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The sexual morph of *Hohenbuehelia subreniformis* (*Pleurotaceae*) discovered in Finland

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Abstract: A fresh collection of a *Hohenbuehelia* from Turku, Finland was determined through phylogenetic analyses of sequences of the nuclear ribosomal internal transcribed spacer (ITS) region, large ribosomal subunit (nLSU), translation elongation factor 1-alpha (*TEF-1α*), and RNA polymerase II second largest subunit (*RPB2*) genes to be conspecific with ex-type cultures of *Hohenbuehelia subreniformis*, originally described from Ontario, Canada. No sexual morph was known; it is a member of the broad *H. atrocoerulea* clade. We provide a detailed description of the macro- and micromorphology of this species, which resembles pale forms of *H. grisea* but differs in having a more spathulate pileus and broader spores. Of the fifteen valid species formerly classified in the anamorph genus *Nematoctonus*, all but three are now linked to conspecific or closely related sexual morphs in *Hohenbuehelia*.

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INTRODUCTION

Hohenbuehelia (Schulzer *et al*. 1866; *Basidiomycota*: *Agaricales*, *Pleurotaceae*) is a genus of agarics with pleurotoid basidiocarps and a nematophagous lifestyle during the mycelial assimilative phase (Thorn & Barron 1986). All species that have been studied in culture produce holoblastic conidia that, previous to 2012 (Taylor 2011), would have been referred to the asexual genus *Nematoctonus* (Drechsler 1941), which is now considered a synonym of *Hohenbuehelia* (Thorn 2013). Ten of the 15 validly described species originally placed in *Nematoctonus* were first described as predators or parasitoids of nematodes, with no associated sexual basidiocarps (Drechsler 1941, 1943, 1946, 1949, 1954, Jones 1964, Giuma & Cooke 1972, Thorn & Barron 1986). A strain of one of these, identified as *N. robustus*, formed a basidiocarp initially identified as *Hohenbuehelia atrocoerulea* in pure culture (now identified as *H. grisea*), making the first recognized connection between the asexual and sexual morphs (anamorph-teleomorph) (Barron 1977, Barron & Dierkes 1977). Subsequently, five species placed in *Nematoctonus* were isolated from basidiocarps of named *Hohenbuehelia* (Thorn & Barron 1986) but complicating the asexual-sexual connections is the fact that single form-species of *Nematoctonus,* having fewer morphological features than the sexual morph, were often associated with multiple species of *Hohenbuehelia*. In addition, the correct species identity of the sexual morphs of the ex-type strains of *Nematoctonus cylindrosporus*, *N. geogenius*, and *N. hamatus* was not realized at the time of their publication (Thorn & Barron 1986). Molecular phylogenetic analyses within the genus *Hohenbuehelia* and, particularly, the fixing of species concepts by designation of neotypes or epitypes of older species names (Consiglio 2016, 2017a, b, Consiglio & Setti 2017, 2018), have resolved the historically controversial applications of many names in this group, and provided finer species resolution where morphology had previously led to multiple species being treated under a broad species concept (Pilát 1935, Coker 1944, Miller 1986, Thorn & Barron 1986, Elborne 1995). In addition, phylogenetic studies have revealed previously unrecognized asexual-sexual connections in this group (Consiglio & Setti 2018), as in other groups of fungi (e.g., Rehner & Buckley 2005, Wingfield *et al*. 2012).

Hohenbuehelia subreniformis is one species for which no sexual morph is known. It was first described as a nematode-attacking fungus, isolated from humic-rotted hardwood in Algonquin Provincial Park, Ontario, Canada (Thorn & Barron 1986). Sequences of the nuclear ribosomal internal transcribed spacer (ITS) region and adjacent 5'-end of the large ribosomal subunit (nLSU) of the ex-holotype and one paratype strain were obtained by Koziak *et al*. (2007b) and remained in an isolated position in phylogenetic trees at that time and since (Consiglio *et al*. 2018, Consiglio & Setti 2018). This report describes a sexual (teleomorphic) specimen recently collected in Finland whose ITS sequences clustered with those of *H. subreniformis* and provides additional sequences of the translation elongation factor 1-alpha (*TEF-1α*), and RNA polymerase II second largest subunit (*RPB2*) genes of Ontario and Finnish materials to test the proposed asexual-sexual connection. Additionally, we present an updated list of asexual-sexual connections for all described *Nematoctonus* species.

MATERIALS AND METHODS

Morphological methods

The macroscopic description was derived from a photograph of the dried specimen. Microscopic structures were observed with a Zeiss Axioscope 40, in bright field, in phase contrast and in interferential contrast, by using 10×, 20×, 40×, and 63× and 100× oil immersion objectives. Gill fragments, transverse sections and edges as well as pileipellis radial sections were mounted in L4 (Clémençon 1972) and stained in Congo red (1 % aqueous). Melzer's reagent (Melzer 1924) was used to determine amyloidity and cresyl blue (Clémençon 1972) was used to assess metachromatism. Spore measurements were made by photographing all the spores (taken from the hymenophore of mature specimens) occurring in the field of view and then using Mycomètre software (Fannechère 2011). Spore dimensions with exclusion of the hilar appendix are given as: average minus standard deviation–average plus standard deviation of length × average minus standard deviation–average plus standard deviation of width; Q = average minus standard deviation–average plus standard deviation of ratio length/width; Qm = average of ratio length/width; Vm = average of the volume (in μm^3). The approximate spore volume was calculated as that of an ellipsoid (Gross 1972, Meerts 1999). Photomicrographs were taken with a Canon PowerShot A640 digital camera.

