

# Generic names in the Orbiliaceae (Orbiliomycetes) and recommendations on which names should be protected or suppressed

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**Abstract** A list of all generic names that have been connected with the Orbiliomycetes is provided. Recommendations are made as to which names should be used in accordance with the rules and the different generic concepts. There is a mismatch in the current generic concepts within Orbiliomycetes regarding the two morphs: a narrow concept is used for the asexual morphs, but a broad concept relies on the sexual morphs. As a consequence, many more generic names have been established for the asexual morphs. A number of previous generic concepts are artificial, since they were based on single characters without molecular support. In order to

provide solutions for this mismatch, we present three different generic concepts within the Orbiliomycetes. A broad concept recognizes a large genus *Orbilia*, with which most of the listed names fall into synonymy, but could be maintained as infrageneric names. Due to the lack of data proving phylogenetic relationships, this broad concept, at present, is the most practicable and recommended one. A moderate concept subdivides *Orbilia* into several genera, with all nematode-trapping fungi merged in *Arthrobotrys*. A narrow generic concept accepts genera based on differences in trapping organs, but also subdivides the remaining groups of *Orbilia* into

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The last eight authors are listed alphabetically, contributing by phylogenetic results or in advisory capacity.

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additional genera. Trapping of invertebrates (zoophagy) is not restricted to *Arthrobotrys* in a broad sense, but occurs also in the more distant basal genera *Hyalorbilia* and *Lecophagus*, which mainly prey on rhizopods and rotifers. Whether these predatory capabilities trace back to a common ancestor is not clear. The following new combinations are proposed: *Hyalorbilia oviparasitica*, *Hyalorbilia quadridens*, *Hyalorbilia tenuifusaria*, and *Orbilia fissilis*.

**Keywords** *Arthrobotrys* · *Hyalorbilia* · *Lecophagus* · *Orbilia* · *Vermispora* · Nematode trapping · Nomenclature · Phylogeny · Stauroconidia

## 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 close to the Pezizomycetes. The main characteristic of the sexual morph is a striking plasmatid structure of the ascospores, the “spore body” (Fig. 2), which is well visible only in the vital state. This vacuolar organelle occurs mostly in the spore apex, more rarely in both ends of the spore. It shows a high morphological diversity among the taxa, varying between lens-shaped, globose, tear-shaped, rod-shaped, and vermiform (straight or flexuous). Further peculiarities of many species of the class involve the ability to trap invertebrates, including protozoa, by means of specialized trapping organs, the connection to some genera of Ingoldian hyphomycetes as asexual morphs, and a high desiccation tolerance of both asexual and sexual morphs.

A serious deficit in previous taxonomic treatments became obvious in the huge number of new species to be described in the monograph in preparation (H.O. Baral, E. Weber & G. Marson, unpubl.). Most of the previously published taxonomic, cultural, and molecular phylogenetic work on the class has been done on the basis of taxa from permanently moist (hygric) or wet (semi-aquatic) environments, but many, mostly undescribed taxa from xeric substrates, which are dry for most of the season, were missing in public fungaria, culture collections, and sequence databases. The ongoing monographic treatment of the class has revealed many misidentifications in such repositories. This is due to the paucity of previous monographic work, especially on the sexual morph. The naming of samples is complicated by inadequate descriptions, which often offer very different interpretations of a species.

Connections between sexual and asexual morphs within the Orbiliomycetes have been known since the end of the 19th century (Brefeld 1891, *Dicranidion*), but most connections have been discovered since the end of the 20th century, starting

with Pfister's (1997) comprehensive study. Scholler et al. (1999) and Hagedorn and Scholler (1999) introduced a new generic concept for asexual morphs of nematode-trapping orbiliaceous fungi based on the types of trapping organs rather than the morphology of conidia and conidiophores. Together with molecular phylogenetic data, the new concept appears sound for those taxa that produce trapping organs in culture. Trapping organs adapted to nematode capture are either adhesive traps or involve constricting or non-constricting rings. Some taxa with adhesive organs capture arthropods such as copepods, mites, collembolans, and dipterans. All these predacious taxa treated by Scholler et al. (1999) are members of *Arthrobotrys* in a broad sense, a subgroup of *Orbilia* s. l.

Two further genera of Orbiliomycetes that possess trapping organs were not treated by Scholler et al. (1999): *Brachyphoris* (the asexual morph of *Hyalorbilia*, earlier classified in *Dactylella*) and *Lecophagus*. Their members trap rhizopods, or rotifers and tardigrades, respectively, through the prey's mouth region by means of adhesive pegs or knobs. One species (*Brachyphoris oviparasitica*) is known to parasitize nematode eggs, a behavior occurring also in the closely related genus *Vermispora*. In our molecular phylogenetic analyses (Fig. 1), the two genera cluster in basal clades and might originate from a common ancestor with predacious capabilities. *Arthrobotrys* s. l. does not seem to be closely related to this clade; therefore, it is unclear whether it developed zoophagy independently.

In the ongoing work on the monograph, predacious capabilities could not be demonstrated in pure culture for the majority of species up to now. 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 molecular phylogenetic hypothesis (Fig. 1) suggest that these taxa can be classified into various groups, most of which appear only distantly related to the predacious groups. Due to the absence of trapping organs, their classification is mainly based on characters of the sexual morph and rDNA data, and, to a certain extent, also on conidial morphology. In some of the groups (e.g., *Pseudotriporiconidium* vs. *Helicoon/Anguillospora*), the conidial morphology is highly characteristic, whereas the sexual morph is hardly distinctive.

The heterogeneity of most non-predacious asexually typified genera is exemplified by those with stauroconidia that are distinguished according to different types of branching. Cultural studies have shown that different branching types often occur within a single isolate (see, e.g., Ando 1992) or in very closely related species. We found representatives of most of these asexually typified genera, for instance *Trinacrium* and *Dicranidion*, in distant clades within the class, and evidence is accumulating that the current generic concept is artificial. Two of these genera, *Dwayaangam* and *Anguillospora*, also include taxa belonging to the Helotiales (e.g., *D. colodena* Sokolski & Bérubé and *A. crassa* Ingold) or Dothideomycetes [e.g., *A. rubescens* Gulis & Marvanová and *A. longissima* (Sacc. &

P. Syd.) Ingold]. These asexual morphs are morphologically difficult to distinguish from their orbiliaceous analogues.

Under the new nomenclature rules, we see two aspects of handling asexually typified genera without known trapping organs. We can either regard these conidium-based “genera” just as descriptive terms. According to recommendations by Seifert et al. (2000), Cannon and Kirk (2000), and Hawksworth (2011), it is convenient to use phrases such as “anguillospora-like” when referring to a given morphology, irrespective of the phylogenetic relationship. Or we have to determine which of these asexually typified generic names can be used in a phylogenetic sense as a holomorph name for a given genus, depending on the position of its type species.

The following alphabetic list treats all generic names that we found to be connected with the Orbiliomycetes. Several names are obligate, homotypic synonyms of others, and many are heterotypic synonyms even when a narrow generic concept is applied. However, the identity of a type species, particularly that of asexually typified genera, is often uncertain when no DNA sequences are available because of convergences, especially in conidial shape.

Below, we have indicated our opinion on all those generic names that compete with a name of a different or the same morph, addressing which name should be used in accordance with the rules and the chosen generic concept. Studies of connections of asexual and sexual morphs within the last several decades have shown that the generic concepts applied up to now are very inconsistent between the two morphs: a narrow concept has been applied to the asexual morph but a broad concept to the sexual morph. As a result, we are dealing with many more generic names that are based on asexual morphs.

We see three main ways of handling the ranks within the class (Table 1). (1) When applying a broad generic concept, most of the listed generic names fall into synonymy with the oldest name of an orbiliaceous sexual morph, *Orbilia*, published by Fries in 1836. Apart from three small undescribed genera, two of which are included in our phylogenetic analysis (Fig. 1), this concept recognizes five genera with very different species numbers: *Hyalorbilia* (~40), *Lecophagus* (~5), *Orbilia* (~500), *Pseudorbilia* (1), and *Vermispora* (~7, including *Microdochiella*) (the species numbers given here include undescribed taxa). The large genus *Orbilia* is subdivided into a system of subgenera, sections, and series. This broad concept is represented in Fig. 1. It is applied in the ongoing monograph of Orbiliomycetes, because many species of *Orbilia* s. l. are at present without molecular data, and because available rDNA data in various cases did not result in significantly supported clades that reflect morphology-based concepts.

(2) A moderate generic concept subdivides the large genus *Orbilia* into a number of genera. For instance, the following four names could be recognized: *Arthrobotrys*, *Habrostrictis*, *Hemiorbilia*, and *Orbilia*. *Arthrobotrys*, published by Corda in 1839, is the oldest available name for an orbiliaceous

**Table 1** Three generic concepts within *Orbilia*. A broad concept is used in the “Monograph of Orbiliomycetes” (Baral et al., unpubl.)

| Broad concept                   | Moderate concept                 | Narrow concept                |
|---------------------------------|----------------------------------|-------------------------------|
| <b><i>Orbilia</i></b>           |                                  |                               |
| subgenus <i>Hemiorbilia</i>     | <b><i>Hemiorbilia</i>*</b>       |                               |
| section <i>Hemiorbilia</i>      | subgenus <i>Hemiorbilia</i>      | <b><i>Hemiorbilia</i></b>     |
| section <i>Lentiformes</i> *    | subgenus <i>Lentiformes</i> *    | <b><i>Lentiformes</i>*</b>    |
| subgenus <i>Habrostrictis</i>   | <b><i>Habrostrictis</i></b>      |                               |
| section <i>Habrostrictis</i>    | subgenus <i>Habrostrictis</i>    | <b><i>Habrostrictis</i></b>   |
| section <i>Helicoon</i>         | subgenus <i>Helicoon</i>         | <b><i>Helicoon</i></b>        |
| section <i>Aurantiorubrae</i> * | subgenus <i>Aurantiorubrae</i> * | <b><i>Aurantiorubrae</i>*</b> |
| subgenus <i>Orbilia</i>         | <b><i>Orbilia</i></b>            |                               |
| section <i>Orbilia</i>          | subgenus <i>Orbilia</i>          | <b><i>Orbilia</i></b>         |
| section <i>Ovoideae</i> *       | subgenus <i>Ovoideae</i> *       | <b><i>Ovoideae</i>*</b>       |
| section <i>Arthrobotrys</i>     | <b><i>Arthrobotrys</i></b>       |                               |
| series <i>Arthrobotrys</i>      | subgenus <i>Arthrobotrys</i>     | <b><i>Arthrobotrys</i></b>    |
| series <i>Dactylella</i>        | subgenus <i>Dactylella</i>       | <b><i>Dactylella</i></b>      |
| series <i>Dactylellina</i>      | subgenus <i>Dactylellina</i>     | <b><i>Dactylellina</i></b>    |
| series <i>Drechslerella</i>     | subgenus <i>Drechslerella</i>    | <b><i>Drechslerella</i></b>   |
| series <i>Gamsylella</i>        | subgenus <i>Gamsylella</i>       | <b><i>Gamsylella</i></b>      |

\* at present unpublished name

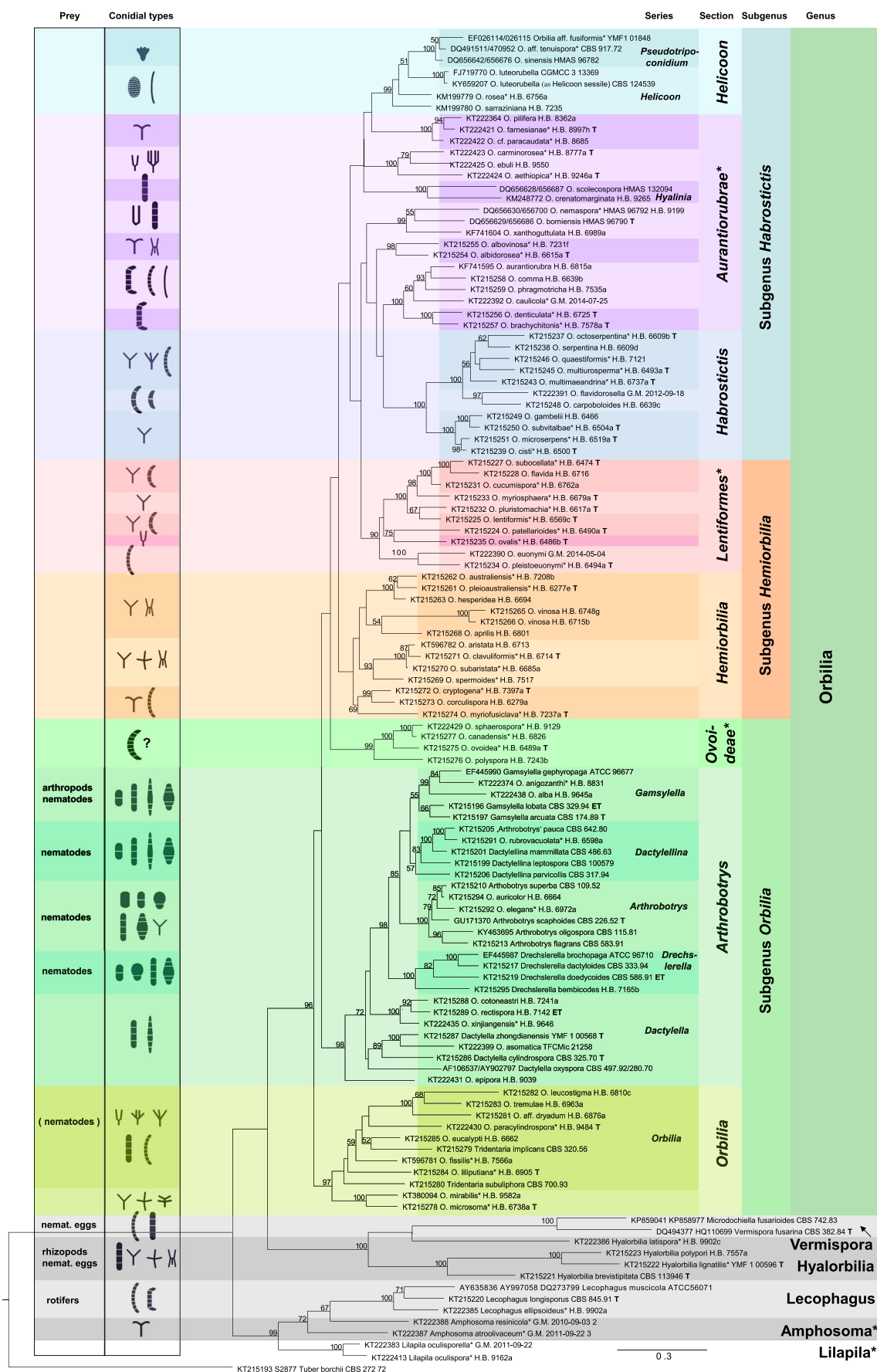
asexual morph, and, under this concept, it would encompass all nematode-trapping species, as well as some closely related non-nematophagous species (*Dactylella* p.p.). (3) A narrow generic concept accepts the system proposed by Scholler et al. (1999) for the nematode-trapping group and also subdivides the remaining three genera of the moderate generic concept into various further genera.

