayish, scattered to gregarious, obconic sporangia with an invaginated apex to form a funnel (0.2-0.6 mm high). Peridium: membranous and hyaline to yellowish-white; covered with a roughened layer of stellate white lime crystals; circumscissile dehiscence to form an operculum. Capillitium: straight to undulating grayish-reddish-brown to grayish-brown threads; branching and anastomosing with cross bars. Spores: subglobose (11-15  $\mu\text{m}$ ); warty (bacula forming an irregular network by SEM); black (in mass) or grayish-reddish-brown to grayish-brown (in transmitted light). Plasmodium: small hyaline to milky white phaneroplasmodium. Habitat: on dead leaf bases of *Puya* and *Copiapoa* spp. in arid regions.

Distribution – northwestern Argentina and northern Chile, rare.

Similar species – *D. umbilicatum* – sessile and does not have a real funnel shape; *D. operculatum* – does not have a funnel-shaped sporotheca and the spores are warty.

Remarks – this taxon appears to be a rather unique desert species

***Didymium intermedium*** J. Schröt., in Hennings, Hedwigia 35: 209. 1896.

= *Didymium excelsum* Lister, in Jahn, Ber. Deutsch. Bot. Ges. 20: 275. 1902.

Types – none known.

Hypothallus – extensive and branching, membranous, white and calcareous. Stalk: long (1-1.3 mm), smooth, filled with coarse non-stellate lime crystals; white to pale-yellow to orange-brown. Columella: discoid in a closed umbilicus. Sporotheca: white, gregarious to united, globose to discoid sporangia (0.4-0.7 mm). Peridium: membranous, fragile and hyaline; densely covered with a white to grayish-white powdery layer of stellate lime crystals. Capillitium: profuse, delicate, and hyaline threads; dichotomously branching and anastomosing. Spores: globose (10-12  $\mu\text{m}$ ); covered with long spines arranged to form a partial reticulum; black (in mass) or dark-violaceous-brown (in transmitted light). Plasmodium: dirty-white phanero-plasmodium. Habitat: on litter and mossy wood.

Distribution – widespread (Asia, Madagascar, South America, US), but rare.

Similar species – *D. laccatipes* - has separate sporangia and pilate spores; *D. floccosum* – has separate sporangia and a dark clavate columella.

Remarks – a conspicuous and distinct species, which is rarely collected; however, DNA studies (Wrigley de Basanta et al. 2015) indicate that a specimen of this taxon is very close to some *D. squamulosum* specimens.

***Didymium iridis*** (Ditmar) Fr., Syst. Mycol. 3: 120. 1829.

= *Cionium iridis* Ditmar, in Sturm, Deutschl. Fl. pilze 1: 13. 1812.

= *Cionium xanthopus* Ditmar, in Sturm, Deutschl. fl. Pilze 1: 87. 1816.

*Didymium xanthopus* (Ditmar) Fr., Syst. Mycol. 3: 120. 1829.

*Physarum xanthopus* (Ditmar) Schwein., Trans. Amer. Philos. Soc. 4: 257. 1832.

*Didymium nigripes* var. *xanthopus* (Ditmar) Lister, Monogr. Mycetoza 98. 1894.

= *Didymium pertusum* Berk., in Smith, Engl. Fl. 5: 313. 1836.

= *Didymium verrucisporum* [“verrucosporum”] A.L. Weldon, Mycologia 46: 98. 1954.

= *Didymium bahiense* Gottsb., Nova Hedwigia 15: 365. 1968.

Types – none known.

Hypothallus – discoid and inconspicuous; membranous and brown. Stalk: long (up to 1 mm), somewhat tapered and striate; light-yellow to pale-reddish brown (may be dark brown under some conditions). Columella: variable discoid to globose in a usually closed umbilicus; white to grayish-white. Sporotheca: white to grayish-white, gregarious, globose to depressed globose sporangia (0.3-0.7 mm). Peridium: membranous and hyaline to pale-brown (areolae can be seen with the scanning electronic microscope); covered with white stellate lime crystals. Capillitium: profuse and hyaline to pale-yellow-brown (with pale tips) threads; branching and rarely anastomosing. Spores: globose (7-9  $\mu\text{m}$ ), faintly warty to nearly smooth (pilate by SEM); brown (in mass) or pale-

purplish-brown (in transmitted light). Plasmodium: usually a brown phaneroplasmodium, but varies to yellowish to pale tan. Habitat: on litter, wood, dung and soil.

Distribution – cosmopolitan and very common.

Similar species – *D. nigripes* - darker stalks, columella and spores.

Remarks – the central species in the iridis group; consist of many biological species and clonal lines that have considerable variations and morphologically merge into other valid species; G. Lister (Lister 1925) considered that the variants in this super complex were all part of *D. nigripes*; a sensible disposition when based solely on morphology.

***Didymium karstensis*** 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: white to pale yellow, gregarious, subglobose to depressed sporangia (0.5-0.7 mm, rarely up to 1.2 mm). Peridium: membranous; hyaline (somewhat iridescent) with brownish areolae; 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  $\mu\text{m}$ ), 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 – the unique characters of this taxon could easily be due to developmental problems.

***Didymium laccatipes*** J. Matsumoto, in Matsumoto & Duguchi, Mycotaxon 70: 154. 1999b.

Types – HIRO (Matsumoto 150), TNS.

Hypothallus – membranous; hyaline to pale-orange-brown. Stalk: short to intermediate (0.3-0.6 mm); glossy, nearly smooth, white to very pale-orange-brown, and filled with rhombic lime crystals. Columella: conical in a closed umbilicus; white to very pale-orange-brown, containing lime crystals. Sporotheca: grayish-white, gregarious, depressed globose to discoid sporangia (0.4-0.6 mm). Peridium: membranous and purplish-brown to pale-orange-brown, with colorless reticulations; covered with white stellate lime crystals. Capillitium: profuse, hyaline to very pale-purplish-brown threads; sparsely dichotomously branching and rarely anastomosing. Spores: globose (9-11  $\mu\text{m}$ ), strongly warted with dark clusters (pilate by SEM); dark-brown (in mass) or pale-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Japan, US, four collections.

Similar species – *D. squamulosum* - has lime on the stalk surface, no lime crystals in stalk, and the spores are less warted.

Remarks – very similar to *D. squamulosum*, but distinct enough to be a valid species; may be widespread.

