Recommendations about Genera to be Protected or Suppressed in the
Orbiliaceae (Orbiliomycetes)


Abstract:
A list of all generic names that have been brought into connection with the Orbiliomycetes is provided. A recommendation is made about which generic names should be used in accordance with the new rules and the chosen generic concept. This concerns cases where different generic names compete not only within the same morph but also with a different morph. There is a high mismatch in the current generic concepts between asexual and sexual morph: a narrow concept was used for the asexual morph, but a rather broad concept for the sexual morph. Therefore, much more anamorph generic names have been established. However, quite a few genera of both morphs turned out to be artificial as they were based on single characters without genetical support.

Three different generic concepts within the Orbiliomycetes are here presented. A broad concept recognizes a large genus Orbilia, with which most of the listed names fall into synonymy. A moderate concept would subdivide Orbilia into a number of genera, with the nematode-trapping fungi merged in Arthrobotrys. A narrow generic concept accepts within the latter group different genera for different trapping organs, but would also subdivide the remaining groups of Orbilia into various further genera. In our monograph we maintained the broad concept because quite a few species included in Orbilia s. l. are difficult to place, and because morphology often does not coincide with molecular data.

Trapping of invertebrates (zoophagy) is not restricted to Arthrobotrys in a wide sense, but occurs also in the more unrelated basal genera Hyalorbilia and Lecophagus which prey on, e.g., rhizopods and rotifers besides nematodes. Whether these capabilities trace back to a common ancestor is not clear.

The following new combinations are proposed: Hyalorbilia oviparasitica, Hyalorbilia tenuifusaria, Orbilia fissilis, Hyalorbilia quadridens.

Introduction

Previously assigned to the Helotiales, an order today recognized in the Leotiomycetes, the family Orbiliaceae was raised to the rank of a class, Orbiliomycetes, based on morphological as well as molecular-phylogenetic data (Eriksson et al. 2003). The class forms a monophyletic group that occupies a rather basal position within the Ascomycota, with the Pezizomycetes appearing most closely related. The main characteristic of the class is a striking plasmatic structure of the ascospores, the spore body (SB, Fig. 1), which is well recognizable only in the vital state. This vacuolar organelle is mostly attached to the spore apex, more rarely to both ends of the spore. It shows a high diversity among the taxa, varying between lens-shaped, globose, tear-shaped, rod-shaped, and vermiform. Further peculiarities concern the ability to trap invertebrates including protozoa by means of specialized trapping organs, the connection to Ingoldian hyphomycetes as asexual morphs, a high desiccation tolerance of both asexual and sexual morph in many species, and a serious deficit in taxonomic studies, which became obvious by the huge number of new species to be described in our monograph (Baral et al. in prep.).

Connections between sexual and asexual morphs within the Orbiliomycetes have been known since the end of the 19th century (Brefeld 1891, Dicranidion), but most of the presently known connections were discovered at the end of the 20th century and later, particularly starting with Pfister's (1997) comprehensive study. Most of the published taxonomic, cultural, and molecular phylogenetic work on the Orbiliaceae has been done on taxa from
permanently moist (hygric or semi-aquatic) environments. Therefore, many, mostly undescribed taxa from xeric substrates (i.e., being dry for most of the time) are almost completely missing in public repositories, such as fungaria, culture collections, and GenBank. On-going monographic treatment of the class by Baral et al. (in prep.) has revealed many misidentifications in these repositories, which is due to the paucity of previous monographic work, especially on their sexual morphs. Naming of samples is actually complicated by the often inadequate descriptions which offer very different interpretations of a species. Comprehensive studies of teleomorph type material by the senior author have clarified in many cases at least the rough application of ancient names, and shed light on the often heterogeneous species concept of a given author.

Scholler et al. (1999) and Hagedorn & Scholler (1999) introduced a new generic concept for asexual morphs of nematode-trapping orbiliaceous fungi, which is founded on the types of trapping organs instead of the previously used conidial and conidiophore morphology. Together with molecular phylogenetic data, this new concept appears rather sound for classification of those taxa that produce the typical trapping organs in culture. Trapping organs adapted to nematodes are either adhesive trapping, or concern constricting or non-constricting rings, but some taxa with adhesive organs prey instead on arthropods such as copepods, mites, collemboles, and dipters. All these predacious taxa are members of Arthrobotrys in a wide sense, a subgroup of Orbilia s. l.

Two further genera of Orbiliomycetes which possess trapping organs were not treated by Scholler et al.: Brachyphoris (the asexual morph of Hyalorbilia, earlier classified in Dactylella), and Lecophagus. Their members trap rhizopods, or rotifers and tardigrades (respectively) in the mouth region by means of adhesive pegs or knobs. One species (Brachyphoris oviparasitica) is known to parasitize nematode eggs. The two genera cluster in a basal clade in our phylogenetic analyses (Fig.) and thus might perhaps originate from a common ancestor with predacious capabilities. Arthrobotrys s. l., however, does not seem to be closely related to this clade, and it is quite unclear whether or not it developed zoophagy independently.

Predacious capabilities could not be demonstrated in pure culture for the majority of species of Orbiliomycetes up to now. Therefore, the aforementioned classification system based on trapping organs does not offer a solution for all those apparently non-predacious taxa. Unpublished morphological data together with the present phylogenetic results (Fig. 5) show that these taxa can be classified into various groups, most of them being rather unrelated to the predacious ones. Due to the unavailability of trapping organs, their classification is based on conidial and conidiophore morphology, though mainly on characters of the sexual morph, and DNA data. In some of the groups (e.g., Pseudotripocconidium vs. Helicoon/Anguillospora), conidial morphology is highly characteristic of a clade, whereas the sexual morphs hardly permit recognition of the clade.

The present heterogeneity of most non-predacious anamorph genera is exemplified by those having stauropsorous conidia. Stauropsorous genera are currently distinguished according to different branching types of their conidia. However, cultural studies have shown that different branching types often occur within a single isolate (see, e.g., Ando 1992), or in phylogenetically very closely related species. Besides the fact that representatives of most of these anamorph genera, for instance Trinacrium and Dicranidion, were found by us to occur in various unrelated clades within the family Orbiliaceae, there is enough evidence that this generic concept is quite artificial. Two of these artificial anamorph genera include also non-orbiliaceous taxa, belonging to the Helotiiales (Dwayaangam and Anguillospora) or Dothideomycetes (Anguillospora), although these unrelated taxa are morphologically difficult to distinguish from their orbiliaceous siblings.

We see two aspects of handling anamorph genera without known trapping organs under these circumstances under the new nomenclatural rules. Firstly, we can regard these conidia-based "genera" just as descriptive terms.
When referring to a given conidial morphotype it is convenient to use phrases such as "anguillospora-like", according to recommendations by Seifert et al. (2000), Cannon & Kirk (2000) and Hawksworth (2011), irrespective of the phylogenetic relationship. Secondly, we must figure out which of these anamorph-generic names can be used as a holomorph name for a given genus. This depends on the position of the type species, not on that of other included species.

The following alphabetic list treats virtually all generic names that have been brought into connection with the Orbiliomycetes. Several names are obligate synonyms of others, and quite a few are taxonomic synonyms even when applying a narrow generic concept. However, the exact identity of a type species, particularly that of anamorph genera, is often uncertain when DNA sequences are wanting, and because of the mentioned convergences in conidial shape.

We have indicated below our opinion on all those generic names that compete with a name of a different or the same morph, concerning which name should be used in accordance with the new rules and the chosen generic concept. The results on anamorph-teleomorph connections of the last decades have shown that the generic concepts applied up to now are very inconsistent between the two morphs: a narrow concept was used for the asexual morph, but a rather broad concept for the sexual morph. As a result, we are dealing with much more anamorph generic names.

