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RESEARCH ARTICLE

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Diversity and systematics of the sequestrate genus *Octaviania* in Japan: two new subgenera and eleven new species

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Key words

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taxonomy

Abstract The sequestrate fungi of Japan, including truffle and truffle-like fungi, have not been well characterized but are potentially diverse. We investigated the diversity and phylogeny of Japanese *Octaviania* specimens using a multifaceted approach including scanning and transmission electron microscopy as well as analysis of nuclear ribosomal DNA (ITS and LSU) and EF-1α (tef1) sequences. Phylogenetic analyses indicate that the genus *Octaviania* is divided into three major clades, and that there are at least 12 species-level lineages in Japan. Accordingly, we describe two new subgenera, *Parcaea* and *Fulvoglobus*, and eleven new species. Subgenus *Parcaea* accommodates four highly divergent, but macromorphologically almost indiscernible cryptic species. We discuss not only the diversity and species delimitation within the genus *Octaviania* but also the phylogeography of the Japanese taxa and their relatives.

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INTRODUCTION

Species in the sequestrate, truffle-like genus *Octaviania* Vittad. (orthographic variant: *Octavianina* Kuntze (Gams 1999); *Boletaceae*, *Boletales*) are characterized by a marbled gleba and dextrinoid or non-amyloid basidiospores with coarse, conical to pyramidal ornamentation. Like many other sequestrate fungi, *Octaviania* species form ectomycorrhizas with woody plants (Chu-Chou & Grace 1983, Frank et al. 2006). Vittadini erected *Octaviania* in 1831 but the genus was broadly interpreted by subsequent authors, resulting in a chaotic taxonomy with competing generic concepts (e.g., Lloyd 1922, Zeller & Dodge, 1936, Cunningham 1944, Cribb 1958). Pegler & Young (1979) thoroughly revised the genus and clarified the taxonomic concepts within the group, but the true diversity within *Octaviania* is still unresolved. Historically, nearly 100 infrageneric taxa have been described at one time or another in *Octaviania*. Many of them were transferred to other sequestrate genera such as *Arcangeliella*, *Gymnomyces*, *Hydnangium*, *Melanogaster*, and *Stephanospora* (e.g., Pegler & Young 1979, Trappe et al. 2002, Vidal 2004), and some others were synonymized into different *Octaviania* species (Lenne 2005). As a result, there are only approximately 15–20 accepted species that fit the current generic concept of the genus.

The evolutionary relationships of the genus with other Agaricomycetes have long been uncertain because of their unique morphology (Thiers 1984). Recent molecular studies of the *Boletales* have placed *Octaviania* within the *Boletaceae* (Binder & Hibbett 2006), but the infrageneric systematics of *Octaviania* has not yet been studied. The well-known type species, *O. asterosperma* Vittad. has been reported worldwide (e.g., Vittadini 1831, Massee 1889, Coker & Couch 1928, Zeller & Dodge 1936, Hawker 1954, Moreno et al. 1991, Cázares et al. 1992, Tao et al. 1998, Montecchi & Sarasini 2000), but morphological diversity among collections from different regions indicates that this may not be a truly cosmopolitan species. Intensive studies in one region using both morphological and molecular techniques may reveal greater species diversity of the genus and provide a more precise understanding of its biogeography.

Three *Octaviania* species have so far been reported from Japan: *O. columellifera* Kobayasi (Kobayasi 1937), *O. asterosperma* (Kobayasi et al. 1987, Yoshimi & Doi 1989), and *O. tuberculata* Hesse (Yoshimi & Doi 1989). However, a recent study by Orihara et al. (2010) revealed that *O. asterosperma* sensu Yoshimi & Doi was a misidentification of *O. columellifera*, and they excluded *O. columellifera* from *Octaviania* and placed it into a new genus, *Heliogaster.* Another doubtful record of *O. asterosperma* from Japan was based on an insufficiently described specimen (Kobayasi et al. 1987) and is treated here as *Octaviania* sp.

The only remaining Japanese *Octaviania* species, *O. tuberculata*, was collected in a subtropical angiosperm forest in Amamioshima Island in the Ryukyu Archipelago (Yoshimi & Doi 1989) and has not been subsequently reported. There are crucial morphological differences between the Japanese *O. tuberculata* described by Yoshimi & Doi (1989) and the authentic *O. tuberculata* from Europe, suggesting that this species report should be re-examined. Our recent intensive collecting of Japanese sequestrate fungi has yielded many unique fruitbodies that do not fit descriptions of any known *Octaviania* species, suggesting that the genus has greater diversity in this region than expected.

The aims of this study are: 1) clarify the diversity and the phylogenetic relationships of *Octaviania* in Japan; and 2) taxonomically evaluate each resulting species using a comprehensive approach that includes morphological, molecular, ecological, and phylogeographic evidence. We therefore conducted

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phylogenetic analyses and molecular comparison using the ITS1-5.8-ITS2 (ITS) region and large subunit (LSU) of nuclear rDNA (nrDNA) and the elongation factor-1α (EF-1α or tef1) gene datasets as well as macro- and micromorphological comparative observations including scanning electron microscopy (SEM) and transmission electron microscopy (TEM). In this publication we present a key to all known Japanese *Octaviania* species and we propose 11 new *Octaviania* species and two new subgenera (*Parcaea* and *Fulvoglobus*). We also propose a substitute name for *O. nigrescens* (Zeller) Singer & A.H. Sm., which is a later homonym of *O. nigrescens* J.W. Cribb.

MATERIALS AND METHODS

Taxon sampling and macro- and microscopic characterization

Fresh basidiomata were collected at various locations throughout Japan. After macro- and micromorphological observation and DNA extraction, the collected basidiomata were air-dried or freeze-dried for later examination. Dried herbarium specimens were obtained from the National Museum of Nature and Science, Tokyo (TNS), Kanagawa Prefectural Museum of Natural History (KPM), the Oregon State University Herbarium, Oregon, USA (OSC), the New York Botanical Garden, New York, USA (NY), and the Royal Botanic Gardens, Melbourne, Australia (MEL). The *Octaviania* specimens collected from Japan were grouped into 9 lineages (i.e., the *Octaviania* lineages A–I) based on morphological and ecological features. For standard light microscopy and differential interference contrast (DIC) microscopy, hand-cut sections of both fresh and dried specimens were mounted in water, 3 % KOH, lactic acid, lactoglycerol, lactophenol-cotton blue (LCB), or 1 % phloxine B aqueous solution. Ectomycorrhizas of *Octaviania* species were collected and examined when they were connected to basidiomata via rhizomorphs. Colours are described in general terms. Spore and spore ornament dimensions were measured based on 50 randomly selected spores unless otherwise noted. Since Orihara et al. (2010) noted that *Octaviania* basidiospore morphology (including spore ornament dimensions) is easily affected by acidic or alkaline solutions, the basidiospores and their ornaments were measured in water. The measurement was done using ImageJ v. 1.4.3 (http://rsbweb.nih.gov/ij/) and excluded both ornamentation and hilar appendages. The 95 % prediction interval of diameter of the basidiospores, shown without parentheses, was calculated as: (the endpoints of the 95 % prediction interval) = $M \pm t \cdot \mathrm{SD}\sqrt{1+1/n}$ (where M = mean value; $t = t$ value under a Student's t-distribution with n-1 degrees of freedom (P = 0.05); SD = standard deviation; n = 50). The actual range in the measurement is shown in parentheses, but is omitted when it is the same as the value of the 95% prediction interval. Average size of basidia was calculated based on 15 randomly selected basidia unless otherwise noted.

SEM was carried out according to Maekawa (1987). TEM protocols for fixation, post-fixation, dehydration, resin impregnation, and observation were those of Shimomura et al. (2007). Specimens examined in this study were deposited in TNS or KPM.

DNA extraction, PCR amplification and sequencing

DNA was extracted from fresh or dried basidiomata using the FTA Classic Card or the Indicating FTA Cards (Whatman International Ltd, Maidstone, England) according to the manufacturer's instructions. PCR amplification of the ITS region and a part of the nLSU of the rDNA was carried out using one or two prepared FTA discs 2 mm diam, Ampdirect Plus and Nova *Taq* (Shimadzu Corporation, Kyoto, Japan) according to the manufacturer's instructions. The primer pairs for PCR were ITS1F (Gardes & Bruns 1993) / ITS4 (White et al. 1990) or ITS4B (Gardes & Bruns 1993), ITS1F / ITS2 (White et al. 1990), and/or ITS3 (White et al. 1990) / ITS4F for the ITS region, LR0R / LR5 (Vilgalys & Hester 1990) for the nLSU, and EF1-983F / EF1-2218R or EF1-1567R (Rehner & Buckley 2005) for EF-1α. Reactions were performed on a Astec Program Temp Control System PC-812 (Astec, Fukuoka, Japan) as follows: initial incubation at 95 °C for 10 min; in ITS amplification, a subsequent step of 10–12 cycles at 94 °C for 30 s, 60 °C for 60 s (decreasing 1 °C per cycle in the last 5 cycles), and 72 °C for 60 s (extending 1 s per cycle in the last 5 cycles), followed by 25 cycles at 94 °C for 30 s, 55 °C for 60 s, and 72 °C for 66 s (extending 1 s per cycle; thus the final elongation time is 90 s); in nLSU amplification, 35 cycles at 94 °C for 30 s, 50 °C for 60 s, and 72 °C for 90 s (extending 1 s per cycle in the last 30 cycles), followed by 5 cycles at 94 °C for 30 s, 50 °C for 60 s, and 72 °C for 120 s; and in EF-1α, 10 cycles at 94 °C for 30 s, 65 °C for 60 s (decreasing 1 °C per cycle), and 72 °C for 90 s, followed by 30 cycles at 94 °C for 30 s, 55 °C for 60 s, and 72 °C for 91 s (extending 1 s per cycle; thus the final elongation time is 90 s). A final elongation step of each run was at 72 °C for 7 min. All amplified PCR products were cleaned with ExoSAP-IT (USB Corporation, Cleveland, Ohio, USA) using the manufacturer's instructions. Bidirectional sequencing of the PCR products was performed using BigDye v. 3.1 terminator cycle sequencing kit (Applied Biosystems, Foster City, California, USA) with the following protocol: initial denaturation at 94 °C for 1 min, 94 °C for 10 s (denaturation), 55 °C (ITS) or 50 °C (nLSU and EF-1α) for 5 s (annealing), and 60 °C for 4 min (elongation). Primer pairs used for sequencing reactions were the same as above for ITS and nLSU rDNA whereas for EF-1α sequencing the primer EF1-2212R was used instead of EF1-2218R. Sequencing was conducted on an ABI 3130 Genetic Analyser or an ABI 3730xl DNA Analyser (Applied Biosystems, Foster City, California, USA). Sequences were edited with Sequence Scanner v. 1.0 (Applied Biosystems, Foster City, California, USA), BioEdit v. 7.0.9 (Hall 1999), and Clustal X v. 1.83 (Thompson et al. 1997).

Phylogenetic analysis

Specimens used for phylogenetic analyses are listed in Table 1 and 2. A total of 77 sequences identified to the species level, including 12 sequences from GenBank/DDBJ/EMBL, were used for nLSU analyses. Sequences of *Tylopilus chromapes* (JN378517) and *Austroboletus* spp. (Table 2) were used as outgroups for the *Octaviania-Leccinum-Leccinellum-Chamonixia-Rossbeevera* clade. GenBank sequences of *Octaviania nigrescens* (HQ328787–HQ328788) and *O. tasmanica* (HQ328790) were identical to those used in this study, but they were considerably shorter (< 624 bp long) and were thus not used in the analyses. For EF-1α analyses, a total of 56 sequences were included and *T. chromapes* JN378457 was selected as the outgroup taxon. For the combined nLSU and EF-1α phylogeny, a total of 65 sequences identified to the species level were selected based on BLAST search and downloaded from GenBank. For the ITS phylogenetic network analyses, sequences of *O. asterosperma* EU784378–EU784379 and *Octaviania* sp. EU414289–EU414290 were retrieved from the database. Multiple sequence alignment was performed using Clustal X and the data were manually adjusted in SeaView (Galtier et al. 1996). Gaps were treated as 'missing' data for all analyses. All alignments and Bayesian trees generated from each alignment are deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S11908).

Bayesian analyses were conducted with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). For the nLSU dataset, the general time reversible model under the assumption of a discrete gamma-shaped rate variation with a proportion of invariable

Table 1 Newly obtained sequences of *Octaviania*, *Leccinum*, *Leccinellum*, *Chamonixia*, *Rossbeevera*, *Turmalinea* and outgroup species. The nLSU sequences excluded from the combined analyses are indicated as asterisks (*). The nLSU sequence of *Rossbeevera eucyanea* (HQ693879) was retrieved from GenBank (**).

Taxon	Locality	Voucher No.	GenBank No.		
			ITS	nLSU	EF-1α
Octaviania lineage A-1	Japan, Kagoshima Pref., Amami-oshima Isl.	KPM-NC-0017748	JN257985	JN378459	JN378403
Octaviania lineage A-1	Japan, Kagoshima Pref., Amami-oshima Isl.	KPM-NC-0017749	JN257986	JN378460	JN378404
Octaviania lineage A-1	Japan, Mie Pref., Kameyama-shi	KPM-NC-0017750	JN257987	JN378461	JN378405
Octaviania lineage A-1	Japan, Hyogo Pref., Shiogahara	KPM-NC-0017751	N257988	JN378462	JN378406
Octaviania lineage A-1	Japan, Hiroshima Pref., Hiroshima-shi, Higashi-ku, Hiroshima Prefecture Ryokka-Center	KPM-NC-0017752	JN257989	JN378463	JN378407
Octaviania lineage A-1	Japan, Oita Pref., Saiki-shi, Shiroyama	KPM-NC-0017745	JN257990	JN378464	JN378408
Octaviania lineage A-2	Japan, Kyoto Pref., Mt Hiei	KPM-NC-0017763	JN257991	JN378465	JN378409
Octaviania lineage A-2	Japan, Kyoto Pref., Mt Ponpon	KPM-NC-0017764	JN257992	JN378466	JN378410
Octaviania lineage A-2	Japan, Aichi Pref., Okazaki-shi, Ohata-cho, Nishiyama	KPM-NC-0017765	–	JN378467*	–
Octaviania lineage A-2	Japan, Oita Pref., Saiki-shi, Ume-Oaza, Shigeoka	KPM-NC-0017767	JN257993	JN378468	JN378411
Octaviania lineage A-2	Japan, Oita-shi, Oaza, Hisado, Yayama	KPM-NC-0017768	JQ619186	JN378469	JN378412
Octaviania lineage A-2	Japan, Nara Pref., Nara-shi, near Mt Kasuga	KPM-NC-0018020	JQ619166	–	–
Octaviania lineage A-3	Japan, Tottori Pref., Hie Shirine	KPM-NC-0017770	JN257994	JN378470	JN378413
Octaviania lineage A-3	Japan, Kyoto Pref., Nanzen-ji Shrine	KPM-NC-0017771	JN257995	JN378471	JN378414
Octaviania lineage A-3	Japan, Kyoto Pref., Kyoto-gyoen	KPM-NC-0017773	JN257996	JN378472	JN378415
Octaviania lineage A-3	Japan, Ehime Pref., Futami-cho	KPM-NC0017724	JQ619167	JQ619187	–
Octaviania lineage A-4	Japan, Nara Pref., Nara-shi, Nara Park	KPM-NC-0017776	JN257997	JN378473	JN378416
Octaviania lineage A-4	Japan, Nara Pref., Nara-shi, Nara Park	KPM-NC-0018026	JQ619169	–	–
Octaviania lineage A-4	Japan, Nara Pref., Nara-shi, near Mt Kasuga	KPM-NC-0018021	JQ619168	JQ619190	JQ619184
Octaviania lineage B	Japan, Hyogo Pref., Akou-shi	KPM-NC-0017778	–	JN378474*	–
Octaviania lineage B	Japan, Kyoto Pref., Kyoto Botanical Garden	KPM-NC-0017780	–	JN378475	JN378417
Octaviania lineage B	Japan, Okayama Pref., Mt Minagasen	KPM-NC-0017782	–	JN378476	JN378418
Octaviania lineage B	Japan, Kyoto Pref., Uji-shi	KPM-NC-0017783	JQ619171	JN378477	JN378419
Octaviania lineage B	Japan, Nara Pref., Nara-shi, Mt Kasuga	KPM-NC-0017785	JQ619170	JN378478	JN378420
Octaviania lineage C	Japan, Tokyo, Hachioji-shi	KPM-NC-0017792	–	JN378479	JN378421
Octaviania lineage C	Japan, Kanagawa Pref., Zushi-shi	KPM-NC-0017793	JQ619173	JN378480	JN378422
Octaviania lineage C	Japan, Tottori Pref., Tottori-shi, Ouchidani	KPM-NC-0017795	–	JN378481	JN378423
Octaviania lineage C	Japan, Ehime Pref., Hutami-cho	KPM-NC-0017727	JQ619172	JQ619189	–
Octaviania lineage D	Japan, Tottori Pref., Mt Daisen, Kagamiganaru	KPM-NC-0017798	–	JN378482	JN378424
Octaviania lineage D	Japan, Akita Pref., near Lake Towada	KPM-NC-0017797	JQ619174	JN378483	JN378425
Octaviania lineage D	Japan, Tottori Pref., Mt Daisen	KPM-NC-0017806	–	JN378484	JN378426
Octaviania lineage D	Japan, Tottori Pref., Yazu-cho	KPM-NC-0017810	JQ619175	JN378485	JN378427
Octaviania lineage D	Japan, Okayama Pref., Kagamino-cho	KPM-NC-0017812	–	JN378486	JN378428
Octaviania lineage E	Japan, Kagoshima Pref., Amami-ohshima Isl.	KPM-NC-0017813	JQ619176	JN378487	JN378429
Octaviania lineage F	Japan, Miyagi Pref., shichigasyuku-cho	KPM-NC-0017814	–	JN378488	–
Octaviania lineage F	Japan, Kanagawa Pref., Minami-ashigara-shi	KPM-NC-0017829	JQ619177	JQ619188	–
Octaviania lineage G	Japan, Hokkaido, Kamikawa-cho, Mt Daisetsu	KPM-NC-0017824	JQ619178	JN378489	JN378430
Octaviania lineage G	Japan, Hokkaido, Kamikawa-cho, Mt Daisetsu	KPM-NC-0017823	–	JQ619185	–
Octaviania lineage H	Japan, Okinawa Pref., Ishigaki Isl., Mt Omoto	KPM-NC-0017818	JQ619179	JN378490	JN378431
Octaviania lineage H	Japan, Okinawa Pref., Ishigaki Isl., Mt Omoto	KPM-NC-0017819	JQ619180	JN378491	JN378432
Octaviania lineage I	Japan, Toyama Pref., Nakashingawa-gun, Teteyama-cho	KPM-NC-0017822	JQ619182	JN378492	JN378433
Octaviania lineage I	Japan, Hyogo Pref., Kobe-shi, Kita-ku	KPM-NC-0017849	JQ619183	–	–
Octaviania lineage I	Japan, Kyoto Pref., Sonobe-cho	KPM-NC-0017820	JQ619181	–	–
Octaviania tasmanica	Australia, Victoria, East Gippsland, Alpine National Park, Black Mountain Road, Rams Horn track	Trappe 18104	–	JN378493	JN378434
Octaviania tasmanica	Australia, Tasmania, Avre River Picnic Area, on road to Terhune Airwalk	OSC132097	–	JN378494	JN378435
Octaviania tasmanica	Australia, Tasmania, Mount Field, Mt Field Nat. Park	MEL2341996	–	JN378495	JN378436
Octaviania tasmanica	Australia, NSW, Southern Tablelands, off Nungatta Rd., 3.5 km from junction with Imlay Rd, off small track to east	MEL2128484	–	JN378496	JN378437
Octaviania asterosperma	Spain, Sella Covallera	Trappe 23377	JN257998	JN378497	–
Octaviania cyanescens	OR, Lane Co., Lanb Butte south of English Mountain	PNW FUNGI 5603	–	JN378502	JN378438
Octaviania cyanescens	Canada, British Columbia	OSC58498	–	JN378503	JN378439
Octaviania nigrescens sensu Singer & A.H. Sm.	USA, Maine, Tunk Lake, off route 182	MES270	–	JN378498	JN378440
Octaviania sp.	USA, Florida, Wakulla Co., Skipper Bay road, St Marks NW refuge	OSC131925	–	JN378499	JN378441
Octaviania sp. (labeled as '*O. asterosperma*')	USA, Iowa, Story County, YMCA woods, Ames	KPM-NC-0017827 (RH30)	–	JN378500	JN378442
Octaviania sp. (labeled as '*O. asterosperma*')	USA, Minnesota, Forestville State Park.	KPM-NC-0017828 (RH1181)	–	JN378501	JN378443
Rosbeevera eucyanea	Japan, Mie Pref., Kameyama-shi	TMI-40253	–	HQ693879**	JN378444
Rossbeevera westraliensis	Australia, Western Australia, Beedelup National Park, Anzac Rd	OSC61480	–	JN378505	JN378445
Rossbeevera vittatispora	Australia, New South Wales, Genoa National Park, junction Imlay road and Nungatta road	OSC61484	–	JN378506	JN378446
Rossbeevera vittatispora	Australia, New South Wales, c. 5 km south of the junction between Princess highway and Eden road	TO-AUS-46	–	JN378507	JN378447
Leccinum aff. *duriusculum*	Japan, Hyogo Pref., Uwano	KPM-NC-0017830	–	JN378510	JN378448
Leccinellum aff. *griseum*	Japan, Hyogo Pref., Uwano	KPM-NC-0017831	–	JN378508	JN378449
Leccinellum aff. *griseum*	Japan, Tottori Pref., Tottori-shi, Ouchidani	KPM-NC-0017832	–	JN378509	JN378450
Leccinum sp. (sect. *Leccinum*)	Japan, Iwate Pref., Appi	KPM-NC-0017838	–	JN378512	JN378452
Leccinum sp. (sect. *Leccinum*)	Japan, Iwate Pref., Appi	KPM-NC-0017839	–	JN378513	JN378453
Leccinum versipelle	UK, Scotland, Aberdeenshire, Dennet Oakwood National Nature Reserve	KPM-NC-0017833	–	JN378514	JN378454
Leccinum scabrum	Japan, Iwate Pref., Appi	KPM-NC-0017837	–	JN378511	JN378451
Leccinum scabrum	UK, Scotland, Aberdeenshire, Burn O' Vat	KPM-NC-0017840	–	JN378515	JN378455
Leccinum vulpinum	UK, Scotland, Aberdeenshire, near Mar Lodge Estate	KPM-NC-0017834	–	JN378516	JN378456
Tylopillus chlomapes	Japan, Tottori Pref., Yazu-cho	KPM-NC-0017835	–	JN378517	JN378457
Austroboletus subvirens	Japan, Tottori Pref., Tottori-shi	KPM-NC-0017836	–	JN378518	JN378458

Table 2 DNA sequences retrieved from GenBank.