***Didymium laxifilum*** [“*laxifila*”] G. Lister & Ross, in G. Lister, Essex Nat. 27: 264. 1945.

= *Didymium aurantipes* T.E. Brooks & Kowalski, Mycologia 58: 169. 1966.

Types – BM (3500), K (Lister & Howard 3501).

Hypothallus – large, discoid, membranous and yellowish-brown to brown. Stalk: generally short (0.5-1.2 mm); translucent and reddish-brown to golden. Columella: generally a large white conical to stalked-hemisphere in a shallow or closed umbilicus (occasionally small to nearly absent); containing lime. Sporotheca: white to grayish-white, gregarious, subglobose to more or less flattened sporangia (0.5-0.8 mm). Peridium: membranous and dark-brown to hyaline with yellowish spots above; densely coated with rather large aggregates of white to yellowish lime crystals. Capillitium: profuse, coarse, hyaline to brown threads which may bear numerous swelling, and have flattened junctions; branching and anastomosing to form a firm reticulum. Spores:

globose (8-12  $\mu\text{m}$ ), densely and minutely warted with a nearly smooth area (verrucose by SEM); black to dark-purple (in mass) or dark-purplish-brown to brown (in transmitted light). Plasmodium: yellow phaneroplasmodium. Habitat: on litter.

Distribution – widespread (Curacao, Chile, England, Spain, California), but rather rare.

Similar species – *D. squamulosum* - has a calcareous stalk and thin capillitia; *D. crustaceum* – has a crustose lime covered peridium; *D. rubropus* – has rounder less firm capillitia.

Remarks – Moreno et al. (1997b) re-described this species and designated a type.

***Didymium leoninum*** Berkeley & Broome, J. Linn. Soc., Bot. 14: 83. 1873.

≡ *Lepidodermopsis leonina* (Berk. & Broome) Höhn., Akad. Wiss. Wien. Sitzungber. Math. – Naturwiss. 118: 439. 1909.

Types – K [K(M)53675].

Hypothallus – cartilaginous, discoid and inconspicuous; orange-yellow, may be frosted with lime. Stalk: short (0.2-0.6 mm), cartilaginous, stout, orange-yellow to buff, frosted with large rhombic lime crystals; spongy internal core containing lime crystals. Columella: globose to hemispheric, in a close umbilicus; brownish-orange to dark-brown; spongy interior material. Sporotheca: white to buff to orange, scattered to gregarious, globose to depressed globose sporangia (0.5-1 mm). Peridium: cartilaginous, glossy-dark-brown to chestnut-brown with thinner yellow lines of dehiscence (breaks up into scale-like fragments); covered with white to buff to orange deposits of large stellate lime crystals. Capillitium: profuse, dark-purplish-brown threads with pale tips; sparsely dichotomously branching and anastomosing. Spores: globose (7-9  $\mu\text{m}$ ), minutely warts arranged in lines (incomplete cristae of bacula by SEM); dark-brown to black (in mass) or dark-purplish-brown (in transmitted light). Plasmodium: orange-red phaneroplasmodium. Habitat: on litter.

Distribution – widespread (Germany, Mexico, Tanzania, Japan, Madagascar, tropical Asia), but rare.

Similar species – *Lepidoderma tigrinum* - has platelets of crystalline lime, and larger darker spores.

Remarks – the plasmodiocarpic form has been described as a new species: *D. panniforme*.

***Didymium lenticulare*** K.S. Thind & T.N. Lakh., Mycologia 60: 1083. 1968.

Types – Thind #453.

Hypothallus – discoid and dark-brown. Stalk: long (1-1.8 mm), tapered and striate; deep-brown (lighter above) and scantily sprinkled with lime crystals on the lower portion. Columella: none. Sporotheca: white, gregarious, discoid sporangia (0.5-0.8 mm). Peridium: membranous, thin, hyaline to translucent; covered with minute white lime crystals forming thick ridges and small to large thin platelets. Capillitium: profuse, stout, subhyaline threads with bead-like nodular thickenings; sparsely branching and anastomosing. Spores: globose (9-11  $\mu\text{m}$ ), distinctly warted with larger and darker clusters of warts; black (in mass) or deep-violaceous-brown (in transmitted light). Plasmodium: unknown. Habitat: on living fern fronds.

Distribution – India (H.P.), single collection.

Similar species – *D. clavus* – has a dark peridium covered with a uniform lime layer, shorter stalks, and nearly smooth smaller spores.

Remarks – possibly a developmental aberrant of *D. dictyopodium*.

***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 short (up to 0.5 mm), reddish and fibrous. Columella: hemispheric and white, in a closed umbilicus. Sporotheca: white, scattered to gregarious, globose to ovoid sporangia (0.4-0.8 mm) to plasmodiocarpous (up to 2.5 mm long). 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  $\mu\text{m}$ ); 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, however, the spore and capillitium differences make this an acceptable specialized taxon.

***Didymium macrospermum*** Rosaf., Sluzowce Mongr. 161. 1874.

= *Didymium macrospermum* var. *leiosporum* L.F. Čelak., Arch. Naturwiss. Landesdurchf. Böhmen 7: 63. 1893.

Types – none known.

Hypothallus – discoid, membranous and white. Stalk: long (1-1.5 mm); white to pale-orange-brown; containing lime. Columella: discoid to globose; white. Sporotheca: white to yellowish, gregarious, irregularly globose sporangia (0.3-1 mm). Peridium: membranous and hyaline to pale-orange-brown; covered with white to yellowish crystalline lime. Capillitium: profuse, slender to coarse, hyaline to brown threads; dichotomously branching and rarely anastomosing. Spores: globose (12.5-13.5  $\mu\text{m}$ ); spinulose; dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Europe.

Similar species – *D. pertusum* - has spores with small warts.

Remarks – an uncertain taxon.

***Didymium marineri*** G. Moreno, Illana & Heykoop, Myxotaxon 34: 630. 1989.

Types – H.AH (U. Alcalá de Henares, Botany) 11040, Nannenga-Bremekamp 16.066.

Hypothallus – discoid, membranous and brown. Stalk: short (0.3-0.4 mm), yellowish to reddish-brown. Columella: discoid to globose, in a closed umbilicus; white. Sporotheca: white, scattered, globose to depressed globose sporangia (0.5-0.7 mm). Peridium: membranous and hyaline; covered with abundant grayish-white lime crystals. Capillitium: profuse, hyaline to light-yellowish-brown threads; dichotomously branching and rarely anastomosing. Spores: globose (9-10  $\mu\text{m}$ ); densely and minutely warted with darker clusters (pilate by SEM); brown (in mass) or pale-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Spain, Japan, Saudi Arabia, rare

Similar species – *D. squamulosum* - has lime on stalk.

