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# Molecular data show that *Topeliopsis* (Ascomycota, *Thelotremataceae*) is polyphyletic

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**Abstract:** A phylogenetic study using DNA sequences of the nuclear ribosomal large subunit from 38 species is used to infer the phylogeny of species currently placed in *Topeliopsis*. The genus is shown to be polyphyletic; monophyly of previous and current circumscriptions of the genus are rejected using two alternative hypothesis tests. *Topeliopsis meridiensis* is shown to be closer to *Chapsa* than *Topeliopsis*, but additional studies are necessary to understand the circumscription of *Chapsa*. The new genus *Melanotopelia* Lumbsch & Mangold is described to accommodate *T. toensbergii* and *T. rugosa*. These species were previously regarded as aberrant in *Topeliopsis* because of their thin-walled ascospores and dark pigmented proper exciple. The new combination *Graphis mexicana* (Hale) Kalb, Lücking & Lumbsch is proposed and *Graphis muscicola* and *Topeliopsis globosa* reduced to synonymy with this species.

**Key words:** *Graphidaceae*, *Melanotopelia*, Ostropomycetidae, phylogenetic analysis

## Introduction

*Topeliopsis* is a small genus in *Thelotremataceae* currently including ten species (Aptroot 2002; Frisch & Kalb 2005; Kantvilas & Vězda 2000). The family belongs to *Ostropales*, which is the largest order within Ostropomycetidae (Hibbett *et al.* 2007; Lumbsch *et al.* 2007; Miądlikowska *et al.* 2007). While most genera in this family have their centre of distribution in tropical or subtropical regions (Hale 1980, 1981), species of *Topeliopsis* are common in oceanic-temperate zones and occur in tropical regions only at high elevations. The genus was described by Kantvilas and Vězda (2000) to accommodate three species with urceolate, almost perithecioid ascomata, a fused proper exciple with lateral paraphyses (*sensu* Henssen 1995, same as periphysoids *sensu* Sherwood 1977, but not *sensu* Eriksson 1982) and hyaline, non-halonate, large, eumuriform ascospores that turn reddish or purple in iodine. When describing the new genus, Kantvilas and Vězda (2000) mentioned that it was heterogeneous and that two species, viz. *T. rugosa* Kantvilas & Vězda and *T. toensbergii* Vězda & Kantvilas "may well be better placed in a separate genus altogether" (Kantvilas & Vězda 2000: 348). These two species were said to differ from the type species in having, at least in part, dark pigmented layers in the proper exciple (vs. a hyaline proper exciple), a reddish reaction of the ascospores with iodine (vs. amyloid ascospores), and the presence of depsidones (vs. secondary metabolites lacking). Consequently, Kalb (2001) reviewed the generic circumscription of *Topeliopsis* and found that ascospores varied in *Topeliopsis*, being thin-walled and non-amyloid (i.e. not reacting blue in iodine) in

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*T. rugosa* and *T. toensbergii* and thick-walled and amyloid in *Topeliopsis* s.str. He suggested excluding the two deviating species from *Topeliopsis* and noted that they ''probably belong to another undescribed genus'' (Kalb 2001: 325), but did not propose any nomenclatural changes. Kalb (2001) further described three additional new species in *Topeliopsis* s.str. from Australia. Later, *Topeliopsis globosa* Aptroot was described from Brazil, which differed in lacking lateral paraphyses (Aptroot 2002). Recently, Frisch and Kalb (2005) revised *Topeliopsis* and accepted seven species in the genus, with the description of three new species and additional nomenclatural changes. *Topeliopsis rugosa, T. toensbergii* and *T. globosa* were not included in their treatment. However, they extended the circumscription of the genus to include taxa with ascomata having a flat disc, an indistinctly layered margin, and non-amyloid ascospores that are morphologically similar to some *Thelotrema* species. Frisch and Kalb (2005) interpreted the non-amyloid ascospores in *T. meridensis* as due to immaturity of the material examined. Further, the distinction from the recently resurrected genus *Chapsa* A. Massal. (Frisch *et al.* 2006) has become less clear with the inclusion of taxa with open discs.