Taxon	Locality	Voucher No.	GenBank No.	
			ITS	nLSU
Octaviania sp. (= *Octaviania* lineage A-2)	Japan, Aichi Pref., Okazaki-shi	Orihara 227	EU414289	EU414290
Octaviania sp. (= *Octaviania* lineage A-2)	Japan, Nara Pref., Nara-shi, Mt Kasuga	Orihara 231	EU414291	EU414292
Octaviania asterosperma	UK, South Hampshire	RBG Kew K(M) 102511	EU784378	–
Octaviania asterosperma	UK, Caernarvonshire	RBG Kew K(M) 81259	EU784379	–
Octaviania asterosperma	Germany: Bavaria	Strain: Octa 1	–	DQ534619
Chamonixia caespitosa	USA	OSC 117571	–	EU669260
Chamonixia caespitosa	USA	Trappe 10517	–	EU669427
Chamonixia caespitosa	Germany	92/83	–	AF336245
Leccinellum carpini (syn.: *Leccinum pseudoscabrum*)	Germany	930808	–	AF139691
Leccinellum carpini (syn.: *Leccinum pseudoscabrum*)	Netherlands, Breukelen	hdb065	–	AF454588
Rossbeevera eucyanea	Japan, Mie Pref., Kameyama-shi	TMI-40253	–	HQ693879
Austroboletus mucosus	N/A	TH6300	–	AY612798
Austroboletus gracilis	USA, MA	Strain: 112/96	–	DQ534624
Austroboletus niveus	New Zealand	M / Strain: 312	–	DQ534622
Austroboletus novae-zelandiae	New Zealand	PDD7252	–	DQ534623

sites (GTR+I+G) was estimated as the best-fit likelihood model with MrModeltest 2.3 (Nylander 2004). The EF-1α dataset was further partitioned by codons and introns, and the best-fit likelihood models were estimated for each partition. For the 1st, 2nd, and 3rd codons and introns, HKY+I+G, F81+I, GTR+G, and GTR+G models were applied for the phylogenetic inference, respectively. For the combined analyses, the incongruence-length difference (ILD) test was conducted on PAUP* 4.0b10 beforehand to test compatibility of phylogenetic signals between the two concatenated DNA regions (Farris et al. 1995). We subsequently compared resultant tree topologies directly to confirm the compatibility. Posterior probabilities (PP) were approximated by the Metropolis-coupled Markov chain Monte Carlo method (Geyer 1991). Two parallel runs were conducted with one cold and seven heated chains each for 5 000 000 generations, starting with a random tree. Temperature of the seven heated chains was set to 0.15. Trees were saved to a file every 100th generation. We judged that the two runs reached convergence when the average SD of split frequencies continuously dropped below 0.01. Trees obtained before reaching convergence were discarded as the burn-in, and the remaining trees were used to calculate a 50 % majority consensus topology and to determine PP values for individual branches.

The nLSU and combined nLSU and EF-1α datasets were further analysed by the maximum likelihood (ML) method with RAxML v. 7.2.6 (Stamatakis 2006). The best-fit ML tree was inferred under the GTR+I+G model. The combined dataset was partitioned in the same way as in the Bayesian analysis, and different α-shape parameters, GTR rates, and empirical base frequencies were assigned to each partition. To check statistical support for the resultant tree topology, the rapid bootstrap option was used under the automatically assigned, GTA+CAT model, setting the number of replicates to 1 000.

The phylogenetic network analysis of the ITS dataset of one *Octaviania* lineage (lineage A) was conducted with SplitsTree 4 (Huson & Bryant 2006). Networks were constructed by the NeighborNet method under the setting of distance estimation to uncorrected P value and of ambiguous states of nucleotides as average states. The resultant networks were visualized with the ClusterNetwork method (Huson & Rupp 2008). Three *O. asterosperma* sequences (EU784378–EU784379 and JN257998) were used as outgroups.

RESULTS

Phylogenetic analyses of the nLSU dataset

The final aligned nLSU dataset was 954 bp long. In the Bayesian inference, the two parallel MCMC runs converged after c. 930 000 generations. Accordingly, the first 9 300 trees in each run were discarded as the burn-in and the remaining 81 402 trees (representing c. 4.07M generations) were used to calculate a 50 % majority consensus tree and to determine PPs (Fig. 1). Likelihoods (ln L) of the best states for cold chains of the two runs were –4839.62 and –4863.13. Maximum likelihood analysis of the same dataset generated one ML tree (ln L = –4650.068186). Branches that were strongly supported by Bayesian PPs (> 0.95) were also present in the best ML topology. The resulting topology represented 10 infrageneric Japanese lineages that were also represented in the multi-gene analyses (i.e., lineages A-2–A-3 and B–I). The phylogeny recovered the three clades within *Octaviania* (clade A–C). Unfortunately only part of the nLSU sequences (557 bp in total) were successfully obtained in one specimen of the lineage A-4 (KPM-NC0017776). Although it was 99 % identical to another sequence of the lineage A-4 (KPM-NC0018021), the monophyly of the lineage was collapsed and the latter sequence formed a clade with the lineage A-1a with weak statistic supports (PP = 0.84, BS = 66 %). Accordingly, monophyly of the lineages A-1a and A-1b was not recovered in the nLSU analyses. Monophyly of *Octaviania* lineage B sequences was not supported in the Bayesian analysis despite that all the sequences were identical.

Phylogenetic analyses of the EF-1α dataset

Preliminary analyses that included either *Tylopilus chromapes* (JN378457) or *Austroboletus subvirens* (JN378458) as an outgroup produced paraphyly of the *Octaviania* clade. This is likely due to long branch attraction caused by the highly divergent *T. chromapes* and *A. subvirens* sequences so we excluded them and re-analysed a dataset without an outgroup. The final EF-1α dataset was 1 145 bp long and included 55 taxa. In the Bayesian inference, the two MCMC runs converged after c. 590 000 generations. Accordingly, the first 5 900 trees in each run were discarded as the burn-in and the remaining 88 202 trees (representing c. 4.41M generations) were used to calculate a 50 % majority consensus tree and determine PPs (Fig. 1). Likelihoods (ln L) of the best states for cold chains of the two runs were –4370.99 and –4378.93. The final optimization likelihood score was ln L = –4308.079165. Branches that were strongly supported by Bayesian PPs (> 0.95) were also present in the best ML topology.

Bayesian and ML analyses based on EF-1α detected 11 species-level lineages (lineages A-1–A-4, B–E and G–I) among the Japanese collections. EF-1α sequences of *Octaviania* lineage F were not available so that these species were not included in the analyses. Lineages A-1a and A-1b were not differentiated in the EF-1α phylogeny and these two groups formed instead

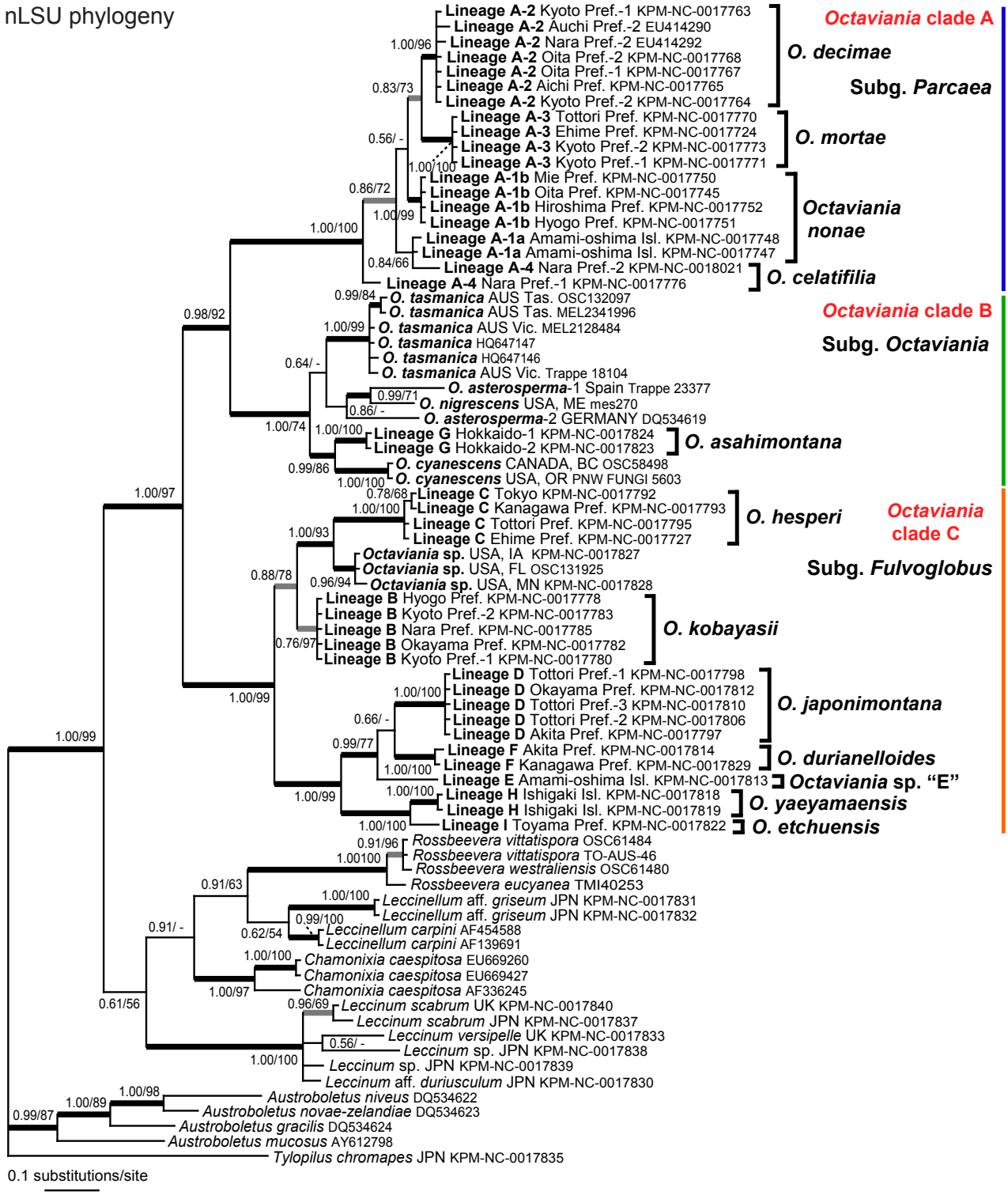


Fig. 1 Bayesian 50 % majority-rule consensus tree of the nLSU rDNA dataset of *Octaviania* and allied genera. Bayesian posterior probabilities (PP) and RAxML bootstrap (BS) values (1 000 replicates; only BS > 50 % are shown) are indicated above or below branches or at nodes as PP/BS. Branches supported by PP greater than 0.95 and BS greater than 70 % are depicted as black thickened lines. Branches supported by either PP less than 0.95 or BS less than 70 % are depicted as grey thickened lines.

a monophyletic clade with strong statistic supports (PP = 1.00, BS = 100 %). As in the nLSU phylogeny, *Octaviania* spp. were divided into three clades (A–C) although monophyly of clade B was not strongly supported by the Bayesian analysis (PP = 0.93).

Phylogenetic analyses of the combined nLSU and EF-1α dataset

The ILD test found no significant incongruence between the nLSU and EF-1α datasets. There was also no topological incongruence in significantly supported clades between the nLSU and EF-1α phylogenies (highlighted with thicked black lines in Fig. 1, 2). Thus, they were combined into a nucleotide alignment that was 2105 bp long. In the Bayesian inference, the two parallel MCMC runs reached convergence after c. 780 000 generations so the first 7 800 trees were discarded as the burn-in. The remaining 84 402 trees (representing c. 4.22M generations) were used to calculate a 50 % majority consensus tree and determine PPs (Fig. 3). Likelihoods (ln L) of the best states for cold chains of the two runs were –9878.35 and –9886.34.

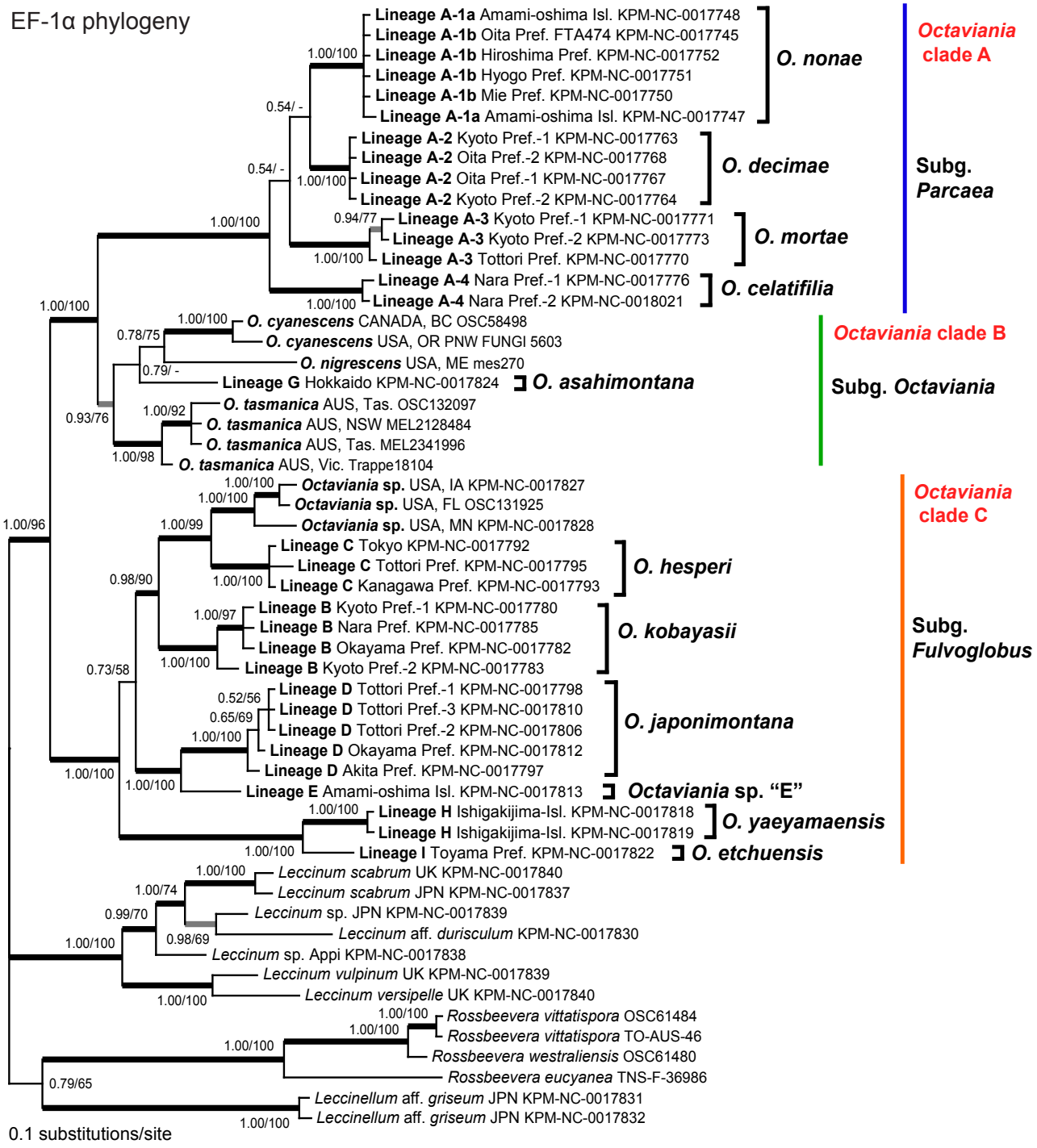


Fig. 2 Bayesian 50 % majority-rule consensus tree of the EF-1α dataset of *Octaviania* and allied genera. Bayesian posterior probabilities (PP) and RAxML bootstrap (BS) values (1 000 replicates; only BS > 50 % are shown) are indicated above or below branches or at nodes as PP/BS. Branches supported by PP greater than 0.95 and BS greater than 70 % are depicted as black thickened lines. Branches supported by either PP less than 0.95 or BS less than 70 % are depicted as grey thickened lines.

Maximum likelihood analysis of the multigene dataset resulted in one ML tree (ln L = –9787.186452). Branches that were strongly supported by Bayesian PPs (> 0.95) were also present in the best ML topology.

Both Bayesian and ML multigene analyses supported monophyly of *Octaviania* and represented 12 phylogenetically divergent infrageneric lineages from Japan (lineages A-1, A-2–A-4 and B–I) that were different from all of the foreign taxa included in the analyses (Fig. 3). The genus *Octaviania* was divided into three phylogenetically distinct clades (clade A–C). Clade A is comprised of four genetically distinct but morphologically and ecologically similar cryptic species (i.e., lineages A-1, A-2, A-3, and A-4). The lineage A-1 diverged further into two lineages that were geographically isolated by a strait with strong statistical supports (i.e., lineages A-1a and A-1b). The relationships among these four lineages, however, were not resolved in both Bayesian and ML analyses. Clade B contains sequences of the type species, *O. asterosperma*, from Germany and Spain (Binder & Hibbett 2006 and this study) as well as several North American and Australian species (i.e., *O. cyanescens* Trappe & Castellano, *O. nigrescens* (Zeller) Singer & A.H. Sm. and *O. tasmanica* (Kalchbr. ex Massee) Lloyd). The two sequences identified as *O. asterosperma* (i.e., DQ534619 and JN378497) actually represent two different species. The only Japanese collection placed within clade B was lineage G, collected on the island of Hokkaido in northern Japan. Clade C contains the

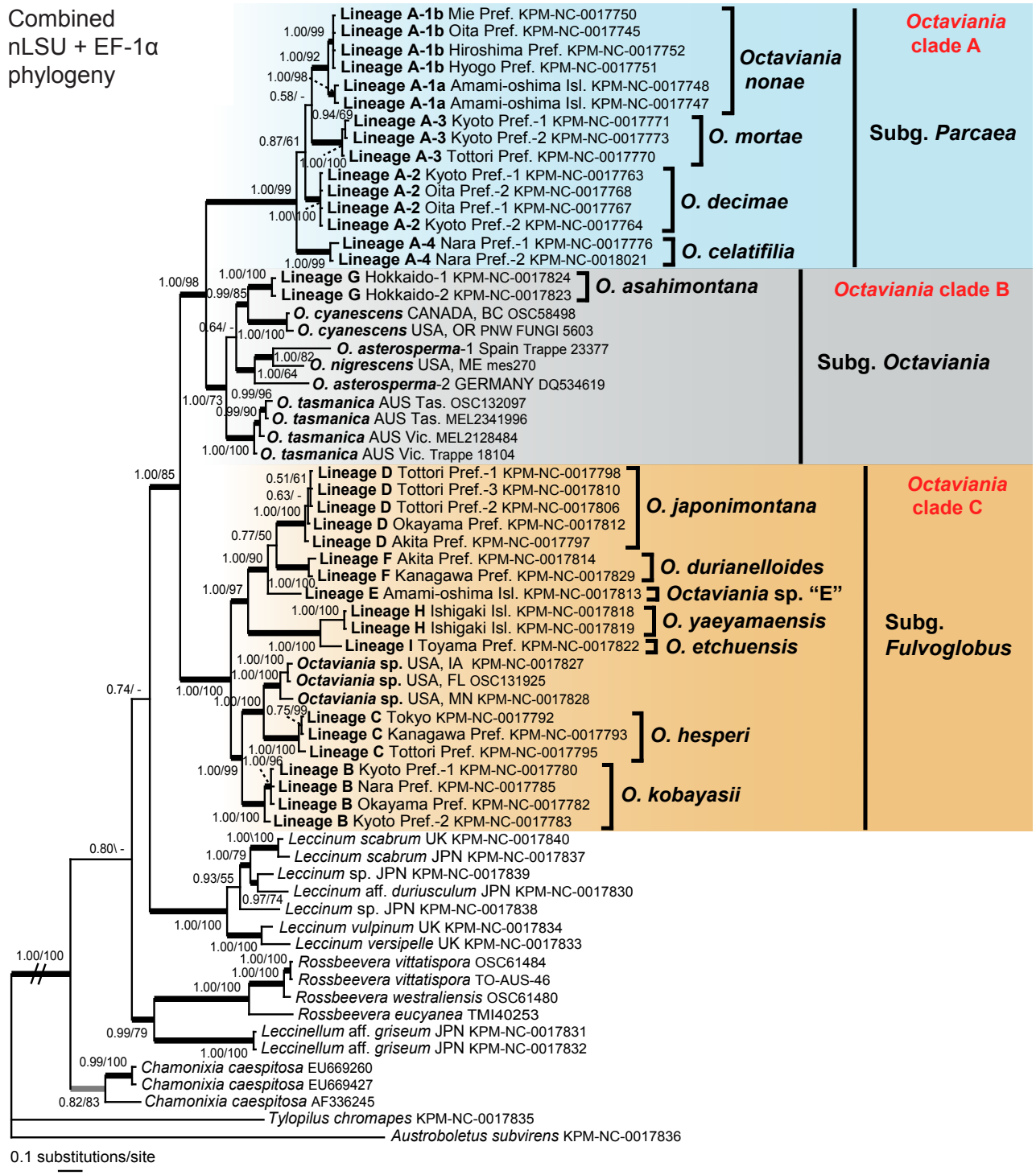


Fig. 3 Bayesian 50 % majority-rule consensus tree of the combined nLSU rDNA and EF-1α (tef1) dataset of *Octaviania* and allied genera. Sequences of *Austroboletus subvirens* and *Tylopilus chlomapes* were used for outgroups. Bayesian posterior probabilities (PP) and RAxML bootstrap (BS) values (1 000 replicates; only BS > 50 % are shown) are indicated above or below branches or at nodes as PP/BS. Branches supported by PP greater than 0.95 and BS greater than 70 % are depicted as black thickened lines. Branches supported by either PP less than 0.95 or BS less than 70 % are highlighted as grey thickened lines.

other Japanese lineages and one unidentified North American species. Although the multi-gene analyses produced a well-resolved phylogeny of the genus *Octaviania*, the relationship between *Octaviania* and its sister group remained unresolved.