Remarks – a developmental form of *D. squamulosum* which lacks lime on its stalk.

***Didymium martinii*** (T.N. Lakh.) H. Neubert, Nowotny & K. Baumann, Myxomycetes 2: 139. 1995.

≡ *Lepidodermopsis martinii* T.N. Lakh. 1978. Norweg. J. Bot. 25: 196.

Types – Univ. Delhi Herbarium Mycologicum; Nannenga-Bremekamp.

Hypothallus – cartilaginous, black and discoid. Stalk: long (1-1.2 mm), striate and dark. Columella: subglobose in a closed umbilicus; brown and containing lime. Sporotheca: ash-gray, scattered, globose to subglobose sporangia (0.5-0.7 mm). Peridium: cartilaginous, shining, yellowish-brown to brown (purplish-brown with spore mass); dehiscence at paler rupture lines; covered with white stellate lime crystals. Capillitium: profuse, stout, orange-brown (hyaline and flattened at the base) threads with pale tips; branching and anastomosing to form a lax network. Spores: globose (10.5-11  $\mu\text{m}$ ); strongly warted with a thinner hyaline area on one side; black (in mass) or deep-violet-brown (in transmitted light). Plasmodium: unknown. Habitat: on wood.

Distribution – India (Simla), single collection.

Similar species – *D. leoninum* – has a short calcareous stalk sporangium or plasmodiocarp, purplish-brown peridium, and smaller minutely warted spores.

Remarks – Neubert, Nowonty & K. Baumann 1995 did not accept *Lepidodermopsis* and placed this taxon in *Didymium*; we consider this to be a developmentally abnormal *D. nigripes*.

***Didymium megalosporum*** Berk. & M.A. Curtis, in Berk. Grevillea 2: 53. 1873.

= *Didymium eximium* Peck Annual Rep. New York State Mus. 31: 41. 1879.

*Didymium nigripes* var. *eximium* (Peck) Lister, Monogr. Mycetozoa 98. 1894.

= *Didymium fulvellum* Masee, Monogr. Myxogastr. 237. 1892.

= *Didymium elegantissimum* Masee, Monogr. Myxogastr. 243. 1892.

= *Didymium discoideum* K.S. Thind & H.S. Sehgal, Mycologia 56: 566. 1964.

= *Didymium crassicolle* Ing, Trans. Brit. Mycol. Soc. 76: 443. 1982.

= *Didymium carnariense* Ing, Stapfia 73: 95. 2000

Types – Curtis 1205, K

Hypothallus – discoid; membranous and brown. Stalk: long (up to 1 mm), striate, translucent, yellow-brown to orange-brown (base darker). Columella: subglobose to discoid, in a closed (usually) umbilicus; sometimes rough or spiny; dull yellow to orange-brown, containing lime. Sporotheca: white to orange-brown, gregarious, depressed-globose to discoid to saddle-shaped sporangia (0.5-0.8 mm wide, 0.4-0.5 mm deep). Peridium: membranous and hyaline to pale-yellow to pale-orange; sparsely (usually) covered with white to yellowish lime crystals. Capillitium: profuse, pallid to pale-orange-brown threads; sparsely dichotomously branching and anastomosing. Spores: globose (8-12 µm); minutely warted to nearly smooth (pilate by SEM); dark-brown to black (in mass) or pale-brown (in transmitted light) Plasmodium: brown phaneroplasmodium. Habitat: on leaves and litter.

Distribution – cosmopolitan but not common.

Similar species – *D. nigripes-iridis* complex – have more globose sporangia which are never yellowish, and no columella spines.

Remarks – a species complex which grades morphologically into *D. iridis*.

***Didymium melanospermum*** (Pers.) T. Macbr., N. Amer. Slime-moulds 88. 1899.

≡ *Physarum melanospermum* Pers., Neues Mag. Bot. 1: 88. 1794

= *Didymium farinaceum* Schrad., Nov. Gen. Pl. 22. 1797.

*Physarum farinaceum* (Schrad.) Pers., Syn. Meth. Fung. 174. 1801.

*Physarum farinaceum* var. *globosum* Alb. & Schwein., Cosp. Fung. Lusat. 96. 1805.

*Trichia farinocea* (Schrad.) Poir., in Lamarck, Encycl. 8. 1808.

*Cionium farinaceum* (Schrad.) Gray, Nat. Arr. Brit. Pl. 1: 571. 1821.

= *Trichia compressa* Trentep., in Roth, Catal. Bot. 1; 229. 1797.

= *Trichia sphaerocephala* Sowerby, Col. Fig. Engl. Fung. 240. 1799.

= *Physarum farinaceum* var. *globosum* Alb. & Schwein., Consp. Fung. Lisat. 1805.

= *Physarum capitatum* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamnten Naturk. 3: 27. 1809.

= *Physarum sinuosum* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamnten Naturk. 3: 27. 1809.

*Didymium sinuosum* (Link) Durieu & Mont., in Durieu et al., Fl. Algérie 1: 411. 1846-69.

= *Cionium lobatum* Spreng., Syst. Veg. 4: 529. 1827.

*Didymium lobatum* (Spreng.) Schwein., Trans. Amer. Philo. Soc. 4: 257. 1832.

*Didymium lobatum* Nees, System. Pilze 112. 1816.

= *Didymium nigrum* Fr., Syst. Mycol. 3: 146. 1829.

= *Didymium farinaceum* var. *confluens* Rostaf., Sluzowce Monogr. 155. 1874.

= *Didymium farinaceum* var. *rufipes* Rostaf., Sluzowce Monogr. 155. 1874.

= *Didymium farinaceum* f. *nigrum* Rostaf., Sluzowce Monogr. 155. 1874.

= *Didymium farinaceum* f. *subsessile* Rostaf., Sluzowce Monogr. 155. 1874.

- = *Didymium fairmanii* Sacc., in Fairman, J. Mycol. 5: 78. 1889.
- = *Didymium melanospermum* var. *bicolor* G. Lister, in Lister, Monogr. Mycetozoa ed. 3 115. 1925.
- = *Didymium melanospermum* f. *erythropus* Buchet, Bull. Soc. Mycol. France 57: 115. 1942,
- = *Didymium melanospermum* f. *calcipes* Y. Yamam. & Shuan L. Chen, in Yamamoto, Chen, Degawa & Hagiwara, Bull. Natl. Sci. Mus. B 28: 69. 2002.
- = *Didymium angularisporum* J. Matsumoto, in Matsumoto & Deguchi, Mycotaxon 70: 157. 1999b.