The moderate as well as the narrow generic concept require a classification system that includes ranks above the generic level. The phylogenetic analysis presented here is based on rDNA alone, because data from protein-coding genes were not available for the majority of taxa. Therefore, the resulting tree topology shows high support only for its terminal branches and leaves the backbone of the tree unresolved.

In the notes on each generic name, we have mentioned the three main generic concepts whenever the acceptance of a name depends on the taxonomic concept chosen. Table 3 lists the recommended generic names and those names of either the sexual or the asexual morph that are considered synonymous even under a narrow concept. If action is required, this is mentioned in the last column.

## Materials and methods

The origin of fungal material will be reported in detail in the monograph in preparation. For the microscope techniques, see Baral (1992). Sequences were either gained from our cultures, for which half-strength cornmeal agar (CMA:2, Rubner 1996) was used, or from apothecia, using standard techniques for DNA extraction, PCR, and Sanger sequencing (e.g., Quijada





**Fig. 1** Maximum likelihood tree illustrating phylogenetic relationships in the Orbiliomycetes as inferred from a 1854 bp alignment of nuclear DNA sequences (18S, 5.8S, and 28S). Branch support is given as maximum likelihood bootstrap percentages from 1000 replicates; values below 50% are not shown. Branch lengths are given in terms of expected numbers of substitutions per nucleotide. GenBank accession numbers are given in the tree for each DNA sequence used. The tree was rooted with *Tuber borchii*. A broad taxonomic concept is shown that includes different subgenera, sections, and series (the latter are only mentioned when published names are available); \*generic, infrageneric, and species names that will be validly published in the “Monograph of Orbiliomycetes” (Baral et al., unpubl.); T = type; ET = epitype; for an explanation of the conidial symbols, see Table 2

et al. 2014) with various primers. The following abbreviations are used: (A) = asexual morph (= anamorph), (S) = sexual morph (= teleomorph), H.B. = private fungarium H.-O. Baral.

### Molecular phylogenetic analysis

Nuclear rDNA sequences comprising partial 18S, ITS, and 28S rDNA were aligned using MAFFT 7 (Kato and Standley 2013) via a web server at <http://mafft.cbrc.jp/alignment/server/>. Gappy alignment blocks caused by inserts in single sequences were excluded. Misaligned isolated sequence fragments in the leading or trailing regions of the alignment were recoded (masked) as missing data, as were

two short strings of three or nine nucleotides, respectively, which apparently had been misaligned because of sequencing errors. The final dataset (alignment) had a length of 1854 nucleotides (see the [supplementary material](#)). The alignment is also deposited in TreeBASE (<http://www.treebase.org>, accession number S20839). We ran five separate heuristic maximum-likelihood analyses using RAXML version 8.2.4 (Stamatakis 2014), as implemented in a parallelized version at the CIPRES portal (<http://www.phylo.org>), each time involving four processors and the GTRCAT model of DNA substitution, with starting trees in each replicate obtained from 1000 rounds of rapid bootstrapping ( $-f a$  option), and different starting seeds. The tree with the highest likelihood inferred in these analyses is shown in Fig. 1.

### Checklist of genera of Orbiliomycetes

*Anguillospora* Ingold, Trans. Br. Mycol. Soc. 25(4): 401 (1942) [“1941”] — Use *Anguillospora* (A) only in the form of “anguillospora-like” when referring to conidial shape; use instead *Helicoon* (A) when applying a narrow generic concept, otherwise use *Habrostictis* (S) or *Orbilbia* (S).

*Anguillospora* was based on *A. longissima*, which had originally been described in *Fusarium*. Index Fungorum (<http://www.indexfungorum.org>) lists a total of 20 names, but only for one of them, *A. rosea*, could a relationship with Orbiliomycetes be demonstrated (Webster and Descals 1979; Descals and Chauvet 1992; Descals et al. 1999, as *Orbilbia* sp.; Pfister 1997, as *O. luteorubella* (Nyl.) P. Karst.).

*Anguillospora* was characterized by filiform (scolecosporous), multiseptate, hyaline conidia that resemble an eel (= *anguilla*). Examples belonging to Orbiliomycetes are shown in Fig. 3h, i. The morphological delimitation from asexual morphs with shorter conidia referable to *Vermispora* is only gradual concerning conidial shape, though *Vermispora* can be separated from *Anguillospora* by a sympodial conidiogenesis. *Lecophagus* differs by sympoduloconidia formed almost simultaneously in fascicles on multilocular conidiophore tips (Fig. 3g).

That *Anguillospora* is heterogeneous was noticed early based on different patterns of conidial secession and connections to very different sexual morphs (Webster and Descals 1979; Nakagiri and 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, holoblastic. This heterogeneity has been confirmed by molecular studies (Belliveau and Bärlocher 2005; Baschien et al. 2006). Accordingly, the former concept of

**Table 2** Conidial symbols as used in Fig. 1

| Symbol | Explanation                                                                                  |
|--------|----------------------------------------------------------------------------------------------|
|        | Conidia straight, none-septate                                                               |
|        | Conidia unbranched, 1-septate                                                                |
|        | Conidia unbranched, multiseptate, straight (dactylella-like, brachyphoris-like)              |
|        | Conidia unbranched, multiseptate, curved (vermispora-like, lecophagus-like)                  |
|        | Conidia unbranched, filiform, multiseptate (anguillospora-like)                              |
|        | Conidia unbranched, multiseptate, with enlarged central cell                                 |
|        | Conidia unbranched, with protuberances (pseudotriapoconidium-like)                           |
|        | Conidia helicoid, multiseptate (helicoon-like)                                               |
|        | Conidia branched, 2-armed, Y- or T-shaped (trinacrium-like)                                  |
|        | Conidia branched, 2- to 4-armed, U-shaped (dicranidion-like)                                 |
|        | Conidia branched, 3-armed, cross-shaped (descalsia-like, curcusporea-like, tridentaria-like) |
|        | Conidia branched, 4-armed, arthropod-shaped (dwayaangam-like, unnamed)                       |

*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 is hardly visible 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 sexual morphs, the conidiogenous cells have been reported to be thalloblastic-percurrent (Baschien et al. 2013). Pycnidial synanamorphs were found in *Anguillospora longissima* (Willoughby & Archer 1973) and in *A. mediocris* J. Gönczöl & Marvanová (Gönczöl and Marvanová 2002), whereas moniliaceous phialidic synanamorphs were observed in *A. crassa* (Webster 1961) and *A. furtiva* Descals (Descals et al. 1999). Besides a pycnidial synanamorph, Webster and 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. However, Baschien et al. (2006) and Descals et al. (1999) stated that *A. rosea* also shows percurrent proliferation, and L. Marvanová observed this feature in her isolates of *A. rosea*.

In the unpublished monograph, anguillospora-like asexual morphs are reported from ascospore isolates of a few teleomorphic species, particularly those adapted to an aero-aquatic habitat (section *Helicoon*, including *A. rosea*). Since *A. longissima* was shown to belong in *Amniculicola* Y. Zhang et al. (2007), the genus *Helicoon* s. str. can be used to also include *A. rosea*, which is phylogenetically closely related to the type species *H. sessile*. A recent proposal (Rossman et al. 2016) recommends to protect *Amniculicola* over *Anguillospora*, or to conserve *Anguillospora* with a new type.

***Anulosporium* Sherb. (1933) — Use *Dactylellina* (A) instead of the dubious older name *Anulosporium* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).**

The genus *Anulosporium* was proposed for *A. nematogenum*, and no further species have been added later. It is characterized by stalked adhesive knobs and non-constricting rings and is, therefore, a clear earlier synonym of *Dactylellina*. 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 identity of the type species remains unclear. For this reason,

Scholler et al. (1999) considered the genus to be dubious, an opinion with which we agree.

***Arthrobotrys* Corda (1839) — Use *Arthrobotrys* (A) when applying a moderate or narrow generic concept, otherwise use *Orbilia* (S).**

*Arthrobotrys* (Figs. 4j, n–p and 5f), which was described with the single species *A. superba*, is one of the largest orbiliaceous genera and also represents the most widely used generic name within the Orbiliomycetes. 105 specific epithets have ever been combined in *Arthrobotrys* (Index Fungorum), but many of them were shown to be synonyms, which illustrates the complicated taxonomy in this group. For instance, *A. superba*, *A. cladodes* Drechsler, and *A. oligospora* form a difficult complex of species to which *Orbilia auricolor* agg. was shown to be connected as the sexual morph (Figs. 2m and 4o, p).

Some *Arthrobotrys* species (in particular *A. oligospora*, Fig. 4p) have been used as model organisms in attempts to develop biocontrol agents and in mycology teaching. It is, therefore, desirable to preserve this name under the new rules. Earlier, the genus was defined by 1-septate conidia formed in roundish clusters on nodules on swollen fertile nodes (“arthrobotryoid” conidiogenesis), combined with the ability to trap nematodes, though without respect to the type of trapping organs. Schenck et al. (1977) extended the generic definition to include species with aseptate and multiseptate conidia and candelabrelloid conidiophores. The Greek suffix *-botrys* describes the clusters of conidia and the prefix *arthro-* refers to the chain-like arrangement of the clusters along the very elongate conidiophore in the type species.

The ICN contains a new passage [Art. 62.2(a)] that all names ending in *-botrys* are treated as masculine. There are, however, a range of fungal genera that have always been treated as feminine in accordance with *Botrytis*, which will require a modification of the Code. We, therefore, do not follow the new rule.

The concept of Scholler et al. (1999) accepts 46 species in *Arthrobotrys*, all of which trap nematodes by means of more or less three-dimensional adhesive networks (Fig. 5f). Based on this concept, the authors considered eight further generic names as synonymous (see below), which include species possessing conidiophores with a single acrogenous conidium, and conidia varying from cylindric-clavate to fusiform. A sexual morph name (*Orbiliella*) and a questionable asexual morph name (*Tripoconidium*) are here added to the list of synonyms. The genus is represented in Fig. 1 as the *Arthrobotrys* clade within the section *Arthrobotrys*.

*Orbilia*, with currently about 80 validly described and accepted species, was erected three years earlier than *Arthrobotrys*, with about 60 species. When applying a broad generic concept, *Orbilia* should be preferred because of its priority and larger species number. Both genera have

**Table 3** Recommended generic names of Orbiliomycetes and their synonyms that compete for use

| Recommended generic name                                                                                                                                                                                                                                                | Synonymous alternate morph generic name                                                                                                                            | Additional synonymous generic names                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       | Action required                                                      |
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| <b><i>Arthrobotrys</i></b> Corda, Pracht-Fl. Eur. Schimmelbild.: 43 (1839) – Type species: <i>A. superba</i> Corda (1839) [= <i>Orbilia auricolor</i> (A. Bloxam) Sacc. (1889)] (use when applying a moderate or narrow generic concept, otherwise use <i>Orbilia</i> ) | <i>Orbiliella</i> Kirschst., Ann. Mycol. 36: 374 (1938) – Type species: <i>O. armeniaca</i> Kirschst. (1938) [= <i>Orbilia auricolor</i> (A. Bloxam) Sacc. (1889)] | <i>Monacrosporium</i> Oudem., Ned. Kruidk. Arch., Ser. 2,4: 250 (1885) – Lectotype species: <i>M. elegans</i> Oudem. (1885) [= <i>Arthrobotrys oudemansii</i> M. Scholler et al. (2000)]<br><i>Didymo zoophaga</i> Soprunov & Galiulina, Mikrobiologiya 20: 493 (1951) [nom. inval., Art. 39] – Lectotype: <i>D. oligospora</i> (Fresen.) Soprunov & Galiulina, basionym: <i>Arthrobotrys oligospora</i> Fresen<br><i>Candelabrella</i> Rifai & R.C. Cooke, Trans. Br. Mycol. Soc. 49(1): 160 (1966) – Type species: <i>C. javanica</i> Rifai & R. C. Cooke (1966) [= <i>Arthrobotrys javanica</i> (Rifai & R.C. Cooke) Jarow. (1970)]<br><i>Genicularia</i> Rifai & R.C. Cooke, Trans. Br. Mycol. Soc. 49: 153 (1966) [nom. illegit., Art. 53 ICN] – Type species: <i>G. cystosporia</i> (Dudd.) Rifai & R.C. Cooke, basionym: <i>Trichothecium cystosporium</i> Dudd. [= <i>Arthrobotrys cystosporia</i> (Dudd.) Mekht.]<br><i>Duddingtonia</i> R.C. Cooke, Trans. Br. Mycol. Soc. 53: 316 (1969) – Type species: <i>D. flagrans</i> (Dudd.) R.C. Cooke (1969), basionym: <i>Trichothecium flagrans</i> Dudd. [= <i>Arthrobotrys flagrans</i> (Dudd.) Mekht. (1964)]<br><i>Geniculifera</i> Rifai, Mycotaxon 2: 214 (1975) – Type species: <i>G. cystosporia</i> (Dudd.) Rifai (1975), basionym: <i>Trichothecium cystosporium</i> Dudd. [= <i>Arthrobotrys cystosporia</i> (Dudd.) Mekht. (1964)]<br><i>Nematophagus</i> Mekht., Mikol. Fitopatol. 9(2): 250 (1975) – Type species: <i>N. azerbaijanicus</i> Mekht. (1975) [= <i>Arthrobotrys azerbaijanica</i> (Mekht.) Oorschot (1985)]<br><i>Monacrosporiella</i> Subram., Kavaka 5: 94 (1978, “1977”) – Type species: <i>M. megalospora</i> (Drechsler) Subram. (1978), basionym: <i>Dactylella megalospora</i> Drechsler [= <i>Arthrobotrys megalospora</i> (Drechsler) M. Scholler et al. (1999)]<br><i>?Tripoconidium</i> Subram., Kavaka 5: 95 (1978) – Type species: <i>T. aphanopagum</i> (Drechsler) Subram. (1978), basionym: <i>Triposporina aphanopaga</i> Drechsler<br><i>Woroninula</i> Mekht., Khishchnye Nematofagovye Griby-Gifomitsety: 109 (1979) – Type species: <i>W. polycephala</i> (Drechsler) Mekht. (1979), basionym: <i>Dactylaria polycephala</i> Drechsler [= <i>Arthrobotrys polycephala</i> (Drechsler) Rifai (1968)] | Asexual type.<br>Approval needed by Nomenclature Committee for Fungi |