In this study we address the issue of the circumscription of *Topeliopsis* using DNA sequences of the nuclear ribosomal large subunit DNA, including taxa of *Topeliopsis* s. str. and one of each taxa having an open disc (*T. meridiensis*) and thin-walled, non-amyloid ascospores and darkly pigmented proper exciple (*T. toensbergii*).

## Material and Methods

### Molecular methods

Sequence data of 40 specimens representing 38 species were assembled using sequences of nuclear large subunit rDNA (Table 1). *Myriotrema desquamans* and *Thelotrema glaucopallens* were used as outgroup, since *Myriotrema* and the *T. glaucopallens* group (*sensu* Frisch *et al.* 2006) clustered basal to the ingroup taxa in a previous phylogenetic study at family level (Mangold *et al.* 2008). Total DNA was extracted from herbarium specimens using the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's instructions. Dilutions ($10^{-1}$ up to $10^{-2}$) of DNA were used for PCR amplifications. Primers for amplification of the nuclear LSU rDNA were: AL2R (Mangold *et al.* 2008), nu-LSU-0042-5′ (=LR0R), nu-LSU-1432-3′ (=LR7), and nu-LSU-1125-3′ (=LR6) (Vilgalys & Hester 1990). PCR and cycle sequencing conditions were as described previously (Mangold *et al.* 2008). Sequence fragments obtained were assembled with SeqMan 4.03 (DNASTAR) and manually adjusted.

### Sequence alignments and phylogenetic analysis

Alignments for the single data sets were done using Clustal W (Thompson *et al.* 1994). Insertion and ambiguously aligned regions were delimited manually. The alignments were analysed by maximum parsimony (MP) and a Bayesian approach (B/MCMC).

Maximum parsimony analyses were performed using the program PAUP* (Swofford 2003). Heuristic searches with 1000 random taxon addition replicates were conducted with TBR branch swapping and MulTrees option in effect, equally weighted characters and gaps treated as missing data. Bootstrapping (Felsenstein 1985) was performed based on 2000 replicates with random sequence additions. To assess homoplasy levels, consistency index (CI) and retention index (RI) were calculated from the parsimony search.

The B/MCMC analyses were conducted using the MrBAYES 3.1.1 program (Huelsenbeck & Ronquist 2001). The analyses were performed assuming the general time reversible model of nucleotide substitution (Rodriguez *et al.* 1990) including estimation of invariant sites, assuming a discrete gamma distribution with six rate categories. No molecular clock was assumed. A run with 20 000 000 generations starting with a random tree and employing 12 simultaneous chains was executed. Every 100th tree was saved into a file. The first 800 000 generations (i.e. the first 8000 trees) were deleted as the 'burn in' of the chain. We plotted the log-likelihood scores of sample points against generation time using TRACER 1.0 (http://evolve.zoo.ox.ac.uk/software.html?id=tracer) to ensure that stationarity was achieved after the first 800 000 generations by checking whether the log-likelihood values of the sample points reached a stable equilibrium value (Huelsenbeck & Ronquist 2001). Of the remaining 384 000 trees (192 000 from each of the parallel runs) a majority rule consensus tree with average branch lengths was calculated using the sumt option of MrBAYES. Posterior probabilities were obtained for each clade. Only clades that received bootstrap support equal or above 75% under MP and posterior probabilities $\geq 0{\cdot}95$ were considered as strongly supported. Phylogenetic trees were visualized using the program Treeview 1.6.6 (Page 1996).

Since the results of the phylogenetic analyses were incongruent with the current classification of *Topeliopsis*, we tested whether our data are sufficient to reject alternative topologies. We tested three topological constraints: 1, monophyly of *Topeliopsis* s.str. + *T. toensbergii*; 2, monophyly of *Topeliopsis* s.str. + *T. meridiensis*; 3, monophyly of *Topeliopsis* s. lat. For the hypothesis