Types – none known.

Hypothallus – discoid, membranous and dark-brown. Stalk: short (0.2-0.5 mm), stout, striate; dark-brown to black. Columella: globose to discoid; dark-brown; containing lime crystals. Sporotheca: white to grayish-white, gregarious, globes to depressed-globose sporangia (0.5-1 mm wide, 0.4-1 mm thick). Peridium: membranous, firm and purplish-brown with colorless reticula; covered with white or grey lime crystals. Capillitium: profuse, rigid, hyaline to purplish-brown threads; sparingly dichotomously branching and anastomosing. Spores: globose (10-14 µm); strongly warty (pilate by SEM); dark-brown to black (in mass) or dull-purplish-brown (in transmitted light). Plasmodium: white or dull-gray phaneroplasmodium. Habitat: on wood (pine) and litter.

Distribution – cosmopolitan and fairly common

Similar species – *D. nigripes* – less robust sporangia with longer thinner stalks, lighter and less marked spores; *D. minus* – less robust sporangia, and has smaller and paler spores.

Remarks – this is a confusing species, due to its rather general morphology.

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

Types – Alcalá de Henares (AH), Nannenga-Bremekamp.

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 or (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); warty and somewhat reticulate (crestae of branched bacula by SEM); dark-purple-brown (in mass) or purple-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter (agave and yucca), in desert.

Distribution – Mexico, rare

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

Remarks – a rare desert “spore” species.

***Didymium minus*** (Lister) Morgan, J. Cincinnati Nat. Hist. 16: 145. 1894.

≡ *Didymium farinaceum* var. *minus* Lister, Monogr. Mycetozoa 97. 1894.

= *Didymium melanospermum* var. *minus* (Lister) G. Lister, in Lister, Monogr. Mycetozoa ed. 2. 129. 1911.

= *Didymium melanospermum* var. *minus* (Lister) Dearn. & House, New York State Mus. Bull. 266: 58. 1925.

?= *Didymium humile* Hazst., Oesterr. Bot. 27: 84. 1877.

Types – BM (1334) (see Lado & Wrigley de Basanta 2018).

Hypothallus – discoid, membranous and dark-brown. Stalk: short (0.2-0.7 mm), striate, and brown to black; containing refuse matter. Columella: clavate to depressed-globose in a closed umbilicus; rough, dark-brown to sordid-white; containing lime. Sporotheca: white to grayish-white, gregarious, globose to depressed-globose sporangia (0.4-0.6 mm wide, 0.4-0.5 mm thick). Peridium: membranous and purplish-brown with colorless reticula; covered with white lime crystals. Capillitium: profuse, hyaline to purplish-brown threads; dichotomously branching and

rarely anastomosing. Spores: globose (8-11 µm), minutely and densely warted (pilate by SEM); dark-brown to black (in mass) or purplish-brown (in transmitted light).

Plasmodium: dark-purplish-gray phaneroplasmodium. Habitat: on wood (dead bark) and litter.

Distribution – cosmopolitan and fairly common.

Similar species – *D. melanospermum* - has a more robust sporangium, darker stalk and capillitium, and larger spores.

Remarks – the present species concept is a mixed bag, with some specimens identified as *D. minus* being short stalked members of the *D. iridis* complex, and some of the rest being small variants of *D. melanospermum*.

***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: white, gregarious, globose sporangia (0.4-0.6 mm). 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. karstenii* – has a double peridium, and reticulate ridged spores; *D. squamulosum* – has smaller minutely warted spores, and hyaline or pallid capillitia.

Remarks – this taxon appears to be a valid “spore” species.

***Didymium nigripes*** (Link) Fr., Syst. Mycol. 3: 119. 1829.

≡ *Physarum nigripes* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamnten Naturk. 3: 27. 1809.

= *Physarum microcarpon* Fr & Palmquist, Symb. Gastrumyc. 23. 1818.

*Didymium microcarpon* (Fr & Palmquist.) Rostaf., Sluzowce Monogr. 157. 1874.

= *Didymium microcephalum* Chevall., Fung. Byss. Illustr. 1. f. 2. 1837.

= *Didymium wallrothii* Rabenh., Deutschl. Krypt.-Fl. 1: 281. 1844.

= *Didymium porphyropus* Durieu & Mont., in Durieu et. al., Exp. Sci. Algérie 1: 409. 1846-69.

= *Didymium tenue* Pat. & Gaillard., Bull. Soc. Mycol. France 4: 96. 1888.

= *Didymium microcarpon* var. *leucotrichum* L.F. Čelak., Arch. Naturwiss. Landesdurchf. Böhmen 7: 60. 1893.

=? *Lepidodermopsis martini* T.N. Lakh., Norweg. J. Bot. 25: 196. 1978.

*Didymium martini* (T.N. Lakh.) H. Neubert, Nowotny & K. Baumann, Myxomyceten 2: 139. 1995.

Types – none known.

Hypothallus – discoid, membranous, and dark-brown to black. Stalk: long (0.5-1.2 mm), striate, and brown to blackish; often filled with refuse matter below, but translucent above. Columella: subglobose to discoid in a usually closed umbilicus; brown and containing lime. Sporotheca: white to grayish-white, gregarious, globose to depressed globose sporangia (0.3-0.6 mm). Peridium: membranous and pale-purplish-brown with colorless reticula; covered with white stellate lime crystals. Capillitium: profuse, hyaline to brown threads; sparingly dichotomously branching and rarely anastomosing. Spores: globose (7-10 µm), minutely warted (pilate by SEM); brown to dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: dark-reddish-brown phaneroplasmodium. Habitat: on litter and wood.

Distribution – cosmopolitan and common.

Similar species – *D. iridis* – has a lighter stalk and columella; *D. megalosporum* – has a yellowish-brown sporangium and spiny columella.

Remarks – considered to be common, but many collections labeled *D. nigripes* are actual dark forms of *D. iridis*.

***Didymium nigrisporum*** Nann.-Bremek., K.G. Mukerji & Pasricha, Proc. Kon. Ned. Akad. Wetensch. C 87: 478. 1984.

Types – Mukerji DU/KRP 558, Nannenga-Bremekamp 13.768.