We see three main ways of handling the ranks within the class. (1) When applying a broad generic concept, most of the listed generic names will fall into synonymy with the oldest teleomorph name Orbilia Fr. 1836. Apart from three small undescribed genera, this concept recognizes presently five published genera which comprise very different numbers of species (Hyalorbilia [-40], Lecophagus [-5], Orbilia [-400], Pseudorbilia [1], and Vermispora [-6]; these numbers include also undescribed species). (2) A moderate generic concept would subdivide the large genus Orbilia into a number of genera, depending on personal considerations. For instance, the following five genera could be recognized: Arthrobotrys, Habrostictis, Hemiorbilia/Descalsia, Hyalinia, and Orbilia. Arthrobotrys Corda 1839 is the oldest available anamorph name and under this concept it would encompass all nematode-trapping species, but also some closely related non-nematophagous species (Dactylella s. str.). (3) A narrow generic concept would accept the system proposed by Scholler et al. (1999) for the nematode-trapping group, and would also subdivide the remaining four genera of the moderate generic concept into various further genera.

The moderate generic concept could result in recognition of subfamilies within one family Orbiliaceae, and the narrow concept in a subdivision of the Orbiliomycetes into several families and subfamilies.

In the notes to each generic name we have mentioned these generic concepts whenever the acceptance of a name depends on the taxonomic concept chosen. Those names that require action under the new rules of the ICN are indicated in Table 1.

The following abbreviations are used: (A) = asexual morph (= anamorph), (S) = sexual morph (= teleomorph), H.B. = private herbarium H.-O. Baral, SB = spore body.

Genera checklist of the Orbiliomycetes:

referring to conidial shape; use instead *Helicoon* (A) when applying a moderate or narrow generic concept, otherwise use *Orbilia* (S).

Index Fungorum lists a total of 18 names in *Anguillospora*, but only for one of them, *A. rosea*, an orbiliaceous teleomorph is known (Webster & Descals 1979, Descals & Chauvet 1992, Descals et al. 1999, as *Orbilia* sp.; Pfister 1997, as *O. luteorubella* [agg.]). In the ongoing monographic study of *Orbiliomycetes* anguillospora-like anamorphs were obtained in pure culture only in a few of the many investigated species, particularly in those adapted to an aero-aquatic habitat, including *A. rosea*. Since *A. rosea* is not the type of *Anguillospora*, the genus *Helicoon s. str.* (type species *H. sessile*) can be used to also include *A. rosea*, which is phylogenetically closely related to *H. sessile*.

*Anguillospora* was characterized by filiform (scolecosporous), multiseptate, hyaline conidia which resemble an eel (= *anguilla*). Examples belonging to *Orbiliomycetes* are shown on Fig. 2h–i. The morphological delimitation from anamorphs with shorter phragmoconidia referable to *Vermispora* is only a gradual one, while differences in conidiogenesis are not easy to assess and inconsistent within the polyphyletic genus *Anguillospora*. *Lecophagus* differs by conidia formed almost simultaneously in fascicles on multilocular conidiophore tips (Fig. 2g).

That *Anguillospora* is heterogeneous was early noticed based on different patterns of conidial secession and connections to very different teleomorphs (Webster & Descals 1979, Nakagiri & Tubaki 1983, Descals et al. 1999). Species of *Anguillospora* also differ in their microconidial synanamorph: non-orbiliaceous members often have subglobose, non-septate microconidia formed on phialides, whereas orbiliaceous members form microconidia similar to the macroconidia: elongate, septate, formed holoblastically. This heterogeneity is confirmed by genetic studies (Belliveau & Bärlocher 2005, Baschien et al. 2006). Accordingly, the former concept of *Anguillospora* encompasses five different ascomycete orders (*Dothideales, Pleosporales, Lulworthiales, Helotiales, Orbiliales*).

Conidial secession in the type species *A. longissima* is rhexolytic, i.e., with a separating cell that splits during secession, though this feature is best seen only shortly after secession, and invisible in some of the published illustrations. In perhaps all of the remaining species conidial secession is schizolytic, i.e., without such a separating cell (Baschien et al. 2006). In taxa of the genus connected to helotialean teleomorphs, the conidiogenous cells are said to be thalloblastic-percurrent (Baschien et al. 2013). Pycnidial synanamorphs were found in *Anguillospora longissima* (Willoghby & Archer 1973) and in *A. mediocris* (Gönczöl & Marvanová 2002), whereas moniliaceous phialidic synanamorphs were observed in *A. crassa* (Webster 1961) and *A. furtiva* (Descals et al. 1999). Besides a pycnidial synanamorph, Webster & Descals (1979) report a tiny phialidic synanamorph with simple conidiophores in *A. longissima*. In those anguillospora-like asexual morphs that we found to be connected to orbiliaceous sexual morphs, neither rhexolytic conidial secession nor percurrent proliferation or formation of phialidic microconidia have been observed, although Baschien et al. (2006) and Descals et al. (1999) stated that also *A. rosea* shows percurrent proliferation.


Although clearly synonymous with *Dactylellina* (see there), this generic name should not be used because the specific identity of the type species is unclear.
Arthrobotrys Corda, Prachtfl. Europ. Schimmelbild.: 43 (1839) – Monotype: A. superba Corda — Use
Arthrobotrys (A) when applying a moderate or narrow generic concept, otherwise use Orbilia (S).

Arthrobotrys (Figs 3j–p, 4f) is one of the largest genera and also represents the most widely used generic
name within the Orbiliomycetes. Some Arthrobotrys species (in particular A. oligospora) have historically been
used as model organisms or in attempts to develop biocontrol agents, and are continuously being used for
teaching mycology. It is, therefore, desirable to preserve this name under the new rules. Earlier the genus was
defined by 1-septate conidia formed on swollen fertile nodes in roundish clusters, combined with the ability to
trap nematodes, though irrespective of the type of trapping organ. Schenck et al. (1977) extended the generic
definition to include species with 0- or several-septate conidia. The Greek suffix -botrys describes these conidial
clusters, and the prefix arthro refers to the chain-like arrangement of the clusters along the very elongate
conidiophore in the type species.

Scholler et al. (1999) and other authors have shown by molecular-phylogenetic methods that the morphology
of the trapping devices provides more valuable key characters to delineate natural groups than conidial and
conidiophore morphology. In their concept all included 46 species of Arthrobotrys trap nematodes by means of
more or less three-dimensional adhesive networks. Based on this concept, the authors considered eight further
generic names as synonymous (see below). A teleomorph name (Orbiliella) and a questionable anamorph name
(Tripoconidium) are here added to the list.

Orbilia with presently about 80 validly described and accepted species has priority over Arthrobotrys with
presently about 53 species. When applying a broad generic concept, Orbilia would be preferred because of its
continuous application over the centuries and its larger species number. When using a moderate generic concept,
Arthrobotrys should be used for the group that includes all nematode-trapping fungi presently included in
Arthrobotrys, Dactylellina, Drechsleriella, and Gamsylella, because it is the oldest of these generic names, and
also because of its large species number. Such a concept should, however, also include the non-predacious
species presently recognized in Dactylella (see below). Under a narrow generic concept, all these anamorph
names could be recognized as distinct holomorph genera under the new rules, because they delineate rather well-
defined phylogenetic but also ecologically distinct groups (but see under these names for competing teleomorph
genera).

oviparasitica (G.R. Stirling & Mankau) Juan Chen, L.L. Xu, Bin Liu & Xing Z.Liu — Use the older name
Hyalorbilia (S) instead of Brachyphoris (A).

Brachyphoris was erected by Chen et al. (2007a, c) for five species previously assigned to Dactylella, but
with shorter conidiophores and a considerable genetic distance to the accepted Dactylella species. Two of the
five species are without DNA sequences and were assigned to the genus merely on the basis of the short
conidiophores. It is quite unlikely, however, that they are related to Brachyphoris because such short
conidiophores are frequently observed in various groups of desiccation-tolerant species of Orbilia s. l.

