

FULL PAPER

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## Three species of *Heterobasidion* (Basidiomycota, Hericiales), *H. parviporum*, *H. orientale* sp. nov. and *H. ecrustosum* sp. nov. from East Asia

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**Abstract** We describe and illustrate three *Heterobasidion* species distributed in East Asia, based on both dried specimens and cultures. *Heterobasidion parviporum*, formerly known as *H. annosum* from Asia, is characterized by effused-reflexed basidiocarps with cuticulate pilei, small round pores, thin context and short tubes in each layer. Examination of the type specimen of *Trametes insularis* revealed that this is distinct from the East Asian species widely known as “*H. insulare*”. No prior correct name for this taxon exists, and thus we propose the name *H. orientale* sp. nov. *Heterobasidion orientale* is characterized by sessile to effused-reflexed basidiocarps covered by a thin crust, reddish brown pileus with a marginal white zone and regular to labyrinthiform pores. *Heterobasidion ecrustosum* sp. nov. is characterized by convex basidiocarps frequently covered by a crust only at the base, large regular pores and long tubes. Morphological characters of these three species are compared with other *Heterobasidion* species. Cultural characters of these three species are also described. All isolates show oedocephaloid conidiophores bearing subglobose to ovoid conidia. Conidia of *H. parviporum* are smaller than those of the other two species. Descriptions and a key to the known species of *Heterobasidion* are provided.

**Key words** *Heterobasidion annosum* · *Heterobasidion insulare* · New species · Polypores · Root rot

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### Introduction

The polypore genus *Heterobasidion* Bref. is characterized by effused-reflexed to sessile basidiocarps, dextrinoid skeletal hyphae, generative hyphae without clamp-connections, finely asperulate basidiospores and a *Spiniger* Stalpers anamorph (Gilbertson and Ryvarden 1986; Buchanan 1988). *Heterobasidion annosum* (Fr.) Bref., the type species, is a serious root rot pathogen and frequently induces necrosis of various conifers and angiosperms (Daniel et al. 1998; Krokene et al. 2001; Johansson et al. 2004; Asiegbu et al. 2005; Bodles et al. 2007). In East Asia, *H. annosum* and *H. insulare* (Murrill) Ryvarden have been widely recognized in both Japan and China (Ito 1955; Teng 1964). However, *H. annosum* s. lat. was shown to comprise several closely related species and the following three biological species are now recognized in Europe: *H. parviporum* Niemelä & Korhonen (formerly known as “Eur S-group”), *H. abietinum* Niemelä & Korhonen (“Eur F-group”) and *H. annosum* s. str. (“Eur P-group”) (Niemelä and Korhonen 1998). Dai et al. (2006) reported that the Chinese “*H. annosum*” represents *H. parviporum*. Phylogenetic studies based on three gene loci revealed that Japanese *H. annosum* s. lat. is also closely related to European and Chinese populations of *H. parviporum* (Ota et al. 2006).

After examination of collections and results of mating tests, Dai et al. (2002) detected three intersterility groups within the *H. insulare* complex in China. Dai et al. (2007b) described *H. linzhiense* characterized by large basidiospores and the presence of cystidioles. The species widely known as *H. insulare* in Japan and China was classified as “N group” by Dai et al. (2002) and was recorded as widely distributed in boreal to temperate areas in China and Japan. This finding contrasts with the tropical distribution of *Trametes insularis* Murrill (= *H. insulare*), described from the Philippines as type locality.

Ota et al. (2006) found that an undetermined *Heterobasidion* sp. distributed in southern areas of Japan represents a distinct phylogenetic species closely related to *H. araucariae* P. K. Buchanan. After a comparative study of

Japanese and Chinese specimens, the undetermined species was considered to be conspecific with the “T-type” of *H. insulare* reported by Dai et al. (2002), although a formal name for this taxon has not been designated.

In this study, we provide detailed descriptions for the three *Heterobasidion* species, i.e., one known species (*H. parviporum*) and two new species (*H. orientale* and *H. ecrustosum*), distributed in Japan and East China, after comparative examination of currently described species in this genus and we designate names for the East Asian taxa.

## Materials and methods

Macroscopic and microscopic characters of basidiocarps were described from dried specimens of the three Asian species. Materials of other *Heterobasidion* species including some type specimens were examined. Color names follow the Color Chart of Botanical Plants of Japan (Ministry of Agriculture, Forestry and Fisheries of Japan 1987) and color codes are after the Munsell System (Color Atlas 1998).

Microscopic characters were checked by examining free-hand sections mounted in Melzer’s reagent (Largent et al. 1977). Non-dextrinoid and non-amyloid reactions were described as IKI–. Basidiospore measurements were made from materials mounted in Melzer’s reagent. The following abbreviations are used in the text: L, mean spore length (arithmetic mean of all basidiospores); W, mean spore width (arithmetic mean of all basidiospores); r, ratio of length to width of a basidiospore; R, arithmetic mean of r. The term “ $n = x/y$ ” refers to  $x$  measurements of basidiospores from  $y$  specimens. In presenting the variation in the size of basidiospores, 5% of the measurements were excluded from each end of the range and are given in parentheses.

Japanese specimens examined in this study were deposited in the Mycological Herbarium of Forestry and Forest Products Research Institute, Tsukuba (TFM). Other herbaria holding specimens were abbreviated according to Holmgren et al. (1990).

Cultural studies were made on 2% malt extract agar (MEA) of the following composition: 20 g malt extract (Kanto, Tokyo, Japan), 20 g agar (Kanto) and 1000 ml water. Inocula from each culture were placed near the edge of the Petri dish (84 mm internal diameter).

Inoculated plates were incubated at 25°C in the dark and cultural characters were described mainly based on 6-week-old cultures. Species codes of Nobles (1965) and Stalpers (1978) were recorded for 6-week-old cultures. Mycelial growth rate  $K_r$  at 25°C was calculated as follows:  $R_1 = R_0 + K_r (t_1 - t_0)$ , where  $R_1$  = colony radius at time  $t_1$  and  $R_0$  = colony radius at time  $t_0$ . Conidial measurements were made as for basidiospores. Extracellular oxidase reactions were tested according to Nobles (1958) and Käärik (1965). Optimal temperature for mycelial growth was estimated by measuring the growth rate at 4, 7, 10, 13, 16, 19, 22, 25, 28,

31, 34 and 37°C, as already mentioned. Five replicates for each of three *H. parviporum* isolates, four *H. orientale* isolates, and three *H. ecrustosum* isolates were measured at each temperature.

Cultures examined in this study were deposited in NIAS Genebank and/or the culture bank of Microbial Ecology Laboratory, Forestry and Forest Products Research Institute and the culture bank of Microbiology Laboratory, Hokkaido Forestry Research Institute.

## Results

Based on the comparative studies of both dried specimens and cultures or only dried specimens, descriptions of the following seven species of *Heterobasidion* are provided below.

***Heterobasidion parviporum*** Niemelä & Korhonen, *Heterobasidion annosum*: biology, ecology impact and control: 31 (1998). Figs. 1, 2

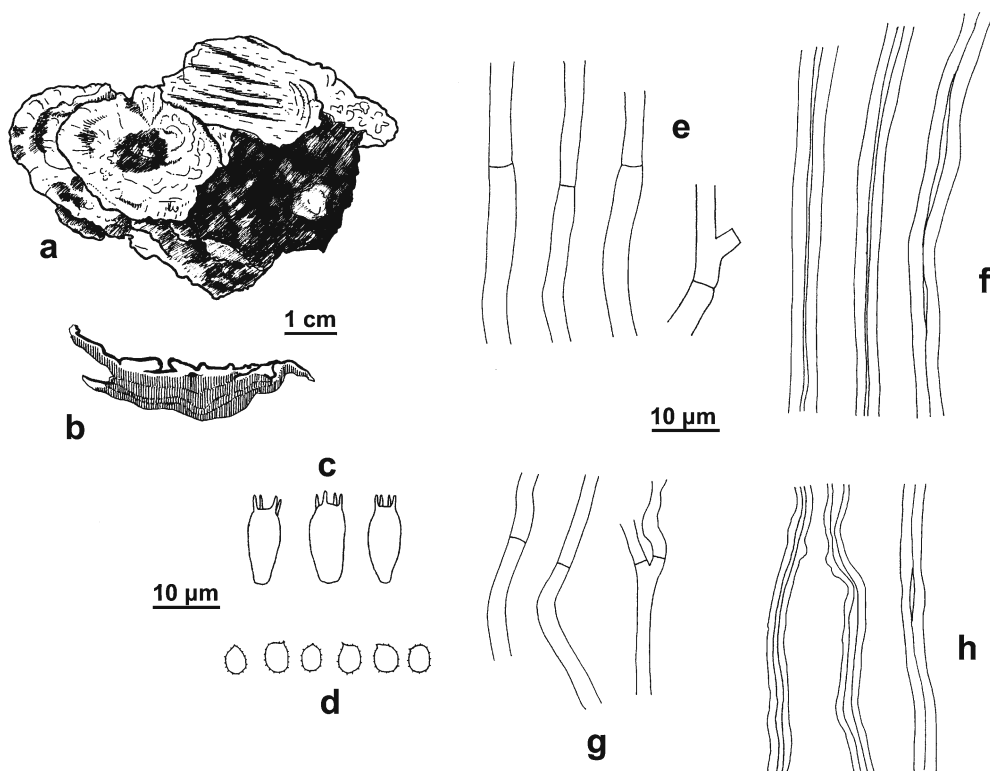
“*Fomitopsis annosa*” (Fr.) P. Karst., auct. non Fries: Ito, Mycological Flora of Japan 2:302 (1955).

“*Heterobasidion annosum*” (Fr.) Bref., auct. non Fries: Imazeki & Hongo, Colored Illustrations of Mushrooms of Japan II:168 (1989).