Hypothallus – discoid, membranous, and orange-brown; hidden by the sporotheca. Stalk: short (0.1 mm), off-white to pale-orange-brown; filled with lime crystals. Columella: subglobose to depressed, in a closed umbilicus; orange-brown; filled with lime. Sporotheca: white, gregarious, depressed globose to hemispherical sporangia (0.9 mm wide, 0.3-0.4 mm thick). Peridium: membranous and hyaline to pale-yellow, with thickened areolae; densely covered with white stellate lime crystals. Capillitium: fairly sparse, slender, lilaceous-brown threads with membranous expansions at the axils; dichotomously branching with cross-bars. Spores: subglobose and slightly angular from mutual pressure (11.5-12.5  $\mu\text{m}$ ); densely, minutely and irregularly warted; black (in mass) or very dark-purple-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – India, Peru.

Similar species – *D. muscorum* and *D. squamulosum* – the spores lack the angular polygonal ridges.

Remarks – recent multiple collections from Peru validate this taxon.

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

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

= *Didymium wilczekii* f. *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: white, gregarious, depressed-globose sporangia to plasmodiocarpous (1-2 mm). 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  $\mu\text{m}$ ) and warted (Pilate by SEM); black (in mass) or brown (in transmitted light). Plasmodium: unknown. Habitat: on litter (Snowmelt).

Distribution – Japan, Europe, Chile, western US, 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 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: pale brown, gregarious, discoid to pulvinate sporangia (0.6-1 mm). 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  $\mu\text{m}$ ); 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, rare.

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

Remarks – Harkonen in “Additions and corrections to the Finnish flora of Myxomycetes” *Karsenia* 19: 3 (1979); found that *D. fulvum* was the same as *D. obducens*.

***Didymium operculatum*** D. Wrigley, Lado & Estrada, *Mycologia* 103: 806. 2011.

Types – Wrigley de Basanta 3142 (MA-Fungi 74050).

Hypothallus – inconspicuous, irregular and membranous; reddish-brown. Stalk: intermediate to long (0.1-0.6 mm), tapering and striate; with internal and external lime crystals; yellowish-white to pale-yellow to grayish-yellow. Columella: none. Sporotheca: light-gray to white, scattered, oblate sporangia with an operculum (0.2-0.8 mm wide, 0.2-0.4 mm deep). Peridium; membranous, hyaline to light-grayish-brown and iridescent; covered with stellate lime crystals; circumscissile dehiscence producing an operculum. Capillitium: light-gray-brown to hyaline threads; sparsely branching and anastomosing with cross-bars. Spores: globose (10-12  $\mu\text{m}$ ); reticulate (reticulum of muri with a second lighter reticulum by SEM); black (in mass) or brown to grayish-brown (in transmitted light). Plasmodium: milky to brownish phaneroplasmodium. Habitat: on dead *Copiopoa* spp.

Distribution – Northern Chile deserts.

Similar species – *D. reticulosporum* - has reticulate banded spores but lacks capillitia and is sessile; *D. infundibuliforme* - has warted spores and a funnel-shaped sporotheca.

Remarks – apparently a specialized desert species.

***Didymium ovoideum*** Nann.-Bremek., *Acta Bot. Neerl.* 7: 780. 1958.

Types – Nannenga-Bremekamp.

See – *D. proximum*.

***Didymium pertusum*** Berk., in Smith, *Engl. Fl.* 5: 313. 1836.

Types – none known.

Hypothallus – discoid and reddish. Stalk: long (1-2 mm), striate, and reddish; filled with crystalline lime nodules. Columella: subglobose, in a closed umbilicus; red-brown. Sporotheca: white, scattered to gregarious, subglobose sporangia (1 mm). Peridium: membranous and very-pale-yellow; dusted with small stellate lime crystals. Capillitium: profuse hyaline threads; sparsely dichotomously branching and anastomosing. Spores: globose (10-13  $\mu\text{m}$ ), with small warts; lilac-gray (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Europe, China, Madagascar, rare.

Similar species – *D. iridis* - does not have lime in stalk.

Remarks – a taxon which has long been considered to be part of the *D. iridis* complex; but its internal stalk lime indicates that it is probably a different taxon.

***Didymium peruvianum*** Lado, D. Wrigley & SL 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 sporangia (0.25-0.5 x 0.07-0.17 mm). 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  $\mu\text{m}$ ), 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. trachyosporum*, 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 which could be a *D. difforme* variant.

***Didymium projectile*** T.N. Lakh. & K.G. Mukerji, Rev. Mycol. 43: 190. 1979.

Types – Univ. Delhi (TNL 730), Nannenga-Bremekamp.

Hypothallus – discoid, sometimes confluent, membranous, calcareous and white. Stalk: short (0.2-0.5 mm), stout, strongly striate, calcareous (amorphous), and white. Columella: small to large, globose to discoid, in a closed umbilicus; calcareous and pallid-white. Sporotheca: white, gregarious, globose to discoid sporangia (0.5-0.8 mm). Peridium: membranous and hyaline; covered with white stellate lime crystals; floccose at maturity. Capillitium: profuse, stout and pale-violaceous to violaceous-brown threads (hyaline at base and tips); base wider and pitted, narrower and spirally twisted towards the apex; dichotomously branching and anastomosing. Spores: globose (9-10  $\mu\text{m}$ ), prominent thick warts forming clusters and appearing sub-reticulate in polar view; black (in mass) or deep-violet-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter and living fern fronds.

Distribution – India (Simla), Netherlands, both single collections.

Similar species – *D. floccosum* - has longer stalks, a dark columella, and a capillitium without a spiral apex; *D. intermedium* – has longer stalks, and a capillitium without spiral tips; *D. squamulosum* – has a usually non-floccose peridium, minutely warted spores, and a capillitium without a spiral tip.

Remarks – Without further collections, that support this taxon, it will be best to consider it a variant of *D. squamulosum*.

***Didymium proximum*** Berk. & M.A. Curtis, in Berkeley, Grevillea 2: 52. 1873.

= *Didymium ovoideum* Nann.-Bremek., Acta Botanica Neerlandica 7, 780. 1958.