DNA extraction, amplification and sequencing

Genomic DNA was extracted and amplified from dry specimens employing the methods reported in Alvarado *et al*. (2010, 2012). The PCR amplifications were performed with the primers ITSF1 and ITSF4 for the ITS region (White *et al*. 1990, Gardes & Bruns 1993); while LR0R and LR3 or LR5 (Vilgalys & Hester 1990, Cubeta *et al*. 1991) were used to amplify the nLSU rDNA region; EF1-728F, EF1-983F and EF1-1567R (Carbone & Kohn 1999, Rehner & Buckley 2005) for the partial translation elongation factor 1-*α* (*TEF-1α*) gene, and bRPB2-6F2 (reverse of bRPB2-6R2), bRPB2-7.1R2 and bRPB2-7R2 for the RNA polymerase II second largest subunit (*RPB2*) gene (Liu *et al*. 1999, Matheny *et al*. 2007).

The sequences obtained were assembled and checked for possible read errors with MEGA v. 6.0 (Tamura *et al*. 2013), aligned with its MUSCLE application and then manually corrected. The ITS, nLSU, *RPB2* and *TEF-1α* alignments were carried out separately, with the 18S region trimmed from the ITS alignment.

Phylogenetic analyses

The ITS matrix had 349 variable sites in 727 bases, the nLSU matrix 153 in 944, the *RPB2* matrix 376 in 768, and the *TEF-1α* matrix 142 in 430. The data matrices of ITS, nLSU, *RPB2* and *TEF-1α* were combined into a single multilocus matrix. This matrix (2869 alignment positions), which covered a total of 236 sequences for four markers (234 ITS, 123 nLSU, 56 *RPB2* and 56 *TEF-1α*), was analysed with Bayesian Inference (BI) and the Maximum Likelihood (ML) criteria using MrBayes v. 3.2.7a (Ronquist & Huelsenbeck 2003) and RAxML (Stamatakis 2014), respectively. Bayesian analysis was performed through the CIPRES Science Gateway v. 3.3 (Miller *et al*. 2010) with the GTR+G+I evolutionary model for all partitions. The analysis was run for 3410000 generations, with 2 simultaneous runs, 6 chains, temperature set at 0.2, sampling every 1000 generations, and the first 25 % of the trees discarded. Maximum likelihood analysis was conducted in RAxML (Stamatakis 2014) using the standard search algorithm with 1000 bootstrap cycles and the GTR+G model, with *Pleurotus ostreatus* as outgroup. The trees in .tre format were read with the software SEAVIEW v. 4 (Gouy *et al*. 2010) and saved in a vector format for printing. Figure 1 shows the BI tree with the maximum likelihood bootstrap values (MLB) and Bayesian posterior probabilities (BPP). Newly derived sequences (shown in **bold**) and reference sequences from GenBank are listed in Table S1. Fungarium acronyms follow Thiers (2020). Nomenclature and author citations follow Index Fungorum (http://www.indexfungorum.org/authorsoffungalnames.htm).

RESULTS

Phylogenetic results

MrBayes and RAxML did not produce the same topology. This being the case, we decided to adopt the MrBayes phylogram as the basic phylogram and use the MLB values from RAxML only where the topology was the same.

The phylogenetic analysis showed that, apart from two minor groupings (*H. pinacearum-H. unguicularis* and *H. algonquinensis-H. boullardii*), the ingroup is divided in two main strongly supported clades (Fig. 1), i.e., clade A (1.0 BPP) with the species *H. mastrucata*, *H. valesiaca*, *H. pachyspora*, *H. tylospora*, *H. faerberioides*, *H. pseudofaerberioides*, *H. leptospora*, *H. auriscalpium*, *H. bonii*, *H. leiospora*, *H. petaloides*, *H. pseudopetaloides*, *H. longipes*, *H. tremula*, *H. thornii*, *H. wilhelmii* and *H. angustata*, and clade B (0.95 BPP) with the species *H. carlothornii*, *H. grisea*, *H. tristis*, *H. subreniformis*, *H. mustialensis*, *H. leightonii*, *H. nimueae*, *H. cyphelliformis*, *H. pseudocyphelliformis*, *H. ilerdensis*, *H. culmicola*, *H. josserandii*, *H. fluxilis*, *H. atrocoerulea*, *H. canadensis* and *H. portegna*. Within these two large clades are the following species groups, all with 1.0 BPP: a) *H. pachyspora* with *H. mastrucata* and *H. valesiaca*; b) *H. faerberioides* and *H. pseudofaerberioides* with *H. tylospora*; c) *H. bonii* with *H. leiospora*; d) *H. petaloides* with *H. pseudopetaloides*; e) *H. longipes* with *H. tremula*; f) *H. thornii*, *H. wilhelmii* and *H. angustata*; g) *H. grisea*, *H. carlothornii*, *H. tristis* and *H. portegna*; h) *H. cyphelliformis* with *H. pseudocyphelliformis*; i) *H. ilerdensis*, *H. culmicola*, *H. josserandii*, *H. fluxilis*, *H. atrocoerulea*, and *H. canadensis*, and j) *H. atrocoerulea* with *H. canadensis*. Some of these groups correspond with what were formerly treated as form-species of *Nematoctonus*, such as *N. angustatus* (*H. angustata – H. wilhelmii*), *N. hamatus* (*H. mastrucata – H. valesiaca*), *N. leiosporus* (*H. leiospora – H. boniii*), *N. robustus* (*H. carlothornii – H. grisea – H. tristis*; but also applied to asexual morphs of *H. pseudocyphelliformis*; Thorn & Barron