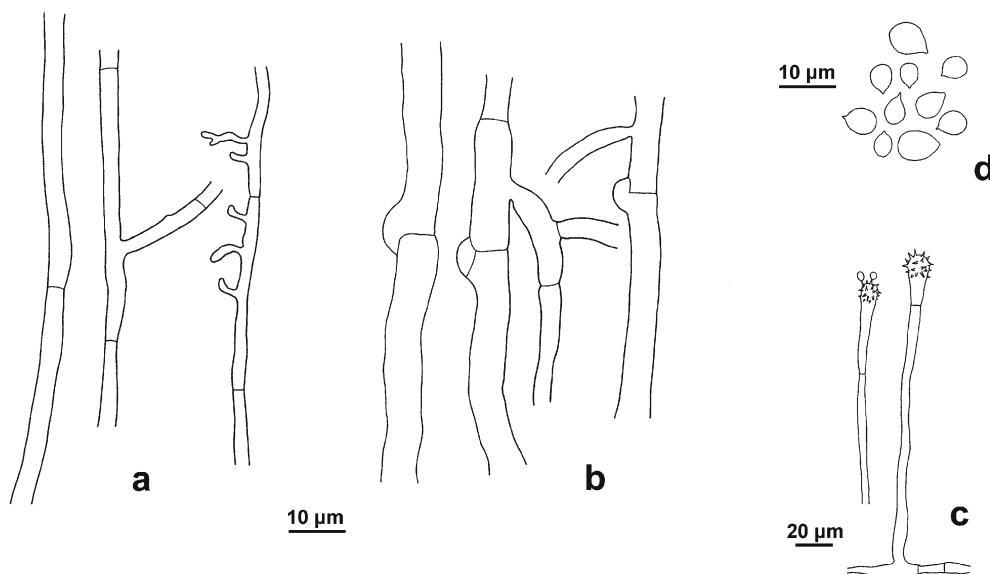
Basidiocarps mostly perennial, effused-reflexed, occasionally sessile or resupinate, usually solitary, easily separable from substrate. Pilei semicircular to irregular, laterally fused then elongated, applanate to slightly convex, 0.6–30 cm long, 0.6–10 cm wide, 0.1–3 cm thick. Pileus surface subtomentose to almost glabrous, tomentum up to 175 µm long, sulcate, azonate to subzonate with narrow bands, partly warty to rugose, rough, brown (5YR-4/4, 5/4, 10YR-5/4, 4/4) to dark brown (5YR-2/2, 2/4, 3/1, 3/2, 3/4), partly almost black (10YR-3/2). Pileus margin rounded to acute, usually thin, often undulating, concolorous with the center or with very narrow whitish bands (pale yellow, 5Y-9/2) in actively growing margin. Pore surface even, at first yellowish white (5Y-9/1) to pale yellow (5Y-9/2), drying pale yellowish orange (10YR-9/4) to yellowish orange (10YR-8/4). Pores round, regular, 4–5(–7) mm, 100–220 µm in diameter, dissepiments at first thick, becoming thin, 30–200 µm thick, entire. Sterile margin concolorous with pore surface, 1–2 mm wide. Context thin, up to 0.5 cm thick, leathery, azonate, yellowish white (5Y-9/1) to light yellow (5Y-9/4), becoming light yellowish orange (10YR-8/4) to light yellowish brown (10YR-7/4) when old, with a distinct crust; crust shiny in vertical section, dark brown to almost black (10YR-3/2), up to 140 µm thick. Tubes corky, concolorous with context, 1–3 mm deep in each layer, indistinctly stratified; occasionally new tube layer develops unevenly and patchily below the previous layer in old and inactive basidiocarps.

Hyphal system dimitic with generative hyphae and skeletal hyphae. Contextual generative hyphae thin walled, without clamp-connections, hyaline, IKI–, 1.5–3(–4) µm in

**Fig. 1.** Structures of *Heterobasidion parviporum*, from specimen (TFM F-21782). **a** Basidiocarp. **b** Vertical section of basidiocarp. **c** Basidia. **d** Basidiospores. **e** Generative hyphae from context. **f** Skeletal hyphae from context. **g** Generative hyphae from trama. **h** Skeletal hyphae from trama



**Fig. 2.** Structures of *Heterobasidion parviporum*, in culture (MAFF-420761). **a** Generative hyphae from aerial mycelium. **b** Generative hyphae with clamp-connections from colony margin. **c** Conidiophores. **d** Conidia



diameter. Contextual skeletal hyphae thick walled, walls up to 2.5 µm thick, hyaline except in cuticle, dextrinoid, 3–4(–5) µm in diameter. Tramal generative hyphae thin walled, hyaline, IKI–, 2–3 µm in diameter. Tramal skeletal hyphae thick walled, walls up to 1.5 µm thick, hyaline, dextrinoid, 2.5–3.5 µm in diameter. Cystidia absent. Basidia broadly clavate, 12–14 × 5–6.5 µm, 4-sterigmate. Basidiospores asperulate, subglobose, hyaline, IKI–, (3.3–)3.6–5.0(–5.6) × (2.9–)3.0–4.3(–4.8) µm, L = 4.4 µm, W = 3.6 µm, r = 1.0–1.5, R = 1.20 ( $n = 673/8$ ).

Cultural characters: Growth moderately fast, 4.8–7.9 mm/day, plates usually covered in 2–3 weeks, but for some

degenerated isolates not covered by 6 weeks. Advancing zone entire except for slow-growing isolates, mycelia usually sparse, appressed, hyaline to white. Mat white (5Y-9/1) to ivory white (5Y-9/2, 9/4), translucent, downy to thinly cottony, later subfelty, farinaceous with erect conidiophores, sometimes brown (5YR-4/4, 4/8, 5/4, 5/8) leathery mycelia develop in the colony and/or partly cover the colony surface after 6 weeks. Reverse unchanged after 6 weeks or partly honey yellow (10YR-7/8, 8/8). Odor indistinctive. Hymenophore not seen within 6 weeks. Optimum temperature for mycelial growth 16–22°C. Generative hyphae from the advancing zone thin walled, usually without clamp-

connections, hyaline, IKI–, 1.5–5.0(–7.5)  $\mu\text{m}$  in diameter. Generative hyphae from aerial mycelium and submerged mycelium hyaline, thin walled, IKI–; clamp-connections rare, present on wide straight hyphae, 2.0–5.5  $\mu\text{m}$  in diameter. Conidiophores arising as erect branches from prostrate hyphae, simple or branched, hyaline, up to 250  $\mu\text{m}$  long, 4–10  $\mu\text{m}$  in diameter, with an apically inflated conidogenous vesicle. Conidogenous vesicle 6–15  $\mu\text{m}$  in diameter, covered with conical denticles on which the conidia are borne. Conidia abundant, ovoid to subglobose, unicellular, smooth, hyaline, IKI–, (3–)3.5–8.0(–10.5)  $\times$  (2.0–)2.5–6.5(–8.0)  $\mu\text{m}$ , L = 5.2  $\mu\text{m}$ , W = 4.0  $\mu\text{m}$ , r = 1.0–2.0, R = 1.32 ( $n$  = 340/4).

Extracellular peroxidase activities: Gum guaiac +, 1-naphthol +, tyrosine –. Nobles' species code: 2, (5), 6, 7, (11), (12), (25), 33, 36, (38), (39), 42, (43), (47), (54), 55, 59. Stalpers' species code: 1, 3, 6, (10), (9), (12), 13, (14), 17, 18, 21, (22), 24, (25), 30, 31, (34), (35), (38), (39), (40), (44), (45), (48), (50), (51), 52, 53, 54, (55), (64), (82), (83), 86, 87, (89), 90, 93.

Hosts and substrates: JAPAN: *Abies sachalinensis* (Fr. Schmidt) Masters (including *A. sachalinensis* var. *mayriana* Miyabe & Kudo), *A. veitchii* Masters, *Picea glehnii* (Fr. Schmidt) Masters, *P. jezoensis* (Sieb. & Zucc.) Carrière. CHINA: *Abies delavayi* Franch., *A. fabri* (Mast.) Craib, *A. fargesii* Franch., *A. forrestii* var. *georgei* (Orr) Farjon, *A. nephrolepis* (Trautv. ex Maxim.) Maxim., *Larix griffithii* Hook. f. & Thomson, *Picea jezoensis*, *P. likiangensis* (Franch.) E. Pritz., *P. schrenkiana* subsp. *tianshanica* (Rupr.) Bykov, *Pinus koraiensis* Sieb. & Zucc., *Tsuga chinensis* (Franch.) E. Pritz., *T. dumosa* (D. Don) Eichler and *Populus* sp. (Dai et al. 2003, 2006, 2007a). On fallen trunks with barks and roots of fallen trees.

Distribution in East Asia: JAPAN: Hokkaido Is., subalpine areas of Honshu Is. CHINA: northern China to eastern Himalayas.

Specimens examined: JAPAN: Hokkaido Pref., Akancho, Lake Akanko, on *Abies sachalinensis*, 20 Sep. 2002, leg. S. Tokuda (TFM F-21781, ex HFB-102; TFM F-21782, ex HFB-103; TFM F-21783, ex HFB-104); same place, on *Picea glehnii*, 20 Sep. 2002, leg. S. Tokuda (TFM F-21784, ex HFB-105); Hokkaido Pref., Ashoro-cho, Mt. Meakandake, on *P. glehnii*, 9 Oct. 1996, leg. S. Tokuda (TFM F-21774, ex HFB-89); same place, on *P. glehnii*, 9 Oct. 1999, leg. S. Tokuda (TFM F-21775, ex HFB-90; TFM F-21776, ex HFB-91); same place, on *A. sachalinensis*, 9 Oct. 1999, leg. S. Tokuda (TFM F-21777, ex HFB-92; TFM F-21778, ex HFB-93); same place, on *A. sachalinensis*, 12 Oct. 2000, leg. S. Tokuda (TFM F-21780, ex HFB-101); same place, on *A. sachalinensis*, 15 Sep. 2002, leg. S. Tokuda (TFM F-21785, ex HFB-106; TFM F-21786, ex HFB-107; TFM F-21787, ex HFB-108); same place, on *A. sachalinensis*, 10 June 2002, leg. S. Tokuda (TFM F-21788, ex HFB-109); same place, on *P. glehnii*, 26 Sep. 2004, leg. Y. Ota (TFM F-21794, ex HFB-130; TFM F-21795, ex HFB-131); same place, on *P. glehnii*, 27 Sep. 2004, leg. S. Tokuda (TFM F-21796, ex HFB-132; TFM F-21797, ex HFB-135); Hokkaido Pref., Memuro-cho, Mt. Memurodake, on *A. sachalinensis*, 5 May 1997, leg. S. Tsukada (TFM F-21779, ex HFB-100); Hokkaido Pref.,