Types – not known; Nannenga-Bremekamp (as *D. ovoideum*)

Hypothallus – discoid, membranous and pale-brown. Stalk: long (0.4-1 mm) striate, translucent, and red-brown. Columella: prolate to discoid, rugulose, in a closed umbilicus; yellowish or white with lime. Sporotheca: white, gregarious, prolate to globose (0.4-0.6 mm, wide, 0.6-1.5 mm deep) sporangia. Peridium: membranous, translucent and hyaline; covered with stellate white lime crystals. Capillitium: profuse, yellowish-brown (with pale tips) threads; dichotomously branching and anastomosing. Spores: globose (7-10  $\mu\text{m}$ ); irregularly and minutely warted (pilate by SEM); dark-brown (in mass) or pale-purple-brown (in transmitted light). Plasmodium: yellow phaneroplasmodium. Habitat: on litter and bark of living trees.

Distribution: cosmopolitan and probably common.

Similar species – *D. iridis* – has a lighter colored stalk, peridium and columella, globose sporotheca, and a cream to brown plasmodium.

Remarks – older collections would record this species as *D. iridis*, *D. nigripes*, or *D. melanosporum*; and newer records as *D. ovoideum*.

***Didymium pseudocolumellum*** H.Z. Li, Y. Li & Q. Wang, Mycosystema 8-9: 173. 1996.

Types – HMAS (69702).

Hypothallus – discoid and white. Stalk: short (0.1-0.3 mm) thick, striate, white and covered with lime crystals. Columella: globose brown pseudocolumella; the stalk attaches to the peridial base, no umbilicus. Sporotheca: white, gregarious, globose to pyriform sporangia (0.3-0.5 mm). Peridium: membranous, translucent and pale-brown; covered with white stellate lime crystals. Capillitium: profuse hyaline branching threads. Spores: globose (8-11  $\mu\text{m}$ ); warted, with the warts sometimes forming columns; black (in mass) or brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – China, single collection.

Similar species – *D. squamulosum* – has a true columella.

Remarks – without further collections, this collection will be considered a developmental abnormality of *D. squamulosum*.

***Didymium radiaticolumellum*** Bellido, G. Moreno, Mar. Mey. & J.F. Moreno, in Bellido, Moreno, Meyer & Castillo Bot.Soc. Micol. Madrid 17. 2017.

Types – AH 46064, 46118, MA-Fungi 89928.

Hypothallus – discoid and blackish. Stalk: intermediate (0.4 to 0.7 mm) consisting of a slightly tapered striate, yellowish-brown to reddish-brown cylinder, darker at the base, and lacking any lime or internal inclusions. Columella: a small pale yellow irregular globose structure in a close umbilicus, covered with a pseudocolumellar like arrangement derived from the abundant lime inclusions at the bases of the capillitial treads. Sporotheca: white, scattered or in small groups, depressed globose to subglobose (0.25-0.35mm high x 0.4 -0.5 mm wide) umbilicate sporangia. Peridium: membranous and yellowish, covered with prominent, large (20-50µm), loose lime crystals with long rays. Capillitium: profuse, flat, thick hyaline to pale yellow dichotomous branching threads with broad nodules of varying morphology and sizes (elongate, fusiform or polygonal) containing abundant lime formations; the lime filled nodules at the base of the threads clumped to form a pseudocolumellar like structure. Spores: globose to subglobose, (17-18 µm), finely warted to nearly smooth (small irregular warts by SEM), dark brown with a paler area. Plasmodium: unknown. Habitat: on fallen *Quercus* leaves.

Distribution – Spain (2 collections).

Similar species – *D. laxifilum* – lack the capillitial nodules containing lime, spores smaller (8-18µm); *D. megalosporum* – lack the flat capillitia with lime filled nodules, spore smaller (8-10µm); *D. rubropus* – has a delicate capillitium lacking lime filled nodules, spore small (9-11µm).

Remarks – we consider this taxon to be a developmental abnormality of *D. laxifilum*.

***Didymium rubropus*** [“*rubeopus*”] G. Moreno, A. Castillo & Illana, in G. Moreno, A. Castillo, Illana & Lizárraga II Int. Congr. Syst. Ecol. Myxomycetes 57. 1996.

= *Didymium rubropus* var. *albocapillitium* G. Moreno, A. Castillo, Illana & Lizárraga 1997b. Cryptog. Mycol. 18: 318.

Types – Univ. Alcalá (AH).

Hypothallus – forming an extended base; membranous and reddish-brown. Stalk: short to intermediate (0.4-1 mm), striate, translucent, and reddish-orange. Columella: globose to hemispherical, in a closed umbilicus; white. Sporotheca: white, scattered, globose to subglobose sporangia (0.4-1 mm). Peridium: membranous and hyaline; covered with abundant white lime crystals. Capillitium: profuse, delicate, flexuous, hyaline to dark-gray (hyaline tips) threads; sparsely dichotomously branching and rarely anastomosing. Spores: globose (9-11 µm); with small warts (pilate by SEM); black (in mass) or dark-violaceous (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – Spain, France, Mexico, rare.

Similar species – *D. laxifilum* – has a flatter thicker capillitium forming a net.

Remarks – Moreno et al. (1997a) separated this species from *D. laxifilum*.

***Didymium rugulosum*** Berk., London J. Bot 4: 308. 1845.

Types – none known.

Hypothallus – not known. Stalk: slender, straw-like and tapering at the apex (1.6 mm tall). Columella: none. Sporotheca: gregarious, discoid sporangium (0.8 mm diameter) with a closed basal umbilicus. Peridium: white and wrinkled. Capillitium: slightly white in color. Spores: black to brownish-purple. Plasmodium: unknown. Habitat: on bark.

Distribution – Ohio, one collection.

Similar species – not enough information to make a good comparison, but may be similar to *D. crassicolle*.

Remarks – a brief Latin description was provided by Berkeley (1845) and not mentioned since; we believe the description is too brief to identify any specimen, and therefore unless a type is found we will consider this taxon to be an uncertain species.

***Didymium simlense*** [“*simlensis*”] T.N. Lakh. & K.G. Mukerji, Rev. Mycol 43: 188. 1979.

Types – Univ. Delhi (TNL 455), Nannenga-Bremekamp.

Hypothallus – large; membranous and pallid to orange-brown. Stalk: long (0.8 mm); striate (fluted), filled with spherical or rhomboid lime granules; orange-brown to whitish. Columella: small thickened base to clavate, in a closed umbilicus; rough, calcareous, and orange-brown to yellowish. Sporotheca: ash-gray, scattered, globose to depressed globose sporangia (0.2-0.4 mm). Peridium: membranous and hyaline; covered with grayish-white lime crystals. Capillitium: profuse, pale-violaceous to subhyaline threads with pale tips and small membranous expansions at the branching points; sparingly dichotomously branching and anastomosing. Spores: globose (9.5-12.5 µm); large prominent spines arranged in lines; black (in mass) or purple-brown (in transmitted light). Plasmodium: unknown. Habitat: on litter.

