A new species of bird’s nest fungi: characterisation of
Cyathus subglobisporus sp. nov. based on morphological
and molecular data

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Abstract Recent collections of bird’s nest fungi (i.e. Crucibulum, Cyathus, Myocalla, Nidula, and Nidularia species) in northern Thailand resulted in the discovery of a new species of Cyathus, herein described as C. subglobisporus. This species is distinct by a combination of ivory-coloured fruiting bodies covered with shaggy hairs, plications on the inner surface of the peridium and subglobose basidiospores. Phylogenetic analyses based on ITS and LSU ribosomal DNA sequences using neighbour-joining, maximum likelihood and weighted maximum parsimony support Cyathus subglobisporus as a distinct species and sister to a clade containing C. annulatus, C. renweii and C. stercoreus in the Striatum group.

INTRODUCTION
The genus Cyathus along with the genera Crucibulum, Myocalla, Nidula, and Nidularia are known as the bird’s nest fungi because of their small vase-shaped or nest-like fruiting bodies containing lentil-shaped or egg-like peridioles. Cyathus is the most speciose genus in the family Nidulariaceae (Agaricales). Cyathus is distinguished from the other three genera in the Nidulariaceae based on grey to black peridioles with funicular cords and peridium composed of three layers of tissues (Brodie 1975). Historically, Cyathus was monographed by Lloyd (1906) and Brodie (1975, 1984), and their species concepts, especially those of Brodie (1975), are followed by most mycologists (Liu & Li 1989, Ren & Zhou 1992, Yang et al. 2002, Chen et al. 2003, Zhou et al. 2004). Recognition of Cyathus species is based on morphological characters such as fruiting body shape, coverings and plications of peridia, anatomy of peridioles, and the size and shape of basidiospores (Brodie 1975).

Molecular phylogenetic studies based on rDNA sequence data including several Cyathus species and other gasteromycetous fungi (e.g., C. striatus in Hibbett et al. 1997, Hibbett & Thorn 2001 and C. stercoreus in Moncalvo et al. 2002) showed that Cyathus nested within the euagarics clade. The most recent treatment of the Agaricales by Matheny et al. (2006) based on sequence analyses of six loci included Crucibulum laeve and Cyathus striatus as representatives of the Nidulariaceae. Their phylogenetic reconstruction indicated that the Nidulariaceae was sister to the Cystodermaeae (represented by Cystoderma amianthinum). Together these two clades appear sister to the Agaricaeae s.l. but without bootstrap support. A phylogenetic study of the genus Cyathus by Zhao et al. (2007) using ITS and LSU ribosomal DNA sequence datasets, and based primarily on type and authentic specimens of 22 taxa of Cyathus, indicated that the genus was monophyletic and included three infrageneric groups recognisable by morphological characters.

In Brodie’s monographs (Brodie 1975, 1984) eight species were known from southeast Asia: C. cheliensis and C. olivaceobrunneus from China; C. crispus, C. ellipsioideus, and C. griseocarpus from India; C. elmeri and C. gracilis from the Philippines, and C. triplex from the West Indies, the Philippines, and Thailand. Within the last 20 years, seven new taxa have been described from south China: C. africanus var. latissporus (Chen et al. 2003), C. comucipoides (Ren & Zhou 1992), C. lijiangensis (Zhou et al. 2004), C. luxiensis (Chen et al. 2003), C. mega- sporus (Ren & Zhou 1992), C. renweii (Zhou et al. 2004), and C. yunnanensis (Liu & Li 1989). Based on morphological analyses of 48 Cyathus taxa, including 30 type specimens in Zhao et al. (2006), three Cyathus species were found to represent synonyms of existing species. Cyathus cheliensis, C. gansuensis (Yang et al. 2002), and C. megasporus were accepted as synonyms of C. limbatus, C. pygmaeus, and C. poepiggii, respectively.