Tsubetsu-cho, Lake Chimikeppu, on *A. sachalinensis*, 30 May 2007, leg. S. Tokuda (TFM F-21773, ex HFB-197); Hokkaido Pref., Shikaoui-cho, Lake Shikaribetsuko, on *A. sachalinensis*, 4 Sep. 2004, leg. S. Tokuda (TFM F-21798, ex HFB-148; TFM F-21799, ex HFB-149; TFM F-21800, ex HFB-150); same place, on *Picea jezoensis*, 17 Sep. 2004, leg. S. Tokuda (TFM F-21789, ex HFB-123); same place, on *A. sachalinensis*, 17 Sep. 2004, leg. S. Tokuda (TFM F-21790, ex HFB-124); same place, on *P. jezoensis*, 22 Sep. 2004, leg. S. Tokuda (TFM F-21791, ex HFB-126); same place, on *A. sachalinensis*, 22 Sep. 2004, leg. S. Tokuda (TFM F-21792, ex HFB-128); same place, on *P. jezoensis*, 26 Sep. 2004, leg. Y. Ota (TFM F-21793, ex HFB-129); Hokkaido Pref., Kamikawa-cho, Sounkyo, 6 Sep. 1973, leg. K. Aoshima (TFM F-14397; F-21803); same place, on *A. sachalinensis*, Aug. 1953, leg. K. Aoshima (TFM F-14652; F-14685); Gunma Pref., Katashina-mura, Marunuma, on *Abies veitchii*, 18 Oct. 1951, leg. K. Aoshima (TFM F-14675); Nagano Pref., Mt. Yatsugatake, May 1951, leg. Hachiya (TFM, F-22380). CHINA: Jilin Prov., Antu County, Changbai Nat. Res., on *Picea* sp., 25 Aug. 2005, leg. Y.-C. Dai (TFM F-21801, ex Dai-6976); Xizang Auto. Reg., Linzhi County, Sejila Mts., on *Larix* sp., 4 Aug. 2004, leg. Y.-C. Dai (TFM F-21802, ex Dai-5725).

Cultures examined: MAFF-420761, ex HF-401, from basidiocarp tissue of F-21785; MAFF-420763, ex HF-407, from basidiocarp tissue of F-21786; MAFF-420764, ex HF-413, from basidiocarp tissue of F-21787; HF-415, from basidiocarp tissue of F-21781; MAFF-420768, ex HF-431, from basidiocarp tissue of F-21784; HF-599, from basidiocarp tissue of F-21799; HF-600, from basidiocarp tissue of F-21800; WD-1211, from decayed wood of *A. sachalinensis* var. *mayriana*, Hokkaido Pref., Akancho, Nov. 1952, leg. S. Kamei; WD-1212, isolated from decayed wood of *A. sachalinensis* var. *mayriana*, Gunma Pref., Katashina-mura, July 1952, leg. K. Aoshima; WD-1213 isolated from decayed wood of *A. sachalinensis*, Hokkaido Pref., Sounkyo, 25 Sep. 1954, leg. K. Aoshima.

Remarks: This species is characterized by perennial and effused-reflexed basidiocarps, subtomentose and sulcate pileus surface and small pores (4–5/mm) compared with other East Asian species of *Heterobasidion*. The European population has more distinctly tomentose pilei and slightly larger pores, but is otherwise similar. In East Asia, this species is mainly distributed in old-growth forests in the boreal and subalpine areas and is considered to be rare.

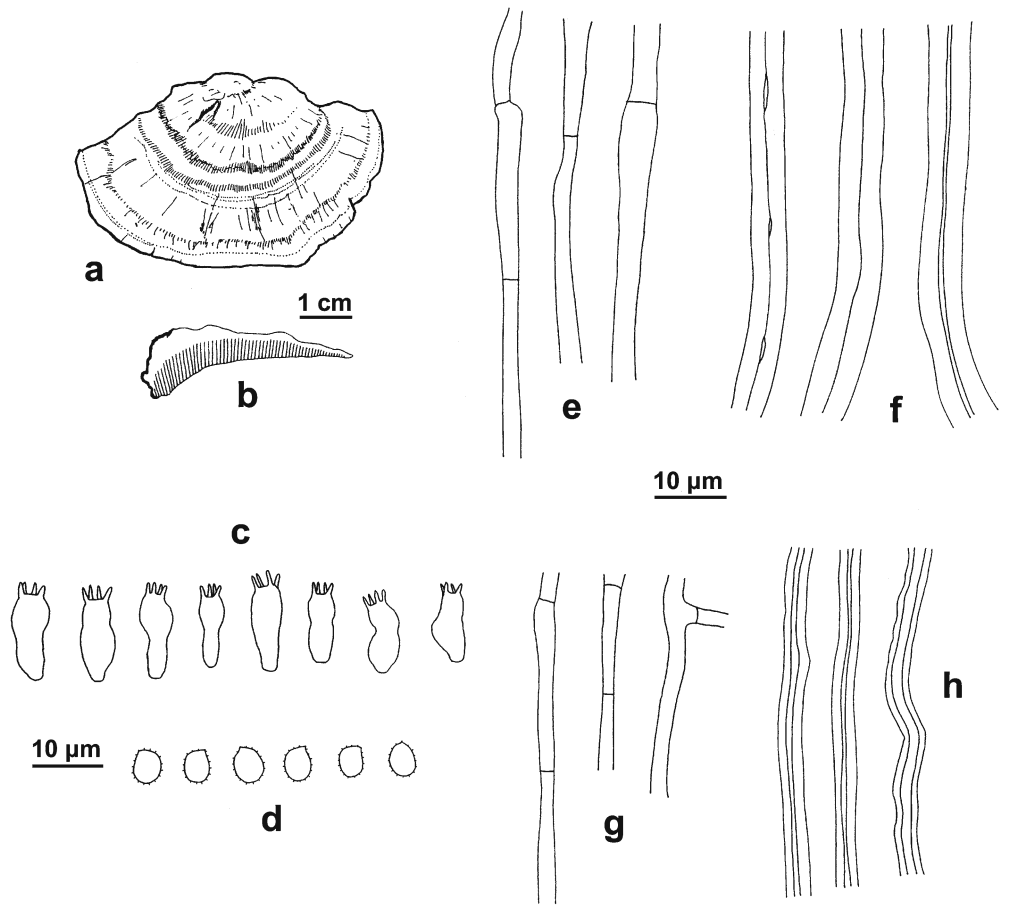
***Heterobasidion orientale*** Tokuda, T. Hatt. & Y.-C. Dai, sp. nov. Figs. 3, 4

“*Polystictus persoonii*” Cooke, auct. non Cooke: Yasuda, Bot. Mag. Tokyo 26:262, 1912. “*Fomitopsis insularis*” (Murrill) Imazeki, auct. non Murrill: Imazeki, Acta Phytotaxonomica et Geobotanica 13:253, 1943.

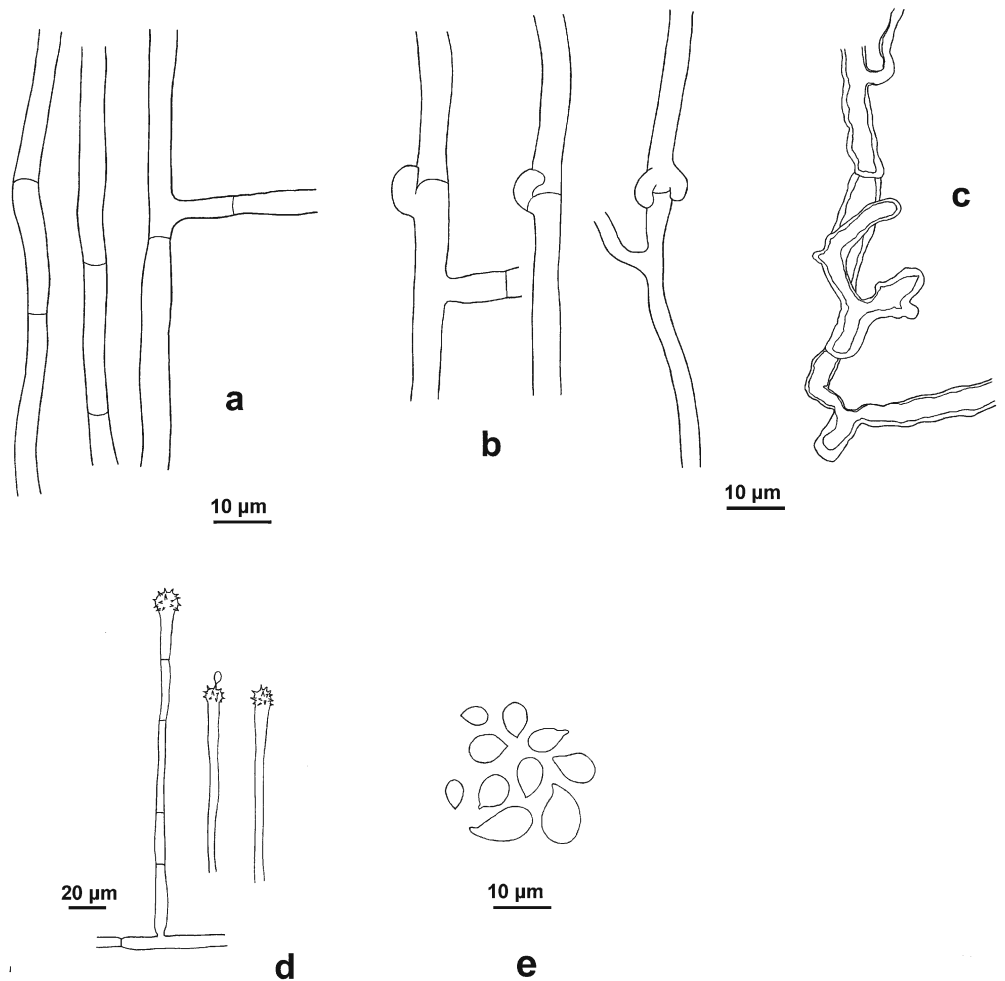
“*Heterobasidion insulare*” (Murrill) Ryvarden, auct. non Murrill: Imazeki & Hongo, Colored Illustrations of Mushrooms of Japan II:168, ut “*H. insularis*”, 1989.

Basidiocarpia annua, sessilia vel effusi-reflexi. Pilei dimidiati, flabelliformes vel elongati, glabri, badii vel fusci.