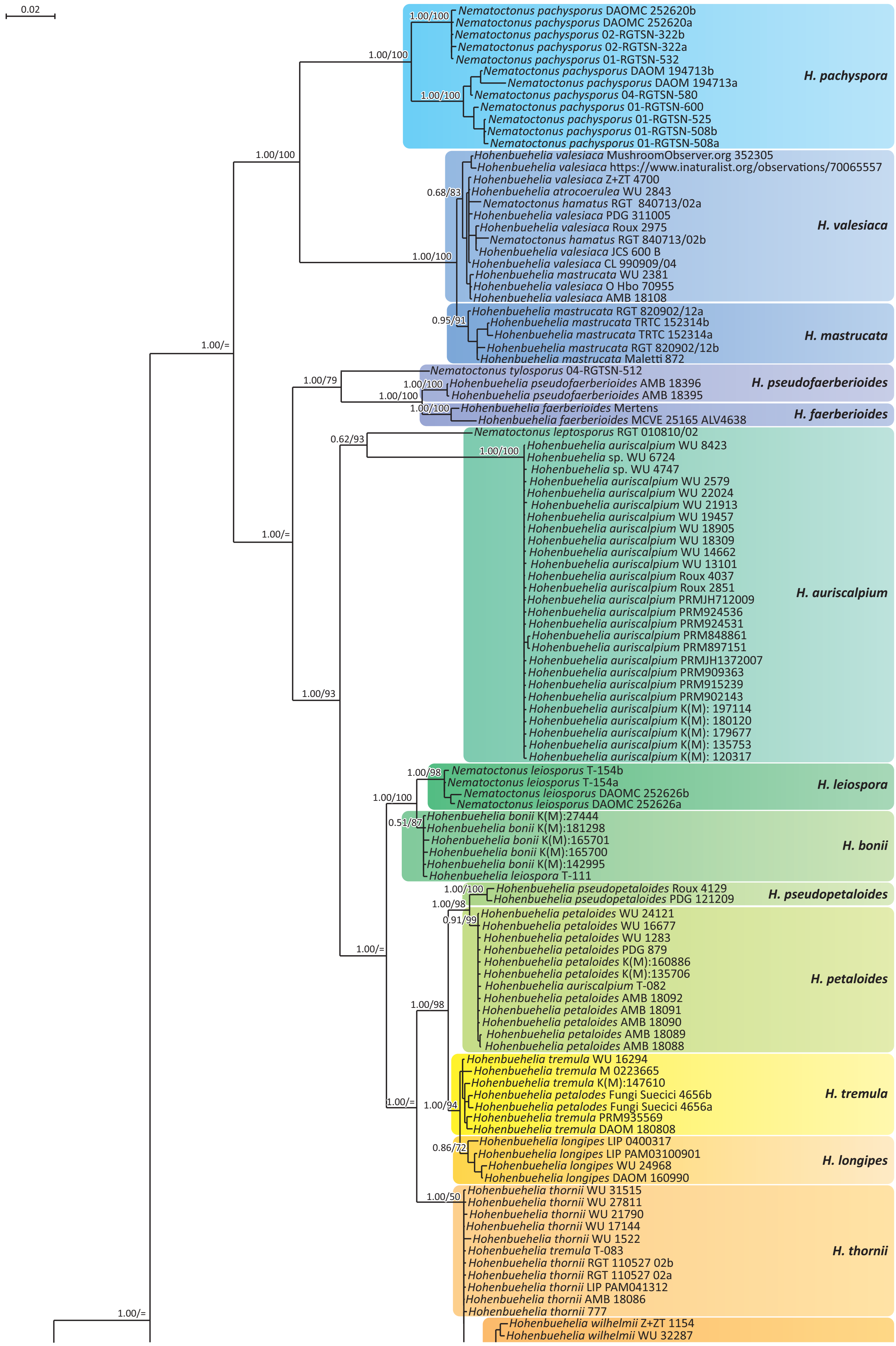

Fig. 1. Bayesian inference phylogram built with nucleotide sequence data of four loci (ITS, nLSU, *RPB2*-exons and *TEF1*-exons) of selected members of *Hohenbuehelia* rooted with *Pleurotus ostreatus*. Bayesian posterior probability values and Maximum Likelihood bootstrap values are shown on the branches. For each taxon, voucher number and original determination are given. The relevant GenBank accession numbers are shown in Table S1.