There has been a recent interest in studies of basidiomycetes in Thailand, particularly around the area of the Mushroom Research Centre (Le et al. 2007a–c, Wannathes et al. 2007). Some Cyathus species have been reported previously from Thailand (Brodie 1975, Ellingsen 1982, Sotyong 1994, Desjardin et al. 2004). However, no new species have been described from Thailand prior to this paper. In this study Cyathus subglobisporus sp. nov. is described and its phylogenetic position is investigated based on ITS and LSU rDNA sequence data.

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MATERIALS AND METHODS

Morphological studies

Macromorphological characters of freshly collected material were documented as follows. Colour terms follow Kornerup & Wanscher (1978). Peridioles were sectioned by hand, mounted in distilled water, and examined using a light microscope. Spore statistics include average dimensions ± SD; Q, the quotient of spore length and spore width in any one spore; and Qw, the mean of Q-values ± SD. Duplicates are deposited in the BIO-TEC Bangkok Herbarium (BBH), Bangkok, Thailand, the H.D. Thiers Herbarium (SFSU) at San Francisco State University, San Francisco, California, USA, and the herbarium of the Mushroom Room Research Centre (MRC), Chiang Mai, Thailand.

Molecular phylogenetic studies

DNA extractions were made from gleba using a commercial DNA extraction kit (E.Z.N.A. Forensic Kit, D3591-01, Omega Bio-Tek). PCR reactions performed with primer pairs LROR and LR5 and ITS4 and ITS5. Sequencing protocols follow those of Zhao et al. (2007).

Newly generated sequences (ITS and LSU sequences from the new species), and those retrieved from GenBank (20 ITS and 19 LSU sequences; Table 1) were initially aligned using Clustal X with default settings (Thomson et al. 1997). Manual adjustments were made in BioEdit v. 7.0.4 and gaps were introduced to improve alignments. The ITS and LSU alignments were separately submitted to TreeBASE (accession number: SN3455). All sequences used in this study were derived from type or paratype specimens or from authentic material determined by us or by H.J. Brodie (cf. Zhao et al. 2007).

Phylogenetic analyses were performed using PAUP v. 4.0b10 (Swofford 2003). Heuristic searches of the ITS, LSU, and ITS+LSU datasets were performed separately under three optimality criteria: weighted parsimony (WP), maximum likelihood (ML), and neighbour-joining (NJ). Unordered characters, random taxon addition sequences, gaps treated as missing data, and tree bisection-reconnection (TBR) branch swapping were used in all analyses. For weighted maximum parsimony, maxtrees was limited to 5 000 trees with 1 000 replications. The weighted parameters were produced using Stratmix (François Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and Lutzoni & Stefan Zoller, Duke University) as described in Miadlikowska et al. (2002). The best nucleotide substitution models for maximum likelihood were chosen by using MrModeltest v. 2.2 (Nylander 2004). Bootstrap values (BS) were obtained from 1 000 replicates. Unconstrained trees (WP, ML, and NJ trees) were compared in PAUP using Kishino-Hasegawa and

Table 1 Taxon information and sequences retrieved from GenBank.

| Taxon Information                  | GenBank Accession Numbers |
|-----------------------------------|---------------------------|
|                                   | ITS          | LSU          |
| Crucibulum laeve                  | DQ463340     | DQ463346     |
| Cystopus africans                 | DQ463344 DQ463341 | DQ463325     |
| C. cylindraceus                   | DQ463354     | DQ463332     |
| C. crassimurus                    | DQ463350     | DQ463329     |
| C. griseocarpus                   | DQ463346     | DQ463327     |
| C. guangshansensis                | DQ463351     | DQ463326     |
| C. helenae                        | DQ463348     | DQ463325     |
| C. hookeri                        | DQ463347     | DQ463324     |
| C. amianthinum                    | DQ463345     | DQ463323     |
| C. subglobisporus                 | DQ463343     | DQ463322     |
| C. pallidus                       | DQ463342     | DQ463321     |
| C. poepigii                       | DQ463349     | DQ463320     |
| C. pygmasus                       | DQ463356     | DQ463319     |
| C. renweii                        | DQ463357     | DQ463318     |
| C. setosus                        | DQ463358     | DQ463317     |
| C. stercoreus                     | DQ463359     | DQ463316     |
| C. subglobisporus sp. nov.        | DQ463360     | DQ463315     |
| C. triplex                        | DQ463361     | DQ463314     |
| C. amianthinum                    | DQ463362     | DQ463313     |
| Nidula niveotomentosa             | DQ463363     | DQ463312     |

1 Refers to the type specimen.
2 Indicates that H.J. Brodie determined the specimen.
Shimodaira-Hasegawa tests (Kishino & Hasegawa 1989). Trees were viewed in TreeView v. 1.6.6 (Page 1996) and exported to graphics programmes.