ITS sequences of Japanese Octaviania lineages

The ITS nuc-rDNA sequences of the lineages A1–A4 were obtained successfully in most cases (Table 1). Those ITS1-5.8S-ITS2 regions were 468–506 bp long. On the other hand, PCR amplicons of the ITS of the lineages B–I are often unusually long and showed polymorphism within individual specimens. Thus, only limited numbers of ITS sequences were obtained successfully. The total length of their ITS1-5.8S-ITS2 region was 709–1461 bp. The sequences had a long insertion within the ITS2 region that will be analysed and discussed in detail in a subsequent publication. It was difficult to align these insertions because they had considerable numbers of gaps and substitutions. Nevertheless, the ITS sequences excluding the insertion had 98 % similarity within each lineage.

Table 3 Comparison of micro- and macroscopic characters among four cryptic species in the *Octaviania* lineage A. Average dimensions (n = 50) are described in **bold**.

	Octaviania nonae (= lineage A-1)	*Octaviania decimae* (= lineage A-2)	*Octaviania mortae* (= lineage A-3)	*Octaviania celatifilia* (= lineage A-4)
Size of basidiospores (excluding spines; µm)	8.5–(8.9–)**10.9**–13.3(–13.8) × (8–)8.1–**9.8**–11.6(–12.4)	(10–)10.3–**11.8**(–13.4) × (9.3–)**10.8**–12.4(–12.9)	11.1–(11.3–)**13**–14.9(–15.6) × 10.2–(10.4–)**12.1**–14.1(–15.6)	(9.9–)**11.4**–12.9(–13.2) × (9.3–)9.4–**10.8**(–12)–12.1
Size of spiny ornaments (length × width; µm)	1.5–(1.6–)**2.2**–2.9 × 1.1–(1.5–)**2.5**–3.9(–4.4)	1.6–(1.7–)**2.7**–3.7(–4.2) × 1.7–(1.9–)**3.1**(–4.4)–4.5	1.9–**2.8**(–3.6)–3.7 × 1.9–(2–)**3.2**(–4.2)–4.5	1.6–(1.8–)**2.6**–3.6 × 1.7–**2.9**(–4)–4.1
Characteristics	Small basidiospores, small ornamentation and clavate basidia	Medium-sized basidiospores, large ornamentation and clavate basidia	Large basidiospores, large ornamentation and short clavate basidia	Medium-sized basidiospores, large ornamentation and clavate basidia; fruitbody often stained with pale yellow

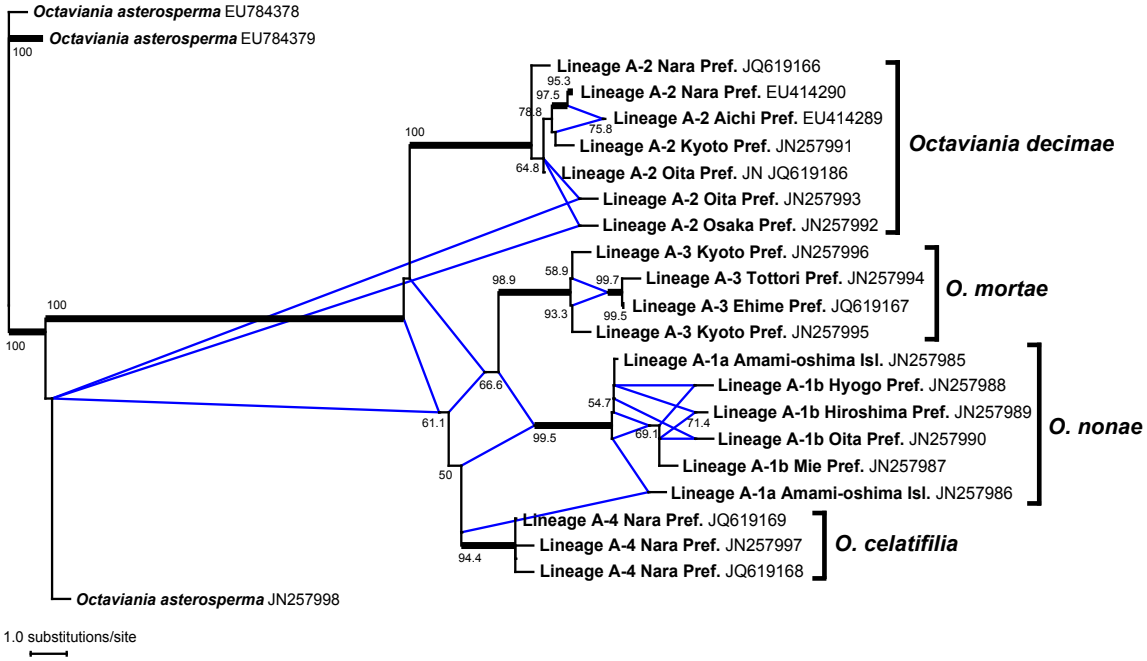


Fig. 4 Phylogram of the cluster network based on the nuclear ITS rDNA dataset of *Octaviania* lineage A1–A4 constructed by the NeighborNet method. *Octaviania asterosperma* sequences (EU784378–784379, JN257998) were used to root the tree. Bootstrap values greater than 50 % are indicated at edges (1 000 replicates). Edges supported by bootstrap values greater than 95 % are highlighted as black thickened lines. Reticulate edges shown as blue lines indicate possible two pathways leading to the descendant lineages in the phylogeny, leaving a possibility of hybridization between lineages.

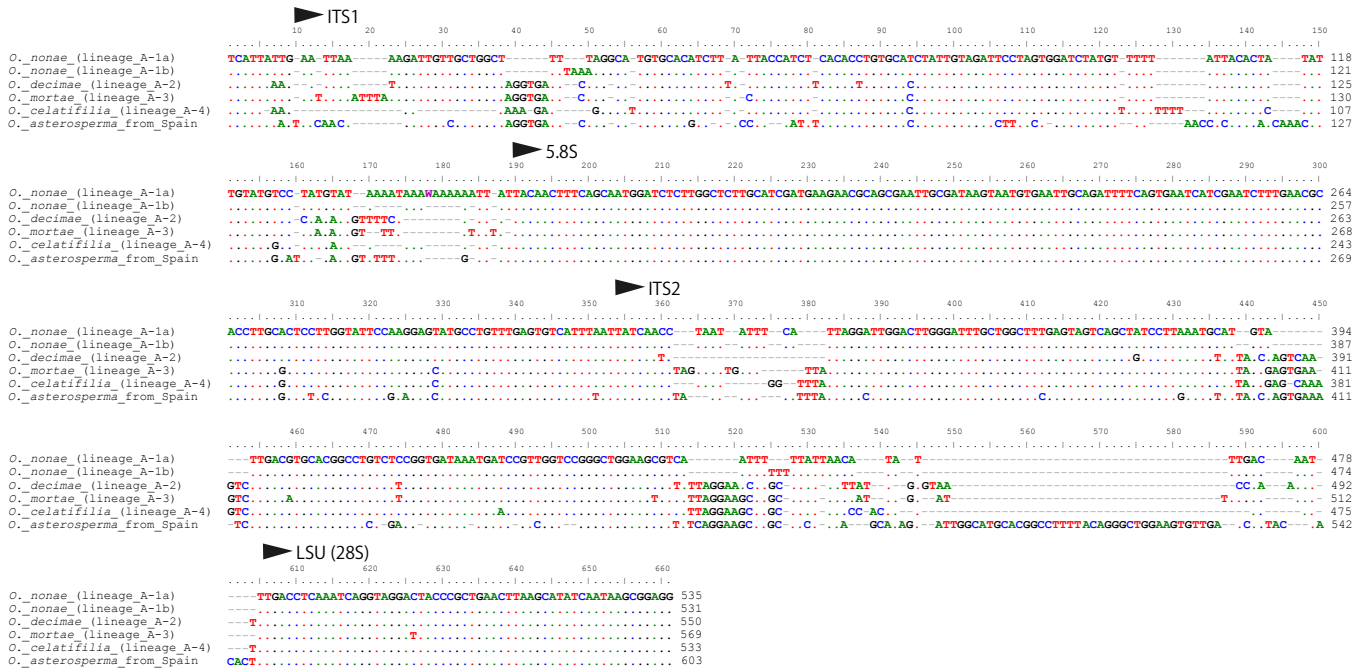


Fig. 5 Comparison of ITS1-5.8S-ITS2 sequences of the *Octaviania* lineages A1a–b and A2–A4. Voucher numbers of the sequences used for the comparison are as follows: *Octaviania* lineage A-1a: JN25986; lineage A-1b: JN257990; lineage A-2: JN257991; lineage A-3: JN257994; lineage A-4: JN257997; *O. asterosperma*: JN257998.

Morphological comparison and ITS network analysis of cryptic species in Clade A

The four cryptic lineages A-1–A-4, which were strongly supported in the EF-1α and the combined analyses (Fig. 2, 3), were further examined based on morphology and ITS phylogenetic analyses. We found that the combination of basidiospore size and spore ornamentation were diagnostic to distinguish lineages A-1, A-2, and A-3 (Table 3, Fig. 7d, 8c, 9c). However, there was no statistically significant difference in both the characters between the lineages A-2 and A-4 (P = 0.05, based on ANOVA, data not shown). Basidia of the *Octaviania* lineage A-3 were significantly shorter than those of the other lineages, suggesting that this character was also useful for species delimitation. There were no clear morphological differences between lineages A-1a and A-1b and analysis of ITS recovered a single monophyletic group. This result was in contrast to the nLSU analysis but congruent with results based on both the EF-1α and multi-gene analyses.

The finally aligned dataset of partial SSU-ITS1-5.8S-ITS2-partial LSU sequences was 735 bp long. To infer not only precise phylogenetic relationships but also traces of recent hybridization among these lineages, we carried out the phylogenetic network analysis using the NeighborNet method. The ITS network (Fig. 4) did not suggest any hybridization among the four extant lineages (A-1–A-4) despite the fact that they are sympatric and occur in the same forest habitat. The four lineages are 88–94 % similar across the ITS1-5.8-ITS2 region in the NCBI BLAST search (Query coverage = 88–100 %; e-value < 1; Fig. 5).

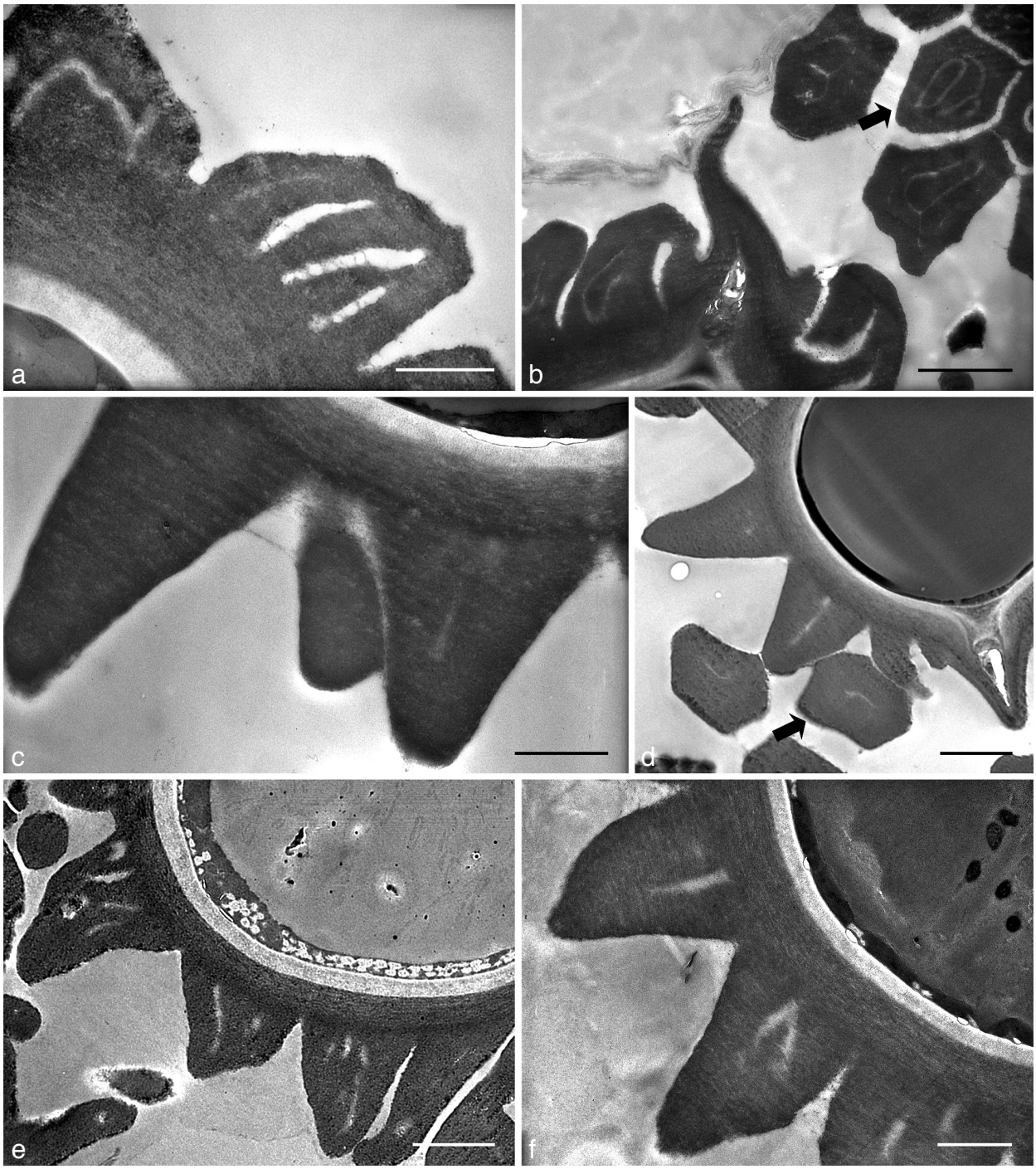


Fig. 6 SEM image of basidiospore ornaments of *Octaviania* spp. a, b. *O. hesperi* (lineage C; KPM-NC0017789): a. vertical section; b. vertical section of the bottom part of the basidiospore and horizontal sections of the ornaments (arrow). — c, d. *O. japonimontana* (lineage D; KPM-NC0017798, holotype). c. Vertical section; d. vertical section of a part of the basidiospore and horizontal sections of the ornaments (arrow). — e. *O. decimae* (lineage A-2; KPM-NC0017757). — f. *O. durianelloides* (lineage F; KPM-NC0017815). — Scale bars: a, c, e, f = 1 µm; b, d = 2 µm.

Ultrastructure of basidiospore ornaments

TEM observation of mature basidiospores of Japanese *Octaviania* showed variation in both the number and shape of cavities inside basidiospore ornaments among the different lineages (Fig. 6, and see individual species descriptions). Although not always distinctive, these cavities were also visible with light microscopy at ×1 000. Under the light microscope, these cavities often look like striations on the surface of spore ornaments, but the TEM photomicrographs showed that they were actually isolated from the surface structure in most cases (Fig. 6b, d). All of the specimens from clade A that we observed had multiple cavities inside their spore ornaments, whereas representatives of some lineages within clades B and C (e.g., lineages D, E, H, and I) had only a single, simple cavity.

TAXONOMY

Octaviania Vittad., Monogr. Tuberac.: 15. 1831, emend. Orihara

Typus generis. *Octaviania asterosperma* Vittad., Monogr. Tuberac.: 17. 1831.

Basidiomata solitary to gregarious, ectomycorrhizal, hypogeous to emergent, mostly less than 5 cm diam, globose, subglobose, reniform or tuberiform, more or less rubbery, sessile or with a rudimentary stipe at the base, surface glabrous, floccose, or occasionally scaly to warty, often discolouring when rubbed or bruised. *Peridium* persistent, context often discolouring when exposed to air, composed of often inflated, more or less interwoven, filamentous hyphae often intermingled with isodiametric to spherical cells especially at maturity and pigmented to colourless, filamentous, granular hyphae; true sphaerocysts absent. *Gleba* whitish at first, becoming brown to blackish at maturity, composed of variously sized, subspherical to hemispherical chambers up to c. 2.5 mm diam, often filled with reddish brown to brown to blackish brown spore mass; each glebal chamber permeated by veins of glebal trama almost concolorous with peridial context to form a marbled gleba. *Sterile base* usually absent to pulvinate, occasionally more or less dendroid, occasionally discolouring when exposed to air, of dense, interwoven, sometimes inflated, filamentous hyphae. *Cystidia* absent. *Hymenium* present but poorly developed in most species, with basidia and interspersed, clavulate to cylindro-clavate basidioles. *Subhymenium* absent or if present then poorly developed. *Basidia* clavulate to cylindro-clavate or doliiform, hyaline, 2–4-spored. *Basidiospores* globose to ellipsoid, thick-walled, more or less dextrinoid, non-amyloid, covered with large, thick-walled, pyramidal to conical ornaments that are polygonal at the base but in some species several spore ornaments adhering to form irregular ridges, with one to several cavities inside ornaments; ornaments usually expand and elongate when soaked in alkaline or acidic solutions; perisporium and ectosporium absent or indistinct. *Clamp connections* absent in all tissues.

Octaviania* subgenus *Parcaea Orihara, *subg. nov.* — MycoBank MB563165

Typus subgeneris. *Octaviania nonae* Orihara.

Etymology. The Latin, *Parcae*, is the name of the three goddesses of fate in Roman mythology (= the Fates), metaphorically expressing that the subgenus contains three morphologically similar sister species named after these three goddesses (i.e., *Nona*, *Decima*, and *Morta*).

Basidiomata solitary to gregarious, hypogeous to emergent, mostly up to 2.5 cm diam, subglobose, depressed-globose, tuberiform or reniform, often with white to whitish rhizomorphs at the basal rudimentary stipe, surface glabrous, white to dirty white occasionally with yellowish to dirty yellow tints, often gradually turning dark grey to black when touched, rubbed or bruised. *Peridium* 0.3–2 mm thick, as the interior concolorous with the surface, hyphae of context filamentous when immature, becoming inflated and thick-walled at maturity. *Gleba* wet, whitish to pale brown when immature, becoming strongly glutinous, fuscous or chocolate-brown to blackish brown at maturity. *Hymenium* and *subhymenium* indistinct, deliquescent at maturity. *Basidia* clavate to clavulate. *Basidiospores* spiny, pale cinnamon to brown, strongly dextrinoid, with pyramidal ornaments that each contain one to several slit-like cavities inside.

Notes — *Octaviania* subg. *Parcaea* is newly proposed to accommodate species belonging to clade A (i.e., *O. nonae*, *O. decimae*, *O. mortae*, and *O. celatifilia*). The subgenus is morphologically characterized by the presence of a thick, white to whitish peridium that gradually discolours to almost black when rubbed or bruised, and the lack of a distinct hymenial layer (i.e., basidia and basidioles are sparsely embedded in a glutinous spore mass). Ecologically, the strong host preference for evergreen plants in the family *Fagaceae* (e.g., *Quercus glauca* Thunb. and *Castanopsis* spp.) is a common feature, suggesting this group is probably of temperate or subtropical origin.

Of all the known species of *Octaviania*, *O. lanigera* Hesse is most morphologically similar to the members of subg. *Parcaea* in having a remarkably thick peridium (c. 1 mm thick) as well as other macroscopic similarities. We have morphologically examined an authentic specimen of *O. lanigera* collected by R. Hesse in Germany in September 1901 (No. NY780603). Basidiospores of *O. lanigera* were more yellowish than those of the species in subg. *Parcaea* described below, and *O. lanigera* spores also had larger spiny ornaments with multiple, distinct cavities inside (2.1–4.6 µm (mean 3.4 µm) wide, n = 30). These characteristics, as well as its association with *Betula*, imply the affinity of the species with *O. asahimontana* Orihara sp. nov. rather than the species in subg. *Parcaea.*

Octaviania nonae Orihara, *sp. nov.* — MycoBank MB563166; Fig. 7; Map 1

Etymology. Latin, *Nona*, is the name of one of the three goddesses of fate in Roman mythology. Nona was the first of the three deities and spun threads of human life, expressing metaphorically that *O. nonae* is a member of the cryptic species group.

Basidiomata solitary or in small clusters, up to 2.2 cm diam but mostly less than 1.5 cm diam, subglobose to depressed globose, firm, rubbery, sessile or with a concolorous, rudimentary stipe at the base, surface glabrous, white to greyish white, gradually becoming dark grey to black when touched, rubbed or bruised, sometimes with sparse mycelial tufts concolorous with the peridial surface, basal rhizomorphs sparse, white, narrow, easily snapping off from the base of basidiomata. *Peridium* 0.3–1.2 mm thick when fresh, 150–500 µm thick in dried specimens, white, context white to cream, not discoloured when cut. *Gleba* pale brownish when immature, becoming fuscous to blackish brown at maturity, composed of various-sized, subspherical to ellipsoidal chambers enclosed by white glebal tramae forming a marbled pattern, glebal chambers filled with a dense, glutinous matrix. *Sterile base* pulvinate, greyish white, often connected to a short, rudimentary stipe, gradually turning blackish when exposed to air. *Ectomycorrhiza* plurifurcate, glabrous, more or less sinuate, light-brown to pale reddish brown. *Odour* unpleasant, a mixture of sweet and dimethyl sulfide smells.