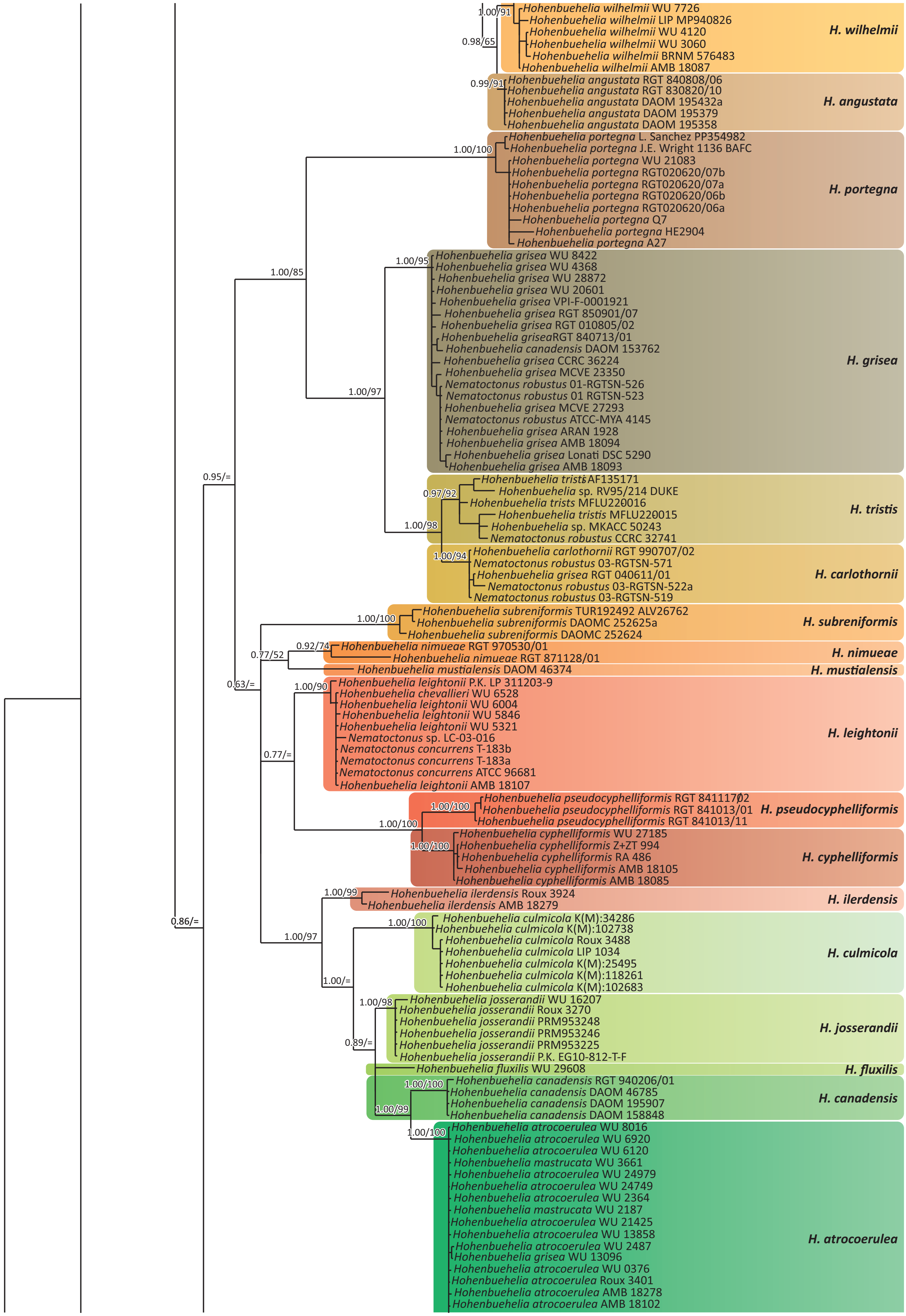

Fig. 1. (Continued).

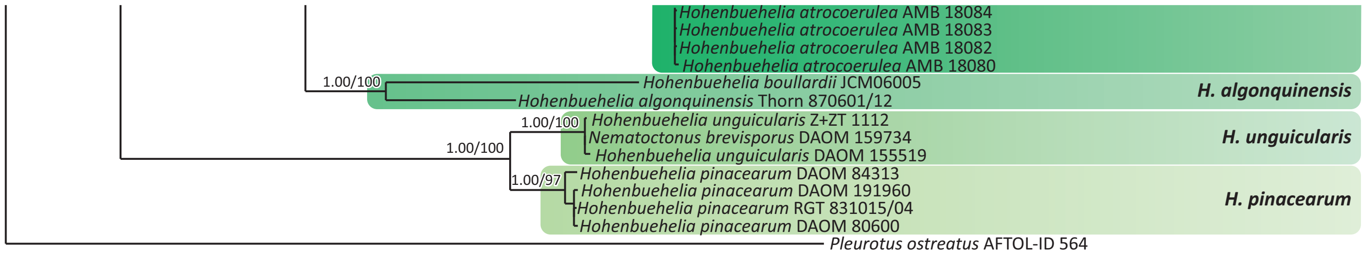

Fig. 1. (Continued).

1986), and *N. brevisporus* (*H. pinacearum* – *H. unguicularis*), whereas other former species of *Nematoctonus* formed isolated clades or single branches, such as *N. pachysporus* (*H. pachyspora*), *N. tylosporus* (*H. tylospora*), *N. leptosporus* (*H. leptospora*), *N. campylosporus* (*H. portegna*), *N. subreniformis* (*H. subreniformis*), and *N. concurrens* (*H. leightonii*).

A sexual collection of *Hohenbuehelia subreniformis*

Hohenbuehelia subreniformis (Thorn & G.L. Barron) Thorn, *Index Fungorum* **16**: 1. 2013. MB 550131. Fig. 2.
Basionym: *Nematoctonus subreniformis* Thorn & G.L. Barron, *Mycotaxon* **25**: 364. 1986.

Typus: **Canada**, Ontario, Algonquin Provincial Park, near the West Gate, approximately 45.44°N, 78.82°W, 440 m.a.s.l., in mature hardwood forest dominated by sugar maple (*Acer saccharum*) with American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), ironwood (*Ostrya virginiana*) and blue-beech (*Carpinus caroliniana*), 18 May 1984, *R.G. Thorn*, N84-240 (**holotype** DAOM 193363, a permanent slide derived from ex-type culture T-137, the latter deposited as ATCC 60607).