The informal infrageneric group names Ollum, Pallidum, and Striatum in *Cyathus* follow the phylogenetic nomenclature established by Zhao et al. (2007). Although these names constitute improper Latin and do not match the specific epithets olla, pallidus, and striatus, they were established by Zhao et al. (2007) to distinguish the clades from similarly named infrageneric groups used by Brodie (1975), viz., Striatus, Pallidus, and Olla, that contain different subsets of species.

**RESULTS**

**DNA alignment and phylogeny**

The ITS dataset consisted of 776 characters of which 371 characters were constant, 109 variable characters were parsimony-uninformative, and 171 characters were parsimony-informative. One hundred and twenty four characters were ambiguous and were excluded. The sequences represent 16 *Cyathus* species (18 strains), *Crucibulum laeve*, and *Nidula niveotomentosa*, while *Cystoderma amianthinum* was used as the outgroup for rooting purposes based on the previous result that *C. amianthinum* (Cystodermateae) is sister to Nidulariaceae (Matheny et al. 2006). In all phylogenies under different optimality criteria (NJ, ML, and WP), the genus *Cyathus* is monophyletic with 100 % bootstrap and all trees have similar topologies. ITS results indicate that *Cyathus* species were partitioned into three main clades as shown by Zhao et al. (2007). Our new taxon, *Cyathus subglobisporus*, belongs to the Striatum group, albeit with weak statistical support (Fig. 1).

The LSU dataset consisted of 797 characters, of which 661 characters were constant, 56 variable characters parsimony-uninformative, and 70 characters parsimony-informative. Ten characters were excluded. The LSU dataset includes 16 *Cyathus* species (17 strains), *Crucibulum laeve*, and *Nidula niveotomentosa*. *Cystoderma amianthinum* was chosen as the outgroup for rooting purposes. Phylogenies (NJ, ML, and WP) show that *Cyathus* is monophyletic with 100 % bootstrap support, and that *C. subglobisporus* clusters with *C. setosus*, and together they are sister to the Pallidum group but this relationship was not statistically supported (Fig. 2).

The combined ITS and LSU sequence dataset consisted of 1573 characters of which 1045 characters were constant; 171 variable characters were parsimony-uninformative, 223 charac-

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**Fig. 2** Phylogenetic relationship of *Cyathus* inferred by maximum likelihood analysis of LSU rDNA sequences. Bootstrap support (BS) values above 50 % are shown.

**Fig. 3** Phylogenetic relationships of *Cyathus* inferred by maximum likelihood analysis of combined ITS and LSU rDNA sequences. Bootstrap support (BS) values above 50 % are shown.
ters were parsimony-informative, and 134 characters were excluded. This dataset represents 10 Cyathus species (11 strains; all taxa for which both ITS and LSU data were available), Crucibulum laeve, and Nidula niveotentomomata. Kishino-Hasegawa and Shimodaira-Hasegawa tests among NJ, ML, and WP indicated that the ML tree was the best tree (Fig. 3). Cyathus is monophyletic with 100% bootstrap support, and C. subglobisporus is sister to C. annulatus, C. renwelli, and C. stercoraceus in the Striatum group with 67% bootstrap support.