Basidiospores globose to subglobose or broadly ellipsoid, spinose, pale cinnamon, dextrinoid, 8.5–(8.9–)13.3(–13.8) × (8–)8.1–11.6(–12.4) µm, mean 10.9 × 9.8 µm (standard deviation [SD]: 1.18 [length], 0.88 [width]), *Q* = 1–1.32, walls 0.8–2.1 µm thick, spinose ornaments ([length] × [width at the base]) 1.5–(1.6–)2.9(–3) × 1.1–(1.5–)3.9(–4.5) µm, mean 2.2 × 2.5 µm, more or less angular at the base, internal cavi-

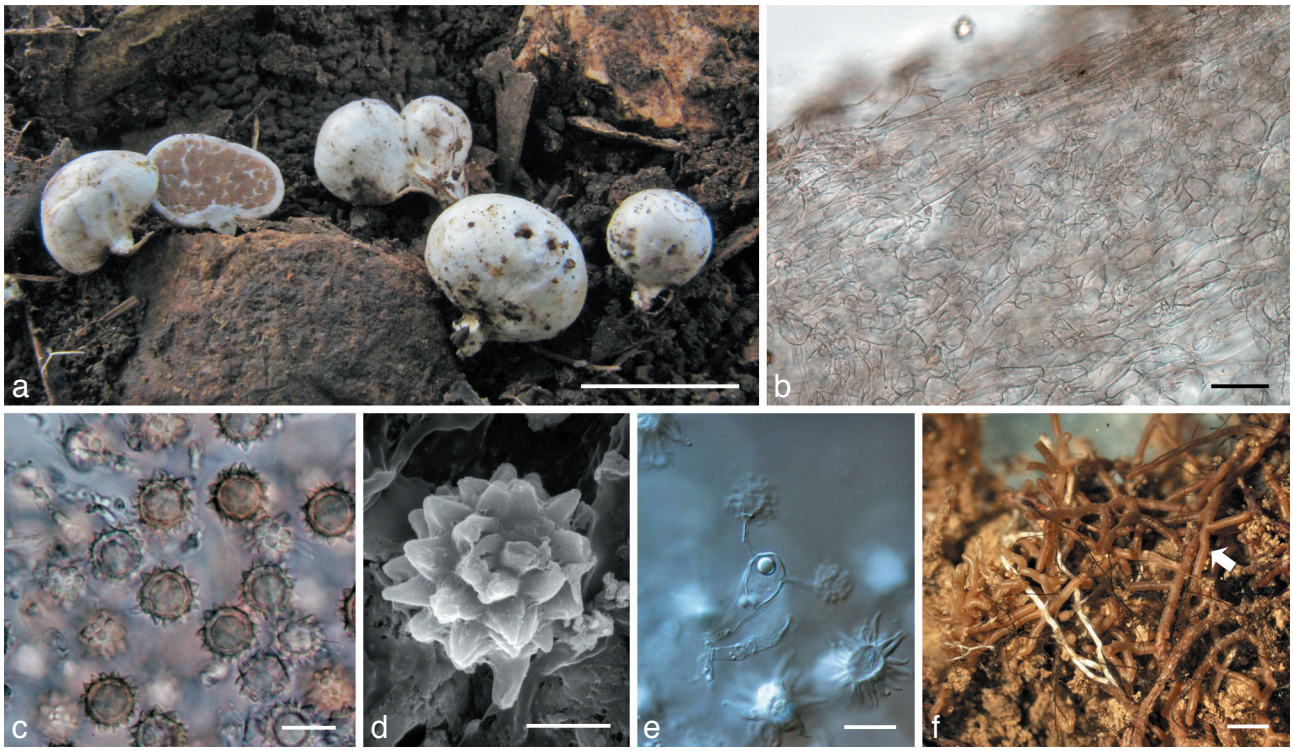


Fig. 7 *Octaviania nonae*. a. Basidiomata (holotype); b. peridium (upper: peridiopellis; lower: context; KPM-NC0017751); c. basidiospores mounted in water (holotype); d. SEM image of basidiospore (holotype); e. basidium mounted in lactoglycerol and observed under DIC microscope (holotype); f. ectomycorrhizas (arrow; holotype). — Scale bars: a = 1 cm; b = 30 µm; c, e = 10 µm; d = 5 µm; f = 1 mm.

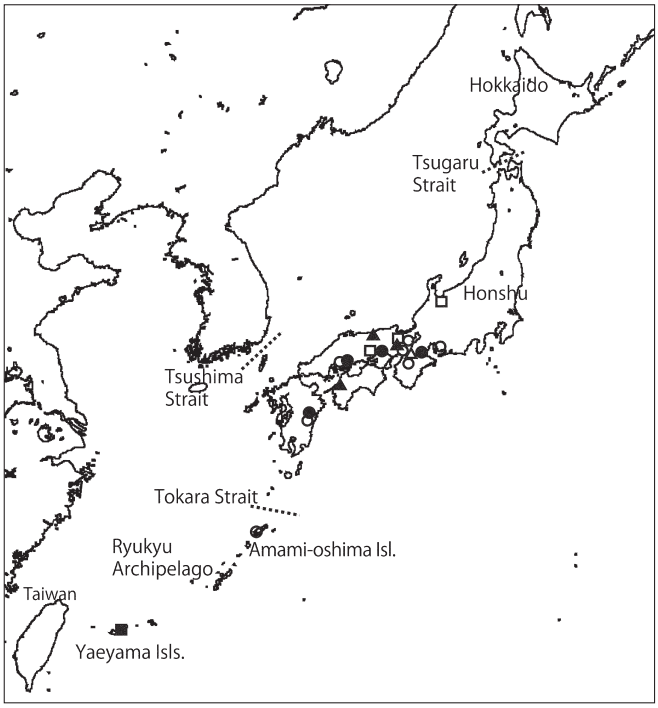
ties of ornaments slit-like in vertical section, labyrinthiform in horizontal section but sometimes indistinct. *Basidia* clavate, hyaline, 2–4-spored, 25–38.5 × 7.5–11 µm, sterigmata up to 9.5 µm long. *Basidioles* clavate, hyaline, almost the same size as basidia. *Hymenia* poorly developed, composed of basidia and interspersed basidioles. Subhymenium absent. *Glebal trama* of parallel, non-inflated, thin-walled (up to 1 µm thick), white, filamentous hyphae 2–5.5 µm broad. *Sterile base* of densely interwoven, more or less inflated, thin-walled (up to 1 µm thick), white to colourless, filamentous hyphae 3–12 µm broad; outermost hyphae mostly dark brown. *Peridium* 300–1200 µm thick (150–550 µm thick in dried specimens): peridiopellis up to 40 µm thick, dark brown, composed of straight, partly inflated, filamentous hyphae 2–12 µm broad forming a cutis, parallel to subparallel to surface, walls up to 1.5 µm thick; peridial context white, of interwoven, inflated, thin- or thick-walled (0.5–2 µm thick) filamentous hyphae 2.3–15 µm broad, hyphae in inner part narrower than in outer part, intermingled with scattered, isodiametric to subspherical cells up to 70 µm diam at maturity. *Clamp connections* absent in all tissues.

Habitat, Distribution & Season — Hypogeous or partially emergent under *Castanopsis sieboldii* (Makino) Hatus, *C. cuspidata* (Thunb. ex Murray) Schottky, and *Quercus glauca*; Honshu, Kyusyu, and Amami-oshima Isl. (Japan); autumn to early spring (October to March).

Holotype. Japan, Kagoshima Pref., Amami-oshima Isl., Yamato-son, north-eastern foot of Mt Yuwandake, under *Castanopsis sieboldii* subsp. *lutchuensis*, 29 Nov. 2008, T. Orihara, KPM-NC0017749 (*Orihara 945*; isotype TNS-F-41401).

Other specimens examined. Japan, **Kagoshima Pref.**, Amami-oshima Isl., Oshima-gun Ukon-son, eastern foot of Mt Yuwandake, 22 Nov. 1988, Y. Doi, TNS-F-11480 (*Yoshimi 7397*) (labelled as '*Octaviania nigrescens*'); the same locality, 22 Nov. 1988, Y. Doi, TNS-F-11479 (*Yoshimi 7401*); Amami-oshima Isl., Yamato-son, north-eastern foot of Mt Yuwandake, under *Castanopsis sieboldii* subsp. *lutchuensis*, 17 Nov. 2007, T. Orihara, KPM-NC0017746 (*Orihara 757*); the same locality, 29 Nov. 2008, T. Orihara, KPM-NC0017748 (*Orihara 944*); Amami-oshima Isl., Tatsugoh-cho, En, under *Castanopsis sieboldii* subsp. *lutchuensis*, 19 Nov. 2007, T. Orihara, KPM-NC0017747 (*Orihara766*); **Hiroshima Pref.**, Hiroshima-shi, Higashi-ku, Hiroshima Prefecture Ryokka-Center, under *Q. glauca*, 23 Oct. 2010, A. Hadano, KPM-NC0017752 (*Orihara1290*); **Hyogo Pref.**, Kobe-shi, Shiogahara, under *C. cuspidata*, 21 Mar. 2010, M. Ohmae, KPM-NC0017751 (*Orihara1157*); the same locality, 21 Nov. 2010, T. Muroi, KPM-NC0017753 (*Orihara1375*); **Mie Pref.**, Kameyama-shi, Seki-cho, under *C. cuspidata*, 31 Oct. 2009, H. Miwa, KPM-NC0017750 (*Orihara1114*); **Oita Pref.**, Saiki-shi, Shiroyama, under *C. sieboldii*, 15 Jan. 2011, T. Orihara, KPM-NC0017745 (*Orihara1362*).

Notes — Thus far we have not found any macroscopic diagnostic character to separate *O. nonae* from other species



Map 1 Geographic distribution of the species of subg. *Parcaea* (= *Octaviania nonae* (●), *O. decimae* (○), *O. mortae* (▲), *O. celatifilia* (△)) and *O. yaeyamaensis* (■), *O. etchuensis* (□).

in subg. *Parcaea*; microscopically the combination of its small basidiospores (mean diam 10.9 µm) and spore ornaments (mean height 2.2 µm) is unique to *O. nonae*. Although *O. nonae* co-occurs with its sister species *O. decimae* at some sites (e.g., the specimens collected from Hiroshima and Oita Prefectures; Map 1), they are nonetheless well-supported as distinct species in analyses of ITS, nLSU, and EF-1α (Fig. 1–4). Maximum identities of the ITS1-5.8S-ITS2 sequence with the other species of subg. *Parcaea* (i.e. *O. decimae*, *O. mortae*, and *O. celatifilia*) in the BLAST search were 88–91 % (Query coverage = 89–94 %).

The ITS and nLSU sequences of *O. nonae* specimens collected from Amami-oshima Island showed slight differences from the other sequences of the species collected from the main island (Honsyu) and Kyusyu (sequence similarity: 97.4 % in ITS and 99.1 % in nLSU [KPM-NC0017748 vs KPM-NC0017750]; e-value = 0; Query coverage = 99–100 %]). This might be due to ancient geological disjunction between the northern Ryukyu Archipelago and the mainland of Japan by the Tokara Strait, which demarcates the border between the Palearctic and Oriental faunal regions. However, it is difficult to examine reproductive ability of their F1 strain because mating tests are not practical. In addition, our analyses show phylogenetic continuity between the two lineages and we therefore currently consider them as a single species.

Octaviania decimae Orihara, *sp. nov.* — MycoBank MB563167; Fig. 6e, 8; Map 1

Etymology. Latin, *Decima*, is the name of one of the three Roman goddesses of fate, who measured the threads of human life, expressing metaphorically that the species is a member of the cryptic species group.

Basidiomata solitary or sparse, up to 2.3 cm diam but mostly less than 1.5 cm diam, subglobose to depressed globose to reniform, firm, rubbery, sessile or with concolorous, rudimentary stipe at the base, surface glabrous, white to greyish white, occasionally with whitish yellow to yellow-brown or more rarely bluish green patches, gradually becoming dark grey to black when touched, rubbed or bruised, rhizomorphs sparse, white, narrow, easily snapping off from the base of basidiomata.

Fig. 8 a–f: *Octaviania decimae*. a. Basidiomata (KPM-NC0017768); b. context of peridium (KPM-NC0017768); c. SEM image of basidiospore (holotype); d. basidiospores mounted in water (KPM-NC0017768); e. basidiospores mounted in LCB after presoaking with Melzer's reagent (KPM-NC0017762); f. 2-spored basidium (KPM-NC0017768). — g, h: "*O. tuberculata*" sensu Yoshimi & Doi (TNS-F-183206). g. Basidiomata; h. basidiospore mounted by lactoglycerol after presoaking with 3 % KOH. — Scale bars: a = 1 cm; b, f = 20 µm; c = 5 µm; d, e, h = 10 µm; g = 5 mm.

Peridium 0.3–1.2 mm thick when fresh, white, context white to cream colour, rarely turning immediately indigo when cut. *Gleba* pale brownish when immature, becoming dark brown to blackish brown at maturity, structure almost the same as *O. nonae*, trama rarely turning immediately indigo when cut. *Sterile base* pulvinate, greyish white, often connected to a short stipe, gradually turning blackish when exposed to air. *Odour* unpleasant, like a mixture of sweet and dimethyl sulfide smells.

Basidiospores globose to subglobose or broadly ellipsoid, spinose, dextrinoid, (10–)10.3–13.4 × 9.3–12.4(–12.9) µm, mean 11.8 × 10.8 µm (SD: 0.78 [length], 0.75 [width]), *Q* = 1–1.23, walls 1–2.3 µm thick, spinose ornaments 1.6–(1.7–)3.7(–4.2) × 1.7–(1.9–4.4)–4.5 µm, mean 2.7 × 3.1 µm, pyramidal, internal cavities of ornaments slit-like in vertical section, labyrinthiform to zonate to cochleae in horizontal section. *Basidia* clavate, hyaline, 2–4-spored, 24–37 × 7.5–11.5 µm, mean 31.5 × 9.9 µm, sterigmata up to 11 µm long. *Basidioles* clavate, hyaline, almost the same size as basidia. *Hymenia* poorly developed, composed of basidia and interspersed basidioles. Subhymenium absent. *Glebal trama* of subparallel, straight or sinuate to strangulated, non-inflated, thin-walled (up to 0.5 µm thick), white, filamentous hyphae 2.2–11.4 µm broad. *Sterile base* of densely interwoven, partly inflated, white to colourless, filamentous hyphae 2–15 µm broad, walls 0.5–1.5 µm thick; in outermost part the hyphae mostly dark brown, narrower. *Peridium* 300–1200 µm thick (200–700 µm thick in dried specimens): peridiopellis up to 80 µm thick, colourless to dark brown, composed of repent, straight, non-inflated, thin-walled (up to 0.5 µm thick), filamentous hyphae 1.7–10 µm broad, subparallel to surface; peridial context white to colourless, of densely interwoven, inflated, thin- or thick-walled (0.5–1.5 µm thick) filamentous hyphae 2–17 µm broad, hyphae in inner part narrower than in outer part, intermingled with scattered, isodiametric to subspherical cells up to 25 µm diam at maturity. *Clamp connections* absent in all tissues.

No distinct morphological and ecological differences from *O. celatifilia* (= *Octaviania* lineage A-4) but c. 90 positions in nuclear ITS rDNA sequence are consistently different between the two species (Fig. 5).

Habitat, Distribution & Season — Hypogeous or partially emergent under *Castanopsis sieboldii*, *C. cuspidata*, and *Quercus glauca*; Honshu, Kyusyu (Japan); early summer to winter (June to January).

Holotype. Japan, Kyoto Pref., Kyoto-shi, Sakyo-ku, south-western foot of Mt Hiei, under *Q. glauca*, 5 July 2008, A. Kajiyama & T. Orihara, KPM-NC0017763 (*Orihara 808*; isotype TNS-F-41402).

Other specimens examined. Japan, **Kyoto Pref**., Kyoto-shi, Sakyo-ku, south-western foot of Mt Hiei, under *Q. glauca*, 17 July 2004, T. Orihara, KPM-NC0017754 (*Orihara 128*); the same locality, 28 June 2004, T. Orihara, KPM-NC0017756 (*Orihara 216*); the same locality, 10 June 2006, T. Orihara, KPM-NC0017760 (*Orihara 394*); the same locality, 3 Sept. 2007, T. Orihara, KPM-NC0017762 (*Orihara 681*); Kyoto-shi, Sakyo-ku, Mt Uryu, 13 June 2004, M Kutsuna, KPM-NC0017755 (*Orihara 147*); the same locality, 3 Nov. 2007, H. Sasaki, KPM-NC0017757 (*Orihara 747*); Kyoto-shi, Saikyo-ku, Mt Ponpon, in *Q. glauca* and *Castanopis* forest, T. Matsumiya, KPM-NC0017764 (*Orihara 1121*); **Nara Pref**., Nara-shi, Mt Kasuga, 11 Dec. 2004, T. Orihara, KPM-NC0015344 (*Orihara 231*); the same locality, 11 July 2005, T. Orihara, KPM-NC0017759 (*Orihara 262*); the same locality, 3 Nov. 2006, T. Orihara, KPM-NC0017761 (*Orihara 536*); the same locality, under *Q. givla*, 24 Dec. 2011, T. Orihara, KPM-NC0018020; **Aichi Pref**., Okazaki-shi, in *Q. glauca* and *Q. serrata* forest, 30 Nov. 2004, S. Honda, KPM-NC0015343 (*Orihara 227*); Okazaki-shi, Ohata-sho, Nishiyama, under *Q. serrata*, 7 Nov. 2009, S. Honda, KPM-NC0017765 (*Orihara 1318*) & TNS-F-41403 (duplicate); **Hiroshima Pref**., Hiroshima-shi, Higashi-ku, Fukuda, in litters under *Q. serrata*, *Q. glauca*, and *P. densiflora*, 18 Oct. 2009, T. Imoto, KPM-NC0017766 (*Orihara 1354*); **Oita Pref**., Saiki-shi, Ume-Oaza, Shigeoka, 1.4 km south-west of Sotaro Station, under *C. sieboldii*, 16 Jan. 2011, Y. Sunada & T. Orihara, KPM-NC0017767 (*Orihara 1367*); Oita-shi, Oaza, Hisado, Yayama, under *Q. glauca*, 17 Jan. 2011, A. Hadano & T. Orihara, KPM-NC0017768 (*Orihara 1373*) & TNS-F-41404 (duplicate).

Notes — This species, which is the most common among the species in subg. *Parcaea*, has intermediate microscopic features between *O. nonae* and *O. mortae*. The average basidiospore size of *O. decimae* is between those of *O. nonae* and *O. mortae* although the basidiospore ornaments are larger than those of *O. nonae* and similar to those of *O. mortae* (Table 3). Another slight difference between *O. decimae* and the other two species is that *O. decimae* sometimes has whitish yellow to yellow-brown patches on the otherwise light coloured surface of the basidiomata. However, these macro- and microscopic traits do not help to discriminate *O. decimae* from *O. celatifilia* (see below). Nonetheless, the ITS1-5.8S-ITS2 sequence of the holotype specimen of *O. decimae* (JN257991) was 88–93 % identical to the other species in subg. *Parcaea* in the BLAST search (Maximum identities; Query coverage = 89–95 %).

Yoshimi & Doi (1989) reported one *Octaviania* species from Amami-oshima Island, Japan, as *O. tuberculata*. We have examined this Japanese specimen (TNS-F-183206; Fig. 8g, h) and compared directly with the holotype specimen of *O. tuberculata* (NY780584; collected by R. Hesse, Oct. 1888 in Germany). The Japanese specimen clearly differed from the holotype in having smaller basidiospores, a smooth rather than verrucose peridium, and it was more similar to *O. decimae* in overall morphology. However, the size of basidiospores of the specimen has much wider range (8.4–18.6 × 7.4–15.7 µm, mean 11.9 × 10.7 [n = 35], SD: 2.71 [length] and 2.32 [width]) than that of typical *O. decimae* specimens. Since we have not been able to successfully extract DNA from this specimen and it differs morphologically from our other collections, we must tentatively identify the Japanese '*O. tuberculata*' as an unknown species of subg. *Parcaea*.

Octaviania mortae Orihara, *sp. nov.* — MycoBank MB563168; Fig. 9a–e; Map 1

Etymology. Latin, *Morta*, is the name of one of the three Roman goddesses of fates, who cut the threads of human life, expressing metaphorically that this is one of the members of the cryptic species group.

Basidiomata solitary or in small clusters, up to 2.3 cm diam, subglobose to irregular tuberculate, firm, rubbery, sessile or with a concolorous reduced stipe at the base, surface glabrous, white to stramineous, gradually becoming dark grey to black when touched, rubbed or bruised, occasionally with sparse mycelial tufts concolorous with the peridial surface, rhizomorphs sparse, white, narrow, easily snapping off from the base of basidiomata. *Peridium* 0.3–2 mm thick when fresh, context white to stramineous, discolouration not observed. *Gleba* pale brownish when immature, becoming dark brown to blackish brown at maturity, structure very similar to *O. nonae*. *Sterile base* pulvinate or not developed, greyish white, sometimes connected to a short stipe, gradually turning blackish when exposed to air. *Odour* strong at maturity, unpleasant, a mixture of burnt and dimethyl sulfide smells.