**Fig. 3.** Structures of *Heterobasidion orientale*, from specimen (TFM F-21825, holotype). **a** Basidiocarp. **b** Vertical section of basidiocarp. **c** Basidia. **d** Basidiospores. **e** Generative hyphae from context. **f** Skeletal hyphae from context. **g** Generative hyphae from trama. **h** Skeletal hyphae from trama



**Fig. 4.** Structures of *Heterobasidion orientale*, in culture (MAFF-420773, ex holotype). **a** Generative hyphae from aerial mycelium. **b** Generative hyphae with clamp-connections from colony margin. **c** Interlocking hyphae from aerial mycelium. **d** Conidiophores. **e** Conidia



Pori angulares vel labyrinthiformes, 2–3/mm; tubi 2–8 mm longi. Contextus suberosus, cremeus vel luteus. Systema hypharum dimiticum; hyphae generativae afibulatae, hyalinae; hyphae skeletales dextrinoideae. Basidiosporae globosae, asperulae, (3.5–)4.0–5.6(–6.4) × (3.0–)3.2–4.5(–5.1) μm.

Holotypus: Japonia, Hokkaido, Mikasa, Minenobu, in truncis *Abietis sachalinensis*, leg. S. Tokuda, 24 Aug. 2002 (TFM F-21825, ex HFB-172).

Etymology: Latin, oriental, after its distribution.

Basidiocarps annual, sessile to effused-reflexed. Pilei dimidiate, flabelliform to elongated, broadly attached, applanate, imbricate with several pilei or solitary, 1.5–9.5 cm across, 0.7–4 cm radius, 1.0–4.5 cm thick at base. When resupinate often widely effused on substrates, then up to 12 cm wide. Pileus surface glabrous, rarely velutinous near the base, radially and/or irregularly rugose when dry, partly warty, subzionate, brown (5YR-4/2, 4/4, 4/8, 5/4, 5/8, 10YR-4/4, 5/4) to dark brown (5YR-3/2, 3/4, 10YR-3/2, 3/4), often zionate with reddish brown (10R-3/4, 3/8, 4/8) to strong orange (5YR-6/12) zones, pale yellow (5Y-9/2, 10YR-9/4) to yellowish white (5Y-9/1) in actively growing margin. Pileus margin acute, occasionally undulate. Pore surface at first yellowish white (5Y-9/1) then pale yellow (5Y-9/2, 9/4, 10YR-9/4) to light yellowish orange (10YR-8/8). Pores angular to round or labyrinthiform, sometimes radially elongated, (1–)2–3(–4)/mm, 70–1500 μm wide, dissepiments eroded, 25–300 μm thick. Sterile margin 0.5–3.0 mm wide, concolorous with pore surface. Tubes 2–8 mm deep, concolorous with context. Context flexible when fresh, drying corky, azonate, yellowish white (5Y-9/1) to pale yellow (5Y-9/2), 2–8 mm thick, up to 20 mm thick at base, with a thin crust except for the margin, up to 50 μm thick near the base.

Hyphal system dimitic with generative hyphae and skeletal hyphae. Contextual generative hyphae thin walled, without clamp-connections, hyaline, IKI–, 2.0–3.5 μm in diameter. Contextual skeletal hyphae dominating, straight to sinuous, thick walled (up to 2.5 μm thick), hyaline except in cuticle, moderately dextrinoid, (2.5–)4.0–5.0(–8.0) μm in diameter. Tramal generative hyphae thin walled, without clamp-connections, hyaline, IKI–, 2–3 μm in diameter. Tramal skeletal hyphae thick walled, walls up to 2 μm thick, hyaline, dextrinoid, (2–)3–4 μm in diameter. Cystidia absent. Basidia clavate, sometimes slightly constricted near the middle, 4-sterigmate, 10–12 × 4–5 μm. Basidiospores finely asperulate, globose to subglobose, hyaline, IKI–, (3.5–)4.0–5.6(–6.4) × (3.0–)3.2–4.5(–5.1) μm, L = 4.9 μm, W = 4.0 μm, r = 1.0–1.6, R = 1.26 (n = 741/9).

Cultural characters: Growth moderately fast, 4.5–8.0 mm/day, growth rate variable among the isolates, plates usually covered in 2–3 weeks but some old isolates take longer than 6 weeks. Advancing zone usually entire but frequently indented and/or partly spread out in very slow growing isolates, mycelia sparse, appressed, hyaline to white. Mat yellowish white (5Y-9/1) to pale yellow (5Y-9/2, 9/4), aerial mycelium abundant, cottony to woolly, later felty, farinaceous with numerous conidia. Reverse unchanged after 6 weeks or partly light yellowish brown (10YR-7/8, 8/8). Odor

indistinctive. Hymenophore not seen within 6 weeks. Optimum temperature for mycelial growth 19–25°C. Generative hyphae from the advancing zone thin walled, usually without clamp-connections, hyaline, IKI–, 2.5–6.0(–8.0) μm in diameter. Generative hyphae from aerial and submerged mycelia hyaline, usually thin walled, rarely thick walled (up to 2 μm), (1.5–)3.0–8.0(–10.0) μm in diameter, rarely with clamp-connections; clamp-connections present on wide and straight hyphae especially near margin, mostly single, extremely rarely double; thin-walled generative hyphae straight, unbranched or branched, rarely with short papillate side branches, cytoplasm with granules or tiny oil droplets; occasionally thick-walled interlocking hyphae present in older parts of colony. Conidiophores arising as erect branches from prostrate hyphae, often constricted at junction with hyphae, almost simple, rarely branched, up to 260 μm long, 4–12 μm in diameter. Apically inflated conidogenous vesicle 8–19 μm in diameter, covered with conical denticles on which the conidia are borne. Conidia abundant, ovoid to subglobose, unicellular, smooth, hyaline, IKI–, (4.1–)5.2–10.0(–15.0) × (2.8–)3.4–6.5(–9.5) μm, L = 7.2 μm, W = 4.8 μm, r = 1.0–2.4, R = 1.5 (n = 379/3).

Extracellular peroxidase activities: Gum guaiac +, 1-naphthol +, tyrosine –. Nobles' species code: 2, (5), 6, 7, (12), 25, 33, 36, 38, 42, 43, (47), (54), (54), 55, 59. Stalpers' species code: 1, 3, 6, 7, (10), (11), (12), 13, (14), (15), 18, (21), 22, (24), 25, 30, 31, (38), (39), (40), 45, (48), (50), (51), (52), 53, 54, (55), (64), 86, 87, (89), 90, 93.

Hosts and substrates: JAPAN: *Abies firma* Sieb. & Zucc., *A. sachalinensis*, *A. veitchii*, *Abies* sp., *Cryptomeria japonica* (L. f.) D. Don, *Fraxinus mandshurica* Rupr. var *japonica* Maxim, *Larix kaempferi* (Lamb.) Carrière, *Picea glehnii*, *P. jezoensis*, *P. maximowiczii* Regel, *Pinus densiflora* Sieb. & Zucc., *P. nigra* Arnold. CHINA: *Abies* sp. and *Pinus* sp. (Dai et al. 2002, 2006). On stumps and fallen trunks.

Distribution: JAPAN: Hokkaido Is., Honshu Is., Kyushu Is., Bonin Is. CHINA: Heilongjiang Prov., Jilin Prov.

Specimens examined. JAPAN: Chiba Pref., Awa-gun, Seicho, 23 Apr. 1964, leg. K. Aoshima (TFM F-11827); Chiba Pref., Awa-gun, Kimitsu-shi, Orikisawa, 9 Jan. 1989, leg. Y. Abe (TFM F-14952); Fukushima Pref., Iwaki, Kawamae, Setogaro, 21 Nov. 1980, leg. Y. Abe (TFM F-21804); Hokkaido Pref., Asahikawa-shi, Kamuikotan, 12 Aug. 1963, leg. K. Aoshima (TFM F-22361); Hokkaido Pref., Ikeda-cho, on *A. sachalinensis*, 3 Oct. 1995, leg. S. Tokuda (TFM F-21821, ex HFB-162); Hokkaido Pref., Mikasa-shi, Horonai, on *A. sachalinensis*, 21 Nov. 1995, leg. S. Tokuda (TFM F-21822, ex HFB-163; TFM F-21823, ex HFB-164); Hokkaido Pref., Mikasa-shi, Minenobu, on *A. sachalinensis*, 24 Aug. 2002, leg. S. Tokuda (HOLOTYPE, TFM F-21825, ex HFB-172); Hokkaido Pref., Bibai-shi, Koshunai, on *P. glehnii*, 14 Sep. 2000, leg. S. Tokuda (TFM F-21824, ex HFB-166); same place, on *P. glehnii*, 24 Aug. 2002, leg. S. Tokuda (TFM F-21819, ex HFB-94); Hokkaido Pref., Chitose-shi, Eniwa, Lake Shikotsuko, 10 Aug. 1963, leg. K. Aoshima (TFM F-14665; F-14676; F-14680; F-14690; F-21805); same place, 14 Sep. 1966, leg. K. Aoshima (TFM F-14655; F-14664; F-14684); Hokkaido Pref., Kamikawa, Soukyo, 14 Aug. 1963, leg. K. Aoshima (TFM F-14618);