Brachyphoris (Figs 3a–b, 4c) is a synonym of Hyalorbilia (Fig. 1c–e), and was established to accommodate
the anamorphs of that genus. Although no DNA sequence of the type species H. berberidis is available, there is
little doubt about its close relationship to B. oviparasitica. The latter species is only known from its asexual
morph, but it is genetically closely related to H. brevistipitata, which also has a brachyphoris-like anamorph. In
fact, many of the anamorphs observed by us in Hyalorbilia have very similar fusoid, brachyphoris-like conidia,
for which an example is shown on Fig. 3a. "Dactylella" passalopaga Drechsler, a species that captures testaceous rhizopods (Fig. 4c), closely resembles these, but due the low diversity in conidial morphology within Hyalorbilia we are unable to decide which teleomorph species belongs to D. passalopaga. The same is true for the predacious isolate figured by Barron (2008) under the name D. passalopaga.

Evidently, only one of the two generic names should stay in use. We give preference to the older name Hyalorbilia, in which presently ten species are described, instead of Brachyphoris with only five species, one of which (B. brevistipitata) being simultaneously published with its teleomorph. Two new combinations are here proposed.

**Hyalorbilia oviparasitica** (G.R. Stirling & Mankau) E. Weber & Baral **comb. nov.**

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**Hyalorbilia tenuifusaria** (Xing Z. Liu, R.H. Gao, K.Q. Zhang & L. Gao) E. Weber & Baral **comb. nov.**

MycoBank MB xxxx


The tetraradiate, ♦-shaped conidia of *Curucispora* differ from those of the similar *Descalsia* in showing two central cells divided by an oblique septum. They also differ in conidial shape, with the arms appearing as a V-shaped primordium in the centre of a bent axis, and later elongating to form a tetra-radiate three-dimensional structure. In *Descalsia*, in contrast, the arms arise oppositely in the middle of the elongate straight main axis, and the conidia are said to remain planar. However, conidia with an obliquely septeal central cell occur occasionally or even frequently also in *Descalsia cruciata*, and in our strains referred to *Descalsia* the arms show a three-dimensional shape, while in preparations with a cover slip the arms are forced to lie in one plane and can easily be mistaken as planar.

Three species have been included in *Curucispora*. Molecular data are lacking, and only the dried holotype culture of *C. ponapensis* was preserved. The conidia in the type species resemble a staurosporous anamorph which was obtained in pure culture of an undescribed species of *Hyalorbilia* similar to *H. fusispora* (Baral et al. unpubl., Fig. 2y), therefore, *C. ponapensis* might be the asexual morph of a *Hyalorbilia* (but Fig. 2y also shows a similarity to *Retiaris superficiaris*). Alternatively, a connection of *C. ponapensis* to *Orbillia* subgenus *Hemiorbilia*, or a non-orbiliaceous sexual morph could be possible. *C. flabelliformis* differs by curved arms, and again resembles an anamorph obtained in pure culture of an unnamed *Hyalorbilia* (Fig. 2x).
In case that DNA can be extracted from the dried type culture of *C. ponapensis*, and it is demonstrated that this species falls within *Hyalorbia*, then *Hyalorbia* should be protected over *Curucispora* in order to avoid a large number of name changes.

**Dactylariopsis** Mekht., Mikol. Fitopatol. 1: 278 (1967) – Type: *D. brochopaga* (Drechsler) Mekht. [= *Drechslerella brochopaga* (Drechsler) M. Scholler et al.] — **Use the older name Drechslerella** (A) instead of *Dactylariopsis* (A) when applying a narrow generic concept. / or: According to all present concepts the synonymy with *Drechslerella* is recognized.

**Dactylella** Grove, J. Bot. 22: 199 (1884) – Monotype: *D. minuta* Grove — **Use Dactylella** (A) when applying a narrow generic concept (epitypification of *D. minuta* required), otherwise use *Arthrobotrys* (A) or *Orbilia* (S).

The type species of *Dactylella* was described as forming always a single terminal conidium (but other species show also apical branching of the conidiophore). The type specimen of *D. minuta* is said to be located in K (Rubner 1996), consisting of a piece of dead wood without any trace of the fungus. A culture was probably not made by Grove, and unambiguous further records are unknown.

The circumscription of *Dactylella* has been emended several times by different authors. It was Rubner (1996) who restricted the genus to non-nematophagous species. Then, Chen et al. (2007a, b) found that *Dactylella* was still heterogeneous, forming three different clades: *Brachyphoris* (teleomorph *Hyalorbia*), *Dactylella* s. str. (teleomorph *Orbilia* s. l.), and *Vermispora* (teleomorph unknown). Under this concept *Drechsleromyces* and *Gangliophragma* are synonyms of *Dactylella*.

Chen et al. accepted 28 species in *Dactylella* s. str., which are saprotrophic though partly capable of invading oospores or nematode eggs. Various phylogenetic studies show that the available sequences of *Dactylella* in this restricted concept form a rather well-defined clade in close vicinity to the nematode-trapping genera *Arthrobotrys*, *Dactylellina*, *Gamsylella* and *Drechslerella*. However, dactylella-like anamorphs were observed in three different groups of *Orbilia* s. l. (Fig. 5): *Dactylella* s. str. (Fig. 3c–g), the group around *O. crenatomarginata* (Fig. 3c, see under *Hyalinia*), and the core of *Orbilia* (Fig. 3d), apart from the dactylella-like asexual state of *Hyalorbia* (*Brachyphoris*).

The morphological similarity of conidial morphs referable to *Dactylella* s. l. is partly remarkably high between species of different clades, therefore, it remains unclear in which of these clades the type species *D. minuta* might have belonged. From its morphology we suspect that it could either be the asexual morph of a member of *Dactylella* s. str. (e.g., *Orbilia cardui*) or the conidial state of *O. crenatomarginata* (*Hyalinia* clade). Hence, when applying a narrow generic concept, the generic name *Dactylella* needs to be fixed by selecting an epitype for *D. minuta*, preferably in the sense of Chen et al.’s *Dactylella* s. str. However, no specimen that matches the large conidial size given by Grove is known to us. CBS cultures deposited under the name *D. minuta* by Gams and re-identified as *D. rhopalota* by Rubner (1996) have conidia of a size much smaller than described by Grove.

Also for the two genera *Gangliophragma* and *Drechsleromyces* no ex-type culture or sequence seems to exist, but sequences under the names of their type species fall in Chen et al.’s clade of *Dactylella* s. str. *Gangliophragma* and *Drechsleromyces* would be available as an alternative to *Dactylella* when applying a
narrow generic concept. Because of the large number of necessary name changes, an epitypification of *D. minuta* would be a better solution.


*Dactylellina* was emended by Scholler et al. (1999) to comprise exclusively species that trap nematodes by means of adhesive knobs, albeit some of them additionally form non-constricting rings (Fig. 4d–e). The conidia are often fusiform (Figs 3h–i) and the apothecia in one species bright red (Fig. 1n). This concept resulted in the synonymy of *Laridospora* and *Kafiaaddinia* with *Dactylellina*. When applying a narrow generic concept, the name *Dactylellina* can be adopted as a holomorph-generic name.

The older genus *Anulosporium* also possesses stalked adhesive knobs and non-constricting rings. However, its author (Sherbakoff 1933) misinterpreted the stalks as conidiophores, the rings as conidia, and the knobs as early stages of the rings. Because no true conidia were observed, the specific identity of the single included species *A. nematogenum* remains unclear. For this reason, Scholler et al. (1999: 109) considered the genus as dubious. We follow this opinion and here propose to protect the name *Dactylellina* for the case that the narrow generic concept is applied.

**Dactylium** Nees, Syst. Pilze: 58 (1816) [1816–1817], : Fr., Syst. Mycol. 3: 382, 412 (1832), nom. rej. [non *Dactylium* Sacc.], nom. illegit., Art. 53 IN] – Monotype: *D. candidum* Nees

The type species is of unclear identity based on its original description. Drechsler (1937a: 523) took up the name *Dactylaria candida* (Nees) Sacc. for an isolate that forms long-stalked adhesive knobs and non-constricting rings, which might be the same as *Monacrosporium haptotylum* (Drechsler) X.Z. Liu & K.Q. Zhang fide Rubner (1996: 74), a species now classified in *Dactylellina*. Gams & Rubner (1996) proposed to reject the names *Dactylium* and *D. candidum* in order to retain the genus name *Monacrosporium*, for the case that Drechsler's redescription would be taken as a neotypification of *D. candidum* (Rubner 1996: 37).