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TABLE 1. *Sequences used in the current phylogenetic study with GenBank accession numbers. Newly obtained sequences in bold*

| Species | Specimen | GenBank acc. no. |
|---|---|---|
| *Acanthotrema brasilianum* | | DQ431928 |
| *Chapsa astroidea* | | EU075614 |
| *C. phlyctioides* | | EU075617 |
| *C. pulchra* | | EU075619 |
| *Chroodiscus coccineus* | | AF465441 |
| *Diploschistes cinereocaesius* | | AY300835 |
| *D. diploschistoides* | | AY605076 |
| *D. elixii* | Australia, Western Australia, *Elix* 32450 (F, isotype) | **EU126644** |
| *D. muscorum* | | AY300836 |
| *D. rampoddensis* | | AF274094 |
| *D. scruposus* | | AF279389 |
| *D. thunbergianus* | | AF274095 |
| *Myriotrema cinereum* | | AY605074 |
| *M. desquamans* | | AY605085 |
| *M. laeviusculum* | | AY605070 |
| *M. olivaceum* | Australia, Queensland, *Lumbsch* 19092 g & *Mangold* (F) | **EU126645** |
| *Ocellularia bahiana* | | AY605067 |
| *O. bonplandii* | Australia, Queensland, *Lumbsch* 19092 f & *Mangold* (F) | **EU126646** |
| *O. kalbii* | Australia, Queensland, *Lumbsch* 19085 h & *Mangold* (F) | **EU126647** |
| *O. microstoma* | Australia, Queensland, *Lumbsch* 19108 c & *Mangold* (F) | **EU126648** |
| *O. postposita* | | AY640008 |
| *O. thelotremoides* | Australia, Queensland, *Lumbsch* 19081 j & *Mangold* (F) | **EU126649** |
| *Thelotrema diplotrema* | | EU075643 |
| *T. lepadinum* | | AY300866 |
| *T. myriocarpum* | Australia, Queensland, *Lumbsch* 19120 d & *Mangold* (F) | **EU126650** |
| *T. pachysporum* | | DQ431925 |
| *T. porinaceum* | Australia, Queensland, *Lumbsch* 19108 d & *Mangold* (F) | **EU126651** |
| *T. porinoides* | Australia, Queensland, *Lumbsch* 19113 s & *Mangold* (F) | **EU126652** |
| *T. suecicum* | | AY300867 |
| *T. weberi* | | AY605084 |
| *T. zebrinum* | | EU075652 |
| *Topeliopsis acutispora* | Australia, New South Wales, *Mangold* 13 f (F) | **EU126653** |
| *T. decorticans* | | EU075654 |
| *T. meridensis* | | EU075655 |
| *T. muscigena* 1 | Australia, Victoria, *Mangold* 5iII (F) | **EU126654** |
| *T. muscigena* 2 | Australia, Victoria, *Mangold* 5 d (F) | **EU126655** |
| *T. muscigena* 3 | | EU075656 |
| *T. subdenticulata* | New Zealand, Otago, 25.4.2006, *Knight* (OTA -59967) | **EU126656** |
| *T. toensbergii* | USA, Washington, *Tønsberg* 32310 (BG) | **EU126657** |
| *Wirthiotrema glaucopallens* | | AY605069 |

testing two different methods were used: a, Shimodaira-Hasegawa (SH) test (2000) and b, expected likelihood weight (ELW) test following Strimmer & Rambaut (2002). The SH and ELW tests were performed using Tree-PUZZLE 5.2 (Schmidt *et al.* 2002) with the combined data set on a sample of 200 unique trees, the best trees agreeing with the null hypotheses, and the unconstrained ML tree. These trees were inferred in Tree-PUZZLE employing the GTR+I+G nucleotide substitution model.

## Results and Discussion

### Phylogenetic analyses

Fourteen new sequences from members of the *Thelotremataceae* were aligned with sequences obtained from GenBank as listed in Table 1. A matrix of 699 unambiguously aligned nucleotide position characters was

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produced, 427 characters in the alignment being constant. Maximum parsimony analysis yielded five most parsimonious trees (754 steps long). The strict consensus tree did not contradict the Bayesian tree topology. In the B/MCMC analysis of the combined data set, the likelihood parameters in the sample had the following mean (variance): LnL= −4636·836 (0·1), base frequencies $\pi(A)_{\{all\}}=0{\cdot}265$ (0·00008), $\pi(C)_{\{all\}}=0{\cdot}213$ (0·00007), $\pi(G)_{\{all\}}=0{\cdot}283$ (0·00008), $\pi(T)_{\{all\}}=0{\cdot}239$(0·00007), rate matrix $r(AC)_{\{all\}}=0{\cdot}079$ (0·0007), $r(AG)_{\{all\}}=0{\cdot}199$ (0·0002), $r(AT)_{\{all\}}=0{\cdot}055$ (0·00007), $r(CG)_{\{all\}}=0{\cdot}053$ (0·00005), $r(CT)_{\{all\}}=0{\cdot}563$ (0·0003), $r(GT)_{\{all\}}=0{\cdot}051$ (0·00006), the gamma shape parameter alpha=0·543 (0·0009), and $p(invar)_{\{all\}}=0{\cdot}292$ (0·00006).