**Table 3** (continued)

| Recommended generic name                                                                                                                                                                                                                                                                                                      | Synonymous alternate morph generic name                                                                                                                    | Additional synonymous generic names                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Action required                                   |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------|
|                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                            | <i>Roigiella</i> R.F. Castañeda, Revta Jardín bot. Nac., Univ. Habana 5(1): 62 (1984) – Type species: <i>R. lignicola</i> R.F. Castañeda (1984) (= <i>Arthrobotrys</i> sp. fide Seifert et al. 2011)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                                   |
| <b><i>Dactylella</i></b> Grove, J. Bot. 22: 199 (1884) – Type species: <i>D. minuta</i> Grove (1884) (use when applying a narrow generic concept, otherwise use <i>Arthrobotrys</i> or <i>Orbilina</i> )                                                                                                                      |                                                                                                                                                            | <i>Gangliophragma</i> Subram., Kavaka 5: 94 (1978, “1977”) – Type species: <i>G. rhopalota</i> (Drechsler) Subram. (1978), basionym: <i>Dactylella rhopalota</i> Drechsler (1943)<br><i>Drechsleromyces</i> Subram., Kavaka 5: 93 (1978, “1977”) – Type species: <i>D. atractoides</i> (Drechsler) Subram. (1978), basionym: <i>Dactylella atractoides</i> Drechsler (1943)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        | <i>Dactylella minuta</i> requires epitypification |
| <b><i>Dactylellina</i></b> M. Morelet, Bull. Soc. Sci. Nat. Archéol. Toulon Var 178: 6 (1968) – Type species: <i>D. leptospora</i> (Drechsler) M. Morelet (1968), basionym: <i>Dactylella leptospora</i> Drechsler (1937) (use when applying a narrow generic concept, otherwise use <i>Arthrobotrys</i> or <i>Orbilina</i> ) |                                                                                                                                                            | ? <i>Dactylium</i> Nees, Syst. Pilze: 58 (1816) [1816–1817], Fr., Syst. Mycol. 3: 382, 412 (1832), nom. dub. – Type species: <i>D. candidum</i> Nees [nom. dub. et rej.; ?non <i>Dactylaria candida</i> (Nees) Sacc. s. Drechsler (1937: 523), = <i>Dactylellina haptotyla</i> (Drechsler) M. Scholler et al.]<br><i>Anulospodium</i> Sherb., Mycologia 25: 262 (1933) – Type species: <i>A. nematogenum</i> Sherb. (1933) (nom. dub., identity unclear at the species level)<br><i>Dactylosporium</i> Mekht., Mikol. Fitopatol. 1: 277 (1967), nom. illegit., Art. 53 ICN [non <i>Dactylosporium</i> Harz 1871] – Type species: <i>D. leptosporum</i> (Drechsler) Mekht., basionym: <i>Dactylella leptospora</i> Drechsler [= (Drechsler) M. Morelet (1968)]<br><i>Laridospora</i> Nawawi, Trans. Br. Mycol. Soc. 66: 344 (1976) – Type species: <i>L. appendiculata</i> (Anastasiou) Nawawi (1976), basionym: <i>Dactylella appendiculata</i> Anastasiou (1964) [= <i>Dactylellina appendiculata</i> (Anastasiou) M. Scholler et al. (1999)]<br><i>Kafiaddinia</i> Mekht. Mikol. Fitopatol. 12: 8 (1978) – Type species: <i>K. fusarispora</i> Mekht. (1978) (= <i>Dactylellina leptospora</i> fide Rubner 1996) | Reject<br><i>Anulospodium</i>                     |
| <b><i>Drechslerella</i></b> Subram., J. Indian Bot. Soc. 42: 299 (1964) [“1963”] – Type species: <i>D. acrochaeta</i> (Drechsler) Subram. (1964), basionym: <i>Dactylella acrochaeta</i> Drechsler (1952) (use when applying a narrow generic concept, otherwise use <i>Arthrobotrys</i> or <i>Orbilina</i> )                 | <b><i>Orbiliaster</i></b> Dennis, Kew Bull. 9: 294 (1954) – Type species: <i>O. pilosus</i> Dennis (1954) [= <i>Orbilina pilosa</i> (Dennis) Baral (1994)] | <i>Dactylariopsis</i> Mekht., Mikol. Fitopatol. 1: 278 (1967) – Type species: <i>D. brochopaga</i> (Drechsler) Mekht. (1967), basionym: <i>Dactylella brochopaga</i> Drechsler (1937) [= <i>Drechslerella brochopaga</i> (Drechsler) M. Scholler et al. (1999)]<br><i>Golovinina</i> Mekht., Mikol. Fitopatol. 1: 275 (1967) – Type species: <i>G. bembicodes</i> (Drechsler) Mekht. (1967), basionym: <i>Dactylella</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           | Later name proposed for protection                |



**Table 3** (continued)

| Recommended generic name                                                                                                                                                                                                                                                                                                                      | Synonymous alternate morph generic name                                                                                                                                   | Additional synonymous generic names                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Action required                     |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------|
|                                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                                           | <i>bembicodes</i> Drechsler (1937) [= <i>Drechslerella bembicodes</i> (Drechsler) M. Scholler et al. (1999)]                                                                                                                                                                                                                                                                                                                                                                                                                                   |                                     |
| <b><i>Gamsylella</i></b> M. Scholler, Hagedorn & A. Rubner, Sydowia 51(1): 108 (1999) – Type species: <i>G. arcuata</i> (Scheuer & J. Webster) M. Scholler et al. (1999), basionym: <i>Dactylella arcuata</i> Scheuer & J. Webster (1990) (use when applying a narrow generic concept, otherwise use <i>Arthrotrichys</i> or <i>Orbilia</i> ) |                                                                                                                                                                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | None                                |
| <b><i>Habrostictis</i></b> Fuckel, Jahrb. Nassau. Ver. Naturkd. 23–24: 249 (1870) – Type species: <i>H. rubra</i> Fuckel (1870) [= <i>Orbilia carpoboloides</i> (P. & H. Crouan) Baral (1994)] (use when applying a moderate or narrow generic concept, otherwise use <i>Orbilia</i> )                                                        |                                                                                                                                                                           | <i>Cheilodonta</i> Boud., Bull. Trimest. Soc. Mycol. Fr. 1: 114 (1885) – Lectotype species: <i>C. carpoboloides</i> (P. & H. Crouan) Boud. (1885), basionym: <i>Peziza carpoboloides</i> P. & H. Crouan (1867) [= <i>Orbilia carpoboloides</i> (P. & H. Crouan) Baral (1994)]                                                                                                                                                                                                                                                                  | None                                |
| <b><i>Helicoon</i></b> Morgan, J. Cincinnati Soc. Nat. Hist. 15: 49 (1892) – Lectotype species: <i>H. sessile</i> Morgan (1892) (use when applying a narrow generic concept, otherwise use <i>Habrostictis</i> or <i>Orbilia</i> )                                                                                                            |                                                                                                                                                                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | None                                |
| <b><i>Orbilia</i> subgenus <i>Hemiorbilia</i></b> Baral, Syst. Ascomycetum 13: 118 (1994) – Type species: <i>O. occulta</i> (Rehm) Sacc. (1889), basionym: <i>Calloria occulta</i> Rehm (1885) (raise <i>Hemiorbilia</i> to generic rank when applying a moderate or narrow generic concept, otherwise use <i>Orbilia</i> )                   | ? <i>Trinacrium</i> Riess in Fresenius, Beitr. Mykol. 2: 42 (1852) – Type species: <i>T. subtile</i> Riess (1852)                                                         | ? <i>Radotinea</i> Velen., Monogr. Discom. Bohem.: 298 (1934) – Type species: <i>R. caudata</i> Velen. (1934) [(?)= <i>Orbilia aristata</i> (Velen.) Velen. (1947)]<br>? <i>Descalsia</i> A. Roldán & Honrubia, Mycol. Res. 92: 494 (1989) – Type species: <i>D. cruciata</i> A. Roldán & Honrubia (1989)                                                                                                                                                                                                                                      | Later name proposed for protection  |
| <b><i>Hyalorbilia</i></b> Baral & G. Marson, Micologia 2000 (Trento): 44 (2001) – Type species: <i>H. berberidis</i> (Velen.) Baral (2001), basionym: <i>Orbilia berberidis</i> Velen. (1934)                                                                                                                                                 | <i>Dwayaangam</i> Subram., Kavaka 5: 96 (1978) – Type species: <i>D. quadridens</i> (Drechsler) Subram. (1978), basionym: <i>Tripasporina quadridens</i> Drechsler (1961) | ? <i>Curucispora</i> Matsush., Matsush. Mycol. Mem. 2: 4 (1981) – Type species: <i>C. ponapensis</i> Matsush. (1981)<br>? <i>Paradactylella</i> Matsush., Matsush. Mycol. Mem. 7: 59 (1993) – Type species: <i>P. peruviana</i> Matsush. (1993)<br><i>Brachyphoris</i> Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu, Fungal Diversity 26: 128 (2007) – Type species: <i>B. oviparasitica</i> (G.R. Stirling & Mankau) Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu (2007), basionym: <i>Dactylella oviparasitica</i> G.R. Stirling and Mankau (1978) | Later name proposed for protection. |
| <b><i>Lecophagus</i></b> M.W. Dick, Mycol. Res. 94: 351 (1990) – Type species: <i>L. fasciculatus</i> M.W. Dick (1990) [= <i>L. muscicola</i> (G.L. Barron et al.) Tanabe et al. (1999)]                                                                                                                                                      |                                                                                                                                                                           |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | None                                |

**Table 3** (continued)

| Recommended generic name                                                                                                                                                                                                                                                                  | Synonymous alternate morph generic name                                                        | Additional synonymous generic names                                                                                                                                                                                 | Action required                            |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------|
| <b><i>Mycoceros</i></b> D. Magyar & Z. Merényi, Mycol. Prog. (2017) – Type species: <i>M. antennatissimus</i> D. Magyar (2017)                                                                                                                                                            |                                                                                                |                                                                                                                                                                                                                     | None                                       |
| <b><i>Orbilbia</i></b> Fr., Fl. Scan.: 343 (1836) – Lectotype species: <i>O. xanthostigma</i> (Fr. : Fr.) Fr. (1849) (designated by Bachmann 1909), basionym: <i>Peziza xanthostigma</i> Fr. (1815)                                                                                       | <i>Dicranidion</i> Harkn., Bull. Calif. Acad. Sci. 1: 163 (1885) – Type species: Harkn. (1885) | <i>Pedilospora</i> Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 111: 1047 [61 ofrepr.] (1902) – Type species: Höhn. (1902)                                                          | None (irrespective of the generic concept) |
| <b><i>Pseudorbilia</i></b> Ying Zhang, Z.F. Yu, Baral & K.Q. Zhang, Fungal Diversity 26: 306 (2007) – Type species: <i>P. bipolaris</i> Ying Zhang et al. (2007)                                                                                                                          |                                                                                                |                                                                                                                                                                                                                     | None                                       |
| <b><i>Pseudotriporconidium</i></b> Z.F. Yu & K.Q. Zhang, in Yu et al., Mycologia 103(1): 168 (2011) – Type species: <i>P. sinense</i> Z.F. Yu & K.Q. Zhang (2011) (use when applying a narrow generic concept, otherwise use <i>Helicoon</i> , <i>Habrostictis</i> , or <i>Orbilbia</i> ) |                                                                                                |                                                                                                                                                                                                                     | None                                       |
| <b><i>Retiarius</i></b> D.L. Olivier, Trans. Br. Mycol. Soc. 71: 194 (1978) – Type species: <i>R. superficialis</i> D.L. Olivier (1978)                                                                                                                                                   |                                                                                                |                                                                                                                                                                                                                     | None                                       |
| <b><i>Vermispora</i></b> Deighton & Piroz., Mycol. Pap. 128: 87 (1972) – Type species: <i>V. grandispora</i> Deighton & Piroz. (1972)                                                                                                                                                     |                                                                                                | ? <i>Microdochiella</i> Hern.-Restr. & Crous, Persoonia 36: 62 (2015) – Type species: <i>M. fusarioides</i> (D.C. Harris) Hern.-Restr. & Crous (2015), basionym: <i>Microdochium fusarioides</i> D.C. Harris (1985) | None                                       |

Recommended names are listed in **bold** in the first column, the second column indicates the oldest competing alternate morph generic name, and the third column in chronological order any further synonymous generic names. The last column indicates the action required, such as protection of sexual morph names without priority or asexual morph names that need protection

continuously been applied over the centuries, but *Arthrobotrys* was mainly used for nematode-trapping species, which represent a comparatively small group within the Orbiliomycetes. When using a moderate generic concept, *Arthrobotrys* should be used for the group that comprises all nematode-trapping fungi included in the series *Arthrobotrys*, *Dactylellina*, *Drechslerella*, 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 non-predacious species currently recognized in *Dactylella* p.p. (see there and Fig. 1: section *Arthrobotrys*). Under a narrow generic concept, all these asexual morph names are recognized as distinct holomorph genera, because they delineate well-defined phylogenetic but also morphologically distinct groups in regard to their trapping organs (but see under these names for competing sexually typified genera).

***Brachyphoris*** Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu (2007) — **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* (with *B. oviparasitica* as the type species) but having shorter conidiophores and a considerable molecular distance to other *Dactylella* species. Two of the five species (*B. helminthodes* and *B. stenomeces*) lack DNA sequences and were assigned to the genus merely on the basis of short conidiophores. It is uncertain, however, whether these two species are related to *Brachyphoris* because such short conidiophores are frequently observed in various groups of desiccation-tolerant species of *Orbilbia* s. l.

*Brachyphoris* is a synonym of the sexually typified genus *Hyalorbilia* (Fig. 2c–e), and was established to

accommodate the asexual morphs of that genus (Fig. 4a, b). Although no DNA sequence of the type species *H. berberidis* is available, there is little doubt about its close relationship to *B. oviparasitica*. That species is only known from the asexual morph, but it is phylogenetically closely related to *H. brevistipitata* B. Liu et al. with its asexual morph *B. brevistipitata* (B. Liu et al.) Juan Chen et al. Many of the asexual morphs observed by us in *Hyalorbilia* have very similar fusoid, brachyphoris-like conidia, for which an example is shown in Fig. 4a. Also, ‘*Dactylella*’ *passalopaga*, a species that captures testaceous rhizopods (Fig. 5c), has such conidia and is undoubtedly a member of *Hyalorbilia*.

*Brachyphoris* and *Hyalorbilia* are competing names and only one of them should now be used. We give preference to the older name *Hyalorbilia*, with ten validly described species, rather than *Brachyphoris*, with only five species. Two new combinations are proposed here for species without a known sexual morph:

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

Mycobank MB 813456

Basionym: *Dactylella oviparasitica* G.R. Stirling & Mankau, *Mycologia* 70(4): 777 (1978).

≡ *Brachyphoris oviparasitica* (G.R. Stirling & Mankau) Juan Chen, L.L. Xu, B. Liu & Xing Z. Liu, *Fungal Diversity* 26(1): 79 (2007).