**Taxonomy**

_Cyathus subglobisporus_ R.L. Zhao, Desjardin, K. Soytong & K.D. Hyde, sp. nov. — MycoBank MB512024; Fig. 4

Peridium obconicum, crassum, 7–10 mm altum, ore 5–8 mm lato, extra palide flavum vel pallide brunneum, pilis resupinatis et fasciis sectatim obtectum, intus griseum, argenteum, tenueret sed distincte striatum, labium minute fimbriatum; epithecum tanum, tenue peridio 1.5–2 mm diam, lentiformia, tunicar peripallide fuscam teretia; cortex simplex; sporae subglobosae vel ellipsoidicae, 13–18 μm longae, 12–16 μm latae.

_Etymology:_ Refers to its subglobose spores.

_Fruiting_ bodies clavate when young, then opening, extending and becoming obconic to infundibuliform, with relatively straight sides in side view; 7–10 mm high, 5–8 mm wide at the top, with the quotient of height by width 1–1.4; external peridium covered by hairs aggregated into shaggy or hirsute clusters, ivory, pale yellow or buff when young, sometimes with a hint of pale orange, then darkening to pale brown with age and the hairs remaining pallid. Inner peridium surface grey to brownish grey, darkening with age, distinctly plicate when young, becoming striate to smooth with age. _Epiphragm_ membranaceous, white, covered by buff to pale orange-white hairs similar to those on the external surface of the peridium, cracking irregularly during maturation and disappearing or leaving a minutely fimbriate lip along the top edge of the peridium. Base of the fruiting bodies narrower than the rest of the fruiting body but lacking a distinct stipe. _Peridioles_ 1.5–2 mm diam, lenticular, greyish brown to pale brown; peridiole covering composed of two layers: a black inner cortex layer, 15–25 μm thick, and a yellowish brown or dark brown outer tonica layer, 25–50 μm thick. _Basidiospores_ 13–18×12–16 μm (av. = 15.8 ± 2.8 × 14.1 ± 2.1, Q = 1–1.31, Qd = 1.12 ± 0.19, n = 50), subglobose or rarely broadly ellipsoidal, hyaline, smooth, thick-walled (1.5–2(–3) μm). _Basidia_ not observed. _Clamp connections_ present.

_Habitat:_ On rotten bamboo stems in moist forest.

_Specimens examined:_ **C. annulatus:** CANADA, Alberta, Cypress Hills, above Elkwater lake, 8 Aug. 1968, H.J. Brodie, holotype DAOM 200366. — **C. berkeleyanus:** CHINA, Sichuan Prov., Chengdu, Nov. 1999, Tongxin Zhou, SWFC 20789. — **C. bulleri:** INDIA, West India, Guadeloupe, 8 Feb. 1966, H.J. Brodie, isotype BPI 727126. — **C. cornucopioides:** CHINA, Yunnan Prov., Luxi county, 4 Sept. 1935, Z.L. Zhao, holotype, SWFC 20414. — **C. crispus:** GHANA, Bunsu, 17 June 1949, S.T. Hughes, holotype DAOM 200373. — **C. duros:** USA, Colorado, Denver, 1900, E. Bethel, isotype BPI 727135, 727134. — **C. griseocarpus:** INDIA, Manipur State, Ukhrul, 29 Aug. 1978, H.J. Brodie, holotype DAOM 200396. — **C. guandishanensis:** CHINA, Shanzhi Prov., Guandishan, 11 Aug. 1987, M.C. Chang, holotype HMAS 81896. — **C. helenae:** CANADA, Alberta, 20 Aug. 1965, H.J. Brodie, holotype DAOM 200384. — **C. olivaceobrunneus:** CHINA, Yunnan Prov., Dalil, 28 Aug. 1939, H.S. Yao, holotype HMAS D1518. — **C. palidus:** CHINA, Guizhou Prov., Aug. 2000, S.K. Bai, SWFC 21160. — **C. setosus:** JAMMUCA, 9 Jan. 1966, H.J. Brodie, holotype DOAM 200815. — **C. subglobisporus:** THAILAND, Chiang Mai Province, Chiang Dao, gregarious on rotten bamboo stem, 22 July 2006, L.-R. Zhao, K.D. Hyde, H.-L. Hu, J.-N. Liu, W. Nilen & C. Ratnadawan, holotype BBH 18348, isotypes MRC 00800 and SFSU zrlc013. — **C. tianshanensis:** CHINA, Neimenggu, collection data unknown, Y.Z. Shang, SWFC 21157. — **C. yunnanensis:** CHINA, Yunnan Prov., 13 Sept. 1935, Q.W. Wang, holotype HMAS 17373.