Since the topologies of the MP and B/MCMC analyses did not show any strongly supported conflicts, only the 50% majority-rule consensus tree of Bayesian tree sampling is shown (Fig. 1). Those nodes that received strong support (i.e. PP$\geq$0·95 in B/MCMC analysis and MP bootstrap $\geq$75%) in both the MP and Bayesian analyses are in bold. In the majority-rule consensus tree, *Topeliopsis* is polyphyletic, with a core group, including the type species *T. muscigena*, and *T. acutispora*, *T. decorticans* and *T. subdenticulata* in a well-supported monophyletic clade, while *T. meridiensis* and *T. toensbergii* cluster in other groups. *Topeliopsis meridiensis*, on the other hand, is basal to a clade including *Chapsa* and *Thelotrema* s.str. While the basal placement of *T. meridiensis* is unsupported, the relationship to this clade is well supported. *Topeliopsis toensbergii* has a basal placement to a clade including the well-supported *Chapsa-Thelotrema* s.str.-*T. meridiensis* clade and *Chroodiscus coccineus*. The relationships of these groups are strongly supported, but the exact position of *T. toensbergii* lacks support. The relationships of *Topeliopsis* s.str. are not resolved with confidence. The genus *Diploschistes* is strongly supported as monophyletic. As shown previously (Mangold *et al.* 2008) and discussed therein, the genera *Chapsa*, *Myriotrema*, *Ocellularia*, and *Thelotrema* as currently circumscribed are not monophyletic.

The results of our phylogenetic analyses do not agree with most current generic concepts of *Topeliopsis*. Neither *Topeliopsis sensu* Kantvilas and Vězda (2000) nor *sensu* Frisch & Kalb (2005) are monophyletic. However, *Topeliopsis sensu* Kalb (2001) is monophyletic. To test whether our data can reject the two former phylogenetic hypotheses, we employed two tests of alternative hypothesis testing as described above. Both tests significantly rejected all three tested alternative topologies (all tests $P<0{\cdot}001$). Hence, *T. toensbergii* needs to be excluded from *Topeliopsis*, as well as *T. meridensis*. The placement of the latter is not entirely clear, especially its relationships to *Chapsa*. Morphologically the species resembles other *Chapsa* species, but it differs in anatomical details, such as the sessile apothecia, inspersed hymenium, brown proper exciple, and thin-walled, non-amyloid ascospores (also in mature ascomata examined in the Costa Rican material of *T. meridensis*). Non-amyloid ascospores are uncommon in *Chapsa*. The generic placement of *T. meridiensis* needs to be addressed with a wider sampling of *Chapsa* species, and at the moment we refrain from drawing any taxonomic conclusions. The deviating morphology of *T. toensbergii* (and the closely related *T. rugosa*) has been recognized several times (Frisch & Kalb 2005; Kalb 2001; Kantvilas & Vězda 2000). Given the isolated position of these two species and the unique combination of morphological characters within *Thelotremataceae* (Frisch *et al.* 2006), we describe below a new genus to accommodate *T. rugosa* and *T. toensbergii*.

We studied the type of *Topeliopsis globosa* and found it to be conspecific with *Graphis muscicola* (Kalb) Staiger (Staiger 2002) for which we found the older available name *Thelotrema mexicanum* Hale (1974). Consequently, a new combination is proposed below and *Topeliopsis globosa* and *Graphis muscicola* are reduced to synonymy with this species.

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FIG. 1. Phylogeny of *Topeliopsis* and allied genera in the *Thelotremataceae* as inferred from a nu LSU rDNA data set. This is a 50% majority-rule consensus tree from a B/MCMC tree sampling procedure. Branches with posterior probabilities $\geq 0{\cdot}95$ and MP bootstrap support values >75% are indicated in bold.