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

Mycobank MB 813463

Basionym: *Dactylella tenuifusaria* Xing Z. Liu, R.H. Gao, K.Q. Zhang & L. Cao, *Mycol. Res.* 100(2): 236 (1996).

≡ *Brachyphoris tenuifusaria* (Xing Z. Liu, R.H. Gao, K.Q. Zhang & L. Gao) Juan Chen, L.L. Xu, Bin Liu & Xing Z. Liu, *Fungal Diversity* 26(1): 124 (2007).

***Candelabrella*** Rifai & R.C. Cooke (1966) — **Use the older name *Arthrobotrys* (A) instead of *Candelabrella* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilia* (S).**

*Candelabrella* with the type species *C. javanica* was proposed for two species with 1-septate conidia and adhesive networks capturing nematodes. It was segregated from *Arthrobotrys* because of its candelabrum-like (candelabrelloid) conidiophore tips. Eight further species have later been included in the genus (Index Fungorum), with mainly adhesive networks, but also with adhesive knobs, the trapping organ of *Dactylellina*. Since Scholler et al. (1999), the synonymy with *Arthrobotrys* has been generally recognized.

***Cheilodonta*** Boud. (1885) — **Use the older name *Habrostictis* (S) instead of *Cheilodonta* (S) when applying a moderate or narrow generic concept, otherwise use *Orbilia* (S).**

*Cheilodonta* was proposed for two species, *C. carpoboloides* and *C. lasia*, based on apothecia with a dentate margin and acuminate-spathulate paraphysis tips. Boudier (1907) transferred both taxa to *Habrostictis* as the older generic name. *C. carpoboloides* was later designated as lectotype. *C. lasia* was early found to be a synonym of *H. rubra*, the type of *Habrostictis*, which in turn was synonymised with *Orbilia carpoboloides* by Baral (1994).

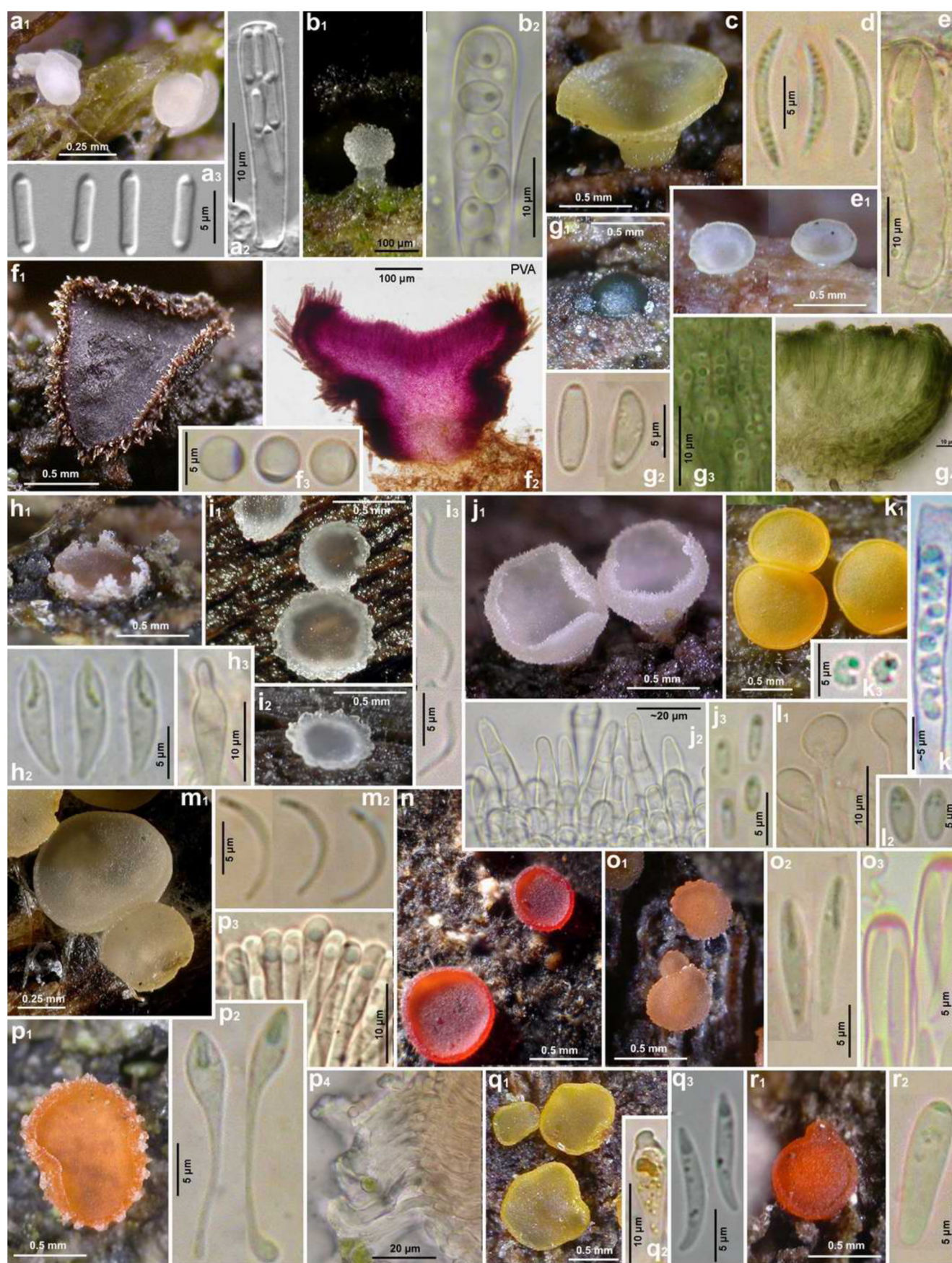
***Curucispora*** Matsush. (1981) — **Protect *Hyalorbilia* (S) over the older *Curucispora* (A) in case of congenericity.**

*Curucispora* was erected with one species, *C. ponapensis*. Two further species have later been included. The name *Cruciconidiifera*, proposed by Matsushima (2005) to replace *Curucispora* (the originally intended spelling) because of homonymy with *Crucispora* Horak, was possibly invalid in case that hard copies have not been provided. The name *Curucispora* should be maintained because Matsushima did not correct his error in a corrigendum of the 1981 volume and because the correction affects the first syllable of the generic name (Art. 60.3 ICN).

The tetra- and radiate conidia of *Curucispora* deviate from those of the similar *Descalsia* in showing two central cells divided by an oblique septum. They also differ in conidial shape, with the arm initials appearing V-shaped in the center of a bent axis, and later elongating to form a tetra- and 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 be typically planar (cross-shaped). However, conidia with an obliquely septate central cell also sometimes occurred in *Descalsia cruciata*, and, in our strains tentatively referred to as *descalsia*-like (Fig. 3z), the arms show a three-dimensional orientation, but in preparations with a cover slip, they are forced to lie in one plane and can be easily mistaken as planar. Also, Descals (pers. comm.) recalls having observed some conidia in *D. cruciata* in which two of the four branches form an acute angle (“V”), which might indicate that they had a three-dimensional orientation.

Molecular data are lacking, and the holotype of *C. ponapensis* was preserved only as a dried culture. The type species resembles in conidial morphology an asexual morph which was observed in association with an undescribed species of *Hyalorbilia* similar to *H. fusispora* (Baral et al., unpubl., Fig. 3y); therefore, *C. ponapensis* might be the asexual morph of a *Hyalorbilia* (but Fig. 3y also shows a similarity to *Retarius superficialis*). *Curucispora flabelliformis* K. Ando differs by curved arms and closely resembles an asexual







◀ **Fig. 2** Sexual morphs of Orbiliomycetes (a<sub>3</sub>, b<sub>2</sub>, d, f<sub>3</sub>, g<sub>2</sub>, h<sub>2</sub>, i<sub>3</sub>, j<sub>3</sub>, k<sub>3</sub>, l<sub>2</sub>, m<sub>2</sub>, o<sub>2</sub>, p<sub>2</sub>, q<sub>3</sub>, r<sub>2</sub>: ascospores with spore bodies; a<sub>2</sub>, b<sub>2</sub>, e<sub>2</sub>, k<sub>2</sub>, o<sub>3</sub>: asci; h<sub>3</sub>, l<sub>1</sub>, p<sub>3</sub>, q<sub>2</sub>: paraphyses; g<sub>3</sub>, j<sub>2</sub>: hairs; p<sub>4</sub>: glassy processes): **a** *Pseudorbilia bipolaris* (from Zhang et al. 2007, H.B. 8794); **b** *Lecophagus 'ellipsoideus'* ined. (16.XI.2013); **c** *Hyalorbilia inflatula* (TAAM 63888); **d** *H. berberidis* (H.B. 8605a); **e** *H. polypori* (H.B. 9361, 7943b); **f** '*Lilapila oculisporella*' ined. (H.B. 7063a, 4822, 9162a); **g** '*Amphosoma atroolivaceum*' ined. (H.B. 9143b, 9136c, 8057); **h** *Orbilia carpoboloides* (section *Habrostictis*, H.B. 9083a, 13.VI.2009, 9233); **i** *O. crenatomarginata* (sect. '*Aurantiorubrae*', H.B. 7683, 9304, P.P. 20070827); **j** *O. pilosa* (series *Drechslerella*, type of *Orbiliaster*, H.B. 9437); **k** *O. xanthostigma* (sect. *Orbilia*, 16.VI.2007, 3.VII.2006, 21.X.2010); **l** *O. eucalypti* (sect. *Orbilia*, H.B. 8427, H.B. 9226f); **m** *O. auricolor* (series *Arthrobotrys*, 8.I.2011, H.B. 8898a); **n** *O. 'rubrovacuolata'* ined. (series *Dactylellina*, H.B. 7719a); **o** *O. vinosa* (sect. *Hemiorbilia*, H.B. 5518, 7861a, 7249c, 18.II.2010); **p** *O. 'subaristata'* ined. (sect. *Hemiorbilia*, H.B. 9163b, 9151d, 10.II.2014); **q** *O. xanthoguttulata* (sect. '*Aurantiorubrae*', H.B. 8170a, 17.III.2011); **r** *O. 'lentiformis'* ined. (sect. '*Lentiformes*', H.B. 9578a, 7891b). Living state, except for ascus in k<sub>2</sub> (in water) and asci and spores in o<sub>3</sub> (in Congo red)

morph obtained in pure culture of an unnamed *Hyalorbilia* (Fig. 3x, Baral et al., unpubl.).

If DNA can be extracted from the dried type culture of *C. ponapensis* and it is demonstrated that this species falls within *Hyalorbilia*, then *Hyalorbilia* should be protected over *Curucispora* in order to avoid a much greater number of name changes.

***Dactylariopsis* Mekht. (1967) — Use the older name *Drechslerella* (A) instead of *Dactylariopsis* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).**

*Dactylariopsis*, with the type species *D. brochopaga*, was segregated from *Dactylella* and *Dactylaria* by the capability of capturing nematodes, from *Dactylella* also by apically at least partly denticulate conidiophores. Mekhtieva (1967) included six species that either form constricting rings (including *D. brochopaga*), adhesive knobs, or adhesive networks. Scholler et al. (1999) placed *Dactylariopsis* in synonymy with *Drechslerella*.

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

*Dactylella* was erected with one species, *D. minuta*, which was described with long unbranched conidiophores with a single terminal phragmoconidium. The holotype of *D. minuta* is located in K but consists of a piece of dead wood without any trace of the fungus (Rubner 1996). However, there is an illustration of *D. minuta* (Grove 1884: tab. 246, fig. 6) which can serve as part of the holotype (Art. 8.1. ICN). A culture was probably not made by Grove, and further unambiguous records are unknown.

The circumscription of *Dactylella* has been emended several times by various authors by including also species with apically

branched conidiophores. It was Rubner (1996) who restricted the genus to non-nematophagous species. Chen et al. (2007a, b) found that *Dactylella* was still heterogeneous with species in three distinct clades: *Brachyphoris* (sexual morph *Hyalorbilia*), *Vermispora* (sexual morph unknown), and *Dactylella* (sexual morph *Orbilia*). Under this generic concept, *Drechsleromyces* and *Gangliophragma* are synonyms of *Dactylella*.

A total of 106 specific epithets have been combined in *Dactylella* (Index Fungorum). Chen et al. (2007a) accepted 28 species in *Dactylella* s. str., which are saprotrophic though partly capable of invading oospores or nematode eggs. Various molecular phylogenetic studies including the present one (Fig. 1) showed that the available sequences of *Dactylella* in this restricted concept form a paraphyletic group in close vicinity of the nematode-trapping genera *Arthrobotrys*, *Dactylellina*, *Gamsylella*, and *Drechslerella*. Its paraphyly and frequently basal placement suggest that *Dactylella* represents the ancestor of the four nematophagous genera.

*Dactylella*-like asexual morphs were observed by us in three different groups of *Orbilia* s. l. (Fig. 1): series *Dactylella* (Fig. 4e–g), section '*Aurantiorubrae*' (two clades, Fig. 4c, see under *Hyalinia*), and series *Orbilia* (Fig. 4d), apart from the *dactylella*-like asexual morph of *Hyalorbilia* (*Brachyphoris*, Fig. 4a, b).

The morphological similarity of some asexual morphs referable to *Dactylella* in a wide sense but belonging to different clades is remarkably high; therefore, it remains unclear to which of these clades the type species *D. minuta* belongs. From its morphology, we suspect that it could either be the asexual morph of a member of series *Dactylella* (e.g., *Orbilia cardui* Velen.) or of *O. crenatomarginata* (section '*Aurantiorubrae*' ined.). When applying a narrow generic concept, the generic name *Dactylella* needs to be fixed by designating an epitype for *D. minuta* in accordance with Chen et al.'s (2007a) concept of *Dactylella*. However, no taxon or specimen that matches the large conidial size given by Grove (1884) is known to us. CBS cultures deposited under the name *D. minuta* by W. Gams and re-identified as *D. rhopalota* by Rubner (1996) have conidia of a size much smaller than that described by Grove.