**DISCUSSION**

At first glance the proposed new species looks like _Cyathus griseocarpus_ (Brodie 1984), which is commonly encountered in northern Thailand. Both species share features of pale yellow or pale brown fruiting bodies, an external peridium covered by pale yellow hairs that aggregate into conic mounds, an inner peridium surface that is striate to plicate, and grey-toned peridioles. The subglobose basidiospores and pale brown peridioles of _C. subglobisporus_, however, can differentiate it from _C. griseocarpus_. The latter species possesses much smaller, more ellipsoid basidiospores (av. = 7.3 ± 0.7 × 5.3 ± 1.3 μm, Q = 1.4 ± 0.6, from holotype) and pale grey peridioles. The LSU tree (Fig. 2) clearly indicates that _C. griseocarpus_ belongs to the Ollum group and is distantly related to _C. subglobisporus_.

Species of _Cyathus_ whose fruiting bodies are pale yellow or pale brown and have a distinctly plicate inner peridium include _C. annulatus_, _C. berkeleyanus_, _C. bulleri_, _C. cornucopioides_, _C. crispus_, _C. duros_, _C. guandishanensis_, _C. helenae_, _C. palidus_, _C. setosus_, _C. tianshanensis_, and _C. yunnanensis_. Only _C. bulleri_, _C. guandishanensis_, and _C. yunnanensis_, however, possess subglobose or globose spores. After comparison of their spore size, _C. subglobisporus_ is distinct in possessing larger spores (av. = 15.8 ± 2.8 × 14.1 ± 2.1, Q = 1.12 ± 0.19) than those of _C. bulleri_ (av. = 7.3 ± 1.7 × 6.8 ± 1.8 μm, Q = 1.08 ± 0.15, from isotype) and _C. guandishanensis_ (av. = 11.6 ± 2.15 × 8.6 ± 1.4 μm, Q = 1.37 ± 0.46, from holotype), and smaller spores than those of _C. yunnanensis_ (av. = 22.38 ± 3.6 × 18 ± 3, Q = 1.25 ± 0.42, from holotype). Of the latter three species sequence data was obtained successfully only from _C. guandishanensis_.

The LSU tree (Fig. 2) clearly indicates that _C. guandishanensis_ belongs to the Ollum group and is distantly related to _C. subglobisporus_.

The spores of _Cyathus olivaceobrunneus_ (named after its olive-brown peridium) are similar to those of _C. subglobisporus_ in shape and size, and the former species has been suspected to be a synonym of _C. poepipigi_ (Brodie 1975). Examination of the type specimen of _C. olivaceobrunneus_ showed the colour of its fruiting bodies to be much darker and to have longer spores (av. = 17.88 ± 8.75 × 13.2 ± 2, Q = 1.36 ± 0.34, from holotype) than those of _C. subglobisporus_. We were unable to generate quality sequence data from available material of _C. olivaceobrunneus_ for comparison with _C. subglobisporus_.

The genus _Cyathus_ was originally subdivided into seven groups based on morphological characters (Brodie 1975, 1984). Brodie’s classification system is not supported by phylogenetic analysis of molecular data, and the recognition of only three infrageneric groups (Ollum, Pallidum, and Striatum) was established based on morphological and molecular data (Zhao et al. 2007). In this study, the combined ITS and LSU phylogenies indicate that _C. subglobisporus_ belongs to the Striatum group.
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Fig. 4  Cyathus subglobosporum (from holotype) a. Fructing body in top view showing peridioles and plications on the inner surface of peridium; b. fructing body in side view showing shaggy hairs; c. opening changes with the development of fructing bodies; d. basidiospores. — Scale bars: a = 1.5 mm; b = 1.8 mm; c = 2 mm; d = 11 μm.

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