Because of its illegitimacy, the name was replaced by *Dactylellina*.

**Descalsia** A. Roldán & Honrubia, Mycol. Res. 92: 494 (1989) – Monotype: *D. cruciata* A. Roldán & Honrubia, Mycol. Res. 92: 495 (1989) — Use *Descalsia* (A, in case a DNA sequence will confirm this synonymy in the future) rather than *Hemiorbilia* (S) (presently existing only at the infrageneric level) when applying a moderate or narrow generic concept.

Only one species was assigned to this genus which has stauroporous, †-shaped conidia similar to *Curucipsisora* (see there). Although there is little doubt that *D. cruciata* belongs in the core of *Orbilia* subgenus *Hemiorbilia*, it cannot be assigned with certainty to a teleomorph species. At least three species are in the narrow selection. *O. aristata*, a close relative of *O. occulta*, forms †-shaped conidia in pure culture very similar to *D. cruciata*, although on the natural substrate we have also often observed trinacrium- and dwayaangam-like...
conidia besides the descalsia-like ones. More or less the same three conidial types were found on the natural substrate and partly also in culture in *O. aff. aristata* and *O. flagellispora* (Baral *et al.* unpubl., Fig. 2g).

Because of the uncertain identity of *D. cruciata* and the impossibility to apply the name to a holomorph, the name *Descalsia* can presently not be used as a holomorph-generic name. No living type culture or sequence exist (A. Roldán & L. Marvanová pers. comm.). As it is quite likely that *D. cruciata* belongs in the complex of *O. occulta*, the type species of subgenus *Hemiorbilia*, the name *Descalsia* should be used instead of raising subgenus *Hemiorbilia* to generic level. However, *Curucispora* might represent an older name in case it would turn out to be congeneric.


The name of the genus refers to the shape of conidia resembling a tuning-fork (from Greek *dikranos*). Such conidia occur in several rather unrelated groups of *Orbilia s. l.* They differ in arm and stipe length, and in the number of branches (Fig. 2i–p). The type species clearly fits the anamorph obtained in ascospore isolates of the frequent, worldwide occurring *O. eucalypti* (W. Phillips & Harkn.) Sacc. (= *O. alnea* Velen., Baral *et al.* unpubl.), which belongs in the core of *Orbilia s. str.*

Due to the scattered occurrence of diconidion-like anamorphs within *Orbilia s. l.* and the widely accepted name *Orbilia*, we shall dismiss the name *Dicranidion* and use *Orbilia* no matter which generic concept is adopted. Further teleomorph connections to *Dicranidion* anamorphs within the core of *Orbilia* concern *D. inaequale* Tubaki & T. Yokoyama = *O. ?tremulae* Velen., *D. gracile* Matsush. (or *D. tenue* Matsush.) = *O. leucostigma* (Fr.: Fr.) Fr. (= *O. delicatula* (P. Karst.) P. Karst.), and the following:

*Orbilia fissilis* (K. Ando & Tubaki) E. Weber & Baral, comb. nov. (Fig. 2o)
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*Didymozoophaga* Soprunov & Galiulina, Mikrobiologiya 20: 493 (1951) [nom. inval., Art. 36; illegit. Art. 52 ICN]
– Lectotype: *D. superba* (Corda) Soprunov & Galiulina (= *Arthrobotrys superba*)

The illegitimate genus is an obligate synonym of *Arthrobotrys*.

*Dicranidion* Subram., J. Indian bot. Soc. 42: 299 (1964) [“1963”] – Monotype: *D. acrochaeta* (Drechsler) Subram. — Protect *Dicranidion* (A) over the older *Orbiliaster* (S) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).

*Drechslerella* was emended by Scholler *et al.* (1999) to comprise exclusively species which trap nematodes by means of constricting rings (Fig. 4h). This concept resulted in the synonymy of *Golovinia* and *Dactylariopsis* with *Drechslerella*. Conidia vary between fusiform, obvoid, and cylindrical (Fig. 3k–m). When applying a narrow generic concept, the name *Drechslerella* can be adopted as a holomorph generic name. However, an isolate referable to the type species of the teleomorph genus *Orbiliaster*, *O. pilosus* Dennis, produced constricting rings in culture (Pfister 1997: 16, as *Orbilia* sp.) and falls genetically in the *Drechslerella* clade, though at a high distance. This suggests that the older name *Orbiliaster* is synonymous with *Drechslerella*. Because *Drechslerella* was widely used since its emendation and presently comprises 15 accepted species, while
only two species were recognized in *Orbiliaster*, the second one being non-nematophagous (Baral et al. unpubl.), we recommend protection of *Drechslerella* over *Orbiliaster* when applying a narrow generic concept.

*Drechsleromyces* Subram., Kavaka 5: 93 (1978, "1977") – Monotype: *D. atractoides* (Drechsler) Subram. (= *Dactylella* atractoides Drechsler) — **Use *Dactylella* (A) instead of the younger *Drechsleromyces* (A) when applying a narrow generic concept.**

*Duddingtonia* R.C. Cooke, Trans. Br. Mycol. Soc. 53: 316 (1969) – Monotype: *D. flagrans* (Dudd.) R.C. Cooke (= *Trichothecium* flagrans Dudd. = *Arthrobotrys* flagrans (Dudd.) Mekht.) — **Use the older name *Arthrobotrys* (A) instead of *Duddingtonia* (A) when applying a moderate or narrow generic concept.**


Subramanian (1978) introduced the genus for a fungus described by Drechsler as *Triposporina quadridens*, with staurosporous conidia arising from short conidiophores and having normally four arms formed by repeated dichotomous branching (the name is derived from Sanskrit: *dwaya* = two, *angam* = branch). No ex-type culture seems to exist, and no type specimen could be located.

Eight species have been recognized, one of which described as the anamorph of *Orbilia juncti* Kohlm. et al. Sequences are only available for *D. colodena* Sokolski & Bérubé, which falls genetically in the *Helotiales* near *Arachnopeziza*. Considering that the conidia of *D. colodena* show a somewhat irregular mode of branching, with usually six arms, all the other species of the genus may well belong in the *Orbiliomycetes*. Studies of Baral et al. (in prep.) revealed some unidentified *Dwayaangam* anamorphs, especially in the *Hemiorbilia* clade but also in species around *O. albovinosa* Maire unpubl. and *Hyalorbilia fuispora* (Velen.) Baral & G. Marson, which resemble more or less closely some of the described *Dwayaangam* species, although we cannot unambiguously name them (Fig. 2A–C).

The original illustration of *D. quadridens* hardly leaves any doubt about its relationship to the *Orbiliomycetes*. The drops in the rather broad cells of the living conidia as drawn by Drechsler are very probably of non-lipidic nature and point to a relationship with *Hyalorbilia*, in which such drops, in contrast to *Orbilia s. l.*, have rather frequently been observed, and branched conidia occur in some species. This hypothesis is supported by Drechsler's observation that *D. quadridens* is predacious on rhizopods, which is also known from "*Dactylella* passalopaga*. The latter anamorph undoubtedly belongs in *Hyalorbilia*, but cannot be unequivocally assigned to a teleomorph species because very similar conidia occur in various species of that genus, including *H. inflatula* (P. Karst.) Baral & G. Marson (Baral et al. unpubl.).

Based on the above data, the anamorph name *Dwayaangam* competes with the teleomorph name *Hyalorbilia*. We recommend protection of the younger *Hyalorbilia* in which presently ten species are described, instead of *Dwayaangam* with only one species for which an affinity to *Hyalorbilia* is highly probable. As a consequence, this species is here combined into *Hyalorbilia*:

*Hyalorbilia quadridens* (Drechsler) Baral & E. Weber **com. nov.**

Mycobank MB xxxx

**Gamsylella** M. Scholler, Hagedorn & A. Rubner, Sydowia 51(1): 108 (1999) – Type: *G. arcuata* (Scheuer & Webster) M. Scholler et al. — Use *Gamsylella* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).