***Dactylellina* M. Morelet (1968) — Use *Dactylellina* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).**

*Dactylellina* was erected with one species, *D. leptospora*, which was proposed as a replacement name for *Dactylosporium*. The genus was emended by Scholler et al. (1999) to comprise all those 17 species known at that time that trap nematodes by means of adhesive knobs or, in some species, additionally by non-constricting rings (Fig. 5d, e). Various further species were later added, partly by including the genus *Gamsylella*, so that, at present, 31 specific epithets have been combined in *Dactylellina* (Index Fungorum). The





◀ **Fig. 3** Conidiophores and conidia of Orbiliomycetes with curved, inversely pyramidal, or stauroconidia (non-predacious taxa except for *Lecophagus*). **Vermispora**: **a** *V. fusarina* (from Chen et al. 2007c); **vermispora-like**: **b** *Orbilia 'brachychitonis'* ined. (sect. 'Aurantiorubrae', H.B. 7578a); **c** *O. aurantiorubra* (sect. 'Aurantiorubrae', 4.I.2013, 3.IV.2013); **d** *O. 'pleistoeuonymi'* ined. (sect. 'Lentiformes', H.B. 9237a); **e** *O. 'patellarioides'* ined. (sect. 'Lentiformes', H.B. 9173h); **f** *O. 'aradi'* ined. (sect. 'Aurantiorubrae', H.B. 7884); **Lecophagus**: **g** *L. muscicola* (H.B. 7771); **anguillospora-like**: **h** *O. yuanensis* (sect. *Helicoon*, from Qiao et al. 2015); **i** *O. 'caulicola'* ined. (sect. 'Aurantiorubrae', G.M. 2013-07-30); **Pseudotriposconidium**: **j** *O. sinensis* (sect. *Helicoon*, from Yu et al. 2011); **Helicoon**: **k** *O. luteorubella* (sect. *Helicoon*, H.B. 9424a); **dicranidion-like**: **l** *O. eucalypti* (sect. *Orbilia*, 10.IV.2013); **m** *O. xanthoguttulata* (sect. 'Aurantiorubrae', H.B. 7884b); **n** *O. 'ovalis'* ined. (presumed, sect. 'Lentiformes', H.B. 7156a); **o** *O. fissilis* (sect. *Orbilia*, H.B. 7566a); **p** *O. abutilonis* (sect. 'Aurantiorubrae', H.B. 8546); **trinacrium-like**: **q** *O. 'obtusispora'* ined. (sect. *Habrostictis*, H.B. 8144); **r** *Hyalorbilia erythrostigma* (H.B. 6209a); **s** *O. 'clavuliformis'* ined. (sect. *Hemiorbilia*, 28.III.2009); **t** *O. pilifera* (sect. 'Aurantiorubrae', H.B. 8076a); **u** 'Amphosoma resinicola' ined. (H.B. 6992a); **tridentaria-like**: **v** *O. septispora* (sect. *Habrostictis*, H.B. 7267a); **unnamed**: **w** *O. 'multimicrosoma'* ined. (sect. *Orbilia*, 7.V.2004); **curucispora-like**: **x** *Hyalorbilia 'latispora'* ined. (H.B. 9902c); **y** *H. 'subfusispora'* ined. (8.XII.2009); **descalsia-like**: **z** '*O. flagellispora*' comb. ined. (H.B. 8264); **dwayaangam-like**: **A** *O. junci* (from Kohlmeier et al. 1998); **B** *O. 'subvinosa'* ined. (H.B. 9173b); **C** *O. aristata* (7.V.2004, z, A–C sect. *Hemiorbilia*). Living state (c and x partly in Cresyl blue), except for t (in water) and u (in KOH)

conidia are often fusiform (Fig. 4h, i). Bright red apothecia are characteristic of *Orbilia 'rubrovacuolata'* ined. (Fig. 2n), which has an asexual morph very similar to *D. mammillata* (S.M. Dixon) M. Scholler et al. In our phylogenetic analysis, the genus is represented as series *Dactylellina* (Fig. 1).

Scholler et al.'s concept resulted in the synonymy of *Laridospora* and *Kafiaddinia* with *Dactylellina*. The type species of the older genus *Anulospodium* is of doubtful identity (see there). Therefore, we propose to protect the name *Dactylellina* in case the narrow generic concept is applied.

**Dactylum** Nees (1816) — **Use Dactylellina (A) instead of the rejected name Dactylum (A) when applying a narrow generic concept, otherwise use Arthrobotrys (A) or Orbilia (S).**

The type species *D. candidum* is of unclear identity based on its original description. Drechsler (1937a: 523) applied the taxon as *Dactylaria candida* (Nees) Sacc. to an isolate that forms long-stalked adhesive knobs and non-constricting rings, which, according to Rubner (1996: 74), might belong to *Monacrosporium haptotylum* (Drechsler) X.Z. Liu & K.Q. Zhang, a species now classified in *Dactylellina*. Gams and Rubner (1997) proposed to reject the names *Dactylum* and *D. candidum* in order to retain the generic name *Monacrosporium* in case Drechsler's redescription would be accepted as a neotypification of *D. candidum* (Rubner 1996: 37). Index Fungorum lists a total of 46 names, many of which belong to other classes.

**Dactylosporium** Mekht. (1967) — **see under Kafiaddinia (A).**

This illegitimate name is a homonym of *Dactylosporium* Harz (hyphomycetes inc. sedis). It was proposed for *D. leptospora* as a segregate of *Dactylella* based on its nematophagy by means of stalked adhesive knobs and non-constricting rings, and often apically branched, denticulate conidiophores. Because of its illegitimacy, it was later replaced by *Dactylellina* (see also under *Kafiaddinia*).

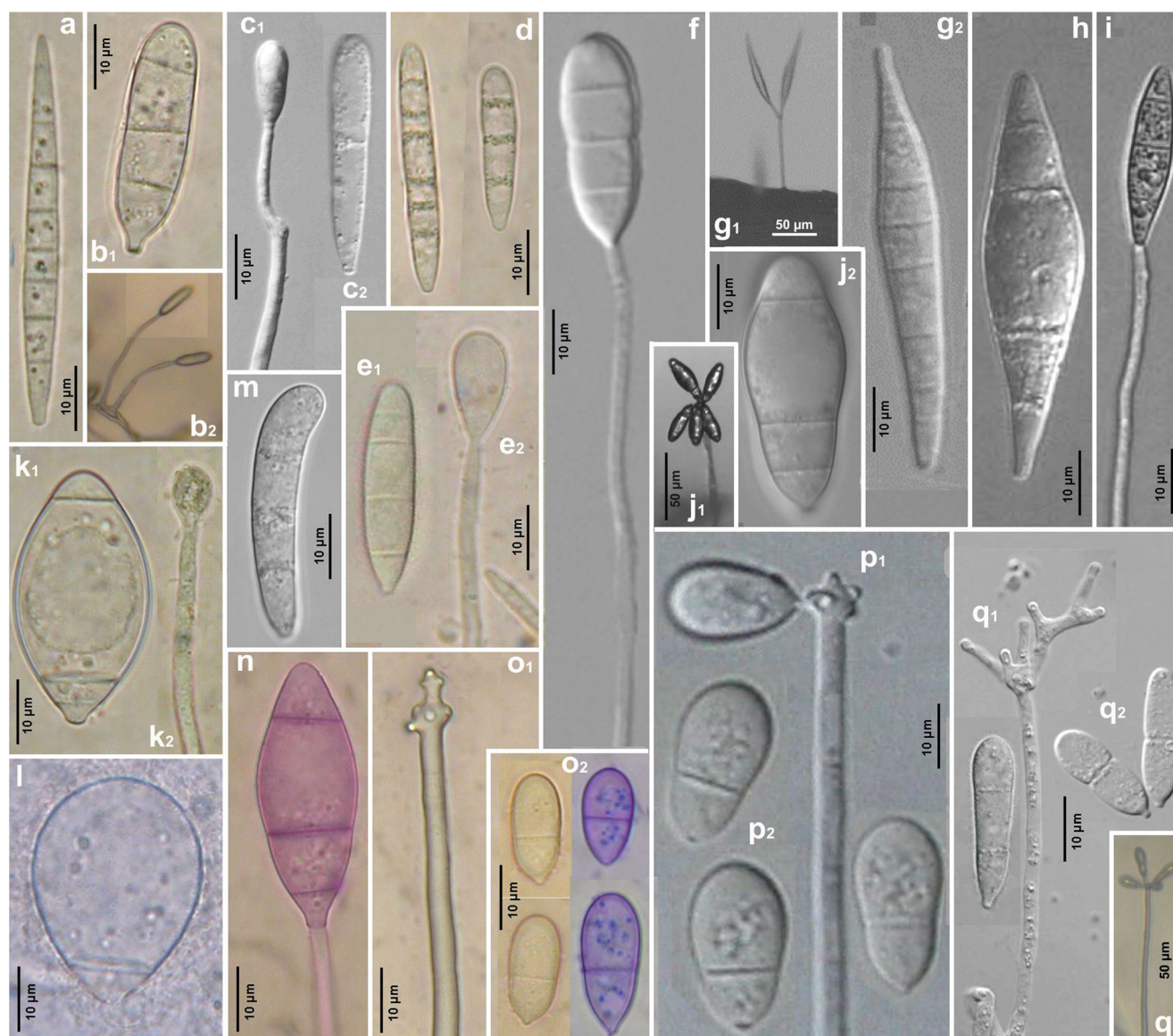
**Descalsia** A. Roldán & Honrubia (1989) — **Use Hemiorbilia (S) (existing at present only at the infrageneric level). Raise Hemiorbilia to genus to be used rather than the unclear Descalsia (A) when applying a moderate or narrow generic concept.**

This genus only includes *Descalsia cruciata*, which has tetrastrate stauroconidia similar to Fig. 3z or in *Curucispora* (see there). There is a possibility that *D. cruciata* belongs to the core of *Orbilia* subgenus *Hemiorbilia*, but, at present, it cannot be connected with certainty to a sexual morph and even its relationship with Orbiliomycetes is not certain. *Orbilia aristata* (Velen.) Velen., a close relative of *O. occulta* (type of subgenus *Hemiorbilia*), forms tetrastrate conidia very similar to *D. cruciata* in pure culture. However, we have also often observed trinacrium- (Fig. 3s) and dwayaangam-like (Fig. 3C) conidia with very similar arm dimensions close to the apothecia of *O. aristata* on the natural substrate, partly also in ascospore isolates of this species, and these three conidial types were also observed in connection with *O. 'subaristata'* (ined.) and *O. flagellispora* (comb. ined.).

Because of the uncertain identity of *D. cruciata*, *Descalsia* cannot now be used as a holomorph-generic name. No living ex-type culture or sequence exists (A. Roldán & L. Marvanová, pers. comm.), and efforts by G. Marson to gain DNA from a permanent slide failed. In case *D. cruciata* would turn out to be closely related to *O. occulta*, the name *Descalsia* could be used instead of raising subgenus *Hemiorbilia* to the generic level. However, *Curucispora* might represent an older name. As long as the phylogenetic relationship remains unclear, we suggest not to use *Descalsia*.

**Dicranidion** Harkn. (1885) — **Use the older name Orbilia (S) instead of Dicranidion (A).**

*Dicranidion* was erected with one species, *D. fragile*, and 12 further specific epithets were later associated with it (Index Fungorum). The name of the genus refers to the shape of conidia resembling a tuning fork (from Greek *dikranos*). Such conidia were found by us to occur in several groups of *Orbilia* (see Fig. 1). They differ in arm and stipe length, and in the number of arms (Fig. 3l–p). The type species clearly fits the asexual morph obtained from ascospore isolates of the common, worldwide *O. eucalypti* (W. Phillips & Harkn.) Sacc. (= *O. alnea* Velen., Baral et al., unpubl.), which belongs to section *Orbilia*.



**Fig. 4** Conidiophores and conidia of Orbiliomycetes with unbranched, mainly uncurved conidia, mainly predacious taxa (except for dactylella-like taxa): **Hyalarbilia** (= **Brachyphoris**): **a** *H. inflatula* (H.B. 9041a); **b** *H. polyperi* (b<sub>1</sub> H.B. 7952a, b<sub>2</sub> H.B. 7557a); **dactylella-like**: **c** *Orbilia vermiformis* (sect. 'Aurantiorubrae', from Yu et al. 2007a); **d** *O. dryadum* (sect. *Orbilia*, H.B. 8224a). **Series Dactylella**: **e** *D. clavispora* (H.B. 8371a); **f** *D. clavispora* (from Chen et al. 2007b); **g** *O. dorsalis* (from Yu et al. 2007b). **Series Arthrobotrys**: **j** *O. blumenaviensis* (=

*A. vermicola*, from Qiao et al. 2012); **n** *A. elegans* (H.B. 6972a); **o** *O. auricolor* (H.B. 8898a, 9553); **p** *A. oligospora* (from Swe et al. 2008). **Series Drechslerella**: **k** *D. cf. bembicodes* (H.B. 9051g); **l** *D. polybrocha* (H.B. 8317a); **m** *O. cf. orientalis* (= *D. brochopaga* agg., YMF 1.01854, from Z.F. Yu et al., unpubl.). **Series Dactylellina**: **h** *D. sichuanensis* (from Li et al. 2006); **i** *D. varietas* (from Li et al. 2006). **Series Gamsylella**: **q** *O. alba* (q<sub>1–2</sub> from Yu et al. 2009, q<sub>3</sub> H.B. 9645a). Living state (n and o<sub>2</sub> in Cresyl blue)

Due to the scattered occurrence of dicranidion-like asexual morphs within *Orbilia* s. l. and the widely accepted name *Orbilia*, we dismiss the name *Dicranidion* and recommend to use *Orbilia* no matter which generic concept is adopted. Some connections between *Dicranidion* species and sexual morphs within the series *Orbilia* are uncertain due to the lack of molecular data. For instance, *D. gracile* Matsush. or *D. tenue* Matsush. fit the asexual morphs of *O. leucostigma* (Fr. : Fr.) Fr. and *O. xanthostigma*, but the ex-type strains appear to have never been subjected to DNA sequencing. In

the following taxon, we could confirm the connection to a sexual morph by molecular data gained from an ascospore isolate that formed the typical conidia (GenBank number of the ex-type culture: LC146730, our strain: KT596781):

***Orbilia fissilis*** (K. Ando & Tubaki) E. Weber & Baral, **comb. nov.** (Fig. 3o)

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Basionym: *Dicranidion fissile* K. Ando & Tubaki, Trans. Mycol. Soc. Japan 25(1): 39 (1984).