Basidiospores globose to subglobose, spinose, dextrinoid, 11.1–(11.3–)14.9(–15.6) × 10.2–(10.4–)14.1(–15.6) µm, mean 13 × 12.1 µm (SD: 0.93 [length], 0.98 [width]), *Q* = 1–1.2, walls 1.2–2.3 µm thick, spinose ornaments 1.9(–3.6)–3.7 × 1.9–(2–4.2)–4.5 µm, mean 2.8 × 3.2 µm, pyramidal, internal cavities of ornaments slit-like in vertical section, labyrinthiform to zonate to cochleae in horizontal section. *Basidia* clavate to clavulate, hyaline, 2–4-spored, 22–31 × 10.1–13.7 µm, mean 25.2 × 11.4 µm, sterigmata up to 10 µm long. *Basidioles* clavulate, hyaline, almost the same size as basidia. *Hymenia* poorly developed. Subhymenium absent. *Glebal trama* of parallel to subparallel, non-inflated, thin-walled (up to 1 µm thick), white, filamentous hyphae 1.6–8 µm broad. *Sterile base* of mostly swollen, colourless, more or less interwoven, thin-walled (up

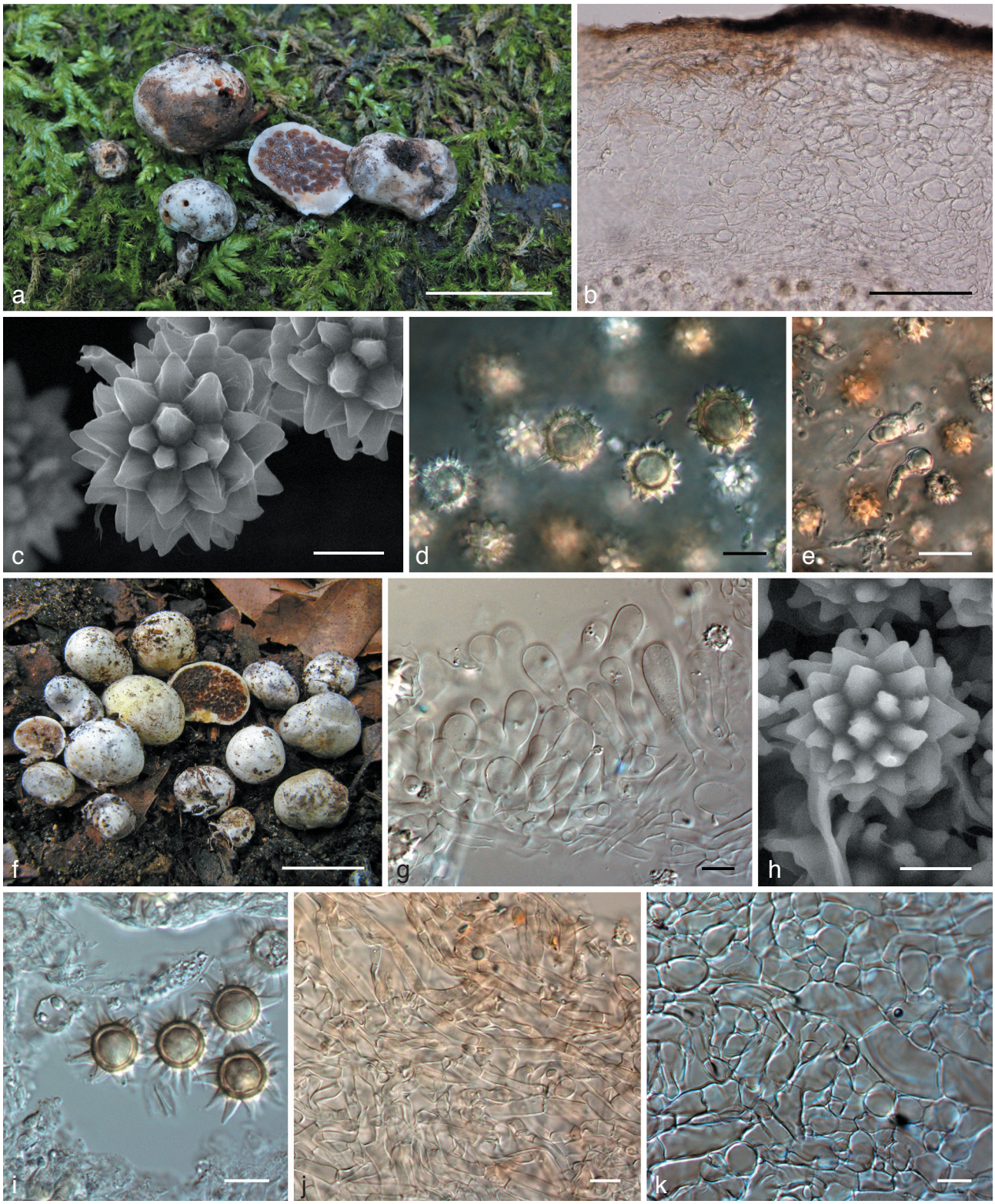


Fig. 9 a–e: *Octaviania mortae*. a. Basidiomata (*Orihara 1208*); b. peridium (KPM-NC0017770); c. SEM image of basidiospores (holotype); d. basidiospores mounted in water (KPM-NC0017772); e. basidium and basidiole mounted in water (KPM-NC0017772). — f–k: *Octaviania celatifilia* (holotype). f. Basidiomata; g. undeveloped hymenium; h. SEM image of basidiospore; i. basidiospores mounted by 3 % KOH; j. peridiopellis; k. context of peridium. — Scale bars: a, f = 1 cm; b = 100 µm; c, h = 5 µm; d, g, i, k = 10 µm; e = 20 µm.

to 0.8 µm thick) hyphae 3–25 µm broad; suprapellis of sterile base up to 50 µm thick, brown, composed of repent to somewhat trichodermial, more or less entangled, branched, non-inflated, pigmented, thin-walled (up to 0.8 µm thick) filamentous hyphae 2–9 µm broad. *Peridium* 150–1300 µm thick in dried specimens: peridiopellis up to 70 µm thick, pigmented in dark brown, of straight, non-inflated, thick-walled (1–2.2 µm thick), filamentous hyphae 2.5–10 µm broad subparallel to surface, forming a cutis; peridial context white, of densely interwoven, inflated, thin- to thick-walled (0.5–1.8 µm thick) filamentous hyphae intermingled with scattered, isodiametric to subspherical cells at maturity, 3–37 µm diam.

Habitat, Distribution & Season — Hypogeous or partially emergent under *Castanopsis sieboldii*, *C. cuspidata*, *Quercus glauca* and *Q. acutissima* Carruth.; Honshu and Shikoku (Japan); summer to autumn (July to November).

Holotype. Japan, Tottori Pref., Tottori-shi, Hie Shrine, under *C. sieboldii*, 16 July 2010, T. Orihara, KPM-NC0017774 (*Orihara 1189*; isotype TNS-F-41406).

Other specimens examined. Japan, **Tottori Pref**., Tottori-shi, Hie Shrine, under *C. sieboldii*, 8 Sept. 2008, T. Orihara, KPM-NC0017770 (*Orihara 852*); the same locality, 4 Oct. 2009, T. Orihara, KPM-NC0017772 (*Orihara 1062*); **Kyoto Pref**., Sakyo-ku, near Nanzen-ji temple, under *C. cuspidata*, 27 Oct. 2002, A. Kajiyama, KPM-NC0017769 (*Orihara 218*); the same locality, 1 Oct. 2009, A. Kajiyama, KPM-NC0017771 (*Orihara 1044*); Kyoto-shi, Kamikyo-ku, Kyoto-gyoen, under *Q. glauca*, 8 Nov. 2009, H. Saiki, KPM-NC0017773 (*Orihara 1118*) & TNS-F-41405 (duplicate); the same locality, 25 Oct. 2010, T. Orihara, KPM-NC0017775 (*Orihara 1326*); **Ehime Pref**., Futami-cho, in *Quercus acutissima* forest, 27 Sept. 2008, F. Nagao, KPM-NC0017724.

Notes — Although macroscopically it is quite difficult to discriminate *O. mortae* from the other members of subg. *Parcaea*, the species has several distinct microscopic features: short basidia (up to 31 µm long) and large basidiospores with large spiny ornaments (Table 3). The strong, burnt smell of the fresh, mature basidiomata is another diagnostic feature that can be determined in the field. Maximum identities of the ITS1-5.8S-ITS2 sequence with the other species of subg. *Parcaea* (i.e., *O. nonae*, *O. decimae*, and *O. celatifilia*) in the BLAST search were 89–93 % (Query coverage = 88–94 %).

Octaviania celatifilia Orihara, *sp. nov.* — MycoBank MB563169; Fig. 9f–k; Map 1

Etymology. The Latin words *celatus* (concealed) and *filia* (daughter) are combined. This epithet conveys the fact that this is a rare species that also belongs to subgen. *Parcaea*.

Basidiomata solitary or in small clusters, up to 1.2 cm diam, subglobose to depressed globose, firm, rubbery, sessile or with a concolorous rudimentary stipe at the base, surface glabrous, white at first, often with yellowish tint or patches, gradually becoming dark grey to black when touched, rubbed or bruised, rhizomorphs sparse, white, narrow, easily snapping off from the base of basidiomata. *Peridium* 0.2–0.8 mm thick when fresh, white, context white to cream colour. *Gleba* pale brownish when immature, becoming dark brown to blackish brown at maturity, structure similar to *O. nonae*. *Sterile base* pulvinate, greyish white to translucent to yellowish, often connected to a short stipe, gradually turning blackish when exposed to air. *Odour* unpleasant, a combination of sweet and dimethyl sulfide smells, similar to that of *O. decimae*.

Basidiospores globose to subglobose, spinose, dextrinoid, 9.9–12.9(–13.2) × (9.3–)9.4(–12)–12.1 µm, mean 11.4 × 10.8 µm (SD: 0.74 [length], 0.68 [width]), *Q* = 0.97–1.16, walls 1–2.2 µm thick, spinose ornaments 1.9(–3.6)–3.7 × 1.9–(2–4.2)–4.5 µm, mean 2.8 × 3.2 µm, conical to pyramidal, internal cavities of ornaments slit-like in vertical section, labyrinthiform to zonate to cochleae in horizontal section. *Basidia* clavate, hyaline, 2–4-spored, 23.8–36 × 8.8–13.2 µm, mean 29.9 × 10.9 µm, sterigmata up to 15 µm long. *Basidioles* clavate, hyaline, almost the same size as basidia. *Hymenia* poorly developed. Subhymenium absent. *Glebal trama* of subparallel, non-inflated, thin-walled (up to 0.6 µm thick), white, filamentous hyphae 2–7 µm broad. *Sterile base* of densely interwoven, narrow, white to colourless, thin-walled (c. 0.5 µm thick) filamentous hyphae 2.5–8 µm broad; suprapellis of sterile base up to 100 µm thick, pigmented in brown to ochraceous, composed of loosely entangled, septate, non-inflated, thin-walled (up to 0.6 µm thick) filamentous hyphae 2–7 µm broad. *Peridium* 300–600 µm thick in freeze-dried specimens; peridiopellis somewhat developed, up to 150 µm thick, pale ochraceous to pale reddish brown in colour, of straight, non-inflated, thin-walled (up to 1 µm thick), filamentous hyphae 3–8.5 µm broad subparallel to surface, forming a cutis; peridial context white to colourless, of dense, strongly inflated, cells up to 17.5 µm broad, walls up to 1.8 µm thick, but in immature basidiomata the context contains less inflated, interwoven filamentous hyphae.

No distinct difference from *O. decimae* found both morphologically and ecologically, but c. 90 positions in nuclear ITS rDNA sequence shown in Fig. 5 different from the latter species at the same level as the other species in subg. *Parcaea.*

Habitat, Distribution & Season — Hypogeous or partially emergent under *Quercus gilva* Blume; Honsyu (Nara Pref., Japan); early summer to winter (June to December).

Holotype. Japan, Nara Pref., Nara-shi, Nara Park, under *Q. gilva*, 3 Nov. 2010, H. Inui & T. Orihara, KPM-NC0017776 (*Orihara 1337*), holotype (isotype TNS-F-41407).

Other specimens examined. Japan, **Nara Pref**., Nara-shi, Nara Park, under *Q. gilva*, 25 June 2011, M. Ohmae, KPM-NC0018026 (*Ohmae 140*); Nara-shi, near Mt Kasuga, under *Q. givla*, 24 Dec. 2011, T. Orihara, KPM-NC018021.

Notes — This rare cryptic taxon has so far been found only in the two localities that are contiguous to each other. Moreover, its microscopic and macroscopic morphological similarities to *O. decimae* make identification extremely difficult: the only morphologically diagnostic character might be the slightly yellowish colour of its basidiomata. The yellowish tint, however, was not observed in every basidioma (Fig. 9f), and this colouration is also occasionally found in specimens of *O. decimae*. In addition, the habitat of *O. celatifilia* is similar to the other three species in subg. *Parcaea*. This species is found sympatrically with *O. decimae*: in one case they both occurred simultaneously within c. 400 m (Map 1). Therefore, the only reliable taxonomic key is unique DNA sequences which clearly distinguish it from the other three species in subg. *Parcaea* (Fig. 1–5). The BLAST maximum identities of the ITS1-5.8S-ITS2 sequence with the other three species in subg. *Parcaea* were 90–94 % (Query coverage = 91–95 %). In the future, the use of other DNA sequences will be helpful to more precisely understand the relationships between *O. celatifilia* and other species in subg. *Parcaea*.

Octaviania* subgenus *Fulvoglobus Orihara, *subg. nov.* — MycoBank MB563193

Typus subgeneris. Octaviania kobayasii Orihara.

Basidiomata hypogeous to emergent, rubbery or firm, surface whitish when immature, then usually tinged with yellowish, or becoming tawny to rusty at maturity. *Peridium* of two layers: peridiopellis thin, of mostly pigmented, filamentous hyphae; context of peridium of polygonal or subspherical cells comprising pseudoparenchyma, intermingled with partly inflated, filamentous hyphae. *Oleiferous hyphae* usually present, pigmented or colourless, context subgranulate.

Notes — Despite considerable phylogenetical divergence from the other clades in *Octaviania*, clade C (= subg. *Fulvoglobus*) has few unique morphological characters. We herein proposed the new subgenus for clade C based mainly on the characters of the peridial context and colour of the mature basidiomata as well as the dissimilarity of the nLSU rDNA and EF-1α sequences from that of the members of subg. *Parcaea* and *Octaviania* (Fig. 1–3). Species in subg. *Parcaea* are not tinged yellow overall but, similar to species in subg. *Fulvoglobus*, they do have a pseudoparenchymatous peridium at maturity. Subg. *Octaviania* is distinguished by the filamentous hyphae of its peridium that are not truly pseudoparenchymatous even at maturity.

Octaviania kobayasii Orihara, *sp. nov.* — MycoBank MB563194; Fig. 10

Etymology. The epithet, *kobayasii*, was named in honour of Dr. Yosio Kobayasi, who greatly contributed to the taxonomy of hypogeous, sequestrate fungi in Japan, including *Octaviania* as well as other groups of fungi.

Basidiomata solitary to gregarious, up to 3.2 cm diam, subglobose, depressed-globose or tuberiform, rubbery, firm, with rudi-

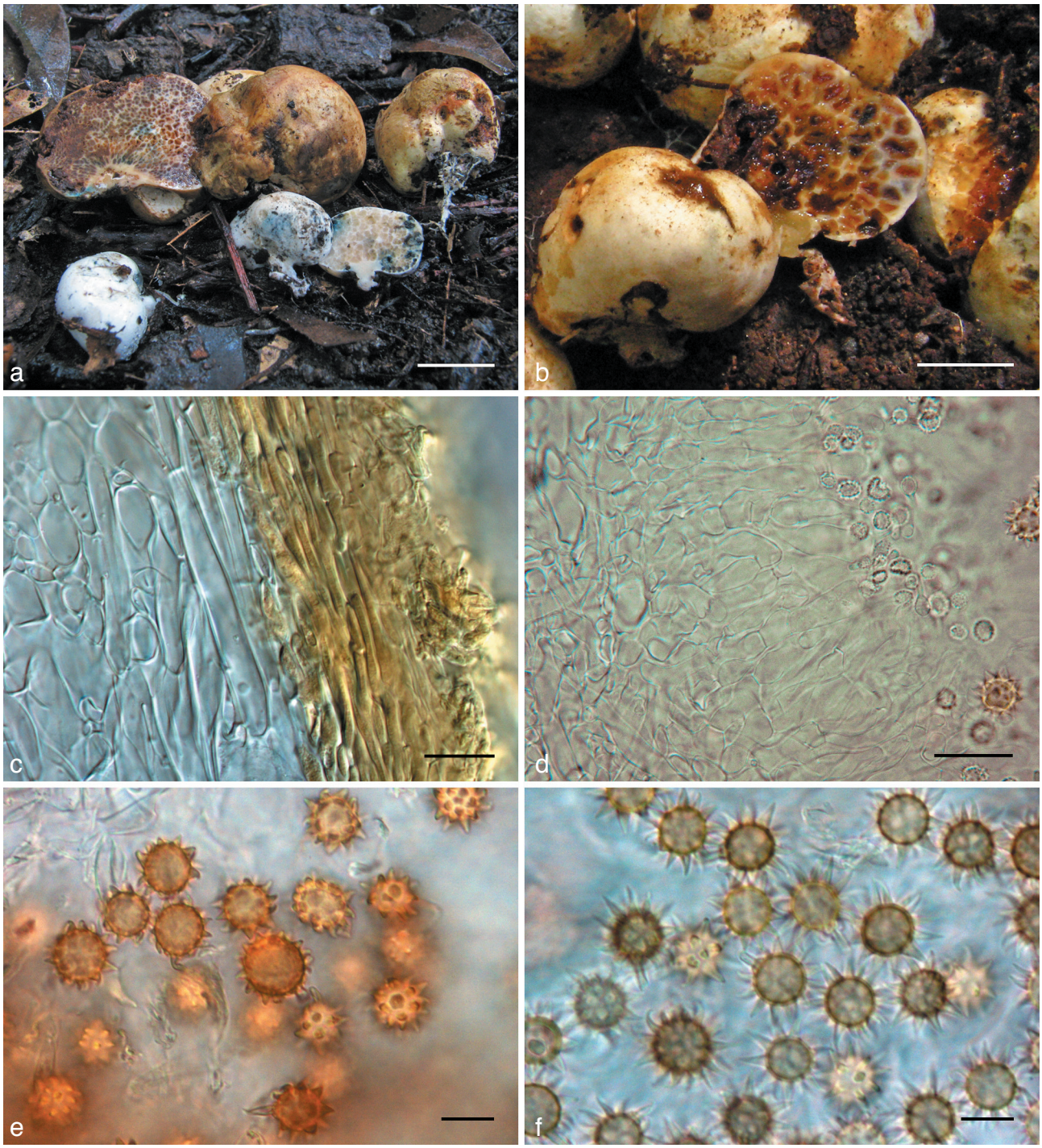


Fig. 10 *Octaviania kobayasii*. a. Basidiomata (KPM-NC0017780); b. longitudinal section of basidioma (KPM-NC0017785); c. peridiopellis (right) and peridial context (left) (KPM-NC0017783); d. developed hymenial and subhymenial layers (KPM-NC0017785); e. basidiospores mounted in water (holotype); f. basidiospores mounted in lactic acid (holotype). — Scale bars: a = 1 cm; b = 5 mm; c, d = 20 µm; e, f = 10 µm.

mentary stipe at the base, surface glabrous or sometimes partly cracked, exposing inner gleba, white in youth, then fulvous to tawny occasionally becoming gradually bluish green to blue, or wine red to reddish brown when touched, rubbed or bruised. *Peridium* up to 0.6 mm thick when fresh, context concolorous with the surface, turning a similar colour to the surface when exposed to air. *Gleba* pale brownish when immature, becoming ochraceous to fuscous at maturity, rubbery in youth, then becoming more or less brittle at maturity, composed of variously shaped chambers enclosed by glebal tramae forming a marbled pattern, spore mass becoming granulate at maturity or rarely somewhat glutinous; glebal trama of two strata: inner opaque, concolorous with the peridium, outer colourless, translucent. *Sterile base* rudimentary or slightly dendroid, concolorous with peridium, occasionally turning bluish green or red to reddish brown when exposed to air. *Rhizomorphs* white, easily snapping off from the base of basidiomata. *Ectomycorrhiza* bifurcate to plurifurcate, glabrous, light-brown to pale reddish brown. *Odour* nutty or like burnt sugar.

Basidiospores globose to broadly ellipsoid, spinose, weakly dextrinoid, pale ochraceous to tawny under the light microscope, (8.4–)8.6–13.6(–14.4) × (7.8–)8.1–12(–12.9) µm, mean 11.1 × 10.1 µm (SD: 1.23 [length], 0.96 [width]), Q = 0.98–1.45, walls 0.5–2 µm thick; ornaments spiny, relatively small, with a single cavity inside the wall, (1.1–)1.2–3.3 × (1.1–)1.2–3.6(–3.9) µm, mean 2.3 × 2.4 µm. *Basidia* clavate to cylindro-clavate, hyaline, evanescent, 2–4-spored, 19–38 × 8.2–11 µm, sterigmata up to 12 µm long. *Cystidia* absent.

Hymenia developed, translucent, composed of basidia and interspersed basidioles. *Glebal trama* comprised of inner white and outer translucent tissues: white part of parallel or subparallel, partly inflated, thick-walled (0.5–1.5 µm thick), filamentous hyphae 2.5–10.5(–20) µm broad; outer, translucent part consisting of subhymenial cells inflated up to c. 40 µm diam and perpendicularly connected to each other from the inner white portion, walls of cells 0.5–1.2 µm thick. *Sterile base* of compact, densely interwoven, white filamentous hyphae 2.3–10 µm broad, walls 0.5–1.3 µm thick. *Peridium* 250–600 µm thick; peridiopellis up to 50 µm thick but absent in some patches, ochraceous, of repent, thin-walled (0.4–0.8 µm thick), filamentous hyphae 2.5–6.5 µm broad forming a cutis; peridial context white to pale ochraceous, of densely interwoven, more or less inflated, filamentous hyphae partly becoming isodiametric to subspherical (pseudoparenchymatous), 2.5–38 µm broad, hyphal walls thin in youth, becoming thick-walled (0.6–1.6 µm thick) at maturity.

Habitat, Distribution & Season — Hypogeous or subepigous under *Castanea crenata* Siebold & Zucc., *Castanopsis sieboldii*, *Quercus dentata* Thunb., *Q. gilva*, *Q. serrata*, and *Pinus densiflora* Siebold & Zucc.; Western Honshu (Japan); mid to late autumn (September to November).

Holotype. Japan, Okayama Pref., Maniwa-shi, Mt Minagasen, under *Q. dentata* and *Castanea crenata*, 15 Nov. 2008, T. Orihara, KPM-NC0017782 (*Orihara 930*; isotype TNS-F-41408).

Other specimens examined. Japan, **Kyoto Pref**., Kyoto-shi, Sakyo-ku, Shimogamo-hangi-cho, under *C. sieboldii*, 25 Sept. 2008, A. Kajiyama, KPM-NC0017779 (*Orihara 887*); the same locality, 29 Sept. 2008, T. Orihara, KPM-NC0017780 (*Orihara 888*); the same locality, 13 Dec. 2009, Y. Kitade, KPM-NC0017784 (*Orihara 1125*); Uji-shi, Taiyo-ga-oka Park, under *P. densiflora*, 28 Nov. 2009, F. Deai, KPM-NC0017783 (*Orihara1122*); **Nara Pref**., Nara-shi, Mt Kasuga, under *Q. gilva*, 3 Nov. 2010, H. Inui, K. Maruyama & T. Orihara, KPM-NC0017785 (*Orihara 1342*), TNS-F-41409 (duplicate) & KPM-NC0017786 (*Orihara 1343*; parasitized by *Sepedonium chrysospermum*); **Hyogo Pref**., Kobe-shi, Kita-ku, Yamada-cho, Shimo-tanigami, under *Q. serrata*, 9 Sept. 2006, T. Orihara, KPM-NC0017777 (*Orihara 483*); Akoh-shi, under *Q. serrata*, 10 Sept. 2006, T. Orihara, KPM-NC0017778 (*Orihara 495*); **Okayama Pref**., Maniwa-shi, Mt Minagasen, under *Q. dentata* and *C. crenata*, 12 Oct. 2008, F. Nagao, KPM-NC0017781 (*Orihara 898*); **Hiroshima Pref.**, Kitahiroshima-cho, Higashiyawatahara, 13 Nov. 2010, M. Arita, KPM-NC0017787 (*Orihara 1355*); **Ehime Pref**., Kuma-kogen-cho, under *Q. acutissima*, 10 Nov. 2007, F. Nagao, KPM-NC0017723.

Notes — The most striking character of *O. kobayasii* is its thick, evanescent hymenial and subhymenial layers that look translucent macroscopically or under DIC microscopy. In addition, the dry and somewhat brittle spore mass at maturity is also diagnostic of *O. kobayasii*. Ecologically, this species tends to fruit in late autumn and is presumed to have weak host specificity since it occurs directly beneath deciduous and evergreen species of the *Fagaceae* (i.e., *Quercus*, *Castanea*, and *Castanopsis* spp.) as well as *Pinus densiflora*. Phenology is helpful for distinguishing *O. kobayasii* from *O. hesperi* (= *Octaviania* lineage C) because *O. hesperi* fruits in summer whereas *O. kobayasii* generally fruits in late autumn. Characters that differentiate *O. kobayasii* from other macroscopically similar species (i.e., *O. japonimontana* and *O. etchuensis*) are found in their descriptions below.