Description: *Basidiocarps* (macroscopic description from photograph of dried specimen). *Pileus* spathulate-orbicular, approximately 2.5 cm long and 2 cm broad, pale creamy beige overlain with whitish to pale greyish yellow tomentum from base almost to margin, margin narrowly acute, decurved and wavy. *Lamellae* close, narrow (approximately 1 mm deep as dried), decurrent onto pseudostipe, whitish to pale yellow, seriate. *Pseudostipe* underside off-white, tomentose, with raised lines extending from base of lamellae and forming a loose reticulum, arising from well-rotted wood without visible rhizomorphs or mycelial cords. *Odour* and *taste* not recorded. *Basidiospores* (Fig. 2A) hyaline, inamyloid, smooth, ellipsoid to broadly ellipsoid, 7.1–8.4 × 4.9–5.9 µm (on average 7.7 × 5.4) (n = 32), Q = 1.31–1.54 (on average 1.43), Vm =121 µm^3, with dull, granular content or with one or more oily drops. *Basidia* 22–26 × 7–8 µm, tetrasporic, clavate, with sterigmata up to 4 µm long. *Hymenophoral trama* irregular, made up of hyphae up to 8 µm broad, hyaline in L4, yellow in Melzer's. *Cheilometuloids* (Fig. 2D) in groups along the lamellar edge, subfusoid, generally with a narrow base, mostly with a lanceolate apical part and partly covered with refringent, yellow or whitish, crystalline granules, 17–33 × 7–9 µm. Mounted in Melzer's (Fig. 2F, G) they react pale reddish (dextrinoid reaction), while in cresyl blue (Fig. 2E) the wall stains vinaceous red (metachromatic reaction). *Cheilocystidia* (Fig. 2D, E) (leptocystidia) of the gloeosphex type (Thorn & Barron 1986), 10–17 × 5 µm, plus a neck and capitulum of 6–12 × 1.5–2 µm, often capped with a tiny, vanishing drop of mucus. *Pleurometuloids* similar to cheilometuloids, 40–60 × 8–10 µm. *Pileipellis* near margin (Fig. 2B) consisting of an ixocutis of variously intertwined, gelatinized, filamentous, smooth hyphae, 6–8 µm wide, yellow in Melzer's, with an intracellular yellowish pigment; halfway from the point of attachment (Fig. 2C) with a trichoderm of often tufted hairs. *Clamp connections* ubiquitous in all tissues.

Habitat and distribution: Originally described from well-decayed hardwood in Ontario, Canada (Barron & Thorn 1986; see *Isolates studied*, below), and found on a rotten branch in a mixed forest in southwest Finland. A search of globalfungi.com (Větrovský *et al.* 2020), a fungal environmental DNA (eDNA) database, yielded only a single full matching ITS1 sequence from a Swedish air sample (SH0815783.10FU) and no exact ITS2 matches (17 Jul. 2025).

Specimen examined: **Finland**, Southwest Finland region, Turku, Ruissalo, Kuuva, east side of the road Kuuvannokantie, in rich mixed forest near field, approximately 60.4109°N, 22.1175°E, 3 m.a.s.l., on fallen rotten branch beside *Alnus glutinosa*, near *Betula* and *Quercus robur*, 6 Aug. 2007, *K. Kokkonen*, 189/07 (TUR 192492, as *Hohenbuehelia mastrucata*?).

Isolates studied: **Canada**, Ontario, Algonquin Provincial Park, near the West Gate, approximately 45.44°N, 78.82°W, 440 m.a.s.l., in mature hardwood forest dominated by sugar maple (*Acer saccharum*) with American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), ironwood (*Ostrya virginiana*) and blue-beech (*Carpinus caroliniana*); recovered using the centrifuge plate technique, infecting unknown rhabditid nematodes (Thorn & Barron 1986) from three samples of well-decayed hardwood, 14 Oct. 1983, *R.G. Thorn*, N83-147 (source of culture T-108 = CBS 858.85); idem., 18 May 1984, *R.G. Thorn*, N84-240 (source of culture T-137 = ATCC 60607, source of holotype specimen, DAOM 193363); idem., N84-243 (source of cultures T-138, T-139 and T-140).

Notes: The basidiocarp of *H. subreniformis* resembles pale versions of *H. grisea* or *H. auriscalpium*, differing from the former by its spathulate, rather than dimidiate, shape and from both by the broad basidiospores, averaging 5.4 µm compared to less than 4 µm broad (Consiglio & Setti 2018). The hardwood (angiosperm) substrate also differs from the gymnosperm (conifer) substrate of *H. auriscalpium* (Consiglio & Setti 2018).

DISCUSSION

It is difficult to know, with just two published observations, whether this species is truly rare or is rarely encountered. Rabinowitz (1981), referring to vascular plants, identified three axes of rarity: small geographic range – related to endemism; high habitat specificity – in fungi, related to a specialized nutritional mode or substrate; and small local population size, or few individuals – which, for fungi and other microbes, is perilously difficult to establish (Burnett