Hokkaido Pref., Sapporo-shi, Mt. Maruyama, on *Picea maximowiczii*, 27 Aug. 1962, leg. S. Kamei (TFM F-14666); Hokkaido Pref., Kamikawa-gun, Shintoku-cho, Iwamatsu, on *P. glehnii*, 10 Oct. 2002, leg. S. Tokuda (TFM F-21820, ex HFB-95); Hokkaido Pref., Sorachi-gun, Yamabe, Kumanosuzawa, Univ. Tokyo Exp. Forest, on *Fraxinus mandshurica*, 24 Sep. 1962, leg. Y. Hayashi (TFM F-14654); Hokkaido Pref., Sorachi-gun, Yamabe-mura, Mt. Tairokusan, 17 Aug. 1963, leg. Y. Hayashi (TFM F-10426); same place, 25 Sep. 1962, leg. Y. Hayashi (TFM F-14660); same place, 17 Aug. 1963, leg. K. Aoshima (TFM F-14614); Hokkaido Pref., Yamabe, Hirasawa, Univ. Tokyo Exp. Forest, on *A. sachalinensis*, 24 Sep. 1962, leg. Y. Hayashi (TFM F-14683); same place, 16 Aug. 1963, leg. K. Aoshima (TFM F-14692); Hokkaido Pref., Yamabe, Rokugo, Tokyo Univ. Forest, on *Pinus nigra*, 26 Sep. 1962, leg. Y. Hayashi (TFM F-11828); Hokkaido Pref., Tomakomai-shi, Maruyama, on *P. jezoensis*, 19 Sep. 1961, leg. Y. Hayashi (TFM F-14687); same place, on *P. jezoensis*, 19 Sep. 1962, leg. Y. Hayashi (TFM F-14616), same place, 19 Sep. 1962, leg. Y. Hayashi (TFM F-14620; F-14679); Kagoshima Pref., Yakushima Is., Anbou, on *Cryptomeria japonica*, 3 Aug. 1955, leg. K. Katsumoto (TFM F-21806); Kagoshima Pref., Kumage-gun, Yakushima Is., 20 Oct. 1961, leg. K. Aoshima (TFM F-14623); Kyoto Pref., Kitakuwata-gun, Kyoto Univ. Exp. Forest, on *Abies firma*, July 1964, leg. H. Furukawa (TFM F-14615); Kyoto Pref., Kitakuwata-gun, Miyama, Ashu, 30 July 1968, leg. K. Aoshima (TFM F-21807); Mie Pref., Ichishi-gun, Misugi-cho, Kawakami, 27 Aug. 1967, leg. H. Furukawa (TFM F-11825); Miyagi Pref., Oshika-gun, Oshika-cho, Mt. Kinkasan, 30 Oct. 1973, leg. T. Kobayashi (TFM F-21808); Miyazaki Pref., Kitamorokata-gun, Mt. Aoidake, 15 Oct. 1962, leg. M. Andou (TFM F-21809); Miyazaki Pref., Takaharu, Miike, on *Pinus densiflora*, 2 July 2000, leg. S. Kurogi (TFM F-20028); Nagano Pref., Nishichikuma-gun, Fukushima-cho, 4 Sep. 1963, leg. H. Furukawa (TFM F-14662); Nagano Pref., Chiisagata-gun, Wada, Wadatouge, 6 Aug. 1964, K. Aoshima (TFM F-11826); same place, 7 Aug. 1964, leg. K. Aoshima (TFM F-21810); Nagano Pref., Hara, Suwa, on *P. densiflora*, 23 Aug. 1998, leg. T. Hattori (TFM F-18941); Nara Pref., Mt. Kasugayama, 17 Oct. 1966, leg. K. Aoshima (TFM F-21811); Bonin Is., Hahajima Is., Kuwanokiyama, 25 June 1990, leg. T. Hattori (TFM F-15916); Osaka Pref., Takatsuki, Mt. Ponponyama, on *A. firma*, 3 Apr. 1990, leg. T. Hattori (TFM F-15366); Saitama Pref., Chichibu, on *Larix leptolepis*, 9 Aug. 1971, leg. Y. Hayashi (TFM F-21812); Shizuoka Pref., Iwata-gun, Misakubo-cho, 14 June 1961, leg. K. Aoshima (TFM F-14681; F-21813); Tokyo Pref., Hachioji, 17 Oct. 1963, leg. Y. Hayashi (TFM F-10175; F-10176; F-10177; F-14624; F-14672; F-14673; F-14691); same place, 23 Oct. 1966, leg. K. Aoshima (TFM F-21814); same place, June 1979, leg. Y. Abe (TFM F-21815); Tokyo Pref., Hachioji, Asakawa, 20 Sep. 1985, leg. Y. Abe (TFM F-13731; F-13732); Yamaguchi Pref., Ooshima-gun, Touwacho, 12 Aug. 1956, leg. K. Katsumoto (TFM F-21816); Yamanashi Pref., Minamitsuru-gun, Narusawa-mura, Mt. Fuji, 28 Aug. 1965, leg. K. Aoshima (TFM F-14611; F-14612); Yamanashi Pref., Mt. Fuji, 6 Oct. 1981, leg. Y.

Hayashi (TFM F-21817); Yamanashi Pref., Minamitsuru-gun, Fujiyoshida, Mt. Fuji, Sep. 1982, leg. T. Kobayashi (TFM F-21818). CHINA: Heilongjiang Prov., Yichun City, Fenglin, on fallen trunk of *Abies* sp., 7 Apr. 2002, leg. Y-C. Dai (TFM F-21829, ex Dai-3601); Jilin Prov., Antu County, Changbai Nat. Res., on rotten wood of *Abies* sp., 29 Aug. 2005, leg. Y-C. Dai (TFM F-21830, ex Dai-7136).

Cultures examined: WD-651, from basidiocarp tissue of F-15366; WD-825, from basidiocarp tissue of F-15916; WD-1280, from basidiocarp tissue of F-10175; WD-1281 from basidiocarp tissue of F-10176; MAFF-420772, from basidiocarp tissue of F-21819; MAFF-420773, from basidiocarp tissue of F-21825.

Remarks: This species corresponds to “*Heterobasidion insulare* N group” reported by Dai et al. (2002). The phylogenetic relationships of this fungus in the genus of *Heterobasidion* were revealed by Ota et al. (2006) as “*H. insulare*”. *Heterobasidion orientale* is characterized by annual and sessile to effused-reflexed basidiocarps, semicircular to flabelliform and applanate pilei, reddish brown and glabrous pileus surface with white margin, thin crust on the pileus surface, and angular to round or labyrinthiform pores. The reddish brown pileus surface with white margin is distinctive when fresh and darkens during drying. This fungus has a wider host range than *H. parviporum* and is common in various forest types, including newly cut artificial stands and old-growth forests.

***Heterobasidion ecrustosum*** Tokuda, T. Hatt. & Y-C. Dai, sp. nov. Figs. 5, 6

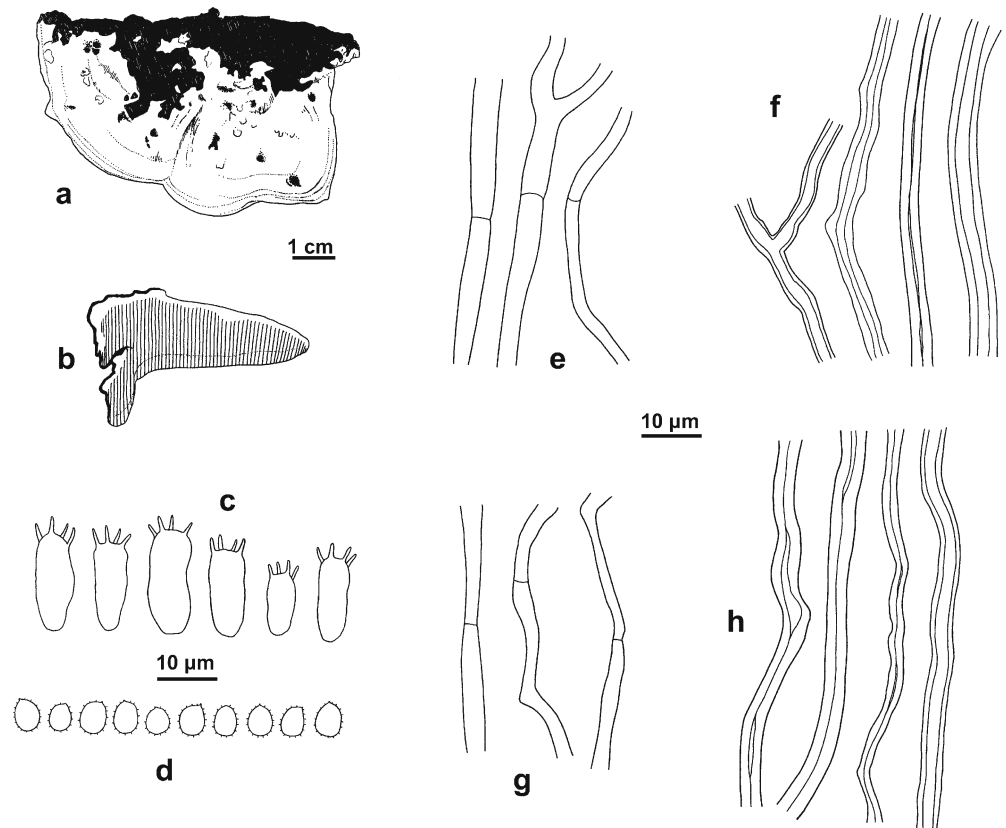
Basidiocarpia annua, sessilia. Pilei dimidiati, glabri, lutei vel ochracei. Pori angulares vel rotundi, 2–3/mm; tubi 10–20 mm longi. Contextus suberosus, cremeus vel luteus. Systema hypharum dimiticum; hyphae generativae afibulatae, hyalinae; hyphae skeletales dextrinoideae. Basidiosporae globosae, asperulae, (3.7–)4.1–5.7(–6.4) × (2.9–)3.3–4.6(–5.3) μm.

Holotypus: Japonia, Okinawa, insula Iriomote, prope flumen Shiira, in truncis *Pini luchuensis*, leg. T. Hattori, 12 Nov. 1997 (TFM F-18051).

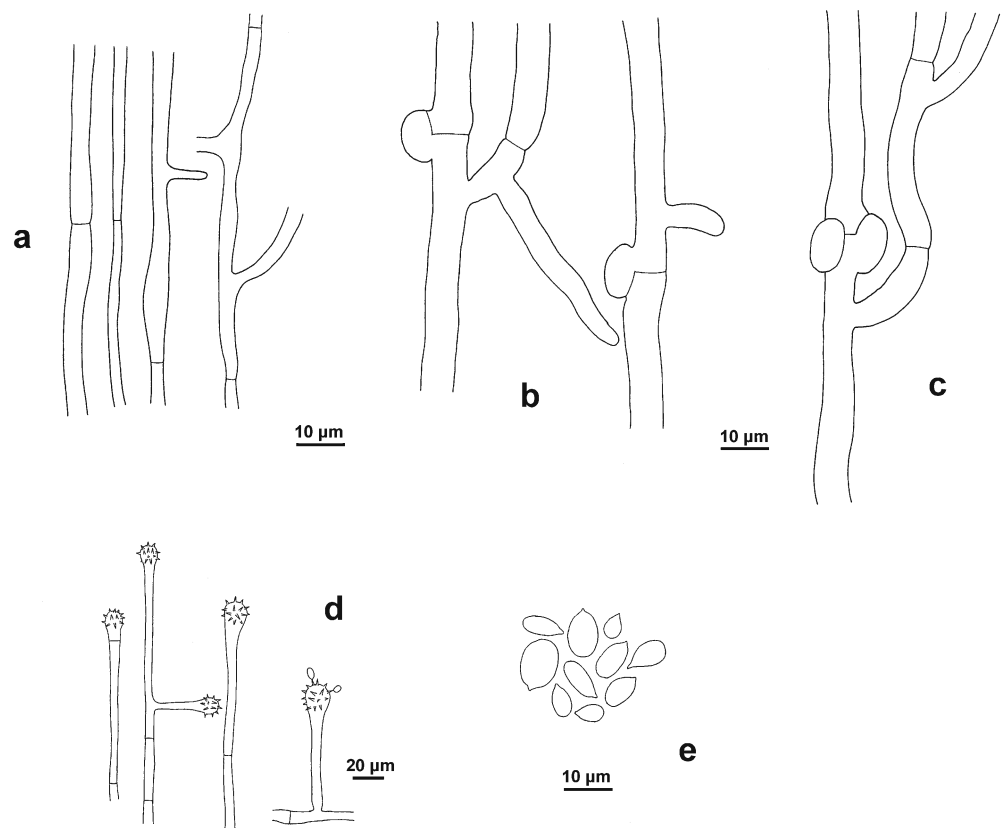
Etymology: Latin, without a crust; after the pileus that frequently lacks a crust.