The EF-1α sequence of the specimen collected under *Pinus densiflora* (KPM-NC0017783) was slightly divergent from the other *O. kobayasii* sequences. This might reflect cryptic differences among isolates from different host plants (i.e., *Pinus* vs *Fagaceae*). However, the nLSU and ITS sequences between the *Pinus*-associated specimen and the other angiosperm-associated specimens were identical, and we could not find any obvious morphological differences. Although we refrain from proposing any infraspecific divisions within *O. kobayasii*, we recognize that there may be cryptic, host-specific diversity within this species.

Octaviania hesperi Orihara, *sp. nov.* — MycoBank MB563195; Fig. 6a, b, 11

Etymology. Latin, *hesperi*, after the Greek term *hesperos* (the evening star), referring to the large, ochraceous basidiospores with large, spiny ornamentation.

Basidiomata solitary or gregarious, up to 2 cm diam, subglobose, depressed-globose or tuberiform, rubbery, solid when immature, often with a rudimentary basal stipe, surface glabrous, sometimes becoming rimose-areolate at maturity forming an areolate pattern, white in youth, then stramineous to ochraceous, finally rusty at maturity, sometimes gradually becoming bluish green to indigo blue where touched, rubbed or bruised. *Peridium* up to 0.35 mm thick when fresh, concolorous with or paler than the surface, turning bluish green in some portions in cross section. *Gleba* whitish to pale brownish when immature, becoming fuscous to blackish brown at maturity, rubbery in youth, becoming glutinous at maturity, trama homogenous. *Sterile base* rudimentary to pulvinate, almost concolorous with the peridial context, occasionally turning bluish green to indigo blue when exposed to air. *Rhizomorphs* white, easily snapping from the base of basidiomata. *Odour* nutty.

Basidiospores globose to broadly ellipsoid, spinose, weakly to moderately dextrinoid, fulvous to tawny with light microscopy, 10–15.6(–18.2) × 9.4–(9.9–)14.8(–17.8) µm, mean 12.8 × 12.1 µm (SD: 1.40 [length], 1.31 [width]), Q = 0.96–1.15, occasionally with a pedicel 5.5–15 × 1.8–3 µm, pedicels sometimes with a ring-like appendage (Fig. 12f), spore walls 1.8–3 µm thick, ornaments spiny, 2–(2.1–)3.6(–4) × 1.3–(1.7–)5.4(–5.7) µm, mean 2.8 × 3.6 µm, large, polygonal at the base, with several large, distinct cavities that appear slit-like in vertical section and labyrinthiform to zonate to cochleae in horizontal section. *Basidia* clavate, hyaline, mostly 4-spored or more rarely 2–3-spored, 21.5–33.3 × 9.2–14.5 µm, sterigmata up to 15 µm long. *Cystidia* absent. *Hymenia* poorly developed, composed of basidia and interspersed basidioles up to 32 × 12.7 µm, deliquescent at maturity. *Glebal trama* of parallel to subparallel, white to more or less translucent, non-inflated or sometimes partly inflated, thin-walled (up to 0.8 µm thick), filamentous hyphae 2–8.5(–20) µm broad. *Sterile base* of compacted, densely interwoven, partly inflated, thin-walled, white filamentous hyphae 3–25 µm broad. *Peridium* 100–350 µm thick; peridiopellis up to 150 µm thick, absent in some portions, of straight, septate, more or less pigmented, partly inflated filamentous hyphae 2–10 µm broad forming cutis, hyphal walls 0.5–1.3 µm thick, outermost hyphae stained ochraceous to fuscous with light microscopy; peridial context 80–300 µm thick, almost colourless, of thick-walled (0.8–2 µm thick), spherical to subspherical, or isodiametric cells up to 92 µm diam intermingled with thin-walled (up to 1 µm thick), inflated filamentous hyphae 4–27 µm broad, but in youth the inflated cells are not yet developed and hyphal walls are thinner. Oleiferous hyphae present in peridium and trama, sinuate or monililform, pigmented, 2–9 µm broad.

Habitat, Distribution & Season — Hypogeous or subepigeous under *Quercus glauca*, *Q. myrsinaefolia* Blume, *Castanopsis sieboldii* or *Lithocarpus edulis* (Makino) Nakai, rare; Honshu (Japan); early summer to early autumn (June to October).

Holotype. Japan, Kanagawa Pref., Zushi-shi, Numama, under *C. sieboldii*, 21 July 2009, T. Orihara, KPM-NC0017793 (*Orihara 984*).

Other specimens examined. Japan, **Ehime Pref**., Hutami-cho, in *Q. actissima* forest, 27 Sept. 2008, F. Nagao, *Nagao 08-09-12-08*, KPM-NC0017727; **Tokyo**, Hachioji-shi, Matsugaya, Otsuka Park, under *L. edulis*, 26 Oct. 2008, T. Orihara, KPM-NC0017792 (*Orihara 841*); **Kanagawa Pref**., Zushi-shi, Numama, under *C. sieboldii*, *Q. glauca*, or *Q. myrsinaefolia*, 5 Sept. 2006, T. Orihara & M. Ohkubo, KPM-NC0017790 (*Orihara 475*); the same locality, 16 July 2007, T. Orihara, KPM-NC0017791 (*Orihara 641*) & TNS-F-41410 (duplicate); the same locality, under *C. sieboldii*, 21 July 2009, T. Orihara, KPM-NC0017794 (*Orihara 985*; parasitized by *Sepedonium chrysospermum*);

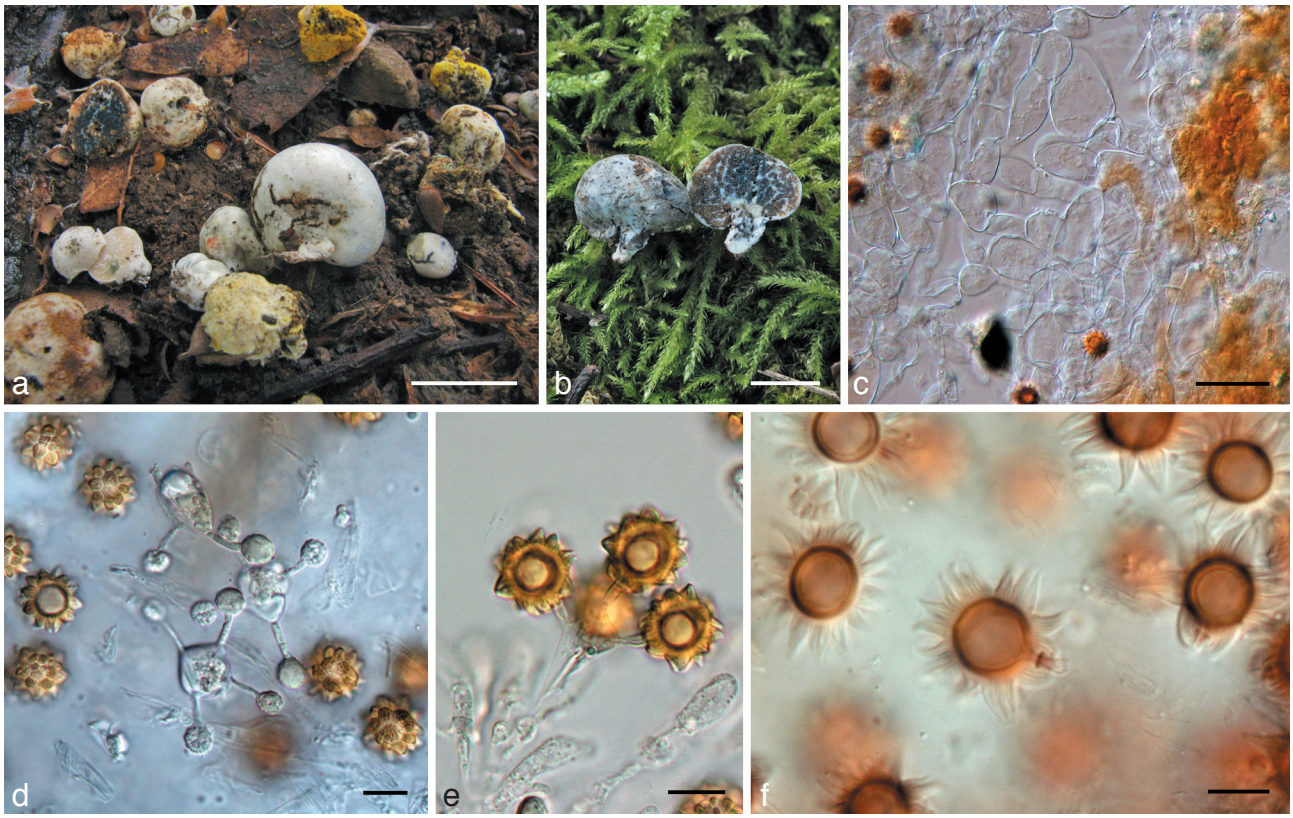


Fig. 11 *Octaviania hesperi*. a. Immature (centre) and mature (upper left) basidiomata (holotype). Upper right basidiomata are parasitized by *Sepedonium chrysospermum*; b. basidioma (section; KPM-NC0017795); c. peridium (KPM-NC0017791); d. basidia mounted in water (KPM-NC0017795); e. basidia with spores mounted in water (KPM-NC0017792); f. basidiospores mounted in lactic acid after presoaking in Melzer's reagent showing weak dextrinoid reaction (KPM-NC0017792). — Scale bars: a = 1 cm; b = 5 mm; c = 30 µm; d–f = 10 µm.

the same locality, under *C. sieboldii*, 23 Oct. 2011, T. Orihara, KPM-NC0018019; **Kyoto Pref**., Kyoto-shi, Sakyo-ku, south-western foot of Mt Hiei, under *Q. glauca*, 27 Sept. 2005, T. Orihara, KPM-NC0017789 (*Orihara 301*) & TNS-F-41411 (duplicate); the same locality, 3 Oct. 2005, T. Orihara, KPM-NC0017788 (*Orihara 300*); **Tottori Pref**., Tottori-shi, Ouchidani, under *C. sieboldii*, 11 July 2010, T. Orihara, KPM-NC0017795 (*Orihara1185*).

Notes — Among members of subg. *Fulvoglobus*, *O. hesperi* (= *Octaviania* lineage C) is characterized by the relatively large basidiospores covered by large ornaments. In addition, the spore ornaments of this species contain multiple, distinct cavities. The macroscopically similar species, *O. kobayasii* is found in the same habitat as *O. hesperi* but the two species are microscopically distinct. In addition, *O. kobayasii* is readily distinguished from *O. hesperi* by its typically translucent hymenium and subhymenium as well as the tendency of *O. kobayasii* to from larger basidiomata.

Octaviania japonimontana Orihara, *sp. nov.* — MycoBank MB563196; Fig. 6c, d, 12

Etymology. Latin, *japoni-*, refers to its wide distribution within Japan, and Latin, *montanus*, refers to its mountainous habitat.

Basidiomata solitary to gregarious, subhypogeous or emergent, up to 4 cm diam, subglobose to reniform, rubbery, usually with a rudimentary basal stipe, surface glabrous to slightly floccose, often becoming partly areolate at maturity, white in youth, becoming stramineous to camel at maturity, gradually turning bluish green to cobalt blue, or red to wine, sometimes later turning blackish when touched, rubbed or bruised. *Peridium* varying in thickness, up to 0.7 mm thick when fresh, context paler than the surface, discolouring the same colour as the surface when exposed to air. *Gleba* whitish to pale brownish when immature, becoming fuscous to blackish brown at maturity, rubbery in youth, then becoming glutinous at maturity, glebal trama homogenous, concolorous with the peridial context. *Sterile base* rudimentary to pulvinate, concolorous with peridial context, discolouring the same colour as the surface when exposed to air. *Rhizomorphs* white, easily snapping off from the base of basidiomata. *Odour* nutty, strong at maturity.

Basidiospores globose to subglobose, spinose, dextrinoid, spadiceous to tawny with light microscopy, (9.1–)9.3–12(–12.1) × 8.7–(8.9–)11.3(–11.4) µm, mean 10.6 × 10 µm (SD: 0.67 [length], 0.64 [width]), Q = 0.93–1.21, with a basal appendage that has a ring-like edge, walls 1–2.4 µm thick; ornaments spiny, pyramidal, with one cavity inside the ornament wall, (1.5–)1.7–3.3(–3.5) × (1.2–)1.4–4.2(–4.3) µm, mean 2.5 × 2.8 µm. *Basidia* clavate, hyaline, 2–4-spored, 19–26.5 × 7–13 µm, mean 23.8 × 9.6 µm, sterigmata 2.5–9.5(–13) µm long and 1.5–2.3 µm broad. *Oleiferous hyphae* often present in the trama and the peridial context, filamentous, white to pigmented, more or less granulate, slightly swollen at hyphal tips. *Hymenia* poorly developed, composed of basidia and interspersed basidioles. *Glebal trama* of parallel to subparallel, non-inflated or sometimes partly inflated, white, thin-walled (up to 0.8 µm thick), filamentous hyphae 2–16 µm broad to surface. *Sterile base* of compacted, densely interwoven, partly inflated, thin-walled (0.4–0.8 µm thick), white filamentous hyphae 3.5–15 µm broad. *Peridium* 180–700 µm thick; peridiopellis 30–200 µm thick, usually well-developed, fulvous to pale brown near surface but whitish in colour toward the interior, of thin-walled (0.4–0.8 µm thick), filamentous hyphae 3–10 µm broad and parallel to subparallel to surface, forming a cutis; peridial context colourless, of densely interwoven, more or less inflated, filamentous hyphae 3–15 µm broad, some hyphal cells becoming subspherical or isodiametric, up to 70 µm diam at maturity; hyphal walls 0.7–1.6(–4) µm thick at maturity.

Habitat, Distribution & Season — Hypogeous or emergent under *Fagus crenata* Blume or *Quercus crispula* Blume; Honshu (Japan); summer to autumn (July to November).

Holotype. Japan, Tottori Pref.: Kofu-cho, Kagamiganaru, under *F. crenata*, 14 Oct. 2007, Y. Ando & T. Orihara, KPM-NC0017798 (*Orihara 724*; isotype TNS-F-41412).

Other specimens examined. Japan, **Aomori Pref**., Aomori-shi, Tashirodiara, under *F. crenata* and *Q. crispula*, 17 Aug. 2005, S. Kudo, KPM-NC0017799 (*Orihara 771*); Aomori-shi, Mt Hakkoda, under *Q. crispula*, 28 Aug. 2008, Y. Ando, KPM-NC0017802 (*Orihara 859*), KPM-NC0017803 (*Orihara 860*; parasitized by *Sepedonium chrysospermum*) & KPM-NC0017805 (*Orihara 864*; parasitized by *Sepedonium* sp.); **Akita Pref**., Kazuno-shi, Hakkatohge, near Lake Towada, 15 Sept. 2007, Y. Ando, KPM-NC0017797 (*Orihara 700*); the same locality, 28 Aug. 2008, Y. Ando, KPM-NC0017804 (*Orihara 861*) & TNS-F-41413 (duplicate); **Aichi Pref**., Kita-shitara-gun, Tengudana, under *F. crenata*, 6 Aug. 1983, S. Honda, KPM-NC0017796 (*Orihara 219*); **Tottori Pref**., Kofu-cho, Kagamiganaru, under *F. crenata*, 8 Sept. 2008, M. Nabe, KPM-NC0017808 (*Orihara 955*); the same locality, 12 Oct. 2008, S. Sato, KPM-NC0017807 (*Orihara 896*); Daisen-cho, Mt Daisen, Nino-sawa, in *F. crenata* forest, 12 Oct. 2008, S. Hirose, KPM-NC0017806 (*Orihara 895*); Yazu-cho, Hattoh, under *F. crenata*, 21 July 2008, S. Hirose, KPM-NC0017801 (*Orihara 824*); the same locality, 24 July 2008, T. Orihara, KPM-NC0017800 (*Orihara 823*); the same locality, 19 Aug. 2009, T. Orihara, KPM-NC0017809 (*Orihara 1035*) & KPM-NC0017810 (*Orihara 1036*); the same locality, 28 Aug. 2010, T. Orihara, KPM-NC0017811 (*Orihara 1246*); **Okayama Pref**., Kagamino-cho, Kami-onbara, under *F. crenata*, 25 Sept. 2010, T. Orihara, KPM-NC0017812 (*Orihara1262*) & TNS-F-41414 (duplicate).

Notes — So far, *O. japonimontana* has been found only under *F. crenata* or *Q. crispula*, the probable host trees for this species, in mountainous areas of Honshu. The morphologically similar species, *O. kobayasii*, *O. hesperi*, and *O. etchuensis* have not been found with these trees. Despite the morphological similarities between *O. japonimontana* and these other three species, our phylogenetic analyses clearly distinguish *O. japonimontana* as a unique taxon (Fig. 1–3). This is a good example of how host preferences might be used as a potential diagnostic feature among morphologically similar taxa.

The basidiospore morphology of *O. japonimontana* is also similar to European *O. asterosperma*, but the surface of *O. japonimontana* fruitbodies become tan to light brown at maturity whereas those of *O. asterosperma* do not. Also, peridial hyphae of *O. asterosperma* do not become pseudoparenchymatous as that of subg. *Fulvoglobus* even at maturity.

Fig. 12 *Octaviania japonimontana*. a, b. Basidiomata (a: KPM-NC0017798, holotype; b: KPM-NC0017801); c. basidiospores mounted in water (KPM-NC0017797); d. basidiospores mounted in 3 % KOH (KPM-NC0017800); e. 3-spored basidium (KPM-NC0017797); f. tips of oleiferous hyphae (holotype); g. hyphae of sterile base (KPM-NC0017797); h. peridiopellis (upper right) and context of peridium (holotype). — Scale bars: a, b = 1 cm; c–f = 10 µm; g, h = 50 µm.

***Octaviania* sp. "E"** — Fig. 13a–c

Only immature basidiomata were collected. *Basidiomata* solitary or in small clusters, hypogeous to subhypogeous, up to 1 cm diam, depressed-globose to tuberiform, rubbery, with a short, often rudimentary basal stipe; surface smooth, white when immature, turning red to dark reddish brown sometimes with an aeruginous tint when touched, rubbed or bruised, finally becoming blackish red to black. *Peridium* thin, up to c. 0.4 mm thick, white, discolouration not prominent. *Gleba* white in youth, gradually becoming dark brown, somewhat watery, discolouring the same colour as the surface when exposed to air, composed of variously shaped cells enclosed by glebal tramae forming a marbled pattern; glebal trama homogenous, whitish. *Sterile base* pulvinate, white. *Rhizomorphs* white.

Basidiospores globose to subglobose, spinose, dextrinoid, pale ochraceous to tawny under the light microscope, 9.1–(9.4–)12.6(–13.1) × 8.5–(8.8)–11.5 µm, mean 10.8 × 10 µm (SD: 0.83 [length], 0.73 [width], n = 30, t = 2.045), Q = 1–1.28, walls 1.5–3.2 µm thick; ornamentation spiny, pyramidal, mostly with one cavity inside the wall, but exceptionally with several cavities, 1.3–(1.5–)3.8 × 1.3–(1.7–)4.1(–4.2) µm, mean 2.5 × 2.7 µm. *Basidia* clavate, hyaline, 2- or 4-spored, 21–36 × 8–11 µm, sterigmata 5.4–11 µm long. *Oleiferous hyphae* present in the tramal tissue and the peridial context, filamentous, pigmented, 2.5–4.5 µm diam. *Hymenia* poorly developed, composed of basidia and interspersed basidioles. *Glebal trama* of parallel or subparallel, colourless under DIC microscopy, non-inflated or sometimes partly inflated, thin-walled (up to 0.8 µm thick), filamentous hyphae 2–8 µm broad. *Sterile base* of compacted, densely interwoven, partly inflated, thin-walled (0.4–0.8 µm thick), white to translucent, filamentous hyphae 3.5–15 µm broad. *Peridium* 100–400 µm thick; peridiopellis 25–150 µm thick, more or less developed, stained with blackish red to black, of subspherical to isodiametric, thin-walled (up to 1 µm thick), cells up to 25 µm diam intermingled with more or less

Fig. 13 a–c: *Octaviania* sp. "E" (KPM-NC0017813): a. Immature basidiomata; b. immature basidiospores mounted in lactic acid after presoaking in 3 % KOH; c. poorly developed hymenium with basidioles. — d–h: *O. durianelloides*. d. Basidiomata (KPM-NC0017829, holotype); e. basidioma with green stains (KPM-NC0017815); f. basidiospores mounted in water (KPM-NC0017815); g. aberrant basidiospore connected directly to a basidium mounted in lactoglycerol after presoaking in 1 % phloxine B and 3 % KOH (centre; holotype); h. peridium (KPM-NC0017815). — Scale bars: a, d = 1 cm; b, f, g = 10 µm; c, h = 20 µm; e = 5 mm.

interwoven, partly inflated, pigmented, filamentous hyphae 4–13 µm broad; peridial context white to translucent under DIC microscopy, of densely interwoven, rarely inflated, filamentous hyphae 2–13 µm broad, mixed with subspherical or isodiametric cells up to 20 µm diam; hyphal walls up to 1 µm thick in youth.

Habitat, Distribution & Season — Hypogeous under *Castanopsis sieboldii* subsp. *lutchuensis*; Amami-oshima Island (the Ryukyu Archipelago, Japan); late autumn (November).

Specimen examined. Japan, **Kagoshima Pref**., Amami-oshima Isl., Yamato-son, north-eastern foot of Mt Yuwan, under *C. sieboldii* subsp. *lutchuensis*, 17 Nov. 2007, T. Orihara, KPM-NC0017813 (*Orihara 761*).

Notes — Unfortunately, the only *Octaviania* sp. "E" collection was immature and therefore inadequate for morphological evaluation and taxonomic delimitation. Thus, we leave it undescribed until mature specimens become available. The *Octaviania* sp. "E" specimen was found almost sympatrically with the holotype of *O. nonae Orihara 945* in evergreen, subtropical forest on Amami-oshima Island in the northern Ryukyu Archipelago. Although these species are found in the same habitat, they are morphologically distinct and fall into different subgenera.

Octaviania durianelloides Orihara, *sp. nov.* — MycoBank MB563197; Fig. 6f, 13d–h

Etymology. The epithet, *durianelloides*, comes from the sequestrate fungus, *Durianella echinulata* (Corner & Hawker) Desjardin, A.W. Wilson & Binder, which is a macro-morphologically similar species. The strong odour of the basidiomata is also reminiscent of durian fruits.