Distribution – India (Simla), single collection.

Similar species – *D. intermedium* – has small dome-shaped columella, and confluent hypothalli; *D. karstenii* – has a double peridium, and smaller spores; *D. squamulosum* – has smaller minutely warted spores; *D. muscorum* – has shorter stalks, larger sporangia, spores and columella.

Remarks – an uncertain taxon, possibly related to *D. intermedium*.

***Didymium squamulosum*** (Alb. & Schwein.) Fr., Symb. Gastromyc. 19. 1818.

≡ *Diderma squamulosum* Alb. & Schwein., Consp. Fung. Lusat. 88. 1805.

*Cionium squamulosum* (Alb. & Schwein.) Spreng., Syst. Veg. 4: 528. 1827.

= *Diderma effusum* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamnten Naturk. 7: 42. 1815.

= *Licea stipitata* DC., in Lamarck & de Candolle, Fl. Franç. Ed. 3. 5: 101. 1815.

= *Tubulina pedicellata* Poir., in Lamarck & Poiret, Encycl. Suppl. 5: 373. 1817.

= *Didymium costatum* Fr., Syst. Mycol. 3: 118. 1829.

= *Didymium squamulosum* var. *costatum* (Fr.) Rosaf., Sluzowcw Monogr. 160. 1874.

= *Didymium herbarum* Fr., Syst. Mycol. 3: 120. 1829.

= *Physarum liceoides* Duby, Bot. Gall. Ed. 2: 861. 1830.

= *Didymium praecox* deBary, in Rabenhorst, Fungi Eur. Editio nova Ser. 2. No. 367. 1861.

= *Didymium radiatum* Berk. & M.A. Curtis, in Berkeley, J. Linn. Soc. Bot. 10: 348. 1868.

= *Didymium neglectum* Berkeley & Broome, J. Linn. Soc. Bot. 14:83. 1873.

= *Didymium fuckelianum* Rostaf., in Fuckel, Jahrb. Nassauischen Verins Naturk. 27-28: 73. 1873.

= *Didymium discoideum* Rostaf., Sluzowce Monogr. 162. 1874.

= *Chondrioderma cookie* Rostaf., Sluzowcw Monogr. Suppl. 17. 1874.

*Didymium cookie* (Rostaf.) Raunk., Bot. Tidsskr. 17: 86. 1890.

= *Didymium angulatum* Peck, Annual Rep. New York State Mus. 31: 41. 1879.

= *Didymium affine* Raunk., Bot. Tidsskr. 17: 88. 1890.

= *Didymium bonianum* Pat., J. Bot. (Morot) 5: 316. 1891.

= *Didymium effusum* var. *maculatum* L.F. Čelak., Arch. Naturwiss. Landesdurchf. Böhmen 7: 64. 1893.

= *Didymium squamulosum* var. *rufipes* L.F. Čelak., Arch. Naturwiss. Landesdurchf. Böhmen 7: 64. 1893.

= *Didymium squamulosum* var. *claviforme* Sturgis, Colorado Coll. Stud. Sci. Ser. 12: 27. 1907.

= *Didymium annulatum* T. Macbr., N. Amer. Slime-moulds ed. 2. 125. 1922.

- = *Didymium applanatum* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. C 75: 352. 1972.
- = *Didymium muscorum* T.N. Lakh. & K.G. Mukerji, Trans. Mycol. Soc. Japan 17: 123. 1976.
- = *Didymium simlense* T.N. Lakh. & K.G. Mukerji, Rev. Mycol. 43: 188. 1979.
- = *Didymium projectile* T.N. Lakh. & K.G. Mukerji, Rev. Mycol. 43: 190. 1979.
- = *Didymium marineri* G. Moreno, Illano & Heykoop, Myxotaxon 34: 630. 1989.
- = *Didymium pseudocolumella* H. Li, Y. Li & Q. Wang, Mycosystema 8-9: 173. 1996.
- = *Didymium balearicum* Ing, Stapfia 73: 94. 2000.

Types – none known.

Hypothallus – discoid, membranous and hyaline to white. Stalk: usually short to intermediate (0.3-1 mm), stout, striate, white to pale-orange; lime on the exterior and between the folded stalk tube membrane. Columella: discoid to globose; white to gray-white, containing lime. Sporotheca: white to grayish-white, gregarious, globose to discoid sporangia (0.3-1 mm). Peridium: membranous and hyaline to pale-orange brown; covered with a thick white crust of white stellate lime crystals (sometimes rugulose). Capillitium: profuse, slender to coarse, hyaline to brown threads; dichotomously branching and rarely anastomosing. Spores: globose (8-11 µm), minute warts which may be clustered (Pilate by SEM); dark-brown to black (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: white to yellowish phaneroplasmodium. Habitat: on litter, wood, dung and the bark of living trees.

Distribution – cosmopolitan and very common.

Similar species – *D. dictyopodium* – generally has a taller, thinner stalk, and a basal plate in a shallow umbilicus, instead of a columella.

Remarks – a large complex of biological sibling species and numerous asexual clones, with a general morphology (El Hage et al. 2000, Winsett & Stephenson 2008), this has produced a large number of taxonomic descriptions.

***Didymium subreticulosporum*** Oltra, G. Moreno & Illana, in G. Moreno, A. Castillo, Illana & Lizárraga, II Int. Congr. Syst. Ecol. Myxomycetes 57. 1996.

Types – Univ. Acala (AH 19047), Nannenga-Bremekamp.

Hypothallus – irregular, membranous and dark-brown. Stalk: short to intermediate (up to 1 mm), striate, somewhat flattened, dark-brown (red-brown in transmitted light). Columella: thick basal plate without an umbilicus; slightly granular and deep-brown. Sporotheca: grayish-white, gregarious, globose sporangia (0.5-1 mm), but sometimes fused or reniform (1 x 1.5-2.5 mm). Peridium: membranous and hyaline to pale-brown; areolae (when stained); covered with stellate white lime crystals. Capillitium: replaced by abundant delicate crystalline lime filaments. Spores: globose (8-11 µm); brokenly reticulate (cristae of fused verruca by SEM); black (in mass) or light-purplish-brown (in transmitted light). Plasmodium: whitish-brown phaneroplasmodium. Habitat: on decaying *Opuntia* cladodes.