*Gamsylella* was erected by Scholler et al. (1999) to comprise six species which trap nematodes by means of unstalked adhesive knobs or two- to multicelled columns which tend to form arches or scalariform bridges (Fig. 4j–l). When applying a narrow generic concept, the name *Gamsylella* could be adopted as a holomorph generic name. However, delimitation from *Dactylellina* proved to be rather difficult, and some authors concluded that both genera should be merged. Teleomorphs are presently unknown in *Gamsylella*, except for unpublished results on two species that cluster with *Gamsylella*, one of which forms large, stalked, elongate adhesive knobs which trap arthropods (*Orbilia alba* Dennis, Figs 3q, 4g).

**Gangliophragma** Subram., Kavaka 5: 94 (1978, "1977") – Type: *Gp. rhopalota* (Drechsler) Subram. (= *D. rhopalota* Drechsler) — Use the older name *Dactylella* (A) instead of *Gangliophragma* (A) when applying a narrow generic concept.


This illegitimate name was replaced by *Geniculifera*.

**Geniculifera** Rifai, Mycotaxon 2: 214 (1975) – Type: *G. cystosporia* (Dudd.) Rifai (= *Arthrobotrys cystosporia* (Dudd.) Mekht.) — Use the older name *Arthrobotrys* (A) instead of *Geniculifera* (A) when applying a narrow generic concept. l or: Synonymy with *Arthrobotrys* has been generally recognized in recent years.


**Habrostictis** Fuckel, Jahrb. Nassau. Ver. Naturkd. 23–24: 249 (1870) – Monotype: *Habrostictis rubra* Fuckel (= *Orbilia carpoboloides* (P. & H. Crouan) Baral) — Use *Habrostictis* (S) when applying a moderate or narrow generic concept, otherwise use *Orbilia*.

When Fuckel (1870) erected *Habrostictis* for *H. rubra*, a species with erumpent, at first closed then lacerate-fimbriate apothecia, he believed that also *Stictis ocellata* (Pers.) Fr. (= *Pezicula ocellata* (Pers.) Seaver) belonged in the genus. He named the genus after its resemblance to *Stictis*, from which it deviated by soft, translucent apothecia (the prefix *habro-* means soft-fleshed), and he placed it in his “Stictæ” between *Naevia* and *Stictis*. Boudier (1907), however, excluded *S. ocellata* from *Habrostictis* and considered the genus as closely related to *Orbilia*. Although later authors even regarded *H. rubra* as a member of *Orbilia* [under the synonymous taxa *O. lasia* (Berk. & Broome) Sacc. or *O. piloboloides* J.H. Haines & Egger], Höhnel (1917) and Nannfeldt (1932) kept *H. rubra* in the vicinity of *Ocellaria* (= *Pezicula*) and *Dermea*, until Spooner (1987) and Baral (1994) definitely accepted *Habrostictis* as orbiliaceous.

According to type studies of the first author, *H. rubra* was found to have various synonyms, including the oldest name *Peziza carpoboloides* P. Crouan & H. Crouan. This species (Fig. 1h) turned out to belong in a very
large group of mainly undescribed desiccation-tolerant species, which share elongate, verrucose to filiform SBs but differ from the type in usually smooth apothecia and capitate paraphyses. In case this group is considered as a genus of its own, Habroscistis would be the appropriate name. When using a broader concept, Habroscistis could also comprise the O. aurantiorubra, O. luteorubella, and O. crenatomarginata clades, with Hyalinia then becoming a synonym, or Habroscistis could be used as an infrageneric group of Orbilia s. l.

H. carpoboloides is associated with a verrucose spora-like anamorph, which was compared with Idriella P.E. Nelson & S. Wilh. by Haines & Egger (1982), whereas most members of Habroscistis in the above narrower sense possess trinacularium-like anamorphs.

*Helicoon* Morgan, J. Cincinnati Soc. Nat. Hist. 15: 49 (1892) – Lectotype: *H. sessile* Morgan — Use *Helicoon* (A) when applying a moderate or narrow generic concept, otherwise use *Orbilia*.

The main characteristics of the genus *Helicoon* are filiform, multiseptate, strongly coiled (helicosporous, barrel-shaped), hyaline to fuscous conidia, coiled more tightly towards the poles, produced on short to long, hyaline to brown conidiophores (Goos et al. 1986). The genus is heterogeneous and, like in Anguillospora, by far the major part of the c. 25 described species belong in other classes. Pfister (1997) found the type species *H. sessile* (Fig. 2k) to be the anamorph of Orbilia luteorubella, but this connection was doubted by Hagedorn & Scholler (1999) who found that the sequences obtained by Pfister were hypocreal. However, Pfister's observation could later be confirmed based on a trustable strain of *H. sessile* isolated and sequenced by H. Voglmayr, and a culture by X. Jiang (pers. comm.) of *O. crenatomarginata* (CGMCC 3.13369, GenBank FJ719770) that produced a *Helicoon* in pure culture (Baral et al. unpubl.).

When using a moderate or narrow generic concept of *Orbilia*, members related to *O. luteorubella* could be considered as a genus of its own, and *Helicoon* would be available for use. A teleomorph very closely related to *O. luteorubella* has *Anguillospora rosea* as anamorph, but the genus *Anguillospora* is unavailable because its type species is non-orbiliaceous.

However, the group around *Helicoon* also includes a subgroup for which the very different anamorph genus *Pseudotriuroconidium* was erected (see below). With a narrow generic concept *Pseudotriuroconidium* would be excluded from *Helicoon*.


The genus was introduced by Boudier for a desiccation-sensitive species with a toothed margin (Fig. 1i, the teeth are composed of long, agglutinated glassy processes), and paraphyses without a distinct apical inflation. However, this combination of characters occurs also in many desiccation-tolerant species of *Orbilia* (e.g., Fig. 1p). Later, Boudier (1907) included species with a smooth margin, many of them being today regarded as members of the Helotiales. The type species of *Hyalinia* is also characterized by narrow, helicoidally twisted ascospores.

Under a broad generic concept, *Hyalinia* becomes a synonym of *Orbilia* (Baral 1994), in which genus its type competes with another name, *O. crystallina* Rodway, therefore, the name *O. crenatomarginata* has to be used. The placement of this species within *Orbilia* s. l. is not easy to assess, particularly because the morphological group in which it seems to belong, based particularly on a combination of helicospores and
presence of glassy processes, clusters in two distant clades (Fig. 5). Nevertheless we believe that these two clades possess some phylogenetic relationship. One of them contains *O. nemaspora* (ined.) and *O. bomiensis* Bin Liu et al. and clustered with high support as sister to *O. xanthoguttulata* Baral, a member of a large assemblage which morphologically groups around *O. aurantiorubra* Boud. The other clade contains *O. crenatomarginata* and *O. scolecospora* (G.W. Beaton) Baral and thus represents the core of *Hyalinia*. Both clades cluster rather unresolved in *Orbilia* s. l., i.e., in a quite marginal position of the "Aurantiorubrae" group (a phylogenetic analysis based on the ITS region is given in Zhang et al. 2015).

Although the presumed anamorph of *O. crenatomarginata* is very similar to species such as *Dactylella rhopalota* or *D. xinjiangensis*, no close relationship of *Hyalinia* to *Dactylella* s. str. could be demonstrated by molecular methods. Therefore, the generic name *Hyalinia* does not compete with *Dactylella* when applying a narrow generic concept, but it could be used if the large assemblage around *O. aurantiorubra* or parts of it are raised to generic level.


This teleomorph genus was segregated from *Orbilia* because of strong morphological differences from more typical members of *Orbilia*, including an ectal excipulum of textura prismatica and ± homopolar ascospores. The ascospores usually contain more than one SB, which occur near both ends of the spore (Fig. 1c–e vs. h–r). Later, connections of *Hyalorbilia* species to some asexual morphs were detected that previously had been described in *Dactylella*, and for which the genus *Brachyphoris* was erected (see there). Mainly unpublished genetic data (ITS, LSU) suggest that *Hyalorbilia* forms a monophyletic group with a high distance to *Orbilia* s. l. Parasitizing on nematode eggs is known for *H. oviparasitica*, and the capture of testaceous rhizopods for "*Dactylella* passalopaga* (Drechsler 1936, Barron 2008, see Fig. 4c).