Basidiomata solitary or in small clusters, subhypogeous or emergent, up to 2.5 cm diam, depressed-globose to reniform, rubbery, with a rudimentary basal stipe; surface covered with minute, somewhat fibrillar, felty warts or squamules, becoming wrinkled when dried, whitish to pale brown when immature, brown at maturity, gradually turning wine red when immature and dark green at maturity where rubbed or bruised, then later turning black to blackish green; tips of the peridial warts usually darker than the surrounding peridial surface. *Peridium* thin, only up to c. 0.4 mm thick when fresh, context white to beige, or somewhat translucent, discolouring dark blue when exposed to air at maturity. *Gleba* fuscous to black at maturity, rubbery in youth, then becoming somewhat glutinous at maturity, occasionally exuding water, composed of variously shaped cells; glebal trama homogenous, white to semi-transparent. *Sterile base* rudimentary to pulvinate, white, opaque. *Rhizomorphs* white. *Odour* slightly nutty or durian-like to unpleasant, with hints of dimethyl sulfide.

Basidiospores globose, subglobose, or broadly ellipsoid, spinose, dextrinoid, yellowish brown to fuscous under the light microscope, 8.1–(8.8–)15.1(–18.5) × 7.5–(8–)13.4(–15.1) µm, mean 11.6 × 10.4 µm (SD: 1.54 [length], 1.46 [width]), Q = 1–1.31, occasionally becoming aberrant and unusually swollen up to 26 µm diam and connected directly to basidia (Fig. 14g), walls 1–2(–2.5) µm thick; basal appendage not distinct; ornamentation spiny, acute, pyramidal, with one to several cavities inside each spore ornament wall, 1.3–3.9(–4.4) × 1.4–(1.5–)3.8(–4.1) µm, mean 2.6 × 2.6 µm, surface almost smooth under the light microscope. *Basidia* clavate to cylindroclavate, hyaline, 2–4-spored, 17.5–35 × 8–11.8 µm, mean 25.7 × 9.7 µm (n = 12), often with sterigmata 5–10 µm long. *Oleiferous hyphae* not observed. *Hymenia* poorly developed. *Glebal trama* semi-transparent under DIC microscopy, of more or less loosely interwoven or subparallel, thin-walled (up to 1 µm thick), partly branched, filamentous hyphae 1.8–8.5(–10) µm broad, intergrading with spherical cells up to c. 30 µm diam. *Sterile base* white under DIC microscopy, collapsed in dried specimens and not rehydrated when soaked in water or 3 % KOH. *Peridium* 200–400 µm thick; peridiopellis 40–100(–150) µm thick, yellow-brown, of partly branched, pigmented filamentous hyphae 2.8–13 µm broad but partly inflated to 23 µm broad, parallel to subparallel to surface, forming a cutis, walls 0.5–1.8 µm thick; peridial context 100–325 µm thick, of colourless, mostly of interwoven, inflated, thick-walled (0.4–2.2 µm thick), filamentous hyphae 3–10.5(–18) µm broad, becoming mostly pseudoparenchymatous up to 35 µm diam at maturity.

Habitat, Distribution & Season — Under *Castanea crenata*, *Quercus serrata*, or *Q. acutissima*; central to northern Honshu (Japan); early to mid summer (June to August).

Holotype. Japan, Kanagawa Pref.: Minami-ashigara-shi, Uchiyama, under *C. crenata*, 4 July 2011, T. Orihara, KPM-NC0017829 (*Orihara 1386*; isotype TNS-F-41415).

Other specimens examined. Japan, **Miyagi Pref**., Shichigasyuku-cho, under *Q. serrata*, 23 July 2004, Yoko Ando, KPM-NC0017814 (*Orihara 148*); Sendai-shi, Izumi-ku, eastern foot of Mt Kurohana, 28 July 2006, H. Sasaki, KPM-NC0017816 (*Orihara 1170*); **Saitama Pref**., Kawagoe-shi, under *Q. serrata* and *Q. acutissima*, 27 June 2006, Ikuo Asai, KPM-NC0017815 (*Orihara 410*); **Shiga Pref**., Hino-cho, Kamagake, 23 Aug. 2007, Y. Kotera, KPM-NC0017817 (*Orihara 1377*).

Notes — *Octaviania durianelloides* is unique in *Octaviania* because of its warty, brown peridium and dark green discolouration where injured, but otherwise it is morphologically similar to the other species in the genus. The macromorphology of *O. durianelloides* is similar to *Durianella echinulata* (syn. *Hydnangium echinulatum*; *Boletales*, *Boletineae*), which was reported from Malaysia and forms greyish orange to golden yellow, durian-shaped basidiomata (Desjardin et al. 2008). However, *D. echinulata* differs from *O. durianelloides* in having larger and more distinct peridial warts (up to 1 mm tall), thicker peridium (1–2 mm thick), and basidiospores covered with collapsible spines. Moreover, rDNA LSU sequences of *D. echinulata* EU293063 and *O. durianelloides* were only c. 86 % similar, indicating that these taxa are not close relatives. Thus, the superficial morphological similarities between these two sequestrate fungi is due to convergent evolution within *Boletales*. The acute ornamentation of basidiospores and relatively wide range of the basidiospore size, some becoming unusually swollen, are additional diagnostic features of *O. durianelloides*.

Octaviania yaeyamaensis Orihara, *sp. nov.* — MycoBank MB563198; Fig. 14a–f; Map 1

Etymology. The epithet refers to the known distribution of the species. The type locality, Ishigaki Island, is one of the Yaeyama Islands, which makes up the southernmost part of the Ryukyu Archipelago, Japan.

Basidiomata solitary to gregarious, hypogeous to subhypogeous, up to 3 cm diam, subglobose, depressed globose or reniform, firm, rubbery, sessile or with rudimentary stipe at the base, surface smooth to slightly tomentose, white when young, then becoming yellowish white to pale stramineous with a reddish brown or bluish green tint at maturity, turning red to reddish brown or bluish green where bruised, with whitish brown rhizomorphs at the base. *Peridium* well developed, 0.2–1 mm thick, rubbery, often gradually turning red to reddish brown when cut. *Gleba* cream-coloured to pale brown when young, then blackish brown to chocolate brown at maturity, glebal chambers filled with numerous basidiospores immersed in a glutinous matrix, trama white at first, but quickly turning indigo blue to blackish blue at maturity when exposed to air. *Sterile base* pulvinate or somewhat dendroid, upper portion turning the same colour as glebal trama at maturity when exposed to air, the lower portion turning the same colour as peridium. *Odour* pleasant, slightly sweet, refreshing, similar to pandan leaves (*Pandanus amaryllifolius* Roxb.).

Basidiospores globose to subglobose, weakly dextrinoid, spinose, 9.3–(9.5–)14.8(–16.6) × 8.4–(9.1–)13.9(–14.4) µm, mean 12 × 11.2 µm (SD: 1.34 [length], 1.33 [width]), *Q* = 0.96–1.23, walls 1–2.3 µm thick, with pedicel up to 10 µm long at the base, surface covered with dense, relatively small, conical to polygonal spines with a single cavity inside the walls of each ornament, 12–16 spines per circumference, 0.9–(1–)2.6(–3.3) × (1.3–)1.4–3(–3.2) µm, mean 1.7 × 2.2 µm in water. *Basidia*

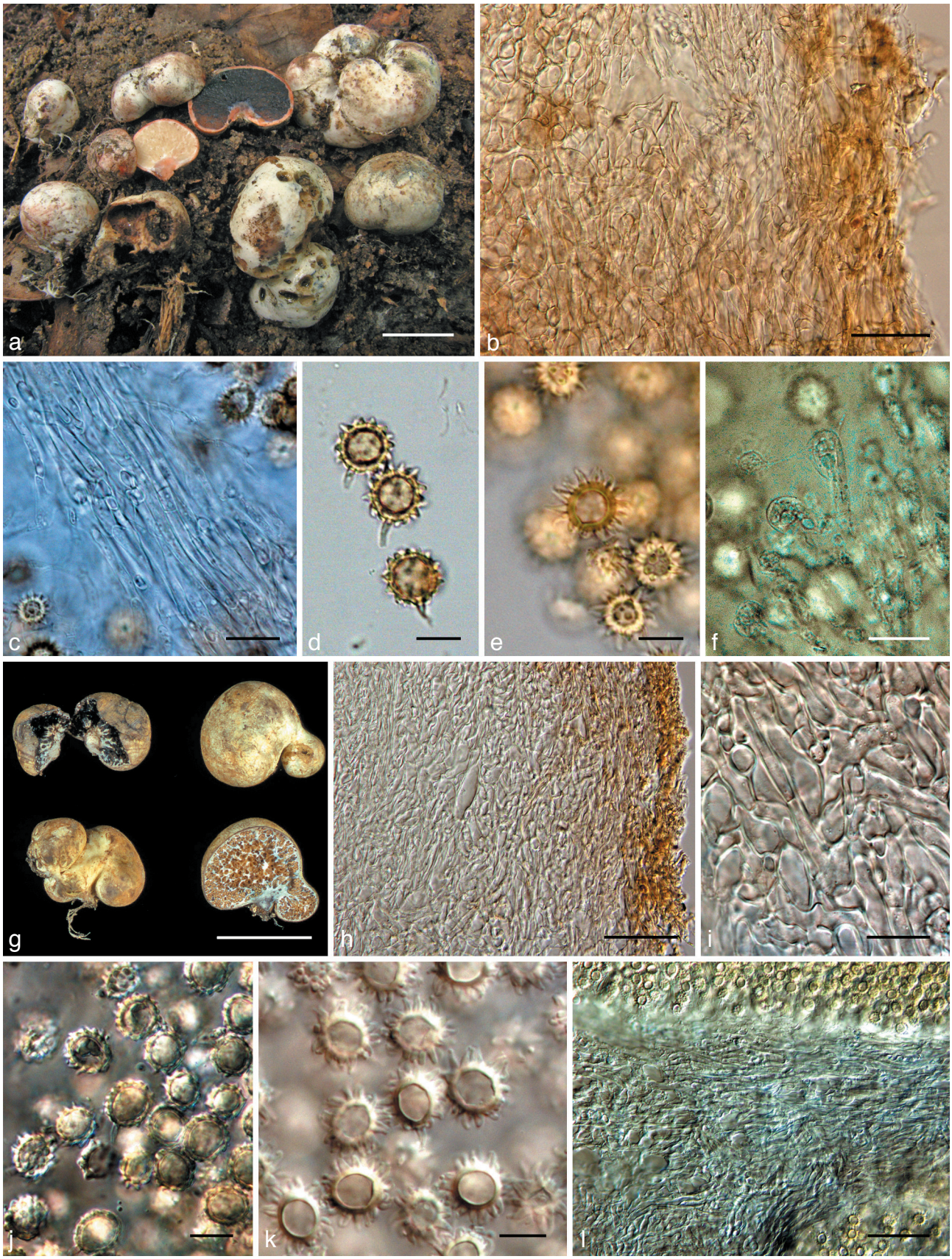


Fig. 14 a–f: *Octaviania yaeyamaensis* (KPM-NC0017819, holotype). a. Basidiomata; b. peridium; c. tramal hyphae; d. basidiospores mounted in water; e. basidiospores mounted by lactoglycerol after presoaking in 3 % KOH; f. basidia. — g–l: *O. etchuensis* (KPM-NC0017822, holotype). g. Basidiomata; h. peridium; i. context of peridium; j. basidiospores mounted in water; k. basidiospores mounted by lactoglycerol after presoaking in 3 % KOH; l. trama. — Scale bars: a, g = 1 cm; b, h, l = 50 µm; c, i = 20 µm; d–f, j, k = 10 µm.

clavate, 2- or 4-spored, 23–33 × 8–12.5 µm, mean 27.6 × 10.5 µm, evanescent, hyaline, sterigmata 3.5–12 µm long. *Cystidia* absent. *Subhymenium* absent. *Hymenia* poorly developed, composed of basidia and interspersed basidioles. *Trama* of white, thin-walled (up to 0.8 µm thick), filamentous hyphae 2.5–9 µm broad, more or less parallel to hymenium. *Sterile base* of densely interwoven, white to ochraceous, thin-walled (up to 1 µm thick), partly inflated, filamentous hyphae 3–15 µm broad. *Peridium* well developed, 400–900 µm thick when fresh; peridiopellis 70–160 µm thick, of repent, thin-walled (up to 1 µm thick), non-inflated filamentous hyphae 2.5–13.2 µm broad, subparallel to surface, hyphae in outermost portion pigmented ochraceous-brown; peridial context white under the DIC microscope, composed of subspherical, thick-walled (0.9–2.7 µm thick), inflated cells up to 78 µm diam intermingled with inflated, thin-walled (up to 1.2 µm thick), filamentous hyphae 4–25 µm broad often filled with oleiferous, intracellular pigments.

Habitat, Distribution & Season — Under *Castanopsis sieboldii* subsp. *lutchuensis*; Ishigaki Isl.; early winter (December).

Holotype. Japan, Okinawa Pref., Ishigaki Isl., Ishigaki-shi, on southern foot of Mt Omoto, 18 Dec. 2009, T. Orihara, KPM-NC0017819 (*Orihara 1137*; isotype TNS-F-41416).

Another specimen examined. Japan, **Okinawa Pref**., Ishigaki Isl., Ishigaki-shi, on southern foot of Mt Omoto, 12 Dec. 2009, T. Orihara, KPM-NC0017818 (*Orihara 1127*).

Notes — The subtropical *O. yaeyamaensis* shares similar microscopic characters (i.e., medium-sized basidiospores surrounded by relatively small spines that each have only a single cavity) and habitat with *Octaviania* sp. "E", which was collected from Amami-oshima Island, about 700 km northeast from Ishigaki Island. Molecular data, however, confirm that they were distinct species in the same subgenus (Fig. 1–3). *Octaviania yaeyamaensis* is also morphologically similar to *O. malaiensis* (Corner & Hawker) Pegler & T.W.K. Young, which is one of the few known tropical species. Both species have whitish peridia, distinctly cyanescent glebae, and small spiny basidiospore ornaments with single cavities. However, *O. malaiensis* differs in its smaller basidiospores (i.e., mostly less than 10 µm diam) and basidiospore ornaments (i.e., less than 1.6 µm high in water). The combination of a rubbery, developed peridium that tinged more or less yellowish at maturity in combination with the pandan-like odour of the mature basidiomata is characteristic to *O. yaeyamaensis*.

Octaviania etchuensis Orihara, *sp. nov.* — MycoBank MB563199; Fig. 14g–l; Map 1

Etymology. The epithet refers to the old name for Toyama Prefecture, Japan, where the holotype specimen was collected.

Basidiomata solitary or in small clusters, subhypogeous, up to 1.5 cm diam, subglobose to depressed globose, firm, rubbery, often with a short stipe up to 4 mm high at the base, surface smooth or partially with concolorous mycelial tufts, whitish in youth, dirty yellow to fulvous with reddish brown tint at maturity, turning bluish green to blackish where touched or bruised, with whitish dirty yellow to light-yellow rhizomorphs at the base. *Peridium* 0.3–1 mm thick when fresh, rubbery, context white. *Gleba* pale brown when immature, then blackish brown at maturity, glebal chambers mostly filled with masses of basidiospores and immersed in a glutinous matrix, trama white, turning bluish green and sometimes finally turning blackish when cut. *Sterile base* pulvinate or somewhat dendroid, beige, occasionally turning blackish when exposed to air. *Odour* faint, pleasant, similar to that of *O. yaeyamaensis*.

Basidiospores globose to broadly ellipsoid, weakly dextrinoid, spinose, 9.3–(9.4–)12.3(–12.8) × 8.1–10.8(–11.6) µm, mean 10.8 × 9.4 µm (SD: 0.75 [length], 0.67 [width]), *Q* = 1.04–1.15–1.36, walls 1–2 µm thick, with pedicel up to 6 µm long at the base, surface covered with dense, relatively small, low, polygonal spines with single cavity inside the walls, 14–21 spines per circumference, 0.8–2.4 × (1–)1.1–2.9(–3) µm in water, mean 1.6 × 2 µm. *Basidia* clavate, colourless, 2- or 4-spored, evanescent, mostly collapsed. *Cystidia* and *subhymenium* not seen. *Hymenia* poorly developed, composed of basidia and interspersed basidioles. *Trama* colourless with light microscopy, composed of densely interwoven to subparallel, non-inflated, thin-walled (up to 0.8 µm thick), filamentous hyphae 2–7.5 µm broad, hyphae in fork of tramal plates loosely interwoven, filamentous. *Sterile base* of densely interwoven, colourless to slightly brownish, non-inflated filamentous hyphae 3.5–10(–14) µm broad, walls c. 1 µm thick. *Peridium* 200–750 µm thick in dried specimen; peridiopellis up to 150 µm thick, ochraceous to golden-yellow at surface, inner paler to colourless, of narrow, non-inflated filamentous hyphae 1.8–6.5 µm broad, partially inflated to 25 µm diam, parallel to subparallel to surface, hyphae in outermost portion strongly pigmented, walls up to 1.3 µm thick; peridial context up to 600 µm thick, colourless to slightly brownish, of densely interwoven to subparallel, filamentous hyphae when immature, then becoming darker and pseudoparenchymatous with cells up to 35 µm diam at maturity intermingled with narrower, thick-walled, filamentous hyphae, mature cell walls up to 3 µm thick, oleiferous hyphae not observed.

Habitat, Distribution & Season — Subhypogeous in *Quercus serrata* and *Pinus densiflora* forests, rare; Honsyu (Japan); autumn (September to November).

Holotype. Japan, Toyama Pref., Nakakniikawa-gun, Tateyama-machi, Tochizu, in *Q. serrata* and *Pinus densiflora* forest, 16 Sept. 2001, M. Hashiya, KPM-NC0017822 (*Orihara 368*; split: *Hashiya 2785*; isotype TNS-F-41417).

Other specimens examined. Japan, **Toyama Pref**., Nakakniikawa-gun, Tateyama-machi, Tochizu, in *Q. serrata* and *Pinus densiflora* forest, 18 Sept. 2000, T. Ohara, KPM-NC0017821 (*Orihara 367*; split: *Hashiya 2449*); **Kyoto Pref**., Sonobe-cho, Ruri-kei, 11 Nov. 2001, A. Kajiyama, KPM-NC0017820 (*Orihara 214*); **Hyogo Pref**., Kobe-shi, Yamada-cho, Shimotanigami, under *Q. serrata*, 24 Sept. 2011, S. Koutoku, KPM-NC0017849.

Notes — *Octaviania etchuensis* is a rare species that is closely related to *O. yaeyamaensis*. Together these species constitute a unique monophyletic group within subg. *Fulvoglobus* (Fig. 1–3). Morphologically, both of these species have firm, moderately developed peridia, reduced appendages on the pedicels, and small spiny ornaments on their basidiospores. However, *O. etchuensis* has only been collected in temperate forests containing species of the deciduous *Fagaceae* and *Pinus* species whereas *O. yaeyamaensis* is known from subtropical forests with *Castanopsis sieboldii* subsp. *lutchuensis*. Morphologically, *O. etchuensis* has slightly smaller basidiospores than *O. yaeyamaensis*. In addition, *O. etchuensis* also has a more yellowish peridium that turns bluish green to blackish when touched or bruised whereas the peridium of *O. yaeyamaensis* has other staining reactions but does not turn black. The basidioma colour and the basidiospore dimensions of *O. etchuensis* are almost the same as those of *O. kobayasii*, but the subhymenial layer of the latter species is translucent and more developed, and the basidiospore ornaments of this species are larger than those of *O. etchuensis*.

Octaviania* subgenus *Octaviania

Typus subgeneris. Octaviania asterosperma Vittad.

Basidiomata hypogeous to subepigeous, soft, surface smooth to floccose to rimose, surface white when immature, then off-white to fuligineous grey at maturity, turning red to reddish brown or bluish green to cyaneous and finally blackish when injured. *Peridium* mostly thin, not becoming rubbery, context of

thin-walled, non-inflated or partly inflated filamentous hyphae usually not exceeding 20 µm broad.

Notes — Subgenus *Octaviania* is an autonym that results from the establishment of subg. *Parcaea* and *Fulvoglobus*. This subgenus is equivalent to *Octaviania* clade B, which includes *O. asterosperma*, *O. cyanescens*, *O. zelleri* (= *O. nigrescens* (Zeller) Singer & A.H. Sm.), *O. tasmanica*, and *O. asahimontana*. The nLSU and multigene phylogeny indicates that the subgenus also includes other European *Octaviania* species that are morphologically similar to *O. asterosperma* (Fig. 1, 3). However, we so far refrain from concluding their subgeneric position since most of them have not been reported for more than 50 years and their comprehensive molecular phylogeny is still infeasible until their reliable specimens are newly collected.

Octaviania zelleri Orihara & M.E. Sm., *nom. nov.* — MycoBank MB564118

≡ *Hydnangium nigrescens* Zeller, Mycologia 40, 6: 641, 1948.

= *Octaviania nigrescens* (Zeller) Singer & A.H. Sm., Mem. Torrey Bot. Club 21, 3: 11. 1960; non J.W. Cribb, Papers of the Department of Botany, University of Queensland 3: 249. 1958 (as '*Octavianina nigrescens*').

Etymology. The epithet is named in honour of the authority of the basionym, Prof. Sanford Myron Zeller (1885–1948), who significantly contributed to taxonomy of sequestrate and gasteroid fungi.