## Taxonomic conclusions

### Melanotopelia Lumbsch & Mangold, gen. nov.

MycoBank no. 511127

Genus *Thelotrematacearum*, algas ad *Trentepohliam* pertinentes in thallo continens. Thallus crustaceus. Apothecia sessilia, subglobosa vel doliiformia, perithecioidea, hemiangiocarpia, primum clausa, demum poro terminali aperientia. Excipulum cupulatum, fuscum vel atrobrunneum, intus paraphysibus lateralis

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hyalinis instructum. Discus ureceolatus. Hymenium non-amyloideum. Paraphyses rectae, simplices. Asci non-amyloidei, cylindrici, ad typum Ostropales dictum pertinentes, 1–4-spori. Ascosporae hyalinae, ellipsoideae, lepto-dermatidae, murali-divisae, non-halonatae, in Iodo rubescentes vel non-amyloideis. Pycnidia ignota.

Species typica: ***Melanotopelia toensbergii* (Vězda & Kantvilas) Lumbsch & Mangold comb. nov.** MycoBank no. MB 511128.

Bas.: *Topeliopsis toensbergii* Vězda & Kantvilas *Lichenologist* **32:** 353 (2000); type: USA, Washington, Clallam Co., Olympic National Park, Lake Ozette N, W of Ozette River, N of trail to Cape Alava, *T. Tønsberg* 25545 (BG—holotypus!).

*Thallus* crustose, thin, sometimes evanescent, covered by a thin epinecral layer. Prothallus not visible. *Photobiont* trentepohlioid.

*Apothecia* sessile, subglobose or barrel-shaped, perithecioid, hemiangiocarpous, closed at first, later opening by a terminal pore, 0·3–1·0 mm diam., more or less denticulate at margin; discs dark brown to blackish, deeply urceolate; true exciple cupulate, dark brown to black-brown, with an internal hyaline, amyloid layer in the upper part bearing lateral paraphyses; hypothecium hyaline, hymenium 150–350 µm tall, hyaline, non-amyloid. *Paraphyses* simple, straight, conglutinated, not thickened apically. *Asci* cylindrical, non-amyloid, *Ostropales*-type, 1–4-spored. *Ascospores* ellipsoid, hyaline, eumuriform, I − to I+ reddish, thin-walled, indistinctly halonate to non-halonate, 75–180 × 20–40 µm.

*Pycnidia* unknown.

*Chemistry*. Depsidones (stictic acid chemosyndrome or protocetraric acid).

*Etymology*. From melano- (greek: very dark) referring to the dark pigmentation of the true exciple and the superficially resembling genus *Topelia* P.M. Jørg. & Vězda (*Gyalectaceae*).

*Notes*. The new genus is characterized within *Thelotrematateaceae* by having perithecioid ascomata, a dark pigmented proper exciple with a hyaline inner layer that bears lateral paraphyses, and large, hyaline, eumuriform and thin-walled ascospores. There are only few genera within *Thelotrematateaceae* having a dark pigmented proper exciple and lateral paraphyses. These include *Diploschistes* and *Thelotrema* s. lat., in particular members of the *T. schizoloma*-group. *Topeliopsis* s.str. is readily distinguished by a hyaline to pale yellowish proper exciple that always lacks a distinctly dark brown or carbonized outer margin and the lack of distinctly amyloid ascospores. Although different types of ascospore development were shown to occur in *Diploschistes* (Lumbsch *et al.* 1997), the ascospore type is usually regarded as an important taxonomic character in *Thelotrematateaceae* (Frisch & Kalb 2005; Frisch *et al.* 2006).

In addition to the type species, one further described species belongs to *Melanotopelia:*

**Melanotopelia rugosa (Kantvilas & Vězda) Lumbsch & Mangold comb. nov.**

MycoBank no. MB 511129

Bas.: *Topeliopsis rugosa* Kantvilas & Vězda, *Lichenologist* **32:** 351 (2000); type: Tasmania, Reservoir lakes, *G. Kantvilas* 177/86 (HO—holotypus!).