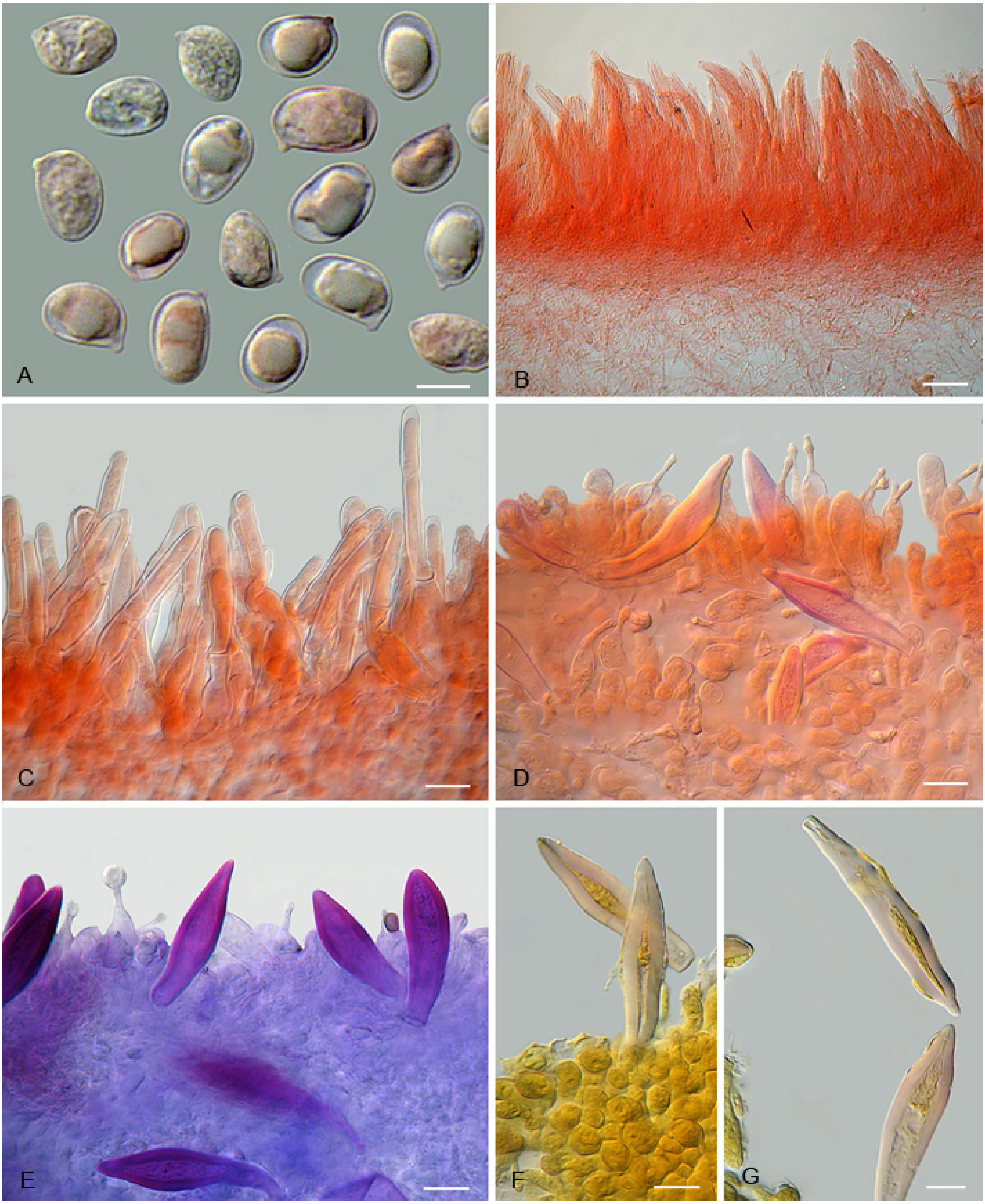

Fig. 2. Photomicrographs of K. Kokkonen 189/07 (TUR *192492*). **A.** Basidiospores. **B.** Pileipellis near pileus margin. **C.** Pileipellis halfway between margin and base. **D.** Gill edge showing cheilometuloids and gloeosphex-type leptocystidia stained with Congo Red. **E.** Gill edge showing metachromatic cheilometuloids and gloeosphex-type leptocystidia stained with cresyl blue. **F, G.** Faintly dextrinoid metuloid cystidia in Melzer's reagent. Scale bars: A = 5 µm; B = 50 µm; C–G = 10 µm.

2003). Adding to these is a low likelihood of encounter; unlike many birds, mammals and vascular plants, fungi and other inconspicuous organisms may be rarely detected without being rare (Kijpornyongpan & Aime 2016). In the case of *H. subreniformis*, it was first encountered in three samples of humic, well-rotted hardwood, the first collected in 1983, followed by two other samples collected in 1984 (Thorn & Barron 1986). The fungus was isolated five times from water agar plates inoculated with fine organic material and baited with rhabditid nematodes (Thorn & Barron 1986) but no inter-compatibility tests or fine-scale sequencing data are available to determine if each isolate was a separate genetic individual (genet), or if all were derived from propagules (infective conidia) of the same one. Many fungal individuals are perennial (Burnett 2003, Zotti *et al*. 2025), so the 1984 isolates could have been of the same individual that persisted since it was first detected in 1983. The most that can be said is that the same taxon was not encountered in any of more than 700 other samples of soil and rotted wood from across Ontario in the same study (Thorn & Barron 1986), and that it has not been reported in other studies of nematophagous fungi worldwide before or since (reviewed in Berhanu *et al*. 2024). With a range spanning over 6000 km, with three detection points, *H. subreniformis* is clearly not "rare and local" or endemic, a pattern also seen in rare wood-inhabiting fungi in New Zealand (Dickie *et al*, 2020). However, its ecological specialization suggests that it may have very spotty distribution at low densities across a circumpolar range and is unlikely to be detected by standardized surveys of basidiocarps or environmental DNAs. There is much work to be done to learn the true abundance and distributions of fungi, even in parts of the world that have been extensively investigated.

The discovery of the sexual morph of *H. subreniformis* marks another connection between the asexual forms previously classified in *Nematoctonus* and named species of *Hohenbuehelia*, first hinted by Drechsler (1941) and established by Barron & Dierkes (1977). Altogether, 15 species have been validly described in *Nematoctonus*, for which the correct names in *Hohenbuehelia* are not readily discoverable in Index Fungorum (https://indexfungorum.org/names/Names.asp). For this reason, we provide here a synopsis of known asexual-sexual connections and the correct names for each species.

Asexual-sexual connections for the 15 species described in *Nematoctonus*

1) *Nematoctonus angustatus* Thorn & Barron, *Mycotaxon* **25**: 333. 1986 (Ontario, Canada) is a synonym of ***Hohenbuehelia angustata*** (Berk.) Singer. The **holotype** of *N. angustatus*, DAOM 193369, is a permanent slide prepared from culture T-91, isolated from a basidiocarp of *H. angustata* (RGT 830820/10; ITS-LSU sequence EF409718), whose sequence is conspecific with the **epitype** of *Panus angustatus* Berk., DAOM 195358 (Consiglio & Setti 2017, 2018).