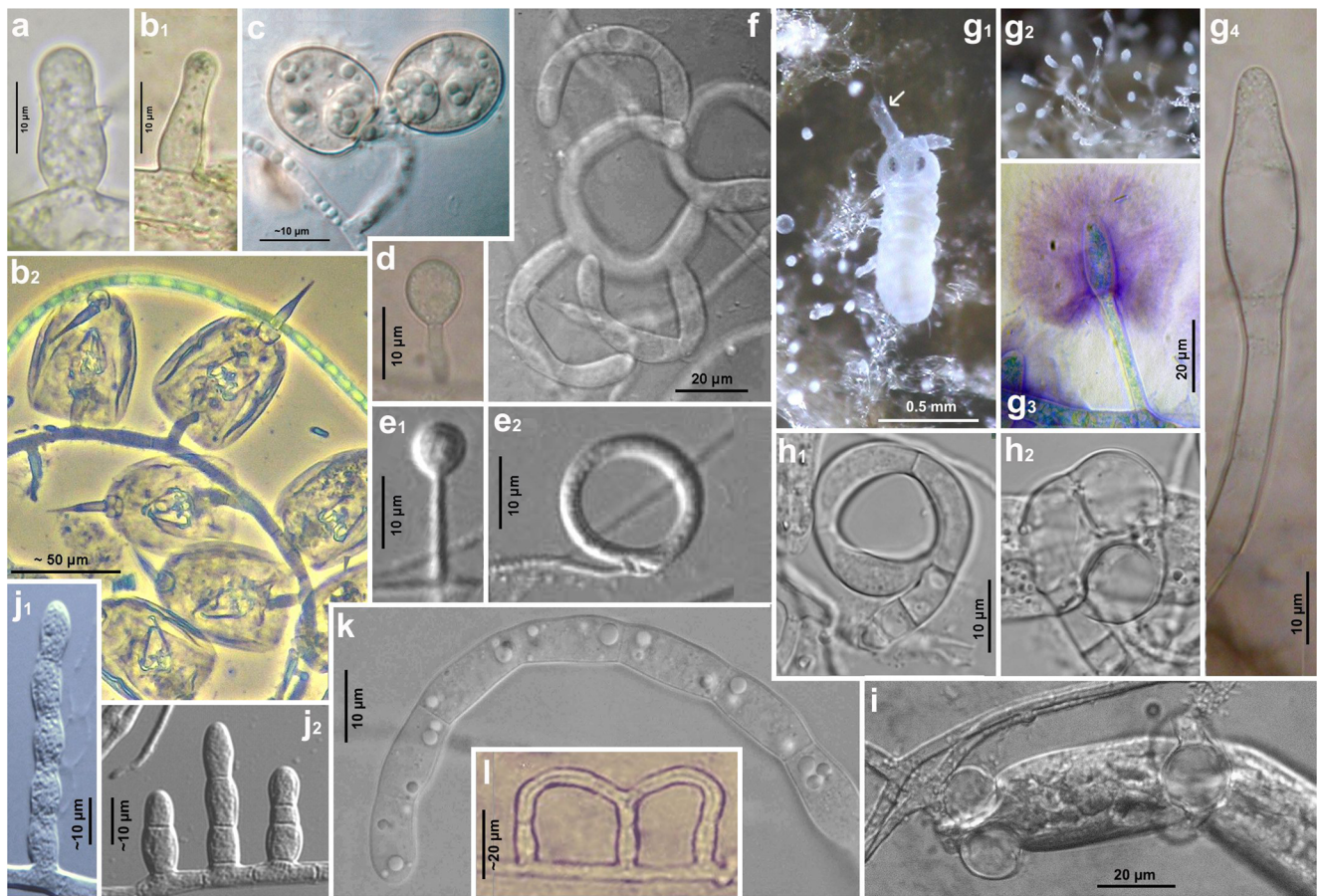
***Didymozaophaga* Soprnov & Galiulina (1951) — Use *Arthrobotrys* (A) instead of the invalid and illegitimate *Didymozaophaga* (A).**

*Didymozaophaga* was proposed to include nine species and some varieties that have 1-septate conidia formed on arthrobotryoid conidiophores and trap nematodes by means of adhesive networks. No type species was designated by the authors. Later, Soprnov (1958) placed the genus in synonymy with *Arthrobotrys*. The name *Didymozaophaga* is invalid because no Latin diagnosis was given (Art. 39 ICN). Schenck et al. (1977) designated *D. oligospora* as the lectotype species, but, later, van Oorschot (1985) selected *D. superba* as the lectotype, obviously overlooking the lectotypification by Schenck et al. We consider the lectotypification by van Oorschot, which would make *Didymozaophaga* illegitimate (Art. 52 ICN), as superfluous.

***Drechslerella* Subram. (1964) — Protect *Drechslerella* (A) over the older *Orbiliaster* (S) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilina* (S).**

*Drechslerella* was erected with one species, *D. acrochaeta*, based on fusiform conidia with a long, filiform apical appendage. The genus was redefined by Scholler et al. (1999) to include 13 species that trap nematodes by means of constricting rings (Fig. 5h, i). At present, it comprises 15 species (Index Fungorum). This concept resulted in the synonymy of *Golovinia* and *Dactylariopsis* with *Drechslerella*. The conidia vary between fusiform, obovoid, and cylindrical (Fig. 4k–m). When applying a narrow generic concept, *Drechslerella* should be adopted as a holomorph name (in Fig. 1, as series *Drechslerella*).

However, the genus *Orbiliaster* was found to provide an older name for this group (see below). *Drechslerella* has been



**Fig. 5** Trapping organs in Orbiliomycetes. ***Lecophagus***: adhesive pegs capturing rotifers: **a** *L. 'ellipsoideus'* ined. (16.XI.2013); **b** *L. muscicola* (H.B. 7771). ***Hyalorbilia* (= *Brachyphoris*)**: adhesive pegs capturing testaceous rhizopods: **c** *Hyalorbilia* sp. (as *Dactylella passalopaga*, from G. Barron, website on fungi). **Series *Dactylellina***: adhesive knobs and non-constricting rings capturing nematodes: **d** *D. mammillata* (H.B. 8372a); **e** *D. sichuanensis* (from Li et al. 2006). **Series *Arthrobotrys***: adhesive network capturing nematodes: **f** *Orbilina blumenavensis* (= *A. vermicola*, from Qiao et al. 2012). **Series *Gamsylella***: adhesive

knobs with thick gel capturing arthropods: **g** *O. alba* (H.B. 9645a, 9051a); adhesive columns and bridges: **j**, **l** *G. cionopaga* (XJ03, from X.Z. Liu et al. unpubl.); **k** *G. cionopaga* (from Z.F. Yu unpubl.). **Series *Drechslerella***: constricting rings capturing nematodes: **h** *O. cf. orientalis* (= *D. brochopaga* agg., YMF 1.01854, from Z.F. Yu et al. unpubl.); **i** *D. doedycoides*, captured nematode (from H.Y. Su unpubl.). Living state, except for **b**<sub>2</sub>, **?e**, **g** [methyl-green in ammonium hydroxide, post-stained by cresyl blue (when hydrated, the gel sheath requires staining for a better visibility)], **j**

widely used since its emendation and, at present, comprises 15 accepted species, whereas only two species were recognized in *Orbiliaster*. Therefore, we recommend protection of *Drechslerella* over *Orbiliaster* when applying a narrow generic concept.

***Drechsleromyces* Subram. (1978) — Use the older name *Dactylella* (A) instead of *Drechsleromyces* (A) in case of congenericity when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilina* (S).**

*Drechsleromyces* was erected with one species, *D. attractoides*, which was segregated from *Dactylella* because of sympodially proliferating conidiophores and from *Gangliophragma* by the constriction between denticle and conidium (narrow attachment). No other epithet was combined in the genus. It was considered a synonym of *Dactylella* by Chen et al. (2007b), based on molecular data.

***Duddingtonia* R.C. Cooke (1969) — Use the older name *Arthrobotrys* (A) instead of *Duddingtonia* (A) when applying a moderate or narrow generic concept, otherwise use *Orbilina* (S).**

*Duddingtonia* was erected with one species, *D. flagrans*, which was segregated from *Arthrobotrys* based on the absence of nodules at the conidiophore tips. No further epithet has been combined in the genus, and its type species was accepted in *Arthrobotrys* by Scholler et al. (1999) because it forms adhesive networks and clusters in that genus (see Fig. 1).

***Dwayaangam* Subram. (1978) — Protect *Hyalorbilia* (S) over *Dwayaangam* (A).**

The genus was introduced for one species, *D. quadridens*, with short conidiophores giving rise to normally four-armed stauroconidia 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 representing the asexual morph of *Orbilina junci* Kohlm., Baral & Volkm.-Kohlm. Out of these, sequence data are only available for *D. colodena*, which, in phylogenetic analyses, clusters 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 to the Orbiliomycetes. Studies of Baral et al. (unpubl.) revealed some unidentified *Dwayaangam* asexual morphs, especially in section *Hemiorbilina*, but also in species around *O. 'albovinosa'* (ined.) of section '*Aurantiorubrae*' and *Hyalorbilia fusispora* (Velen.) Baral & G. Marson (Figs. 1 and 3A–C), which more or less closely resemble

some of the described *Dwayaangam* species, although we cannot unambiguously name them.

The original illustration of *D. quadridens* hardly leaves any doubt about its relationship to the Orbiliomycetes. The drops in the broad cells of the living conidia as drawn by Drechsler are probably of non-lipidic nature and point to a relationship with *Hyalorbilia*, in which such drops, in contrast to *Orbilina* s. l., have 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 asexual morph undoubtedly belongs to *Hyalorbilia*, but cannot be unequivocally assigned to a sexual morph 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 asexual morph name *Dwayaangam* competes with the sexual morph name *Hyalorbilia*. We recommend protection of the younger *Hyalorbilia*, in which, until now, ten species have been combined, 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, comb. nov.**

Mycobank MB 813462

Basionym: *Tripasporina quadridens* Drechsler, Sydowia 15(1–6): 19 (1962) ["1961"]

≡ *Dwayaangam quadridens* (Drechsler) Subram.

***Gamsylella* M. Scholler, Hagedorn & A. Rubner (1999) — Use *Gamsylella* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilina* (S).**

*Gamsylella* with the type species *G. arcuata* was erected to accommodate six species that trap nematodes by means of unstalked adhesive knobs or two- to multicelled columns, which tend to form arches or scalariform bridges (Fig. 5j–l). A seventh species (*G. cionopaga*) was later invalidly combined. The conidia vary between cylindrical and fusiform. When applying a narrow generic concept, the name *Gamsylella* could be adopted as a holomorph generic name. However, delimitation from *Dactylella* proved to be difficult, and some authors concluded that both genera should be merged. In our phylogenetic analysis, the two genera are separated as sister clades, though with low support (Fig. 1). Sexual morphs are unknown at present in *Gamsylella*, except for unpublished results on two further species that cluster with *Gamsylella*. One of them, *Orbilina alba* Dennis, forms large, stalked, elongate adhesive knobs which trap arthropods such as collembolans or dipterans (Figs. 4q and 5g).



***Gangliophragma* Subram. (1978) — Use the older name *Dactylella* (A) instead of *Gangliophragma* (A) in case of congenericity when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilina* (S).**

*Gangliophragma* with the type species *G. rhopalota* was segregated from *Dactylella* because of sympodially proliferating conidiophores and from *Drechsleromyces* by a “gangliar” conidiogenesis, i.e., without constriction between denticle and conidium (broad attachment). Only three specific epithets were combined in the genus, which was considered a synonym of *Dactylella* by Chen et al. (2007b) based on molecular data.

***Genicularia* Rifai & R.C. Cooke (1966) — see under *Geniculifera*.**

This illegitimate name, which is a homonym of *Genicularia* Rouss. (algae), was later replaced by *Geniculifera*.

***Geniculifera* Rifai (1975) — Use the older name *Arthrobotrys* (A) instead of *Geniculifera* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilina* (S).**

*Geniculifera*, a replacement name for *Genicularia*, with the type species *G. cystosporia*, was proposed because of the geniculate conidiophore apex in combination with adhesive networks that capture nematodes. Nine specific epithets have been combined in the genus, mostly by Rifai (Index Fungorum). Since Scholler et al. (1999), its synonymy with *Arthrobotrys* has been generally recognized.

***Golovinina* Mekht. (1967) — Use the older name *Drechslerella* (A) instead of *Golovinina* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilina* (S).**

*Golovinina* with the type species *G. bembicodes* was segregated from *Dactylella* and *Dactylaria* based on fusiform conidia with mostly more than one septum, formed acrogenously or on candelabrelloid conidiophores. A total of 32 specific epithets were combined in the genus by Mekhtieva (1967), comprising nematophagous species with different trapping organs (adhesive networks, adhesive knobs, non-constricting and constricting rings). Because the type species forms constricting rings, Scholler et al. (1999) placed *Golovinina* in synonymy with *Drechslerella*.

***Habrostictis* Fuckel (1870) — Use *Habrostictis* (S) when applying a moderate or narrow generic concept, otherwise use *Orbilina* (S).**

A total of 15 specific epithets have been combined in *Habrostictis* (Index Fungorum), of which only four are considered to be orbiliaceous (Baral et al., unpubl.). When Fuckel erected *Habrostictis* for *H. rubra*, a species with erumpent, at

first closed then lacerate-fimbriate apothecia, he also placed *Stictis ocellata* (Pers.) Fr. [= *Pezicula ocellata* (Pers.) Seaver] and *Schmitzomia chrysophaea* (Pers.) Fr. [= *Ramonia chrysophaea* (Pers.) Vězda] in this genus. Fuckel placed it in his tribe *Sticti* between *Naevia* and *Stictis*. Boudier (1907), however, restricted *Habrostictis* to *H. carpoboloides* and *H. lasia* (= *H. rubra*). He referred *Stictis ocellata* to *Ocellaria* but considered this genus close to *Orbilina*. Other authors regarded *H. rubra* to be a member of *Orbilina* [under the synonymous names *O. lasia* (Berk. & Broome) Sacc. and *O. piloboloides* J.H. Haines & Egger]. Von Höhnelt (1917) and Nannfeldt (1932) kept *H. rubra* in the vicinity of *Ocellaria* (= *Pezicula*) and *Dermea*, until Spooner (1987) and Baral (1994) accepted this species as orbiliaceous.

According to type studies by the first author, *H. rubra* was found to have several synonyms, including the oldest name *Peziza carpoboloides* P. Crouan & H. Crouan. This species (Fig. 2h) belongs to a very large, highly supported monophyletic group of mainly undescribed desiccation-tolerant species (section *Habrostictis*, Fig. 1), that share elongate, vermiform to filiform spore bodies but differ from the type species in usually having smooth apothecia and capitate paraphyses. In a narrow concept, this group of desiccation-tolerant species is considered a genus of its own, and *Habrostictis* would be the appropriate name for it. When using a moderate concept, *Habrostictis* also comprises sections ‘*Aurantiorubrae*’ and *Helicoon*, and, with a broad concept, it is recognized as a subgenus of *Orbilina* s. l. (note that some of these groupings are paraphyletic in Fig. 1, and their delimitation is morphology-based). *Habrostictis carpoboloides* is associated with a vermispore-like asexual morph with small, 1-septate conidia, which was compared with *Idriella* P.E. Nelson & S. Wilh. by Haines and Egger (1982). According to molecular phylogenetic analyses, *Idriella* belongs to Sordariomycetes (Hernández-Restrepo et al. 2015). Most members of the section *Habrostictis* possess trinacrium-like (Fig. 3q) and some tridentaria-like asexual morphs (Fig. 2v).