Further, we also propose a new combination for the muscicolous *Graphidaceae* that has currently been known as *Graphis muscicola* (Kalb) Staiger:

**Graphis mexicana (Hale) Kalb, Lücking & Lumbsch comb. nov.**

MycoBank no. MB 511130

Bas.: *Thelotrema mexicanum* Hale *Phytologia* **27:** 495 (1974); type: Mexico, Tamaulipas, Gomes Farias, 1120 m, *S. Nakanishi* 82 (US—holotypus!).

*Graphis muscicola* (Kalb) Staiger *Bibl. Lichenol.* **85:** 243 (2002).—*Graphina muscicola* Kalb, *Lich. Neotrop., Fasc. X* (nos 401–450) (Neumarkt): 8 (1988); type: Ecuador, Napo, bei Sarayacu, zwischen Tena und Baeza, 2000 m, 10 Sept. 1987, *K. & A. Kalb* [Kalb, *Lich. Neotrop.* 422] (hb. Kalb—holotypus!).

*Topeliopsis globosa* Aptroot, *Fungal Diversity* **9:** 25 (2002); type: Brazil, São Paulo, Serra da Mantiqueira, Campos do Jordão, Mirante de São José dos Alpes, 1750 m, *A. Aptroot* 41709 t42 (ABL—isotypus!).

*Note. Graphis mexicana* superficially resembles a *Topeliopsis* species, especially

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with its often muscicolous growth habit, but can be distinguished by its short slit-like apothecial openings and its completely (also basally) carbonized exciple.

### Key to *Topeliopsis* and similar genera in *Thelotremataceae* and *Graphidaceae*

1 Exciple hyaline to pale yellow . . . . . 2
Exciple dark brown to black, at least in outer parts . . . . . 3

2(1) Hymenium clear; ascospores thick-walled, amyloid; disc remaining half-closed . . . . . **Topeliopsis s. str.**
Hymenium inspersed; ascospores thin-walled, non-amyloid; disc fully exposed when mature . . . . . **'Topeliopsis' meridensis**

3(1) Apothecial opening slit-like; excipulum completely carbonized; ascospores I+ violet-blue . . . . . **Graphis mexicana**
Apothecial opening rounded to irregular; excipulum laterally dark brown to black; ascospores I− to I+ reddish . . . . . **Melanotopelia**

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## References

Aptroot, A. (2002) New and interesting lichens and lichenicolous fungi in Brazil. *Fungal Diversity* **9:** 15–45.

Eriksson, O. (1982) The families of bitunicate Ascomycetes. *Opera Botanica* **60:** 1–209.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39:** 783–791.

Frisch, A. & Kalb, K. (2005) The lichen genus *Topeliopsis*, additions and corrections. *Lichenologist* **38:** 37–45.

Frisch, A., Kalb, K. & Grube, M. (2006) Contributions towards a new systematics of the lichen family *Thelotremataceae*. *Bibliotheca Lichenologica* **92:** 1–539.

Hale, M. E. (1974) Studies on the lichen family *Thelotremataceae*. 2. *Phytologia* **27:** 490–501.

Hale, M. E. (1980) Generic delimitation in the lichen family *Thelotremataceae*. *Mycotaxon* **11:** 130–138.

Hale, M. E. (1981) A revision of the lichen family *Thelotremataceae* in Sri Lanka. *Bulletin of the British Museum (Natural History), Botany Series* **8:** 227–332.

Henssen, A. (1995) *Sagiolechia atlantica*, eine neue Flechte von den Atlantischen Inseln (Ascomycotina, Ostropales). *Bibliotheca Lichenologica* **58:** 123–136.

Hibbett, D. S., Binder M., Bischoff, J. F., Blackwell, M., Cannon, P. F., Eriksson, O., Huhndorf, S., James, T., Kirk, P. M, Lücking, R., Lumbsch, H. T., Lutzoni, F., Matheny, P. B., McLaughlin, D. J., Powell, M. J., Redhead, S., Schoch, C. L., Spatafora, J. W., Stalpers, J. A., Vilgalys, R., Aime, M. C., Aptroot, A., Bauer, R., Begerow, D., Benny, G. L., Castlebury L. A., Crous, P. W., Dai, Y. C., Gams, W., Geiser, D. M., Griffith, G. W., Gueidan, C., Hawksworth, D. L., Hestmark, G., Hosaka, K., Humber, R. A., Hyde, K., Koljalg, U., Kurtzman, C. P., Larsson, K., Lichtwardt, R., Longcore, J., Miądlikowska, J., Miller, A., Moncalvo, J. M., Mozley-Standridge, S., Oberwinkler, F., Parmasto, E., Reeb, V., Rogers, J. D., Roux, C., Ryvarden, L., Sampaio, J. P., Schuessler, A., Sugiyama, J., Thorn, R. G., Tibell, L., Untereiner, W. A., Walker, C., Wang, Z., Weir, A., Weiss, M., White, M., Winka, K., Yao, Y. J., Zhang, N. (2007) A higher-level phylogenetic classification of the *Fungi*. *Mycological Research* **111:** 509–547.