2) *Nematoctonus brevisporus* Thorn & Barron, *Mycotaxon* **25**: 337, 1986 (Ontario, Canada) is a synonym of ***Hohenbuehelia unguicularis*** (Fr.) Singer. The **holotype** of *N. brevisporus*, DAOM 193368, is a permanent slide prepared from culture T-47, isolated from a basidiocarp of *H. unguicularis* (DAOM 159734; ITS-LSU sequences EF409721, MH861918 and MH873607). These sequences are conspecific with that of the **neotype** of *Agaricus unguicularis* Fr., Z+ZT 1112 (Consiglio 2016, Consiglio & Setti 2018). The asexual morph of *H. pinacearum* Thorn (Thorn 1986) is morphologically identical, so the asexual morph description in Thorn & Barron (1986) includes both species, which are closely related in molecular phylogenies (Fig. 1).

3) *Nematoctonus campylosporus* Drechsler, *J. Wash. Acad. Sci.* **44**: 82, 1954 (Louisiana, U.S.A.; no type was designated and there is no living or preserved original material) is a synonym of ***Hohenbuehelia portegna*** (Speg.) Singer, as fixed by the epitypification below. **Lectotype** for *N. campylosporus*, here designated (MBT 10017554): Drechsler's original illustrations, figs 1–6 (J. Wash. Acad. Sci. 44: 83, 1954). For both *N. campylosporus* and *H. portegna*, the **epitype**, here designated (MBT 10017555 and MBT 10017556, respectively): **Argentina**, Buenos Aires, Llavallol, Santa Catalina, 3 Nov. 1968, *J.E. Wright* 1136, (specimen BAFC 29143; culture T-007 = ATCC 60630 = BAFC 280; ITS-LSU sequence AF139959.2), which cements the synonymy of the two species.

4) *Nematoctonus concurrens* Drechsler, *Mycologia* **41**: 382, 1949 (Oregon, U.S.A.; no type was designated and there is no living or preserved original material) is a synonym of ***Hohenbuehelia leightonii*** (Berk.) Watling ex Courtec. & P. Roux. **Lectotype** for *N. concurrens*, here designated (MBT 10017557): Drechsler's original illustrations, figs 1–4 (Mycologia 41: 371, 374, 378, 381, 1949, all illustrating the same mycelial individual). **Epitype** for *N. concurrens*, here designated (MBT 10017558): **USA**, California, Bodega Bay, 5 Dec. 1994, *B.A. Jaffee* (culture ATCC 96681; preserved in a metabolically inactive state; ITS-LSU sequence EF546658). This species is a synonym of *H. leightonii*, based on apparent conspecificity of sequences of the epitype, designated above, and that of the **epitype** of *Agaricus leightonii* Berk., AMB 18107 (Consiglio 2016, Consiglio & Setti 2018).

5) *Nematoctonus cylindrosporus* Thorn & Barron, *Mycotaxon* **25**: 344, 1986 (Oxford, England) is a synonym of ***Hohenbuehelia petaloides*** (Bull.) Schulzer. The **holotype** of *N. cylindrosporus*, DAOM 193366, is a permanent slide prepared from culture T-82 (= CBS 102.82 and CSAV 373; E. Jones), isolated from a basidiocarp of *H. petaloides*. This identification is based on apparent conspecificity of the sequences of this strain with those of the **epitype** of *Agaricus petaloides* Bull., AMB 18091 (Consiglio 2016, Consiglio & Setti 2018). Thorn (2013) incorrectly indicated the sexual morph to be *H. auriscalpium*.

6) *Nematoctonus geogenius* Thorn & Barron, *Mycotaxon* **25**: 348, 1986 (California, USA). The correct name in *Hohenbuehelia* is unresolved. The **holotype** of *N. geogenius*, DAOM 193365, is a permanent slide prepared from culture T-180, isolated from a basidiocarp of what was probably *Hohenbuehelia thornii* Consiglio & Setti, but there are no sequence data for this collection (BL Thompson 411, HSC), and the ex-type culture is lost. The species *H. thornii* is often found growing from soil of potted house plants and horticultural beds (e.g., https://inaturalist.ca/observations/63193326

and https://inaturalist.ca/observations/63193323), as was BL Thompson 411. The epithet *geogenius* is not available for transfer from *Nematoctonus* to *Hohenbuehelia* because of the prior existence of *H. geogenia* (DC.) Singer (1951) so, if *N. geogenius* and *H. thornii* are synonymous, the correct name for this species would be *H. thornii*. Consiglio & Setti (2018) showed that sequences identified as *N. geogenius* fall in four separate clades of *Hohenbuehelia*, a situation requiring further study. **Epitype** for *N. geogenius*, here designated (MBT 10017559): **USA**, California, Sacramento, growing from soil of a potted house plant, 22 Aug. 1984, *B.L. Thompson*, 411 (the portion of the sexual morph, BL Thompson 411, preserved as DAOM 195416).

7) *Nematoctonus hamatus* Thorn & Barron, *Mycotaxon* **25**: 351, 1986 (Ontario, Canada) is a synonym of ***Hohenbuehelia valesiaca*** (Ces. ex Sacc.) Singer. The **holotype** of *N. hamatus*, DAOM 193364, is a permanent slide prepared from culture T-23, isolated from soil nematodes; the sequences of this strain are conspecific with those of the **epitype** of *H. valesiaca* (F. Fouchier, FF13115a), fide Consiglio & Setti (2018). The asexual morph of *H. mastrucata* (Fr.) Singer is morphologically identical, so the asexual morph description in Thorn & Barron (1986) includes both species, which are closely related in molecular phylogenies (Fig. 1).

8) *Nematoctonus haptocladus* Drechsler, *Mycologia* **38**: 19, 1946 (Colorado, U.S.A.; no type was designated and there is no living or preserved original material) is a synonym of ***Hohenbuehelia haptoclada*** (Drechsler) Thorn (2013), but no sexual morph or sequence data are known. **Lectotype** for *N. haptocladus*, here designated (MBT 10017560): Drechsler's original illustrations, figs 1–7 (Mycologia 38: 3, 5, 7, 11, 13, 14, 15, 1946). Designation of an epitype awaits living material that is geographically and morphologically appropriate.