Distribution – Canary Islands, Mexico, rare.

Similar species – *D. disciformis* – has an eggshell peridium, and lacks the crystalline capillitium.

Remarks – a morphologically unique species.

***Didymium tehuacanense*** Estrada, D. Wrigley & Lado, Fungal Diversity 36: 31. 2009.

Types – Estrada-Torres, Lado, Wrigley de Basanta, Lado 14784 (MA-Fungi 73605), TLXM (AE 9159).

Hypothallus – discoid, membranous and brownish-orange. Stalk: intermediate to sessile (0.4-0.9 mm); filed with lime and refuse matter; white to dark-brown. Columella: column-like in a closed umbilicus; white (lime), with calcareous capillitial projections. Sporotheca: whitish, gregarious, subglobose to hemispheric sporangia (0.4-0.9 mm wide, 0.2-0.5 mm thick). Peridium: membranous and iridescent brownish-gray to yellowish-brown; covered with white stellate lime crystals. Capillitium: brownish-grey threads with pale tips; derived from calcareous columella projections and often having crystal inclusions; branching and anastomosing. Spores: subglobose

(8-10 µm); uniformly warted (bacula by SEM); black (in mass) or light-grayish brown (in transmitted light). Plasmodium: unknown. Habitat: on Agave (arid region).

Distribution – Mexico, several collections.

Similar species – *D. subreticulosporum* – capillitium consist of filaments of lime; *D. squamulosum* – usually has a round columella and lacks crystals in its capillitium.

Remarks – clearly related to *D. squamulosum*, but the columella and related capillitium are distinct.

***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: pale-grey to white, gregarious to grouped, discoid sporangia (0.2-0.7 mm) to irregular (fused sporocarps 0.6-1.3 mm long) often with a 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-grayish-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 grayish-brown to brown (in transmitted light). Plasmodium: hyaline to pinkish-white phaneroplasmodium. Habitat: on Yucca and Agave litter.

Distribution – Mexico.

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 & Evrard. Bull. Soc. Mycol. France 36: 110. 1920.

≡ *Diderma vaccinum* Durieu & Mont., in Durieu et al., Exp. Sci. Algérie 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. 1979.

Types – BM (1904A) (see Lado & Wrigley de Basanta 2018).

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: white to brownish-white, scattered to gregarious, hemispheric to turbinate sporangia (0.6-1.4 mm wide, 0.5-1.5 mm thick). 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 dehiscent 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, Chile, Canary Islands, Europe, Israel, Japan, Mexico, US, Uruguay, Peru), but rare.

Similar species – *Diderma* spp. – do not have crystalline lime. *Didymium rubropus* – has thinner less flattened capillitia that does not form a net

Remarks – *D. diciforme* and *D. haretianum* are apparently variants of this species.

***Didymium verrucisporum*** [“*verrucosporum*”] A.L. Welden, *Mycologia* 46: 98. 1954.

Types – IBP (Weldon 7545).

Hypothallus – inconspicuous, membranous and dark-brown. Stalk: long (0.5-1.2 mm), striate, and somewhat tapering; translucent orange-brown, dark-brown at base. Columella: globose, in a closed umbilicus; white and containing lime. Sporotheca: white to grayish-white, gregarious, globose sporangia (0.2-0.8 mm) nodding on the stipe. Peridium: membranous and hyaline; covered with scattered white stellate lime crystals. Capillitium: profuse, hyaline to yellow-brown threads with pale tips; dichotomously branching and anastomosing. Spores: globose (8-9  $\mu\text{m}$ ), usually coarsely and distinctly warted, the warts often in groups and sometimes forming ridges (pilate by SEM); dark-brown (in mass) or pale-purplish-brown (in transmitted light). Plasmodium: brown phaneroplasmodium. Habitat: on litter.

Distribution – cosmopolitan but rare.

Similar species – *D. nigripes* – has a dark columella and peridium, less warted spores; *D. iridis* – has a lighter colored stalk, less warted spores.

Remarks – part of the *D. iridis* complex; the nodding is an environmental effect.

***Didymium wildpretii*** Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado, in Lado, Mosquera, Beltrán-Tej., D. Wrigley. *Mycologia* 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: whitish to pale orange-yellow, gregarious, subglobose to slightly reniform sporangia (0.1-0.5 mm wide, can be 1-2.5 mm long). 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  $\mu\text{m}$ ); densely and uniformly warted (baculate by SEM); brown-black (in mass) or grayish-brown (in transmitted light). Plasmodium: orange-yellow to reddish-orange phaneroplasmodium. Habitat: on decaying cacti.

Distribution – Mexico, Peru, Chile and the Canary Islands, 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 xerophilum*** Lado, Estrada, & D. Wrigley, in Wrigley, Lado, Garcia-Torres & Estrada. *Mycologia* 107: 161. 2015.

Types – Lado 22243 (MA-fungi 868851).

Hypothallus – large, white and calcareous; often connecting several sporangia. Stalk: subcylindrical, intermediate in length (0.25-1.5 mm) and width (0.15-0.25 mm), calcareous (upper region covered with white lime crystals and the entire stalk filled with rhomboidal lime crystals). Columella: yellowish white to olive-brown dome or disk filled with rhomboidal lime crystals. Sporotheca: gregarious, slightly oblate to sub-hemispherical sporangia (0.5-2.0 mm wide) with deep funnel-shaped apical invaginations. Peridium: membranous, light-yellow and covered with white lime crystals (may be sparse on lower region); circumscissile dehiscence of upper region. Capillitium: slender yellow-brown threads with pale tips, dichotomously branching and anastomosing with cross connections. Spores: globose (11-18  $\mu\text{m}$ ), densely warted (bacula by SEM); black (in mass) or dark-brown (in transmitted light). Plasmodium: unknown. Habitat: grass blades and leaf litter and twigs of arid plants.

Distribution – Argentina and Peru.

Similar species – *D. intermedium* – has the connecting calcareous hypothallus but not the funnel-shaped apical invagination or rhomboidal crystals in the stalk; *D. infundibuliforme* has a funnel-shaped apical invagination, but lacks a columella and rhomboidal lime crystals; *D. squamulosum*, *D. laccatipes*, *D. operculatum*, and *D. floccosum* all lack the connecting hypothallus, funnel shaped apical invagination and rhomboidal stalk crystals.

Remarks – one of a number of distinct species from arid regions of South America

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This guide is an attempt to distill the work and ideas of many people; 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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