Huelsenbeck, J. P. & Ronquist, F. (2001) MrBAYES, Bayesian inference of phylogenetic trees. *Bioinformatics* **17:** 754–755.

Kalb, K. (2001) The lichen genus *Topeliopsis* in Australia and remarks on Australian *Thelotremataceae*. *Mycotaxon* **79:** 319–328.

Kantvilas, G. & Vězda, A. (2000) Studies on the lichen family Thelotremataceae in Tasmania. The genus *Chroodiscus* and its relatives. *Lichenologist* **32:** 325–357.

Lumbsch, H. T., Guderley, R. & Feige, G. B. (1997) Ascospore septation in *Diploschistes* and the taxonomic significance of macro- and microcephalic spore types. *Plant Systematics and Evoution* **205:** 179–184.

https://doi.org/10.1017/S0024282908007366 Published online by Cambridge University Press

Lumbsch, H. T., Schmitt, I., Lücking, R., Wiklund, E. & Wedin, M. (2007) The phylogenetic placement of *Ostropales* within Lecanoromycetes (Ascomycota) revisited. *Mycological Research* **111:** 257–267.

Mangold, A., Martín, M. P., Lücking, R. & Lumbsch, H. T. (2008) Molecular phylogeny suggests synonymy of *Thelotremataceae* within *Graphidaceae* (Ascomycota: Ostropales). *Taxon* in press.

Miadlikowska, J., Kauff, F., Hofstetter, V., Fraker, E., Grube, M., Hafellner, J., Reeb, V., Hodkinson, B. P., Kukwa, M., Lücking, R., Hestmark, G., Garcia Otalora, M., Rauhut, A., Büdel, B., Scheidegger, C., Timdal, E., Stenroos, S., Brodo, I. M., Perlmutter, G., Ertz, D., Diederich, P., Lendemer, J. C., Tripp, E., Yahr, R., May, P., Gueidan, C., Arnold, E. A., Robertson, C. & Lutzoni, F. (2007) New insights into classification and evolution of the Lecanoromycetes (Pezizomycotina, Ascomycota) from phylogenetic analyses of three ribosomal RNA- and two protein-coding genes. *Mycologia* **98:** 1088–1103.

Page, R. D. M. (1996) Treeview: an application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* **12:** 357–358.

Rodriguez, F., Oliver, J. F., Martín, A. & Medina, J. R. (1990) The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* **142:** 485–501.

Schmidt, H.A., Strimmer, K., Vingron, M. & von Haeseler, A. (2002) TREE-PUZZLE: maximum likelihood phylogenetic analysis using quartets and parallel computing. *Bioinformatics* **18:** 502–504.

Sherwood, M. A. (1977) The ostropalean fungi. *Mycotaxon* **5:** 1–277.

Shimodaira, H. & Hasegawa, M. (2000) Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* **16:** 1114–1116.

Staiger, B. (2002) Die Flechtenfamilie Graphidaceae. Studien in Richtung einer natürlicheren Gliederung. *Bibliotheca Lichenologica* **85:** 1–526.

Strimmer, K. & Rambaut, A. (2002) Inferring confidence sets of possibly misspecified gene trees. *Proceedings of the Royal Society London, Series B Biological Sciences* **269:** 137–142.

Swofford, D. L. (2003) *PAUP*. Phylogenetic Analysis Using Parsimony* (**and Other Methods*). Sunderland, Mass.: Sinauer Associates.

Thompson, J. D., Higgins, D. G. & Gibson, T. J. (1994) Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22:** 4673–4680.

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172:** 4238–4246.

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