***Helicoon* Morgan (1892) — Use *Helicoon* (A) when applying a narrow generic concept, otherwise use *Orbilina* (S).**

A total of 27 specific epithets have been combined in *Helicoon* (Index Fungorum). The main characteristics of the genus are multiseptate, strongly coiled (helicosporous, barrel-shaped), hyaline to fuscous conidia, coiled more tightly towards the poles, produced sympodially on denticles on short to long, hyaline to brown conidiophores (Goos et al. 1986).

Similar to the case of the heterogeneous genus *Anguillospora*, most of these taxa belong to other classes, but only the type species *H. sessile* (Fig. 3k) is orbiliaceous with certainty (except for a discrepancy in the sense of rotation of the conidia, Voglmayr 1994). Pfister (1997) obtained *H. sessile* in an ascospore isolate of *Orbilina luteorubella*, but this connection was doubted by Hagedorn and Scholler (1999), who found that



the sequences obtained by Pfister were hypocrealean. However, Pfister's observation could later be confirmed based on a trustable strain of *H. sessile* isolated and subjected to DNA sequencing by H. Voglmayr (pers. comm.) and on an ascospore isolate of *O. luteorubella* by X.Z. Jiang (pers. comm.) (CGMCC 3.13369, GenBank FJ719770) that produced a *Helicoon* asexual morph in pure culture.

When using a narrow generic concept of *Orbilina*, species related to *O. luteorubella* could be placed in a genus of its own, and *Helicoon* would be available for use. A sexual morph closely related to *O. luteorubella* has *Anguillospora rosea* as the asexual morph, but the genus *Anguillospora* is unavailable because its type species belongs in Dothideomycetes (see under *Anguillospora*).

Section *Helicoon* (Fig. 1) also includes a highly supported monophyletic subclade for which the very different asexually typified genus *Pseudotriporiconidium* was erected (see there). With a very narrow generic concept, *Pseudotriporiconidium* would be segregated and accepted as distinct from the paraphyletic genus *Helicoon*.

***Orbilina* subgenus *Hemiorbilina* Baral — Use *Hemiorbilina* (S) by raising it to the generic level rather than *Descalsia* (A), *Radotinea* (S), or *Trinacrium* (A) when applying a moderate or narrow generic concept.**

Subgenus *Hemiorbilina* with the type *Orbilina occulta* was proposed by Baral (1994) to include taxa with a hemispherical, thick-walled ascus apex (Fig. 2o<sub>3</sub>), in contrast to a truncate, shouldered ascus apex typical of subgenus *Orbilina* (Fig. 2k<sub>2</sub>). When applying a moderate or narrow concept, we recommend raising subgenus *Hemiorbilina* to the generic rank (see under the above-listed possibly competing generic names).

***Hyalinia* Boud., Bull. Soc. Mycol. Fr. 1: 114 (1885) — Use *Orbilina* (S) instead of the illegitimate name *Hyalinia* (S) when applying a broad concept and *Habrostictis* (S) when applying a moderate concept.**

A total of 58 specific epithets have been combined in *Hyalinia* (Index Fungorum), most of them by Boudier (1907). The genus was introduced for *Helotium crystallinum*, a desiccation-sensitive species with a toothed apothecial margin (Fig. 2i, the teeth are composed of long, agglutinated glassy processes) and paraphyses without a distinct apical inflation, but this combination of characters occurs also in many desiccation-tolerant, distantly related species of Orbiliomycetes (e.g., Fig. 2p). The type species is also characterized by narrow, helicoidally twisted ascospores. In 1907, Boudier included species with a smooth margin, many of them today being regarded as members of the Helotiales.

According to Art. 53.3 (ICN), *Hyalinia* Boud. is an illegitimate homonym of the older, legitimate *Hyalina* Stackh. (brown algae), despite the different spelling [see Index

Fungorum, note that Kirk et al. (2008) erroneously spelled both names as *Hyalinia*].

Under a broad generic concept, *Hyalinia* falls into synonymy with *Orbilina* (Baral 1994), in which genus its type species competes with another name, *O. crystallina* Rodway, and needs to be renamed as *O. crenatomarginata*. The phylogenetic position of the *Hyalinia* clade is difficult to determine. We have included it in the paraphyletic section 'Aurantiorubrae' because of morphological similarities to *O. 'nemaspora'* (and *O. vermiformis*), which clusters in a distant clade (Fig. 1).

***Hyalorbilia* Baral & G. Marson (2001) — Use the older name *Hyalorbilia* (S) instead of *Brachyphoris* (A).**

*Hyalorbilia* was introduced to include five species with *H. berberidis* as the type. At present, it comprises 13 validly combined species. The genus was segregated from typical members of *Orbilina* because of strong morphological differences, including an ectal excipulum of textura prismatica and  $\pm$  homopolar ascospores that usually contain spore bodies near both ends of the spore and asci with a broad, unstalked base arising from croziers (Fig. 2c–e). Later, connections of some *Hyalorbilia* species to asexual morphs were detected that had previously been described in *Dactylella*, and for which the genus *Brachyphoris* was erected (see there). Parasitism on nematode eggs is known for *H. oviparasitica* (Stirling and Mankau 1978) and capture of testaceous rhizopods for '*Dactylella*' *passalopaga* (Drechsler 1936; Barron 2008, see Fig. 5c).

In our molecular phylogenetic analysis, *Hyalorbilia* forms a highly supported clade with the asexually typified genus *Vermispora*, which clusters distantly from *Orbilina* s. l. (Fig. 1). Based on this phylogenetic relationship and on morphological and ecological similarities in the asexual morph, the generic separation between *Hyalorbilia* and *Vermispora* is questionable (see under *Vermispora*).

***Kafiaddinia* Mekht. (1978) — Use the older name *Dactylellina* (A) instead of *Kafiaddinia* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilina* (S).**

*Kafiaddinia* was erected for *K. fusariispora* apparently as a replacement name for the illegitimate *Dactylosporium*. Rubner (1996) regarded the species as a synonym of *Dactylellina leptospora*, which is the type species of both *Dactylosporium* and *Dactylellina*. The two species form stalked adhesive knobs and non-constricting rings, but *K. fusariispora* might represent a different species based on its shorter macroconidia and much shorter microconidia with fewer septa. Only one further species was placed in *Kafiaddinia*, *K. haptospora* (Drechsler) Mekht., which, likewise, forms stalked adhesive knobs but no non-constricting rings.

***Laridospora* Nawawi (1976) — Use the older name *Dactylellina* (A) instead of *Laridospora* (A) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).**

*Laridospora* was erected for one species, *L. appendiculata*, based on long and filiform conidial branches that resemble appendages, the semi-aquatic habitat, and non-predacious habit. However, Rubner (1996: 98, as *Monacrosporium tentaculatum* A. Rubner & W. Gams) showed that the type species forms stalked adhesive knobs. No further taxa were combined in *Laridospora*. Scholler et al. (1999) placed the genus in synonymy with *Dactylellina*.

***Lecophagus* M.W. Dick (1990) — At present, *Lecophagus* (A) is without a competing name.**

*Lecophagus* with the type species *L. fasciculatus* was proposed for two species. Up to now, six specific epithets have been used in the genus, which is recognized for asexual morphs with very broad mycelial hyphae and the ability to capture rotifers and tardigrades by means of adhesive pegs (Fig. 5a, b). The conidia (Fig. 3g) resemble those of *Vermispora* or *Anguillospora*, and we have evidence of a connection to an undescribed sexual morph (Fig. 2b, Baral et al., unpubl.) that forms minute white apothecia on xeric wood and bark, with broad anchoring hyphae emerging from dead rotifer bodies.

Phylogenetically, the monophyletic genus falls in the Orbiliomycetes (Tanabe et al. 1999), which is supported by ascospore morphology: the living spores contain a conspicuous globose spore body close to one end (Fig. 2b<sub>2</sub>). In our analysis, *Lecophagus* clusters in a highly supported clade with two unpublished, mainly resinicolous genera, ‘*Lilapila*’ ined. and ‘*Amphosoma*’ ined. (Fig. 1), which are morphologically very different from *Lecophagus* and for which no predatory capabilities are known.

Since no competing sexual or asexual morph name is known, *Lecophagus* will be extended to include also the sexual morph. Recently, Magyar et al. (2016) widened the generic concept by including a species with sessile adhesive knobs that capture nematodes.

***Microdochiella* Hern.-Restr. & Crous (2015) — Use the older name *Vermispora* (A) when considering both as congeneric.**

*Microdochiella* was erected for a single species, *M. fusarioides*, which was isolated from *Phytophthora* oospores. Morphologically, it is very similar to *Vermispora*, and its ecology was considered a main difference. However, the authors overlooked that the capability to invade spores of oomycetes occurs in both genera. LSU rDNA sequences of *M. fusarioides* clustered with *Vermispora* spp. in Hernández-Restrepo et al.’s (2015) phylogenetic analysis, though in a distinct clade. The same result is obtained when the ITS region is analyzed (unpubl.).

At present, we consider separation of *Microdochiella* from *Vermispora* at the generic level as questionable. No sexual morph is known in either of the two asexually typified genera. Both resemble also the brachyphoris-like asexual morph of the closely related genus *Hyalorbilia* (see under *Vermispora*).

***Monacrosporiella* Subram. (1978) — Use the older name *Arthrobotrys* (A) instead of *Monacrosporiella* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilia* (S).**

*Monacrosporiella* was erected for *M. megalospora*, a species forming adhesive networks; one further species was added later. As in *Monacrosporium*, the genus was based on conidiophores that produce a single acrogenous fusiform conidium, differing in a “distinct basal hilum” (Subramanian 1978), which is a conidial scar “modified by a lump-like deposit of opaque material” (Drechsler 1954). Subramanian believed that, in contrast to *Monacrosporiella*, the conidia of *Monacrosporium* were not blastic but “gangliar”, as they were formed by the transformation of the swollen tip of a conidiophore and, therefore, lacked the “conspicuous basal conidial scar”. *Monacrosporiella* has rarely been used and is today regarded as a synonym of *Arthrobotrys*.

***Monacrosporium* Oudem. (1885) — Use the older name *Arthrobotrys* (A) instead of *Monacrosporium* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilia* (S).**

*Monacrosporium* was erected for *M. elegans* and *M. subtile* Oudem. with long, unbranched conidiophores with single acrogenous conidia, which are fusiform in *M. elegans* (Fig. 4n) and clavate in *M. subtile*. The lectotype species *M. elegans* forms adhesive networks, whereas *M. subtile* is possibly non-predacious (Rubner 1996). By including also species with apically branched, candelabrelloid conidiophores, a total of 70, mainly predacious, species have been added to the genus (Index Fungorum). By accepting all types of orbiliaceous trapping organs, Rubner (1996) restricted *Monacrosporium* to nematophagous taxa in her revision of the *Dactylella*–*Monacrosporium* complex. Scholler et al. (1999) considered *M. elegans* as congeneric with *A. superba*, the type species of *Arthrobotrys*, despite very different conidiophores and conidia. This congenericity is supported by rDNA data (see Fig. 1).

***Mycoceros* D. Magyar & Z. Merényi (2017) — At present, *Mycoceros* (A) is without competing names.**

Like *Retiarius*, *Mycoceros* was introduced for a species that captures wind-borne pollen grains (*M. antennatissimus*). Its conidia resemble those of *Dwayaangam* but are usually three times dichotomously branched. Mainly molecular data distinguish *Mycoceros* from *Retiarius*. In Magyar et al.’s (2017a, b) molecular phylogenetic analysis of different classes of

ascomycetes, it nested with high support as a sister clade to all the remaining *Orbiliomycetes*; nevertheless, it was considered to belong in this class.

***Nematophagus* Mekht. (1975) — Use the older name *Arthrobotrys* (A) instead of *Nematophagus* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilia* (S).**

*Nematophagus* was erected for one species, *N. azerbaijanicus*. The genus closely resembles the classical concept of *Arthrobotrys* because of its arthrobotryoid conidiophores having nodules aggregated on  $\pm$  swollen nodes. It was segregated based on conidia that tend to form more than one septum. Five further taxa were later included in the genus by Mekhtieva, although only some of them exceptionally showed conidia with more than one septum. Most of them, including the type species, capture nematodes by adhesive networks, but one by constricting rings.

***Orbilia* Fr. (1836) — Use *Orbilia* (S) in a wide or narrow sense, depending on the applied concept.**

*Orbilia* is the oldest available generic name of all competing sexually and asexually typified genera recognized in the Orbiliomycetes. About 260 specific epithets have been validly combined in *Orbilia* (Index Fungorum), of which ca. 80 are accepted at present.

When *Orbilia* was firstly established, it contained two species, *O. leucostigma* and *O. xanthostigma*. Although currently believed to be lectotypified by Clements and Shear (1931) with *O. leucostigma*, the earliest known lectotypification was that by Bachmann (1909) based on *O. xanthostigma*. Type material does not exist for either of these, and the original descriptions are without ascospore data. A neotype will be proposed for *O. xanthostigma* (Baral et al. unpubl.) in the sense of *O. delicatula* (P. Karst.) P. Karst. *Orbilia xanthostigma* and *O. leucostigma* are exceptional within the Orbiliomycetes by their warted spores (Fig. 2k).

Depending on the applied concept, the name *Orbilia* will be used at the generic level for section, subgenus, or genus *Orbilia* as represented in Fig. 1.

***Orbiliaster* Dennis (1954) — Protect *Drechlerella* (A) over the older *Orbiliaster* (S) when applying a narrow generic concept, otherwise use *Arthrobotrys* (A) or *Orbilia* (S).**

The genus *Orbiliaster* was erected for one species, *O. pilosus*, to accommodate an orbiliaceous sexual morph with septate hairs (Fig. 2j). The single later included species is distantly related and a member of section ‘*Aurantiorubrae*’. An isolate from a sexual morph tentatively referred to *O. pilosus* (Baral et al., unpubl.) produced constricting rings in culture, and molecular data confirmed its placement in the

*Drechlerella* clade (Pfister 1997: 16–17, as *Orbilia* sp./*Monacrosporium* ?*doedycoides*). This suggests that *Orbiliaster* is an older synonym of *Drechlerella*. For reasons stated under *Drechlerella*, we propose to protect this name over *Orbiliaster*.

***Orbiliella* Kirschst. (1938) — Use the older name *Arthrobotrys* (A) instead of *Orbiliella* (S) when applying a moderate or narrow generic concept, otherwise use *Orbilia* (S).**

*Orbiliella* was based on a single species, *O. armeniaca*, and no further taxa were later added to the genus. The holotype was re-examined (Baral et al., unpubl.) and found to fit *Orbilia auricolor* agg. The asexual morph growing in association on the natural substrate matches *Arthrobotrys cladodes* or *A. superba* (Fig. 4o), which were both found to be connected to *O. auricolor*. *Orbiliella* is a clear synonym of the older *Arthrobotrys* and should not be used.