Basidiocarps annual, sessile, broadly attached, solitary to imbricate with several pilei. Pilei dimidiate, applanate to convex or triquetrous, 1.5–8.7 cm across, 1.5–5.0 cm radius, 1.2–6.0 cm thick. Pileus surface glabrous, subzonate to azonate, often indistinctly sulcate, occasionally warty, pale brown (10YR-8/2) to pale yellow (10YR-9/2, 9/4) or yellow brown (10YR-7/4, 7/8, 7/12, 8/8), partly orange brown (5YR-6/12), usually without a crust or with crust only at the base; occasionally a crust develop in patches on the pileus surface, then dark brown (10YR-3/4) or blackish (10YR-2/2, 3/2). Pileus margin rounded, usually flat and entire. Pore surface even, cream to ivory (10YR-9/4) or pale to light yellowish orange (10YR-8/4, 9/4), pores angular to round, rarely labyrinthiform, sometimes elongated, (1–)2–3(–4)/mm, 120–700 μm in diameter, dissepiments entire, 50–270 μm thick. Sterile margin 1.0–2.5 mm wide, or absent. Tubes concolor-

**Fig. 5.** Structures of *Heterobasidion ecrustosum*, from specimen (TFM F-18051, holotype). **a** Basidiocarp. **b** Vertical section of basidiocarp. **c** Basidia. **d** Basidiospores. **e** Generative hyphae from context. **f** Skeletal hyphae from context. **g** Generative hyphae from trama. **h** Skeletal hyphae from trama



**Fig. 6.** Structures of *Heterobasidion ecrustosum*, in culture (**a, d, e** WD-1945, ex holotype; **b, c** WD-2220). **a** Generative hyphae from aerial mycelium. **b** Generative hyphae with clamp-connections from colony margin. **c** Generative hyphae with double clamp-connections from colony margin. **d** Conidiophores. **e** Conidia





ous with pore surface, 10–20 mm deep. Context corky, cream (5Y-9/2) to white yellow (5Y-9/4), light yellowish orange (10YR-8/4, 9/4), 1.0–2.5(–5.0) mm thick, up to 10 mm thick at base, with or without a thin crust, crusts dark brown, up to 100 µm thick.

Hyphal system dimitic with generative hyphae and skeletal hyphae. Contextual generative hyphae thin walled, without clamp-connections, hyaline, IKI–, 2–4(–9) µm in diameter. Contextual skeletal hyphae thick walled (up to 2 µm thick), hyaline, moderately dextrinoid, (2–)3–4(–5) µm in diameter. Tramal generative hyphae thin walled, without clamp-connections, hyaline, IKI–, 2.0–3.5 µm in diameter. Tramal skeletal hyphae thick walled, walls up to 1.5 µm thick, hyaline, dextrinoid, (2.5–)3–4(–5) µm in diameter. Cystidia absent. Basidia clavate, 12–20 × 5–7 µm, 4-sterigmate. Basidiospores asperulate, globose to subglobose, hyaline, IKI–, (3.7–)4.1–5.7(–6.4) × (2.9–)3.3–4.6(–5.3) µm, L = 4.9 µm, W = 3.9 µm, r = 1.0–1.6, R = 1.25 (n = 1120/9).

Cultural characters: Growth moderately fast, 9.1–11.5 mm/day, plates covered in 1–2 weeks. Advancing zone entire, mycelia sparse, appressed, hyaline to white. Mat white (5Y-9/1) to ivory white (5Y-9/2, 9/4) or light brown (10YR-7/4, 8/4), translucent, downy to cottony or partly woolly, later felty to subfelty, partly farinaceous with erect conidiophores. Reverse unchanged after 6 weeks. Odor indistinctive. Hymenophore not seen within 6 weeks. Optimum temperature for mycelial growth 22–28°C. Generative hyphae from the advancing zone thin walled, occasionally with clamp-connections, hyaline, IKI–, 3.5–6(–9) µm in diameter. Generative hyphae from aerial mycelium and submerged mycelium thin walled, rarely thick walled, walls up to 2 µm thick, simple septate or with clamp-connections, clamp-connections single or double, present on wide and straight hyphae especially near margin, hyaline, IKI–, (2–)3–8(–9) µm in diameter. Conidiophores arising as erect branches from prostrate hyphae, often constricted at junction with hyphae, simple or branched, variable in length, up to 300 µm long, 4–10 µm in diameter. Apically inflated conidiogenous vesicle 8.3–18.1 µm in diameter, covered with conical denticles on which conidia are borne. Conidia abundant, ovoid to subglobose, sometimes oblong ellipsoid, unicellular, smooth, hyaline, IKI–, (3.2–)4.8–9.7(–17.1) × (2.9–)3.5–6.6(–12) µm, L = 6.9 µm, W = 4.6 µm, r = 1.1–2.6, R = 1.50 (n = 341/4).

Extracellular peroxidase activities: gum guaiac +, 1-naphthol +, tyrosine –. Nobles' species code: 2, (5), 6, 7, (11), (12), 33, 36, 38, 42, (47), 55, 59. Stalpers' species code: 1, 3, 6 (12), 13, 14, (17), 18, (19), 21, (22), 24, (25), 30, 31, (38), (39), (40), (44), 45, (48), (51), 52, 53, 54, (55), (64), (82), (83), 86, 87, 90, 93.

Hosts and substrates: JAPAN: *Pinus densiflora*, *P. luchuensis* Mayer, *P. thunbergii* Parlatore, *Pinus* sp. CHINA: *P. massoniana* Lamb., *P. luchuensis*, *Pinus* sp. (Dai et al. 2002). On dead standing trees, cut stumps and recently fallen trees.

Specimens examined. JAPAN: Kagoshima Pref., Kimotsuki-gun, Oonejime, 18 Oct. 1963, leg. K. Aoshima (TFM F-14682); Kanagawa Pref., Manazuru, on *Pinus den-*

*siflora*, 22 May 1999, leg. M. Hisataka (TFM F-19272); Kumamoto Pref., Kumamoto-shi, Tatsuta-yama, on *Pinus* sp., 12 Oct. 2003 (TFM F-21295); Okinawa Pref., Iriomote Is., along Shiira River, on *P. luchuensis*, 12 Nov. 1997, leg. T. Hattori (HOLOTYPE, TFM F-18051); Okinawa Pref., Kunigami-son, Mt. Yonaha-dake, on *P. luchuensis*, 2 Nov. 2001, leg. Y. Ota (TFM F-19882); same place, on *P. luchuensis*, 2 Nov. 2001, leg. Y. Ota (TFM F-22384); Okinawa Pref., Miyako Is., Shimoji, on *P. luchuensis*, 22 June 2004, leg. Y. Kawabe (TFM F-21297); Yamaguchi Pref., Shimonoseki, Chohu-cho, on *P. thunbergii*, 26 Jan. 1956, leg. K. Katsumoto (TFM F-14668). CHINA: Jiangsu Prov., Nanjing, Mt. Zijingshan, on stump of *Pinus* sp., 10 Oct. 2003, leg. Y-C. Dai (TFM F-21827, ex Dai 5236); same place, on stump of *Pinus* sp., 11 Oct. 2003, leg. Y-C. Dai (TFM F-21828, ex Dai 5251).

Cultures examined: WD-1945, from basidiocarp tissue of F-18051; WD-2080, from basidiocarp tissue of F-19272; WD-2220, from basidiocarp tissue of F-19882; WD-2221, from basidiocarp tissue of F-22384.

Remarks: This fungus was identified as "*Heterobasidion insulare* T group" by Dai et al. (2002) and is conspecific with the "undetermined *Heterobasidion* sp." reported by Ota et al. (2006). *Heterobasidion ecrustosum* is characterized by the convex basidiocarps with semicircular pilei, pale-colored pileus surface with or without a crust usually restricted to near the base, thin context, long tubes, and angular to round pores measuring 2–3/mm.

***Heterobasidion annosum*** (Fr.) Bref. Unters. Gesamtg. Mykol. 8:154 (1888).

Basidiocarps annual to perennial, pileate or sessile to effused-reflexed, imbricate with several pilei or solitary. Pilei variable in shape, often semicircular. Pileus surface subtomentose to almost glabrous, brown (5YR-4/4) to dark brown (5YR-2/4, 3/4, 10R-3/2), partly almost black (5YR-2/2, 10R-2/2), margin light yellow (5Y-9/4). Pileus margin round to acute, variable in thickness, entire or undulating. Pore surface light yellow (5Y-9/4). Pores round to angular, 2–3/mm. Context corky, up to 7 mm thick, with a distinct crust. Tubes concolorous with the context, up to 7 mm deep in each layer.

Hyphal system dimitic. Contextual generative hyphae thin walled, without clamp-connections, 2–4.5 µm in diameter. Contextual skeletal hyphae (2–)3–4(–5) µm, thick walled, hyaline except in cuticle, dextrinoid. Tramal generative hyphae thin walled, without clamp-connections, 1.5–3 µm in diameter. Tramal skeletal hyphae 3–4 µm, thick walled, hyaline, dextrinoid. Basidiospores asperulate, subglobose, hyaline, IKI–, 3.6–4.8(–4.9) × (2.6–)2.8–3.6(–3.7) µm, L = 4.1 µm, W = 3.1 µm, R = 1.2–1.5, r = 1.32 (n = 52/1).