9) *Nematoctonus leiosporus* Drechsler, *Phytopathology* **31**: 779, 1941 (Wisconsin, U.S.A.; no type was designated and there is no living or preserved original material) is a synonym of ***Hohenbuehelia leiospora*** (Drechsler) Thorn (2013). **Lectotype** for *N. leiosporus*, here designated (MBT 10017561): Drechsler's original illustration, fig. 2A–K (Phytopathology 31: 776, 1941). **Epitype** for *N. leiosporus*, here designated (MBT 10017562): **Canada**, Ontario, London, isolated from infected nematodes from soil in urban lawn, 13 Jun. 1984, *R.G. Thorn*, subculture of culture T-148 (DAOMC-252626, a culture preserved in metabolically inactive state). No sexual morph is known. A closely related sequence of one isolate previously identified as this species, but with shorter-than-average conidia (T-111 = ATCC 60605, from Morriston, Ontario, Canada; Thorn & Barron 1986, Koziak *et al*. 2007b) has been found to be conspecific with a sequence of the **holotype** of *Hohenbuehelia bonii* A.M. Ainsw., K(M) 165701, fide Consiglio & Setti (2018). *Hohenbuehelia bonii* and *H. leiospora* are seen as sister species in molecular phylogenies (Fig. 1).

10) *Nematoctonus leptosporus* Drechsler, *J. Wash. Acad. Sci*. **33**: 188, 1943 (Maryland, U.S.A.; no type was designated and there is no living or preserved original material) is a synonym of ***Hohenbuehelia leptospora*** (Drechsler) Thorn (2013). **Lectotype** for *N. leptosporus*, here designated (MBT 10017590): Drechsler's original illustration, fig. 2 (J. Wash. Acad. Sci. 33: 186, 1943). Designation of an epitype awaits living material that is geographically and morphologically appropriate. A culture identified as *N. leptospora* (Koziak *et al*. 2007a) was isolated from a basidiocarp of a *Hohenbuehelia* [RGT 010810/02 (UWO), La Selva, Costa Rica 10 Aug. 2001 (culture since lost; ITS-LSU sequence EF409743; Koziak *et al*. 2007b)], but description of the sexual morph awaits better material.

11) *Nematoctonus pachysporus* Drechsler, *J. Wash. Acad. Sci*. **33**: 185, 1943 (Maryland, U.S.A.). **Lectotype** for *N. pachysporus*, here designated (MBT 10017591): Drechsler's original illustration, fig. 1 (J. Wash. Acad. Sci. 33: 184, 1943) is a synonym of ***Hohenbuehelia pachyspora*** (Drechsler) Thorn, ***comb. nov.*** (MB 851648; basionym *Nematoctonus pachysporus* Drechsler, *J. Wash. Acad. Sci.* **33**: 185, 1943). Thorn (2013) reported that a culture matching this asexual morph description had been isolated from a basidiocarp identified as *Hohenbuehelia izonetae* Singer and that *N. pachysporus* may represent an earlier name for *H. izonetae*. However, sequences of cultures identified by this name form two or three separate clades (Koziak *et al*. 2007b, Fig. 1), so designation of an epitype and clarification of possible synonymy awaits studies to determine which clade best fits Drechsler's original species.

12) *Nematoctonus robustus* F.R. Jones, *Trans. Brit. Mycol. Soc*. **47**: 57, 1964 (Ghana, **holotype** IMI 102541) is a synonym of ***Hohenbuehelia robusta*** (F.R. Jones) Thorn (2013). Previously regarded as a synonym of *H. atrocoerulea* (Barron & Dierkes 1977) or *H. grisea* (Thorn & Barron 1986), but likely an independent species. Unfortunately, the ex-type culture has been lost and no similar cultures from the same geographic region are known.

13) *Nematoctonus subreniformis* Thorn & Barron, *Mycotaxon* **25**: 364, 1986 (Ontario, Canada, holotype DAOM 193363) is a synonym of ***Hohenbuehelia subreniformis*** (Thorn & Barron) Thorn (2013) and herein connected with its sexual morph.

14) *Nematoctonus tripolitanius* Giuma & Cooke, *Trans. Brit. Mycol. Soc*. **59**: 215, 1972 (Libya, holotype IMI 162669) is a synonym of ***Hohenbuehelia tripolitania*** (Giuma & Cooke) Thorn (2013). No sexual morph or sequences are known, and the ex-type culture has apparently been lost. The culture IMI 162669, as received, was morphologically identical to CBS 129.68(*Nematoctonus concurrens*, also from R.C. Cooke); that is, it did not conform to the original description of the species and had identical ITS-LSU sequence to CBS 129.68 (R.G. Thorn, unpubl. data).

15) *Nematoctonus tylosporus* Drechsler, *Phytopathology* **31**: 779, 1941 (Maryland, District of Columbia, and Virginia, U.S.A.; no type was designated and there is no living or preserved original material) is a synonym of ***Hohenbuehelia tylospora*** (Drechsler) Thorn (2013). **Lectotype** for *N. tylosporus*, here designated (MBT 10017592): Drechsler's original illustration, fig. 1 (Phytopathology 31: 774, 1941). Designation of an epitype awaits geographically and morphologically suitable living material. The culture 04-RGTSN-512, isolated from infected nematodes from Costa Rica, 1 Jun. 2004, has been

identified as this species (Koziak *et al*. 2007a) and has ITS-LSU sequence EF409766 (Koziak *et al*. 2007b), but no sexual morph is known.

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Supplementary Material: http://fuse-journal.org/

Table S1. Sequences used and generated in this study. Newly sequenced collections are **in bold.** Two-letter province codes are added for Canada and the U.S.A. An emdash (—) indicates data lacking.