***Paradactylella* Matsush. (1993) — Protect *Hyalorbilia* (S) over the older *Paradactylella* (A) in case of congenericity.**

According to Seifert et al. (2011), *Paradactylella* is a synonym of *Dactylella*. The short conidiophores would, however, rather point to *Brachyphoris*. Thus, it cannot be excluded that the genus *Paradactylella* with, so far, only one species, *P. peruviana*, may provide an older name for the genera *Brachyphoris* and *Hyalorbilia*. However, although not specifically mentioned, conidial secession could be rhexolytic, according to the original drawing (re-drawn in Seifert et al. 2011), which would question a relationship with the Orbiliomycetes.

In case *Paradactylella peruviana* can be restudied including DNA sequence analysis, and is found to fit *Hyalorbilia*, we prefer to protect *Hyalorbilia* because of the many otherwise required name changes.

***Patinella* Sacc., Grevillea 4: 22 (1875) — not orbiliaceous.**

The genus was proposed for one species, *P. hyalophaea* Sacc. Over 60 species have been combined in *Patinella* (Index Fungorum). Nannfeldt (1932) placed the genus in a very restricted sense in Orbiliaceae because of capitate paraphyses and a paraplectenchymatic excipulum in the type species. Molecular data gained from a recent specimen described in Baral and Carter (2013) revealed that *P. hyalophaea* is very distant from Orbiliomycetes but related to *Holwaya* Sacc. (Tympanidaceae, Leotiomyces).

***Pedilospora* Höhn. (1902) — Use the older name *Orbilia* (S) instead of *Pedilospora* (A).**

Peek and Solheim (1958) and Matsushima (1981) considered *Pedilospora* as a synonym of *Dicranidion*, based on their belief that the type species of the two genera (*P. parasitans*



and *D. fragile*) and also *P. episphaeria* Höhn. and *P. ramularioides* Bubák might be conspecific. *Pedilospora parasitans* was described by Höhnelt (1902) as growing “In *Helotio citrino* (?) parasitica” ( $\equiv$  *Calycina citrina*  $\equiv$  *Bisporella citrina*), and, possibly, Höhnelt confused *Orbilia eucalypti* (asexual morph *D. fragile*) with the helotialean *Calycina citrina*. Drechsler (1934) included a species in *Pedilospora*, *P. dactylopaga* Drechsler, which is exceptional in preying on testaceous rhizopods and having very long conidiophores. Four further species have been combined in *Pedilospora*, according to Index Fungorum.

***Pseudorbilia* Ying Zhang, Z.F. Yu, Baral & K.Q. Zhang (2007) — *Pseudorbilia* (S) is, at present, without competing names.**

*Pseudorbilia* was erected for *Ps. bipolaris*, in which both ends of the ascospores contain a spore body (bipolar spore body arrangement, Fig. 2a). In this respect, the fungus resembles *Hyalorbilia* and particularly ‘*Amphosoma*’ ined. (Fig. 2g), from which it differs, e.g., in asci with a truncate, shouldered apex (similar to Fig. 2k<sub>2</sub>). No further species was, so far, included in the genus, no asexual morph is known, and no molecular data are available.

***Pseudotriporiconidium* Z.F. Yu & K.Q. Zhang (2011) — Use *Pseudotriporiconidium* (A) or *Helicoon* (A) when applying a narrow generic concept, otherwise use *Habrostictis* (S) or *Orbilia* (S).**

Yu et al. (2011) introduced *Pseudotriporiconidium* to accommodate *Ps. sinense* for an asexual morph obtained in an ascospore isolate of an *Orbilia* referred to *O. aff. luteorubella*. Its inversely pyramidal, non-septate conidia possess more or less pronounced distal nipples and are formed on denticles at the conidiophore apex (Fig. 3j). Shortly after, some closely related species were also found to produce this peculiar type of asexual morph, e.g., *O. acicularis* Baral & Hong Y. Su (Su et al. 2011), but the asexual morph was not given a separate name. The genus *Pseudotriporiconidium* resembles *Triporiconidium*, which differs in septate conidia formed singly at the conidiophore tip.

In the morphology of the sexual morph, this group does not markedly differ from *O. luteorubella* and allied taxa with anguillospora- and helicoon-like conidia very different from *Pseudotriporiconidium*. In molecular phylogenetic analyses, *Pseudotriporiconidium* forms a highly supported monophyletic clade, whereas the group with anguillospora- and helicoon-like conidia appears paraphyletic. The two groups form a monophyletic clade which, under a moderate generic concept, would receive the older name *Habrostictis*. When applying a narrow generic concept, *Pseudotriporiconidium* and *Helicoon* can either be used as two separate genera or *Pseudotriporiconidium* can be regarded as a synonym of *Helicoon* (Fig. 1).

***Radotinea* Velen. (1934) — Use *Orbilia* in the broad concept, or, by raising *Hemiorbilia* (S) to the generic level (existing at present only at the infrageneric level), use *Hemiorbilia* rather than the unclear *Radotinea* (S) when applying a moderate or narrow generic concept.**

The single species included in *Radotinea*, *R. caudata*, 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 (1934) saw a relationship to *Orbilia*, but placed it in the Hyaloscyphaceae because of the hairs. The original description appears to refer to *O. aristata* or an undescribed very close relative of it (*O. ‘subaristata’* ined.), but a further, comparatively distant species (*O. ‘pseudoaristata’* ined.) cannot be excluded with certainty. Since no apothecia could be found in the holotype, we consider *R. caudata* as a nomen dubium. *Radotinea* competes with the subgenus *Hemiorbilia* when using a moderate or narrow generic concept. We recommend not using *Radotinea* because the type material does not permit to clarify the identity of the species, and the name has never been taken up by other authors.

***Retiarius* D.L. Olivier (1978) — *Retiarius* (A) is, at present, without competing names.**

*Retiarius* was introduced for two species that capture wind-borne pollen grains. Two further species will be added to the genus (Magyar et al. 2017b). The type species, *R. superficialis* D.L. Olivier, has trinacrium- to tripospermum- or dwayaangam-like conidia. The second included species, *R. bovicornutus* D.L. Olivier, was considered to belong to *Trinacrium* by Matsushima (1993: 30). Magyar et al. (2017a, b) gained rDNA sequences from the ex-type cultures of the two *Retiarius* species (IMI 223459 and 223460) and one of their new species, which, in their phylogenetic analysis, formed a separate group within the clade containing *Lecophagus*.

***Roigiella* R.F. Castañeda (1984) — Use the older name *Arthrobotrys* (A) instead of *Roigiella* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilia* (S).**

Only one species, *R. lignicola*, has been combined in *Roigiella*. According to Seifert et al. (2011), the genus is a synonym of *Arthrobotrys* in its narrow sense. An unpublished sequence of the ex-type strain (CBS 222.85) clustered near *Arthrobotrys dendroides* Kuthub., Muid & J. Webster (alignment tool in <http://www.cbs.knaw.nl/collections/>). Both species form synnemata. No trapping organs were reported in pure culture of *R. lignicola*, probably because no nematodes were added.

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

The genus *Tricellula* was originally proposed for *T. inaequalis* Beverw., a species with 3-celled holoblastic stauroconidia composed of a stalk and usually two arms, with strong constrictions at the indistinct septa, formed on dichotomously branched conidiophores. Nine species have been included according to Index Fungorum. Matsushima (2003) obtained *T. inaequalis* and its sexual morph in pure culture from a Japanese soil isolate, and described the sexual morph 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 organelles 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 to the Helotiales rather than the Orbiliomycetes. A more detailed morphological study should be carried out on this species 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 von Arx (1970), whereas *Volucrispora graminea* Ingold et al., a species added later, was segregated in the genus *Ypsilina* J. Webster et al. (Descals et al. 1999). A BLAST search of three ITS sequences of *Y. graminea* in GenBank against the nucleotide database of the NCBI (<http://www.ncbi.nlm.nih.gov>) revealed relationships with *Oculimacula* Crous & W. Gams (= *Helgardia* Crous & W. Gams) and other members of Ploettnerulaceae (Helotiales), where it clusters also in the analysis of Baschien et al. (2013).

***Tridentaria* Preuss, Linnaea 25: 74 (1852) — Use *Tridentaria* (A) (in the sense of Drechsler 1937b) only in the form of “tridentaria-like” when referring to conidial shape.**

The original description was based on *Tridentaria alba* Preuss, which forms acervuli containing unbranched conidia arranged in fascicles that suggest a branched conidium. The brief description is inadequate for modern systematics. Because the type specimen did not bear a fungus which agreed with the protologue (van der Aa and van Oorschot 1985), the identity of *T. alba* remains unclear. Probably, it represented a non-orbiliaceous fungus.

Drechsler (1937b, 1940, 1962, 1964) adopted the name *Tridentaria* to accommodate four new hyphomycetous, nematode- (*T. implicans* Drechsler) and, particularly, rhizopod-trapping species (*T. carnivora* Drechsler, *T. glossopaga* Drechsler, and *T. tylota* Drechsler). Three further species for which no trapping capabilities are known have been added to the genus by other authors (Index Fungorum), one of which (*T. setigera* Grove) was later transferred to

*Tetracladium* De Wild. and belongs to the Helotiales based on molecular data.

With exclusion of the type species and *T. setigera*, *Tridentaria* represents a group of apparently orbiliaceous asexual morphs with a peculiar conidial shape, being somewhat intermediate between *Dicranidion* and *Trinacrium*, with three or more  $\pm$  equal arms and a stipe of varying length, formed on short or long conidiophores. In contrast to *Dicranidion* and *Trinacrium*, the arms are usually constricted at the branching point, which enables a considerable motility of each arm (Fig. 3v). Drechsler's three rhizopod-capturing species might belong to *Hyalorbilia* because of predacious similarities to ‘*Dactylella*’ *passalopaga* (see under *Brachyphoris*), whereas the DNA sequences of two strains of *Tridentaria* (CBS, identified as *T. implicans* and *T. subuliphora* Matsush.) cluster in the series *Orbilia* (Fig. 1). A few species of the section *Habrostictis* were found to possess undescribed tridentaria-like asexual morphs (Baral et al., unpubl.), e.g., *O. septispora* Baral (Fig. 3v).

Because of the unsettled identity of the type species, *Tridentaria* should not be used as a holomorph name, but only for characterizing asexual morphs when referring to them as “tridentaria-like”. The type species of the aquatic hyphomycete genus *Flabellocladia* Nawawi (1985), *F. gigantea* Nawawi, strongly resembles orbiliaceous asexual morphs of *Tridentaria*, but the large size of the conidia would be unusual. The type should be investigated by molecular methods to elucidate its phylogenetic relationship.

***Trinacrium* Riess (1852) — Use *Orbilia* (S) in the broad concept. When applying a moderate or narrow generic concept, raise *Hemiorbilia* (S) to the genus rank (existing at present only at the infrageneric level) and use it rather than the unclear *Trinacrium* (A).**

*Trinacrium* was erected for *T. subtile*, and 16 species were later added to the genus (Index Fungorum). 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.

Conidia of the trinacrium-type occur in various groups of Orbiliomycetes (Fig. 1) and are typical of, e.g., many members of the *Habrostictis* clade (Fig. 3q), but also the subgenus *Hemiorbilia* (Fig. 3s), or a clade around *O. pilifera* Baral & R. Galán, in which the arms are bent downwards (Fig. 3t). *Trinacrium iridis* Ts. Watan. is nematophagous and belongs to *Arthrobotrys*, and, also, species of *Hyalorbilia* (Fig. 3r) and ‘*Amphosoma*’ ined. (Fig. 3u) have trinacrium-like asexual morphs. The type species cannot be identified with certainty, but it is probably the asexual morph of one of a couple of species of the section *Hemiorbilia*. Because of this uncertainty, we do not recommend to use *Trinacrium* as a generic name.

***Tripicoxidium* Subram. (1978) — Use *Arthrobotrys* (A) instead of *Tripicoxidium* (A, in case of congenericity) when applying a moderate generic concept, use *Orbilbia* (S) when applying a broad concept.**

Only one species was combined in *Tripicoxidium*, which is characterized by inversely pyramidal, multiseptate conidia with terminal nipple-like protrusions, formed singly at the tip of long conidiophores (for the differences to *Pseudotripicoxidium*, see there). The species seems to belong to the Orbiliomycetes as inferred from its morphology and because it is weakly predacious on nematodes. Since 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 groups of *Arthrobotrys* s. l. remains unclear.

***Vermispora* Deighton & Piroz. (1972) — is presently without competing names (but see under *Microdochiella*); protect *Hyalorbilia* (S) over *Vermispora* (A) when considering both genera as congeneric.**

*Vermispora* was erected for *V. grandispora* based on large, elongate-fusoid phragmoconidia that are slightly curved towards the ends and are formed in small number on rather short, sympodial conidiophores. Further five species were later added to the genus. Chen et al. (2007a, c) provided DNA sequences for three of them, but excluded *V. obclavata* V. Rao & de Hoog for morphological reasons (e.g., faintly pigmented conidiophores). DNA data of the type species, which is only known from the type collection and obviously had not been taken into culture, is not available. One of the species with available DNA data, *V. fusarina* Burghouts & W. Gams (Fig. 3a), is known to parasitize nematode eggs.

Available sequences of *Vermispora* form a highly supported monophyletic clade with *Hyalorbilia* distant from *Orbilbia* s. l. (Fig. 1). *Vermispora* would provide an older name for *Hyalorbilia* when applying a wider generic concept, based on its close molecular affiliation with *Hyalorbilia*, the paraphyly of *Hyalorbilia*, and morphological as well as ecological similarities in the asexual morphs (parasitism on nematode eggs occurring in both genera). Sexual morphs are unknown in *Vermispora*. In our opinion, merging of the two genera should consider also the morphology of the sexual morph; therefore, we refrain hereof at present. Since more combinations would be necessary when adopting *Vermispora*, we recommend protecting *Hyalorbilia* with presently 13 combined taxa over *Vermispora* (see also under *Microdochiella*) in case they are congeneric.

Morphologically, *Vermispora* resembles unpublished asexual morphs in various groups of *Orbilbia* s. l., for instance, in species related to *O. aurantiorubra* (Fig. 3b, c, f) or in section ‘*Lentiformes*’ (Fig. 3d, e) (see Fig. 1). Because of a morphological similarity of *Vermispora* to asexual morphs observed

within *Orbilbia* s. l., we use the term “vermispora-like” for them, but this type of conidia is not sharply separated from the longer conidia that resemble those of *Anguillospora*.

***Woroninula* Mekht. (1979) — Use the older name *Arthrobotrys* (A) instead of *Woroninula* (A) when applying a narrow or moderate generic concept, otherwise use *Orbilbia* (S).**

*Woroninula* with the type species *W. polycephala* was proposed for three species based on 2–4-septate, large, elongate fusoid to ellipsoid conidia formed on arthrobotryoid conidiophores. All three species form adhesive networks, and no further taxa have later been added to the genus. Scholler et al. (1999) referred it to *Arthrobotrys*.

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