Specimens examined: POLAND: Podanin, on *Betula* sp., 17 Aug. 2004, leg. K. Korhonen (TFM F-21326); same place, on *Pinus sylvestris*, 17 Aug. 2004, leg. N. La Porta (TFMF-21327), same place, 17 Aug. 2004, leg. P. Łakomy (TFM F-27080). CZECH REPUBLIC, Cesky Krumlov, Žofinsky prales, 25 Apr. 1990, leg. P. Vampola (TFM F-22389).

***Heterobasidion parviporum*** Niemelä & Korhonen, *Heterobasidion annosum*, biology, ecology impact and control: 31 (1998), "European Form".

Basidiocarps annual to perennial, effused-reflexed to resupinate or pileate, imbricate with several pilei or solitary. Pilei variable in shape, applanate to slightly convex. Pileus surface tomentose, brown (5YR-4/4, 5/4) to dark brown (5YR-2/4, 3/4, 10YR-3/4), partly almost black (5YR-2/2) near the base, margin light yellow (5Y-9/4) to yellowish white (5Y-9/1), tomentum brown, dense, up to 280 µm long. Pileus margin round to acute, usually thin, often undulating. Pore surface pale yellowish orange (10YR-9/4) to light yellowish orange (10YR-8/4), pores round to angular, 3–4(–5)/mm, rarely elongated. Context corky, up to 3 mm thick, with a distinct crust. Tubes concolorous with the context, up to 6 mm deep in each layer.

Hyphal system dimitic. Contextual generative hyphae thin walled, without clamp-connections, 2–4 µm in diameter. Contextual skeletal hyphae (2–)3–4.5 µm, thick walled, hyaline except in cuticle, dextrinoid. Tramal generative hyphae thin walled, without clamp-connections, 2–3 µm in diameter. Tramal skeletal hyphae 2–4 µm, thick walled, hyaline, dextrinoid. Basidiospores asperulate, subglobose, hyaline, IKI–, (3.4–)3.8–5.1(–5.5) × (2.5–)2.8–4.0 (–4.6) µm, L = 4.4 µm, W = 3.4 µm, R = 1.0–1.6, r = 1.29 (n = 231/3).

Specimens examined: POLAND: Suwałki, on *Picea abies*, 17 Aug. 2004, leg. P. Łakomy (TFM F-27081); Białowieża, on *P. abies*, 21 Aug. 2004, leg. P. Łakomy (TFM F-21332; F-21328); same place, on *Picea* sp., 21 Aug. 2004, leg. N. La Porta (TFM F-21329); same place, on *P. abies*, 21 Aug. 2004, leg. K. Korhonen (TFM F-21330; F-21334); same place, on *Picea* sp., 21 Aug. 2004, leg. K. Korhonen (TFM F-21331); same place, on *P. abies*, 21 Aug. 2004, leg. Y. Ota (TFM F-21333).

Remarks: This form is morphologically similar to the East Asian population of *H. parviporum* except for the more tomentose pilei and slightly larger pores. Mating tests revealed that the Chinese "*H. annosum*" belongs to the same biological species as *H. parviporum* described from Europe (Dai et al. 2006). Phylogenetic studies also revealed that the Japanese "*H. annosum* s. lat." is closely related to the European and Chinese *H. parviporum* (Ota et al. 2006). Therefore, the East Asian population is conspecific with *H. parviporum*.

***Heterobasidion abietinum*** Niemelä & Korhonen, *Heterobasidion annosum*, biology, ecology impact and control: 31 (1998).

Basidiocarps perennial, pileate to effused-reflexed. Pilei semicircular or elongated. Pileus surface subtomentose to almost glabrous, brown (5YR-4/4, 4/8, 10YR-4/4, 5/4, 5/8) to dark brown (5YR-2/4, 3/4, 10YR-3/4), partly almost black (5YR-2/1, 2/2), margin light yellowish orange (10YR-8/4) to pale yellowish orange (10YR-9/4), upper tomentum short. Pileus margin round to acute, thin, entire. Pore surface light yellowish orange (10YR-8/4) to pale yellowish orange (10YR-9/4), pores round to angular, 2–3/mm. Context

corky, up to 3 mm thick, with a distinct crust. Tubes concolorous with the context, up to 4 mm deep in each layer.

Hyphal system dimitic. Contextual generative hyphae thin walled, without clamp-connections, 2–4 µm in diameter. Contextual skeletal hyphae (2–)3–4 µm, thick walled, hyaline except in cuticle, dextrinoid. Tramal generative hyphae thin walled, without clamp-connections, 2–3 µm in diameter. Tramal skeletal hyphae 2–4 µm, thick walled, hyaline, dextrinoid. Basidiospores asperulate, subglobose, hyaline, IKI–, (3.3–)3.5–5.0(–5.1) × (2.6–)2.7–4.2(–4.5) µm, L = 4.3 µm, W = 3.3 µm, r = 1.0–1.7, R = 1.30 (n = 57/1).

Specimen examined: POLAND: Siemianice, on *Abies alba*, 17 Aug. 2004, leg. P. Łakomy (TFM F-27082).

***Heterobasidion araucariae*** P. K. Buchanan, *Mycotaxon* 32: 325 (1988).

Basidiocarps annual to perennial, sessile to effused-reflexed, solitary to imbricate with several pilei. Pilei variable in shape, applanate, convex or unguulate. Pileus surface glabrous, sulcate in narrow to broad bands, brown (10YR-4/4, 5/4, 5YR-4/4, 4/8, 5/8) to dark brown (5YR-2/4, 3/2, 3/4), partly dark grayish brown (5YR-2/2), occasionally pale yellowish orange (10YR-9/2, 9/4) in marginal part. Pileus margin rounded, entire. Pore surface even, pale to light yellowish orange (10YR-8/4, 9/4). Pores round to angular or partly irregular, 1–2/mm. Context corky, up to 20 mm thick, with a thin crust. Tubes concolorous with the context, 6–12 mm deep in each layer.

Hyphal system dimitic. Contextual generative hyphae thin walled, without clamp-connections, 2.5–4(–5) µm in diameter. Contextual skeletal hyphae 3–5.5(–6) µm, thick walled, hyaline except in cuticle, dextrinoid. Tramal generative hyphae thin walled, without clamp-connections, 2.5–4 µm in diameter. Tramal skeletal hyphae 3–4.5(–7) µm, thick walled, hyaline, dextrinoid. Cystidioles with one small apical bulb present. Basidiospores asperulate, subglobose, hyaline, IKI–, (3.9–)4.2–6.0(–6.4) × (3.1–)3.4–4.7(–5.3) µm, L = 5.1 µm, W = 4.0 µm, R = 1.0–1.6, r = 1.26 (n = 497/5).

Specimens examined: NEW ZEALAND: Northland, Waipoua Forest Sanctuary, Yakas Kauri Track, on *Agathis australis*, 25 Sep. 1985, leg. P.K. Buchanan (holotype, PDD 48002); Northland, Puketi State Forest, on *A. australis*, 12 Sep. 1984, leg. P.K. Buchanan (PDD 48004); Northland, Trounson Kauri Park, on *A. australis*, 10 Sep. 1984, leg. P.K. Buchanan (PDD 48005); same place, on *A. australis*, 14 Sep. 1984, leg. P.K. Buchanan (PDD 48007); same place, on *A. australis*, 18 Jan. 1988, leg. P.K. Buchanan (PDD 48376); Northland, Omahuta Forest Sanctuary, *A. australis*, 11 Sep. 1984, leg. P.K. Buchanan (PDD 48577); same place, on *A. australis*, 11 Sep. 1984, leg. P.K. Buchanan (PDD 49000); Auckland, Waitakere Ranges, Cascade Loop Tr., on *A. australis*, 6 Apr. 1986, leg. P.K. Buchanan (PDD 48535).

***Heterobasidion insulare*** (Murrill) Ryvarden, *Norw. J. Bot.* 19:237, 1972.

"*Trametes insularis*" Murrill, *Bull. Torrey Bot. Club* 35: 405, 1908.

Basidiocarps annual, sessile to effused-reflexed. Pilei irregular in shape, 2–4 × 3–7 × 1–1.5 cm according to the original description (Murrill 1908). Pileus surface mostly glabrous, subtomentose on crust, incrustated only at the base, mostly light brown (10YR-6/4, 7/4, 8/4), partly brown (5YR-4/8, 5/8, 7/8) to light brown (5YR-6/8) or dull orange (5YR-7/8) with reddish brown tint (10R-3/8, 4/8), crust dark brown (5YR-2/2, 2/4, 3/2, 3/4, 4/4; 10YR-3/4) to almost black (10YR-3/2). Margin rounded, dull, mostly flat and entire. Pore surface even, pores round to angular, partly elongated, 2–3/mm, dissepiments thick, partly thin, sterile margin up to 2 mm. Context up to 3 mm thick, corky hard, concolorous with tubes, becoming gradually thinner toward the margin. Tubes up to 6 mm long at base, becoming gradually shorter toward the margin.

Hyphal system dimitic. Contextual generative hyphae thin walled, without clamp-connections, 3–4 µm in diameter according to the descriptions by Murrill (1908) and Dai et al. (2002). Contextual skeletal hyphae 2.5–6.0(–7.5) µm, thick walled, sinuous, hyaline except in cuticle, dextrinoid. Tramal hyphae dimitic, tramal generative hyphae not seen because of poor condition of type material, tramal skeletal hyphae (2.0–)2.5–3.5(–4.5) µm, thick walled, hyaline, dextrinoid. Basidiospores asperulate, globose to subglobose, hyaline, (4.0–)4.3–5.7(–6.0) × (2.9–)3.2–4.4(–4.8) µm, L = 5.0 µm, W = 3.8 µm, R = 1.0–1.5, r = 1.31.

Specimens examined: PHILIPPINES, Luzon Is., Benguet Province, Baguio, altitude 1500 m, on prostrate logs of *Pinus insularis*, Oct.–Nov. 1905, leg. E.D. Merrill (holotype, NY 00705030).

## Discussion

*Heterobasidion annosum* was originally described by Fries (1821) as *Polyporus annosus* based on a specimen from *Betula* sp. In addition to three distinct species from Europe, two biological species have been discriminated in North America from *H. annosum* s. lat.: North American pine group (Nam P-group) and North American spruce group (Nam S-group) (Korhonen et al. 1998). Stalpers (1996) accepted five species in the genus *Heterobasidion* in addition to *H. annosum* s. lat. Among these five species, Hattori (2001) accepted *H. araucariae* and *H. insulare* in this genus but rejected *H. pahangense* Corner, *H. perplexum* (Ryvarden) Stalpers and *H. rutilantiforme* (Murrill) Stalpers because of differences in hyphal characteristics. On the other hand, *H. arbitrium* (Corner) T. Hatt., which is characterized by a thick corky context without a crust, was included in *Heterobasidion* (Hattori 2001).