The genus *Lecophagus* represents a small group of aero-aquatic anamorph species that capture rotifers and tardigrades by means of adhesive pegs formed on very broad mycelial hyphae (Fig. 4a–b). The conidia (Fig. 2g) resemble those of *Vermispora*, and we have evidence that an undescribed sexual morph (Fig. 1b) is connected which forms minute white apothecia on xeric wood and bark, with broad anchoring hyphae emerging from dead rotifer bodies.

Phylogenetically the genus falls in the *Orbiliomycetes* (Tanabe et al. 1999), a placement which is supported by ascospore morphology: the living spores contain a conspicuous globose, apically attached spore body (Fig.
Since no competing teleomorph names are known, \textit{Lecophagus} will be extended to include also the sexual morph. Due to its extraordinary features the genus could well deserve a family of its own.

\textbf{Monacrosporium} Oudem., Ned. Kruidk. Arch., Ser. 2,4: 250 (1885) – Lectotype: \textit{M. elegans} Oudem. (\textit{= Arthrobotrys oudemansii} M. Scholler et al.) — \textbf{Use the older name \textit{Arthrobotrys} (A) instead of \textit{Monacrosporium} (A) when applying a narrow generic concept.}

\textbf{Monacrosporiella} (Subram., Kavaka 5: 94 (1978, "1977") – Monotype: \textit{M. megalospora} (Drechsler) Subram. [\textit{= Arthrobotrys megalospora} (Drechsler) M. Scholler et al.] — \textbf{Use the older name \textit{Arthrobotrys} (A) instead of \textit{Monacrosporiella} (A) when applying a narrow generic concept.}

\textbf{Nematophagus} Mekht., Mikol. Fitopatol. 9(2): 250 (1975) – Type: \textit{N. azerbaijanicus} Mekht. [\textit{= Arthrobotrys azerbaijanica} (Mekht.) Oorschot] — \textbf{Use the older name \textit{Arthrobotrys} (A) instead of \textit{Nematophagus} (A) when applying a narrow generic concept.}

\textbf{Orbilia} Fr., Fl. Scan.: 343 (1836) – Lectotype: \textit{Peziza leucostigma} Fr. (designated by Clements & Shear 1931) — \textbf{Use \textit{Orbilia} (S) instead of any other competing generic name, no matter which of the present concepts is applied.}

\textit{Orbilia} is the oldest available and indispensable generic name of all competing teleo- and anamorph genera recognized in the \textit{Orbiliomycetes}. When the genus was described by Fries (1836), it contained only two species, \textit{O. leucostigma} Fr. and \textit{O. xanthostigma} Fr. Type material does not exist for either, and the original description is without ascospore data. A neotype will be proposed for \textit{P. leucostigma} (Baral et al. in prep.) in order to fix the name on a species previously identified as \textit{O. delicatula} (P. Karst.) P. Karst.

\textbf{Orbiliaster} Dennis, Kew Bull. 9: 294 (1954) – Monotype: \textit{Orbiliaster pilosus} Dennis [\textit{= Orbilia pilosa} (Dennis) Baral] — see under \textit{Drechslerella}.

The genus was introduced to accommodate orbiliaceous teleomorphs with septate hairs (Fig. 1j). However, the two so far included species turned out to be rather unrelated among each other (see under \textit{Drechslerella}).

\textbf{Orbiliella} Kirschst., Ann. Mycol. 36: 374 (1938) – Type: \textit{Orbiliella armeniaca} Kirschst. (\textit{= Orbilia auricolor}) — \textbf{Protect \textit{Arthrobotrys} (A) over the younger \textit{Orbiliella} (S) when applying a narrow generic concept.}

The holotype of this teleomorph genus was reexamined and found to fit \textit{Orbilia auricolor} (Fig. 1m), and the anamorph associated with the apothecia matches \textit{Arthrobotrys cladodes} or \textit{A. superba} (Fig. 3o, Baral et al. unpubl.). Therefore, \textit{Orbiliella} is a synonym of \textit{Arthrobotrys}, and should not be used for a narrow generic concept as it was not taken up by later workers.


Based on morphological similarities of conidiophores and conidia, it cannot be excluded that the anamorph genus \textit{Paradactylella} Matsush. (1993) coincides with the younger genera \textit{Brachyphoris} and \textit{Hyalorbilia}. 

1b, Baral et al., in prep.).
According to Seifert et al. (2011), *Paradactylella* is a synonym of *Dactylella*. Although not specifically mentioned, conidial secession could be rhexolytic according to the original drawing of *P. peruviana* and on the re-drawing in Seifert et al., which questions a relationship with the *Orbiliomycetes*. However, the protologue shows also schizolytic cases, and those collapsed cells drawn by a dashed line were obviously without turgor while the adjacent cells were alive and turgescent (Matsushima used to mount in water, in which medium the differences between living and dead cells are often striking).

Matsushima argued that *Paradactylella* is non-predacious, which is, however, also true for *Dactylella*. In case *Paradactylella peruviana* can be restudied and sequenced, and is found to fit *Hyalorbilia*, we prefer to protect *Hyalorbilia* because of the many otherwise required name changes.


Peek & Solheim (1958) and Matsushima (1981) considered *Pedilospora* as a synonym of *Dicranidion*, based on their belief that the type species of both genera and also *P. episphaeria* Höhn. and *P. ramularioides* Bubák are quite possibly conspecific. *P. parasitans* was described by Höhn (1902) as growing "*In Helotio citrina (?)* parasitica" (= *Calycina citrina* = *Bisporella citrina*), and possibly Höhnel confused *O. eucalypti* (anamorph *D. fragile*) with the helotialean *Calycina citrina*. Drechsler (1934) included a species in *Pedilospora*, *P. dactylopa*ga Drechsler, which is exceptional in preying on testaceous rhizopods and having very long conidiophores.


This genus was erected for a species in which both ends of the ascospores contain a spore body (bipolar arrangement, Fig. 1a). In this respect the fungus resembles *Hyalorbilia*, from which it differs in isodiametrical excipular cells, asci with a truncate, shouldered apex, and hymenial elements not embedded in gel. No anamorph is known, and no genetic data are available.


Yu et al. (2011) introduced the genus to accommodate a single anamorph species obtained from a teleomorph identified as *Orbilia* aff. *luteorubella*. Its inversely pyramidal, non-septate conidia possess more or less pronounced distal nipples and are formed from denticles on plurilocular conidiogenous cells (Fig. 2j). Some further, closely related teleomorph species were also found to produce this peculiar type of anamorph, e.g., *O. acicularis* Baral & Hong Y. Su, but the anamorph was not given a separate specific name. The genus *Pseudotripoconidium* resembles *Tripoconidium*, which differs in septate conidia formed singly at the conidiophore tip.

In the morphology of the telemorphs this group is hardly different from the group around *O. luteorubella* which forms anguillospora- and helicoon-like conidia very different from *Pseudotripoconidium*. In phylogenetic analyses *Pseudotripoconidium* forms a monophyletic clade, whereas the group around *O. luteorubella* is paraphyletic in relation to this. Together they form a monophyletic group which, under a moderate concept,
could receive the older name *Helicoon*. When applying a narrow generic concept, then *Pseudotripoconidium* and *Helicoon* could be used as two separate genera.

**Radotinea** Velen., Monogr. Discom. Bohem.: 298 (1934) – Monotype: *R. caudata* Velen. [≡ *Orbilia aristata* (Velen.) Velen.] — **Protect Descalsia** (or *Orbilia* subgenus *Hemiorbilia* (S)) over *Radotinea* (S) when applying a moderate or narrow generic concept (by raising *Hemiorbilia* to generic level).