Notes — The species was first described by Zeller (1948) as *Hydnangium nigrescens* based on a specimen collected from New York, USA. The species was later transferred to *Octaviania* by Singer & Smith (1960). However, Cribb (1958) had already proposed the name *O. nigrescens* based on a different type collected from Queensland, Australia. Thus, *Octaviania nigrescens* (Zeller) Singer & A.H. Sm. is nomenclaturally illegitimate. Although the taxonomic treatment of this species was not a main objective of this publication, we consider this nomenclatural

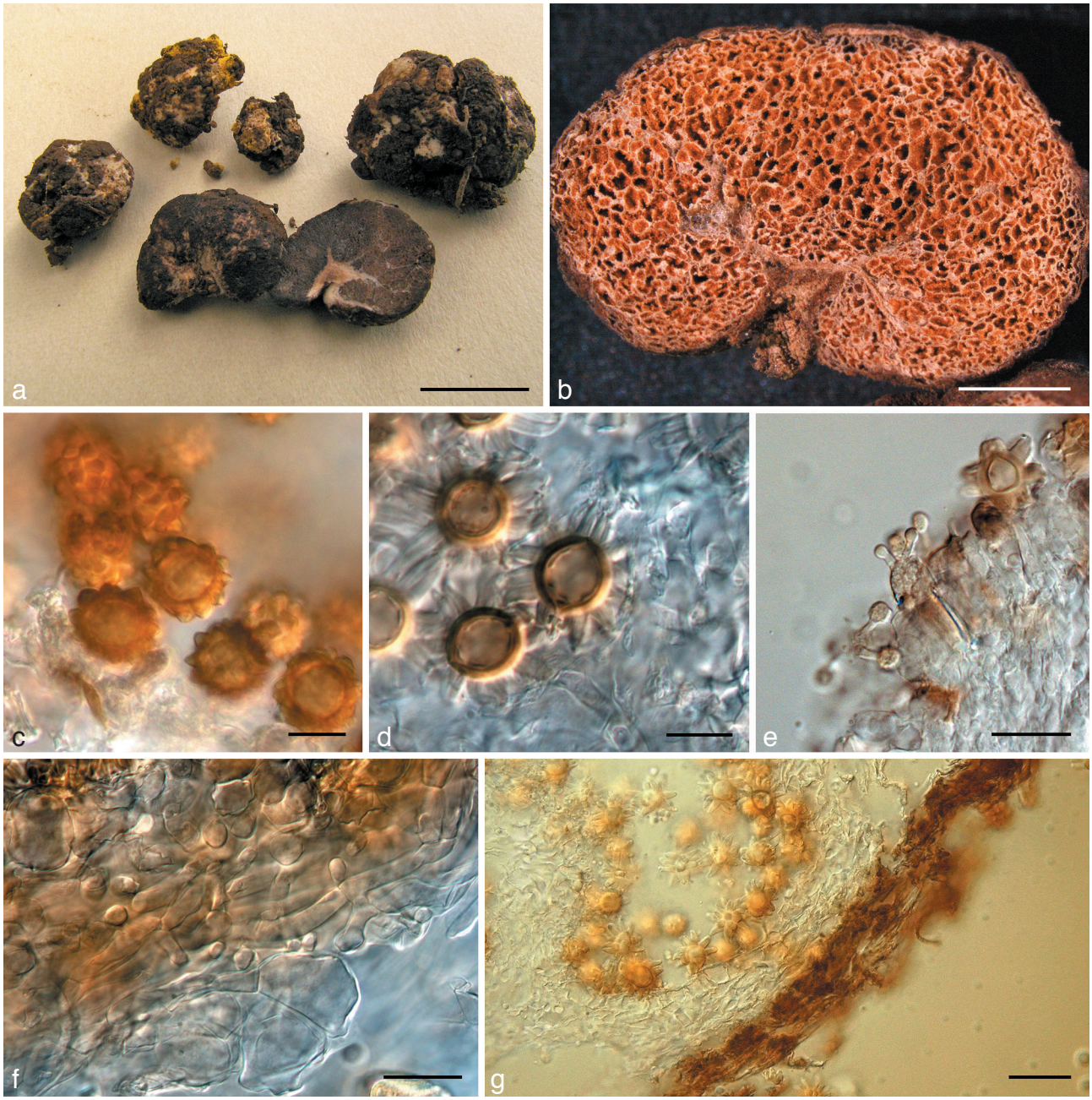


Fig. 15 *Octaviania asahimontana*. a. Basidiomata (KPM-NC0017825). The yellow basidiomata are parasitized by *Sepedonium chrysospermum*; b. longitudinal section of air-dried basidioma (KPM-NC0017823, holotype); c. basidiospores mounted in water (holotype); d. basidiospores mounted in lactoglycerol after presoaking in 3 % KOH (KPM-NC0017825); e. basidia (KPM-NC0017824); f. tramal hyphae and inflated cells (KPM-NC0017824); g. peridium mounted in lactoglycerol after rehydration with 3 % KOH.

revision necessary in order to clarify the taxonomy of the genus *Octaviania*. Accordingly, we herein propose a substitute name, *O. zelleri*, for this taxon.

Octaviania asahimontana Orihara, *sp. nov.* — MycoBank MB563200; Fig. 15

Etymology. The epithet referring to the type locality for the species, Mt Daisetsu, which is located in the middle of Hokkaido. Mt Asahi-dake is a part of Mt Daisetsu.

Basidiomata solitary to gregarious, hypogeous to subhypogeous, up to 2.5 cm diam, subglobose to tuberculate, soft, more or less fragile, sessile, surface smooth to slightly tomentose, pure white to greyish white, turning red when touched or bruised, finally becoming dark reddish brown to black. *Peridium* not well developed, very thin but persistent. *Gleba* cream-coloured to pale brown when young, then blackish brown at maturity, glebal chambers minute (< 0.2 µm diam), with only a minimal glutinous matrix, trama whitish in thick portion but somewhat translucent in the narrower portion, the narrow portion of trama gradually turning blackish when exposed to air. *Sterile base* usually well developed, dendroid, white to pale whitish brown and columella-like. *Rhizomorphs* white. *Odour* unknown.

Basidiospores globose to broadly ellipsoid, weakly dextrinoid, warty to spiny, brown at maturity, 12.6–(13–)17.1(–17.7) × 11.3–15.6(–15.8) µm, mean 14.9 × 13.4 µm (SD: 1.11 [length], 1.07 [width]), *Q* = 0.95–1.27, walls 1.8–3 µm thick but exosporium gradually swollen up to 3.5 µm thick when mounted in acidic or alkaline solutions, surface densely covered with large, polygonal spines 1.5–3.7(–3.8) × 2.2–(2.4–)5.5(–6.4) µm, mean 2.6 × 3.9 µm with 1–3 cavities inside each spore ornament wall. *Basidia* clavulate to doliiform, 2–4-spored, hyaline, evanescent, 17–30 × 8.5–14.2 µm, mean 24 × 11.5 µm, sterigmata 4–10 µm long. *Hymenium* composed of basidia and clavulate, doliiform or subspherical basidioles. *Trama* of white, thin-walled (up to 0.8 µm thick), non-inflated filamentous hyphae 2.5–6(–7) µm broad with translucent, polygonal to subspherical cells up to 33 µm diam, with bundles of parallel, filamentous hyphae running in the centre of the tramal plates. *Peridium* thin, 30–200 µm thick, composed of only one layer, of thin-walled (up to 0.8 µm thick), white to ochraceous, filamentous hyphae 2–7 µm broad, hyphae almost congeneric with the tramal hyphae. *Oleiferous hyphae* often present within tramal tissue and peridial context, sinuate, reddish brown, partly inflated, 3.5–9 µm broad. *Clamp connections* absent in all tissues.

Habitat, Distribution & Season — Under *Betula ermanii* Cham. in the mountain areas in central Hokkaido (Japan); summer (August).

Holotype. Japan, Hokkaido, Kamikawa-cho, on the mid-slope of Mt Daisetsu, 16 Aug. 2006, S. Sato, KPM-NC0017823 (*Orihara 501*), holotype (isotype TNS-F-41418).

Other specimens examined. Japan, **Hokkaido**, Kamikawa-cho, on the mid-slope of Mt Daisetsu, 10 Aug. 2009, S. Sato, KPM-NC0017824 (*Orihara 1023*); the same locality, 12 Aug. 2009, S. Sato, KPM-NC0017825 (*Orihara 1024*) & KPM-NC0017826 (*Orihara 1027*; parasitized by *Sepedonium chrysospermum*).

Notes — Among Japanese *Octaviania* spp., *O. asahimontana* is unique in having a well-developed, dendroid sterile base (columella) and clavulate to doliiform basidia as well as its association with *Betula* trees in the boreal region. Two morphologically similar European species, *O. lanigera* Hesse and *O. lutea* Hesse are also collected under *Betula* trees in Germany. *Octaviania lanigera*, however, is morphologically distinct from *O. asahimontana* in having an undeveloped, pulvinate sterile base and a thicker peridium (nearly 1 mm) (Dodge & Zeller 1936, Singer & Smith 1960). We observed an authentic specimen of *O. lanigera* (NY780603) that was collected by R. Hesse in Germany 10 years after the holotype description, and confirmed that its basidiospores were also smaller than *O. asahimontana* (mean 11.8 × 10.6 µm excl. ornamentation, n = 15). Basidiospores of an authentic *O. lutea* specimen collected by R. Hesse (NY780607) were almost identical to that of *O. lanigera* and, thus were also smaller than basidiospores of *O. asahimontana* (mean 12.5 × 11.3 µm excl. ornamentation, n = 12). *Octaviania cyanescens* Trappe & Castellano, the probable sister species of *O. asahimontana* (Fig. 3, 4), has similar basidiospore morphology to *O. asahimontana* but differs in having strongly cyanescent basidiomata and a gleba filled with a blackish brown spore mass.

The almost non-glutinous glebal cavities and the basidiospore walls that become swollen when mounted in acidic or alkaline solutions, are reminiscent of the genus *Heliogaster*, another morphologically similar, but independent sequestrate genus (Orihara et al. 2010). Phylogenetic analyses clearly indicate that these similarities were the result of convergent evolution and also clarified that *O. asahimontana* is nested within the subclade B with Australian, European, and North American taxa and not with other Japanese taxa (Orihara et al. 2010 and this study). This suggests a biogeographical history that is independent from the other Japanese species.

DOUBTFUL SPECIES

Octaviania asterosperma sensu Minakata ex Kobayasi, Otani, & Hagiw., Fungal enumeration by Kumagusu Minakata 1: 92. 1987; non Vittad., Monogr. Tuberac.: 17. 1831.

In November 1932, one basidioma of an *Octaviania* species was collected in Iwatamura, Kii (known today as Wakayama Prefecture). Mr. Kumagusu Minakata examined the basidioma and named it *Octaviania atrovirens* Minakata nom. inval., leaving a colour sketch and description (Kobayasi et al. 1987). Kobayasi et al. (1987) later examined the sketch and description and identified the specimen as *O. asterosperma*. Undoubtedly, however, this description is insufficient to accurately identify the specimen (i.e., the description is based on only one basidioma and lacks microscopic observations), but it is not likely conspecific with the holotype of *O. asterosperma.* The yellowish tinge and bluish green stains mentioned in the description indicate that the specimen probably belongs to subg. *Fulvoglobus* and could represent either *O. kobayasii* or *O. hesperi.* However, since we have not been able to examine the specimen, its identity remains uncertain.

Key to the Japanese species of Octaviania (with notes on morphologically similar taxa from other world regions)

1. Basidiomata whitish, occasionally with an yellowish tinge, finally turning black when touched or bruised, peridium thick, usually exceeding 0.4 mm thick, occurring under *Castanopsis* or evergreen *Quercus* spp., basidiospore ornamentation containing several longitudinal cavities inside the walls . . . . . Subg. *Parcaea* (see Table 3, Fig. 4, 5)
1. Basidiomata becoming yellowish to brown at maturity, or turning reddish or bluish green when touched or bruised, found beneath trees in the *Fagaceae* or *Betulaceae* . . . 2
2. Basidiomata off-white to fuligineous grey at maturity. Peridium composed of thin-walled, filamentous hyphae, thick-walled pseudoparenchymatous hyphae absent . . . . . 3 (Subg. *Octaviania*)
2. Basidiomata firm or rubbery, becoming more or less yellowish or brownish at maturity, found beneath trees in the *Fagaceae*.

Peridial context of inflated, isodiametric to polygonal hyphae in most part at maturity, becoming pseudoparenchyma . . . . . 6 (Subg. *Fulvoglobus*)

3. Average size of basidiospores exceeding 14 µm diam. — Japan or North America 4
3. Average size of basidiospores not exceeding 14 µm diam. — Europe. 5
4. Basidiomata fragile, not becoming deep blue when rubbed or bruised, found under *Betula* sp. Sterile base more or less developed becoming a dentroid columella . . . . . *O. asahimontana*
4. Basidiomata firm, distinctly cyanescent, found under conifers (e.g., *Tsuga mertensiana*). Sterile base reduced, indistinct . . . . . *O. cyanescens* (North American species phylogenetically close to *O. asahimontana*)
5. Ornaments of basidiospores mostly contain one, simple cavity. Basidiomata found beneath trees in the *Fagaceae* . . . . . *O. asterosperma* (the generic type species)
5. Ornaments of basidiospores contain multiple (2–6) cavities that look labyrinthiform to zonate to cochleae in horizontal section. Basidiomata found under trees in the *Betulaceae* . . . . . *O. lanigera* / *O. lutea* species complex (the European group that needs taxonomic re-evaluation based on molecular data)
6. Peridium well developed, exceeding 0.8 mm thick in some portions. Basidiospore ornaments small, mostly less than 2.6 × 3 µm in water (on average less than 2 µm high), with a single cavity inside each spore ornament. Appendages on the basidiospore pedicels reduced and indistinct . . . 7
6. Peridium thin, less than 0.7 µm thick. Basidiospore ornaments larger, with average height in water exceeding 2 µm. Appendages on the basidiospore pedicels somewhat developed and usually visible under light microscopy at ×1000 9
7. Average size of basidiospores less than 10 µm diam . . . *O. malaiensis* (species known from the Malay Peninsula)
7. Average size of basidiospores exceeding 10 µm diam . 8
8. Basidiomata not staining yellow. Average size of basidiospores 12 × 11.2 µm (Q = 0.96–1.23). — The Yaeyama Islands (the south-western Ryukyu Archipelago). . . . . *O. yaeyamaensis*
8. Basidiomata pale yellow to ochraceous at maturity. Average size of basidiospores 10.8 × 9.4 µm (Q = 1.04–1.36). — Honsyu (the mainland of Japan) *O. etchuensis*
9. Surface of peridium warty or scaly, brown, turning dark green when bruised . . . . . *O. durianelloides*
9. Surface of peridium smooth to slightly floccose, turning reddish or bluish green when bruised 10
10. Average size of basidiospores exceeding 12 µm diam, basidiospore ornaments large, containing multiple cavities in each spore ornament that are slit-like in vertical section and labyrinthiform to zonate to cochleae in horizontal section . . . . . *O. hesperi*
10. Average size of basidiospores not exceeding 12 µm diam. Basidiospore ornaments less than 4.5 µm in width, usually containing 1–3 cavities in each spore ornament that are simple to curved in horizontal section 11
11. Glebal trama consisting of two distinct layers: inner layer white to cream colour and composed of filamentous hyphae; outer layer translucent, of developed hymenia and subhymenia . . . . . *O. kobayasii*
11. Glebal trama of a single, whitish to cream coloured layer 12
12. Basidiomata soft, occurring under *Castanopsis sieboldii* subsp. *lutchuensis*. — Amami-oshima Island (the northern Ryukyu Archipelago) . . . . . *Octaviania* sp. "E"
12. Basidiomata firm, rubbery, occurring under *Fagus crenata* or *Quercus crispula*. — Mainland of Japan . . . . . *O. japonimontana*

DISCUSSION

In this study we have proposed 11 new species and 2 subgenera (plus 1 autonym) in the genus *Octaviania*. At least one additional species (i.e., *Octaviania* sp. "E") was shown to be phylogenetically unique but will await formal description until mature specimens can be obtained and studied. The description of 11 species from Japan constitutes an approximately 60 % increase in the number of accepted *Octaviania* species to c. 30 species (Kirk et al. 2008 and see introduction of this paper). Since the Japanese Archipelago has partially and repeatedly been connected to the continent until the late of the Pleistocene (Fujii 1990), these findings suggest that the genus *Octaviania* is probably highly diverse in Asia. It is likely that many more species remain to be described, particularly from Asian tropical and subtropical habitats where a few unique *Octaviania* species have already been reported (Corner & Hawker 1953, Pegler & Young 1979).

All of the phylogenetic analyses in this study recovered the three highly divergent clades within the genus *Octaviania* (clades A–C; Fig. 1–3). Clade A is morphologically and ecologically distinct and we have proposed a new subgenus *Parcaea* for this group. The other two have fewer distinct diagnostic morphological characters, despite the significant phylogenetic divergence among the three subgenera. One important character that differentiates subg. *Octaviania* is the peridial context that consists of thin-walled filamentous hyphae and does not become truly pseudomarenchymatous at maturity. In contrast, subg. *Fulvoglobus* is characterized by basidiomata that become yellowish to tawny to rusty at maturity and a peridial context that consists of inflated hyphae intermingled with pseudoparenchymatous cells. However, immature specimens are very difficult to identify morphologically to the species level. Therefore, other methods that are applicable to identification of specimens at any stage, such as chemotaxonomical approaches as well as molecular techniques, would be helpful to facilitate subgenus-level delimitation in the genus *Octaviania*.

At the species level, we found few morphological characteristics that can be routinely used to discriminate among the Japanese *Octaviania* spp. Variations in the ultrastructure of cavities inside basidiospore ornaments is informative overall, but these characteristics are not always distinctive. It is possible, in most cases, to morphologically distinguish similar species by a combination of spore ornaments, basidiospore size, and habitat requirement or ectomycorrhizal host plant association. It should be noted here that the presence of cavities is not a character unique to the genus *Octaviania* (Orihara et al. 2010).

The phylogenetic analyses of the nLSU and combined dataset showed two different lineages of *O. asterosperma* (Fig. 1, 3). DNA sequences from the Spanish specimen (Trappe23377; nLSU sequence: JN37847) were recently generated as part of this study. This specimen was morphologically congruent with the lectotype specimen of the species (a duplicate sent from Muséum national d'Histoire naturelle [PC] to the USDA Forest Service Herbarium, Oregon, USA), and it was conspecific to *O. asterosperma* specimens collected from UK in the ITS phylogeny (Fig. 4). This indicates that the name *O. asterosperma* has erroneously been applied to more than one European species.

The widespread use of the name *O. asterosperma* may obscure the true species distribution and confuse the taxonomy of other European *Octaviania* species, many of which have not been reported or closely studied in recent decades.

Although it is possible to identify most of the Japanese species of *Octaviania* morphologically, it is difficult or in some cases almost impossible to discriminate between the species in the subg. *Parcaea* (= *Octaviania* clade A) based on morphology alone. Accurate species delimitation within this subgenus is only currently possible via DNA sequences. All the phylogenetic analyses except nLSU single-gene analyses were highly informative and clearly separated the four cryptic species of subg. *Parcaea* (Fig. 1–5). To evaluate the fidelity of these cryptic species, we also conducted distance-based network analyses, which visualize all the possible topology inferred from a dataset and, thus, can help to identify traces of hybridization, recombination or horizontal gene transfer (Huson 2009, Huson & Bryant 2006). Although we cannot conclude reproductive isolation of each species based only on the few DNA loci used in this study, given the sympatric nature of these species (i.e., geographic distribution and vegetation), we consider that the networks shown in Fig. 4 authenticate that these cryptic species are reproductively independent (e.g., would be recognized by the biological species concept; Mayr 1942). Although the description of morphologically cryptic species is confusing, it is indispensable for precise understanding of speciation, phylogeography, and accurate conservation of species in the subg. *Parcaea*. This study also shows that phylogenetic network methods can contribute to species-level or infraspecific delimitation of sequestrate fungi, since many of these fungi are so difficult to culture that it is unrealistic to directly apply the biological species concept to their taxonomy.

Phylogeography of Octaviania

Despite the fact that only two taxonomically undetermined *Octaviania* spp. had previously been reported in Japan (Kobayashi et al. 1987, Yoshimi & Doi 1989) our data indicate that the genus is highly diverse across the country (Fig. 1–4). In the most well resolved phylogeny based on the multigene dataset (Fig. 3), the 12 species-level lineages were scattered across the 3 subgenera (i.e., clades A–C). *Octaviania asahimontana* is nested within the subclade B, which also includes European, Australian, and North American taxa. Furthermore, this species and *O. herperi* have independent sister relationships with the North American taxa in subg. *Octaviania* and *Fulvoglobus*, respectively (Fig. 1–3). Geographically, the mainland of Japan had repeatedly been connected to the Asian continent until the middle Pleistocene via Tsushima and Tsugaru Straits (c. 0.16 Mya B.P. and 0.13 Mya B.P., respectively; Kizaki & Oshiro 1977, Fujii 1990, Oshima 2000; Map 1). Given that sequestrate fungi depend largely on animal mycophagy for their spore dispersal (Kretzer et al. 2005) and that overseas spore dispersal by these fungi is thought to be rare, the extant species in Japan are considered to have been derived from the continent before the last submergence of these land bridges. From a phylogeographical standpoint, this strongly suggests that *Octaviania* is also highly diverse in China and Southeast Asia, where the genus has not been adequately sampled. This also implies that records of the East Asian *Octaviania* species need to be re-evaluated since Asian specimens are usually assigned to European or North American species names (e.g., Tao et al. 1998). Additionally, more extensive examination of the East Asian *Octaviania* collections will be essential for more precise understanding of biogeographical history of Japanese *Octaviania* spp. as well as that of Southeast Asian species such as *O. borneensis* and *O. malaiensis*.

Within *O. nonae*, there were slight but distinct differences in the ITS and nLSU sequences between Amami-oshima and Honsyu/Kyusyu (mainland) specimens (i.e., 2.6 % in ITS and 0.9 % in nLSU). This could reflect geographic isolation of the northern Ryukyu superisland including Amami-oshima Island from the continent by the Tokara Strait, which had been formed by the early Pleistocene (Hikida & Ota 1997, Ota 1998, Otsuka & Takahashi 2000; Map 1). The Tokara Strait is biogeographically considered to be the border between Palearctic and Oriental regions, and similar divergence is widely recognized in amphibians and reptiles between these regions (Hikida & Ota 1997, Toda et al. 1999). This strongly suggests that the four cryptic species of subg. *Parcaea* had speciated by the Gelasian in the early Pleistocene (1.806–2.588 Mya B.P.), the era that the Japanese Archipelago had been connected to the Asian continent. Based on this estimation, subg. *Parcaea* is considered to be of continental origin and it is highly possible that other unknown species of the subgenus are present in East or Southeast Asia. As far as we know, this is the first example of distinct phylogeographic divergence of sequestrate fungi between the mainland of Japan and the Ryukyu Archipelago.

Another phylogeographically notable relationship is that the *O. etchuensis* specimen collected from Toyama Prefecture, central Honsyu (the mainland of Japan), was sister to *O. yaeyamaensis* collected from Ishigaki Island, one of the southernmost islands of Japan and c. 1 800 km distant from Toyama Prefecture (Map 1). This seems strange based on the present geography of Japan, but can be explained in accordance with paleogeography of the region. The Ishigaki Island had been repeatedly connected to Taiwan and China via a land bridge until the middle or late Pleistocene (Ota 1998, Kimura 2000). Thus, we presume that the common ancestor between *O. etchuensis* and *O. yaeyamaensis* was present on the Asian continent and it had already diverged from the other lineages of the clade C shown in Fig. 3. This also implies that extant species closely related to *O. etchuensis* and *O. yaeyamaensis* might still be present in the region.

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