Each member of *H. annosum* s. lat. has somewhat different characteristics in morphology and ecology. The main diagnostic differences among the three European species are pore size, thickness of basidiocarps, shape of the pileus margin, length and abundance of the tomentum on pileus surfaces, and color of the heterokaryotic pure culture on malt extract agar (Mitchelson and Korhonen 1998; Niemelä and Korhonen 1998). The East Asian population of *H. par-*

*viporum* closely resembles the European population of *H. parviporum* in morphological characteristics, such as small pore size, thin basidiocarps and the brown leathery sclerotial covering on the surface of the colony. However, the East Asian population has subtomentose to almost glabrous pilei while the European population has a well-developed tomentum on young pilei, which is considered to be a good macroscopic character for this species (Niemelä and Korhonen 1998). Additionally, the Japanese specimens are usually effused-reflexed with a thin and leathery context whereas the European specimens frequently have a thicker context and well-developed semicircular pilei. The Chinese specimens have morphological characteristics intermediate between those of the European and the Japanese specimens.

In addition to morphological differences, host preference is another important character for discrimination within the *H. annosum* complex (Korhonen 1978; Doğmuş-Lehtijärvi et al. 2006). European *H. parviporum* shows relatively strict specialization for *Picea abies* (L.) Karst. and occurs primarily in areas where *P. abies* is distributed naturally (Korhonen 1978; Korhonen et al. 1998; Asiegbu et al. 2005). It mostly attacks *P. abies* but also saplings of *Pinus sylvestris* L. planted in areas previously occupied by spruce in Europe and has the potential to infect many other tree species (Korhonen 1978; Stenlid and Swedjemark 1988; Swedjemark and Stenlid 1995). In addition to *Picea abies* and *Pinus sylvestris*, *A. alba* Mill., *A. sibirica* Ledeb., *Betula pendula* Roth, *Larix sibirica* Ledeb., and *Pinus contorta* Dougl. ex Loud. var. *latifolia* Wats. are seldom infected by this fungus in Europe, while it seriously attacks *A. sibirica* in the Ural region of Russia (Piri 1996; Korhonen et al. 1997; Dai and Korhonen 1999; Łakomy and Werner 2003).

In contrast to the European population, the East Asian population does not show high specificity to *Picea* spp. (Dai et al. 2006; Tokuda et al. 2007). It frequently occurs on various species of *Abies* and *Picea* in Japan and China, but also on *Tsuga*, *Larix* and *Pinus* (Dai et al. 2003, 2006; Tokuda et al. 2007). Moreover, the high pathogenicity shown by European *H. parviporum* on *Picea abies* and *A. sibirica* in Europe and western Siberia appears to decline in eastern Asia (Dai et al. 2003). Dai et al. (2006) suggested that *H. parviporum* in China is not an aggressive pathogen on native tree species. There is also no record of mortality caused by *H. annosum* s. lat. in Japan and the fungus did not cause tree decline even in stands with serious root and butt rot damage caused by this fungus (Tokuda et al. 2007). However, we conclude that the East Asian population belongs to the same species, *H. parviporum*, as recognized in Europe because strains from both regions are interfertile and phylogenetically related (Dai et al. 2006; Ota et al. 2006); morphological and ecological differences indicated here are considered to relate to the local population level.

As Murrill (1908) indicated in the original description, the type material of *H. insulare* has an anoderm pileus surface, a round pileus margin and angular to round pores. However, the East Asian species known as "*H. insulare*" is characterized by a reddish brown pileus surface with a thin

crust, a thin and acute margin and angular to round or labyrinthiform pores, and it is apparently distinct from the type material of *H. insulare*. It does not key out in published keys to species of *Heterobasidion* or match the descriptions (Buchanan 1988; Stalpers 1996; Hattori 2001), and thus is herein described as a new species, *H. orientale*. Hyphal characteristics of *H. orientale* and the type material of *H. insulare* are also distinct. Contextual skeletal hyphae are mostly straight and smooth in *H. orientale* but flexuous and sinuous in *H. insulare* type material. Ota et al. (2006) revealed that *H. orientale* (as “*H. insulare*”) is phylogenetically related to *H. araucariae* and *H. ecrustosum* (as “undetermined *Heterobasidion* sp.”). It is also related to pine-specialized species of *H. annosum* s. lat. Eur P-group and Nam P-group, showing a main lineage in the genus (Ota et al. 2006). These species frequently occur on *Pinus* spp. Morphologically, *H. orientale* is characterized by the annual basidiocarps, thin crust, glabrous and reddish pileus surface, frequently labyrinthiform pores and thin and small basidiocarps.

*Heterobasidion ecrustosum* is characterized by annual basidiocarps with semicircular, applanate to convex or triquetrous pilei, thin context (up to 2.5 mm thick) without a crust or encrusted only at the base, long tubes measuring 10–20 mm deep, and round pores (2–3/mm). Among members of *Heterobasidion*, *H. insulare* and *H. arbitrarium*, both known only from type specimens, lack a distinct crust on the pileus surface whereas other members of this genus usually have a distinct crust. In addition to the pileus characteristics, *H. ecrustosum* is only known from warm temperate to subtropical areas in Japan and China, suggesting that it has a more southern distribution than most other Northern Hemisphere *Heterobasidion* spp. *Heterobasidion insulare* and *H. arbitrarium* were described from Southeast Asia and possibly also have a southern distribution, as does *H.*

*ecrustosum*. The type specimen of *H. insulare* has a thicker context and shorter tubes toward the margin compared with *H. ecrustosum*, which has a thin context and distinctly longer tubes. Additionally, contextual skeletal hyphae in *H. ecrustosum* are mostly straight and smooth as in *H. orientale*, but they are flexuous and sinuous in *H. insulare*. The holotype of *H. arbitrarium* has a distinctly thicker and corky context, considerably shorter tubes, and slightly smaller pores than *H. ecrustosum*.

*Heterobasidion ecrustosum* and *H. araucariae* are phylogenetically related (Ota et al. 2006) and share some morphological characteristics, such as long tubes and mostly regular pores. However, *H. araucariae* has larger (up to 34 cm across) and thicker (up to 8 cm thick) pilei than those of *H. ecrustosum* and usually has a well-developed crust on the pileus surface, whereas the crust of *H. ecrustosum* is usually lacking or is found only at the basal area of the pileus. Additionally, pores of *H. araucariae* are slightly larger [1–2(–3)/mm] than those of *H. ecrustosum* [(1–)2–3(–4)/mm]. *Heterobasidion araucariae* can be also distinguished from *H. ecrustosum* by the occurrence of cystidioles with small apical bulbs and by differences in host relationships and geographic distribution.

In culture, *H. parviporum* has the smallest conidia among the three East Asian *Heterobasidion* species, although the ranges of spore size overlap and it is difficult to discriminate them only by this character. Korhonen and Stenlid (1998) suggested that the mycelium of *H. annosum* s. lat. in culture is at first white and then may turn orange brown or dark brown, and the colony may be partly covered by thin and brown pseudosclerotial plates. In our examination, heterokaryotic cultures of *H. parviporum* partly become brown and leathery but those of *H. orientale* and *H. ecrustosum* remain white to cream and lack a brownish tint even 6 weeks after inoculation. Aerial mycelia are abundant and

**Table 1.** Key to the world species of *Heterobasidion*

1.	Pileus surface without crust, or incrustated only at base	2
1.	Pileus surface covered with crust except at margin	4
2.	Pores 3–4/mm, context woody to corky, thick, tubes shorter than thickness of context (Hattori 2001)	<i>H. arbitrarium</i>
2.	Pores 2–3/mm, tubes much longer than thickness of context	3
3.	Context thin, 1–2.5 mm thick, tubes more than ten times longer than thickness of context, well developed even at the margin, sterile margin on the pore surface usually inconspicuous, pores round to angular, rarely labyrinthiform. Context skeletal hyphae mostly straight and smooth; Asian species	<i>H. ecrustosum</i>
3.	Context thicker, up to 3 mm thick, tubes up to three times longer than thickness of context, becoming gradually shorter toward the margin, sterile margin on the pore surface distinct, pores round. Context skeletal hyphae sinuous; Asian species	<i>H. insulare</i>
4.	Pores 1–2(–3)/mm, round to angular or sublabyrinthiform. Basidiocarps corky, pilei up to 34 cm wide and 8 cm thick, up to 50 cm wide when resupinate, cystidioles present; Southern Hemisphere species	<i>H. araucariae</i>
4.	Pores smaller, round to angular or labyrinthiform. Basidiocarps leathery to corky, smaller; known from the Northern Hemisphere	5
5.	Basidiospores large, 5.7–7.8 × 4.1–6.1 μm, cystidioles present, pores 2–4/mm; known from China (Dai et al. 2007b)	<i>H. linzhiense</i>
5.	Basidiospores smaller, up to 5 × 4 μm on average	6
6.	Pores 3–5(–7)/mm, regular, pileus surface subtomentose to almost glabrous, brown to dark brown, with distinct crust	<i>H. parviporum</i>
6.	Pores 2–3/mm, regular to irregular	7
7.	Pileus surface glabrous, reddish brown with white margin, covered by thin crust except for the marginal part. Pores angular to round or frequently labyrinthiform. Usually on stumps or fallen trunks of <i>Abies</i> , <i>Picea</i> , <i>Pinus</i> , etc.; Asian species	<i>H. orientale</i>
7.	Pileus surface subtomentose to almost glabrous, brown to dark brown, with distinct crust. Pores round to angular	8
8.	Tomentum on pileus surface short (mean length, 20.9 μm). Species frequently causes serious root rot of <i>Pinus</i> and many other tree species including broad-leaved trees	<i>H. annosum</i>
8.	Length of tomentum on pileus surface variable but longer than in <i>H. annosum</i> (mean length, 54.8 μm), Frequently cause root rot of <i>Abies</i>	<i>H. abietinum</i>

woolly in cultures of *H. orientale*, but those of *H. parviporum* and *H. ecrustosum* are more appressed and colonies of these two species are usually at least partly translucent.

We accept nine species in *Heterobasidion*. A key to the world species of *Heterobasidion* is provided in Table 1 based on our observations and the published descriptions.

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