The genus was named by Velenovský after a village in Czechia. The single species was described with solid (glassy), 15–35 µm long hairs with a lumen only at the very base, and spores with a thin tail. Velenovský saw a relationship to *Orbilia* but placed it in the *Hyaloscyphaceae* because of the hairs. The original description undoubtedly refers to *O. aristata* or an undescribed very close relative of it (*O. subaristata* nom. prov.), although a further undescribed, rather unrelated species (*O. pseudoaristata* nom. prov.) cannot be excluded with certainty. Since no apothecia could be found in the holotype, *R. caudata* is better considered a nomen dubium. The generic name competes with subgenus *Hemiorbilia*. When using a moderate or narrow generic concept, we recommend not to use *Radotinea* because the type material does not permit a more detailed clarification of critical features, and the name has never been taken up by other authors.


The genus *Retiarius* was introduced for two species that capture wind-borne pollen grains. The type species *R. superficialis* has trinacrium- to curucispora- or dwayaangam-like conidia, and is here considered as orbiliaceous, although we are unable to decide whether it is a member of *Hyalorbilia* or *Orbilia* s.l. The second included species *R. bovicornutus* D.L. Olivier was stated by Matsushima (1993: 30) to belong in *Trinacrium*. Cultures of the two species would be available at IMI 223459, 223460 for inferring their relationship by DNA sequencing.

**Tricellula** Beverw., Antonie van Leeuwenhoek 20: 15 (1954) – Monotype: *T. inaequalis* Beverw. — **Probably not orbiliaceous.**

The genus *Tricellula* was originally described with 3-celled stauroporous holoblastic conidia composed of a stalk and usually two arms, with strong constriction at the indistinct septa, formed on dichotomously branched conidiophores. Eight species are presently included, according to Index Fungorum. Matsushima (2003) obtained *T. inaequalis* and its teleomorph in pure culture of a Japanese isolate, and described the teleomorph in *Orbilia* as a new species *O. tricellularia* Matsush. He placed it in subgenus *Hemiorbilia* obviously because of the slightly thickened apical wall of immature asci. No information on the iodine reaction was supplied. Whether a spore body or other contents occurred in the ascospores remains unclear, because all elements were illustrated in the dead state.

The conical ascus apex and the presence of croziers excludes *Orbilia*, also a relation to *Hyalorbilia* does not seem very probable. Probably *O. tricellularia* belongs in the *Helotiales* rather than the *Orbiliomycetes*. A more detailed morphological documentation and a molecular study on this species should be carried out to find out its genuine placement. Molecular data do not seem to exist for any of the species of *Tricellula*. *Volucrispora* Haskins was synonymized with *Tricellula* by Arx (1970), whereas a later added species, *Volucrispora graminea* Ingold et al., deviating morphologically from *Tricellula*, was later segregated as *Ypsilina graminea* (Ingold et al.) Descals et al. (1999). A BLAST of the latter (in GenBank as *Volucrispora graminea*) reveals relationships with
**Tridentaria** Preuss, Linnaea 25: 74 (1852) – Monotype: *T. alba* Preuss — **Use Tridentaria (in the sense of Drechsler 1937b) only in the form of "tridentaria-like" when referring to conidial shape.**

The original description given by Preuss concerns a fungus that forms acervuli, which contain unbranched conidia arranged in fascicles that suggest a branched conidium. The brief description is rather inadequate for modern systematics. Because the type specimen did not bear a fungus which agreed with the description van der Aa & van Oorschot (1985), the identity of *T. alba* remains unclear, though it probably represented a non-orbiliaceous species.

Drechsler (1937b, 1940, 1962, 1964) adopted the name *Tridentaria* to accommodate four new hyphomycetous, nematode-trapping (*T. implicans*) and particularly rhizopod-trapping species (*T. carnivora*, *T. glossopaga*, *T. tylota*). In this sense the name represents a group of orbiliaceous anamorphs with a peculiar conidial shape, being somewhat intermediate between *Dicranidion* and *Trinacrium*, with three or more ± equal arms and a stipe of varying length, formed on short or long conidiophores. The arms are usually constricted at the branching point, which enables a considerable motility of each arm (Fig. 2v). The three rhizopod-capturing species described by Drechsler in *Tridentaria* might possibly belong to *Hyalorhilia* because of the predacious similarities to "Dactylella" passalopaga, whereas two sequenced strains of *Tridentaria* (CBS, identified as *T. implicans* and *T. subuliphora*) fall in the core of *Orbilia s. str.* A few species of the *Habrostictis* group were found to possess tridentaria-like anamorphs (Baral et al. in prep., e.g., *O. septispora* Baral or *O. quaestiformis* unpubl.).

Because of the unsettled identity of the type species, *Tridentaria* should not be used as a holomorph name, but only for characterizing anamorphs when referring to them as "tridentaria-like".

**Trinacrium** Riess in Fresenius, Beitr. Mykol. 2: 42 (1852) – Monotype: *T. subtile* Riess — **Protect Descalsia/Orbilia subgenus Hemiorbilia (S) over Trinacrium (A) when applying a moderate or narrow generic concept.**

*Trinacrium* was erected for a single species, and 15 species were later added to the genus. The main characteristics are the triradiate (Y-shaped), hyaline conidia with a main axis (stipe) and two divergent, usually equal arms formed by dichotomous branching. A type specimen does not seem to exist and a culture was obviously not made by Fresenius.

Conidia of the *Trinacrium*-type occur in various groups of *Orbiliomycetes* and are typical, e.g., of many members of the *Habrostictis* clade (Fig. 2q), but also of subgenus *Hemiorbilia* (Fig. 2s), or of a clade around *O. pilifera* Baral & R. Galán, in which the arms are always bent downwards (Fig. 2t). A single species (*T. iride* Ts. Watan.) is nematophagous and belongs in *Arthrobotrys*, and also species of *Hyalorhilia* (Fig. 2r) and "Amphosoma" (ined.) (Fig. 2u) have trinacrium-like anamorphs. The type species cannot be identified with certainty, but it could well be the anamorph of a couple of teleomorph species of the *Hemiorbilia* clade. Because of this uncertainty and since the anamorphs of these species are morphologically indistinguishable, we recommend not to use *Trinacrium* as generic name.
**Tripoconidium** Subram., Kavaka 5: 95 (1978) – Monotype: *Trip. aphanopagum* (Drechsler) Subram. (as "aphanophagum") — (In case of synonymy use *Arthrobotrys* (A) instead of *Tripoconidium* (A) when applying a narrow generic concept.)

Only one species was combined in *Tripoconidium*, which is characterized by inversely pyramidal, multi-septate conidia with terminal nipple-like protrusions, formed singly at the tip of long conidiophores (for the differences to *Pseudotripoconidium* see above). The species seems to belong to the *Orbiliomycetes* as inferred from its morphology and because it is weakly predacious on nematodes. As it does not form conspicuously differentiated trapping organs, and since no ex-type culture or a DNA sequence is available, its placement within the nematode-trapping genera remains unclear (possibly *Arthrobotrys* s. str.).

**Vermispora** Deighton & Piroz., Mycol. Pap. 128: 87 (1972) – Monotype: *V. grandispora* Deighton & Piroz. — *Vermispora* (A) is presently without competing name.

*Vermispora* was erected for a single species that is characterized by elongate-fusoid conidia being slightly curved towards the ends, formed in small number on rather short conidiophores. Further five, mostly rather similar species were later added to the genus (one is represented in Fig. 2a). Chen et al. (2007a, c) sequenced three of them, while excluding *V. obclavata* V. Rao & de Hoog for morphological reasons. No sequence can be obtained from the type species which is only known from the type collection and obviously had not been taken into culture. One of the sequenced species (*V. fusarina* Burghouts & W. Gams) is known to parasitize nematode eggs.

Morphologically, *Vermispora* resembles unpublished asexual morphs that were observed in various groups of *Orbilia* s. l., particularly in species related to *O. aurantiorubra* (Fig. 2b–c, f) and in a group that includes *O. euonymi* Velen. (Fig. 2d–e). However, *Vermispora* forms a monophyletic clade quite remote from both *Hyalorbilia* and *Orbilia* s. l., though obviously belonging in the *Orbiliomycetes*. Because of the morphological similarity of *Vermispora* to the asexual morphs observed within *Orbilia* s. l., we use for those morphs the term "vermispora-like".

Sexual morphs are unknown in the *Vermispora* clade. Because of its marginal position the genus might even deserve a family of its own, but presently this family would lack any morphological characteristics of a teleomorph.


References:
Brefeld O (1891) Untersuchungen aus dem Gesammtgebiete der Mykologie, 10. Ascomyceten II. Münster/Westfalen, Germany.


Sherbakoff CD (1933) A new fungus parasitic on nematodes. Mycologia 25: 258–262, pl. 35.


<table>
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<tr>
<th>Recommended generic name</th>
<th>Synonymous alternate morph generic name</th>
<th>Additional synonymous generic names</th>
<th>Action required</th>
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</table>
Dactylella Grove, J. Bot. 22: 199 (1884) – Monotype: *D. minuta* Grove
(use when applying a narrow generic concept, otherwise use *Arthrobotrys* or *Orbilia*)


None

(use when applying a narrow generic concept, otherwise use *Arthrobotrys* or *Orbilia*)

Anulosporium Sherb., Mycologia 25: 262 (1933) – Monotype: *A. nema togenum* Sherb. (nom. dub., identity unclear at the species level)


ICN [non Dactylosporum Hae. 1871] – Monotype: *Dactylina leptospora* (Drechsler) M. Morelet


Reject Anulospori

(use when applying a moderate or narrow generic concept, otherwise use *Orbilia*)

Orbilia subgenus Hemitortilia Baral, Syst. Ascomycetum 13: 118 (1994) – Type: *Orbilia occulta* (Rehm) Sacc. (to be raised to generic level)

?Trinacrium Riess in Fresenius, Beitr. Mykol. 2: 42 (1852) – Monotype: *T. subtile* Riess


(use when applying a narrow generic concept, otherwise use *Arthrobotrys* or *Orbilia*)

Orbiliaster Dennis, Kew Bull. 9: 294 (1954) – Monotype: *Orbiliaster pilosus* Dennis [= *Orbilia pilosa* (Dennis) Baral]


(use when applying a narrow generic concept, otherwise use *Arthrobotrys* or *Orbilia*)

None

(use when applying a moderate or narrow generic concept, otherwise use *Orbilia*)


None

(use when applying a moderate or narrow generic concept, otherwise use *Orbilia*)

None


None
<table>
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<tr>
<th>Genus/Species</th>
<th>Description/Notes</th>
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<tr>
<td><em>Fr. 1: 114 (1885) – Monotype: Helotium crystallinum Quél. (= Orbilia crenatomarginata (Höhn.) Succ. &amp; Trotter) (use when applying a moderate or narrow generic concept, otherwise use Orbilia)</em></td>
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<td>*Orbilia Fr., Fl. Scan.: 343 (1836) – Lectotype: <em>Peziza leucostigma</em> Fr. (designated by Clements &amp; Shear 1931, = <em>Orbilia leucostigma</em>)</td>
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Table 1: Overview of all generic names occurring in the *Orbiliomycetes*, and their nomenclatural status.

Protec *Hyalorbilia* that one of the questionable anamorph names are synonymous.
Figure 1. Teleomorphs of Orbiliomycetes (a, b, d, f, g, h, i, j, k, l, m, o, p, q, r, s): ascospores with SBs; a, b, e, k, o: asci; h, l, p, q: paraphyses; g, j, z: hairs; p: glassy processes: a. Pseudorbilia bipolaris (Zhang et al 2007, H.B. 8794); b. Lecophagus ellipsoides (16.XI.2013); c. Hyalorbilia inflataula (TAAAM 63888), d. H. berberidis (H.B. 8605a), e. H. polyspori (H.B. 9361, 7943b); f. Lilapila ocellispora unpubl. (H.B. 7063a, 4822, 9162a); g. Amphosoma atrofibulaca unpubl. (H.B. 9143b, 9136c, 8057); h. Orbilia carpoboloides (Habrostictis, H.B. 9083a, 13.VI.2009, 9233), i. O. crevatomarginata (Hyalinia, H.B. 7683, 9304, P.P. 20070827), j. O. pilosa (Orbiliaster, H.B. 9437), k. O. leucostigma (Orbilia s. str., 16.VI.2007, 3.VII.2006, 21.X.2010), l. O. eucalypti (Orbilia s. str., H.B. 8427, H.B. 9226), m. O. auricula (Arthrobotrys, 8.1.2011, H.B. 8898a), n. O. rubrospulicola unpubl. (Dactylellina, H.B. 7719a), o. O. vinosa (Hemiorbilia, H.B. 5518, 7861a, 7249c, 8.11.2010), p. O. subaristata unpubl. (Hemiorbilia, H.B. 9163b, 9151d, 10.11.2014), q. O. xanthoguttulata ("Aurantiorubra", H.B. 8170a, 17.3.II.2011), r. O. lentiformis unpubl. ("Lentiformis", H.B. 9578a, 7851b). Living state, except for 1k2 (in water), 1o3 (in Congo Red).
(Kohlmeier et al. 1998), B. O. subvinosa unpubl. (H.B. 9173b), C. O. aristata (07.V.2004). Living state (c, x in Cresyl blue), except for t (in water), u (in KOH).

Figure 3. Conidiophores and conidia of Orbiliomycetes with unbranched, mainly uncurved conidia, mainly predacious taxa (except for daetylella-like taxa): Brachyphoris: a. Hyalorbilia inflatula (H.B. 9041a), b. H. polypori (H.B. 7557a, 7952a); daetylella-like: c. Orbilia vermisformis (Yu et al. 2007a), d. O. dryadum unpubl. (H.B. 8224a), e. O. vestimenti (H.B. 8371a); Dactylella: f. D. clavispora (Chen et al. 2007b), g. O. dorsalis (Yu et al. 2007b); Arthrobotrys: j. O. blumenaviensis (= A. vermicola, Qiao et al. 2012), n. A. elegans (H.B. 6972a), o. O. auricolar (H.B. 8806a, 9553), p. A. oligospora (Swé et al. 2008); Drechslerella: k. Dr. cf. bembicodes (H.B. 9051g), l. Dr. polybrocha (H.B. 8317a), m. O. orientalis (= Dr. brochopaga agg., YMF 1.01854); Dactylellina: h. Da. sichuanensis (Li et al. 2006), i. Da. varietas (Li et al. 2006); Gamsylella: q. O. alba (Yu et al. 2009, q. H.B. 9645a). Living state (n, o; in Cresyl blue).
Figure 4. Trapping organs in Orbiliomycetes: Adhesive pegs capturing rotifers: a. Lecophagus ellipsoides (16.XI.2013), b. L. muscicola (H.B. 7771); adhesive pegs capturing testaceous rhizopods: c. Hyalorbilia sp. (as Dactylella passalopaga, phot. G. Barron, website on fungi); adhesive knobs and non-constricting rings capturing nematodes (Dactylellina): d. Da. mammillata (H.B. 8372a); e. Da. sichuanensis (Li et al. 2006); adhesive network capturing nematodes (Arthrobotrys): f. Orbilia blumenavensis (= A. vermicola, Qiao et al. 2012); adhesive knobs with thick gel capturing arthropods (Gamsylella): g. O. alba (H.B. 9645a, 9051a); constricting rings capturing nematodes (Drechslerella): h. O. orientalis (= Dr. brochopaga agg., YMF 1.01854); i. Dr. doedycoides, captured nematode (?H.Y. Su unpubl.); adhesive columns and bridges: j. Gamsylella cf. cionopaga (XJ03, X.Z. Liu et al. unpubl.); k. G. cionopaga (Z.F. Yu unpubl.). Living state, except for b, e?, g (methyl-green in ammonium hydroxide, post-stained by cresyl blue [when hydrated the gel sheath requires staining for a better visibility]), j, ?I.
Figure 5. Combined phylogenetic analysis of selected species of Orbiliomycetes (RAxML) based on the partial SSU (ca. 360 nt), ITS (ca. 360 nt, without variable regions), and partial LSU rDNA region (ca. 620 nt). — arthro = arthropods, nem/nemat = nematodes, rhiz = rhizopods, rot = rotifers