# Morphological studies in Veluticeps, Pileodon, and related taxa

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In this study, type specimens of Fomes angularis, Pileodon megasporus, Veluticeps philippinensis, V. pini, V. setosa, and V. tabacina are described and illustrated. Fomes angularis and V. pini are conspecific with V. berkeleyi. Basidia and basidiospores of V. philippinensis are described for the first time, and the new combination Pileodon philippinensis is proposed. Veluticeps australiensis Nakasone nom. nov. is proposed for V. setosa G. Cunn., an illegitimate name. The new genus Campylomyces is proposed to accommodate V. tabacina and V. heimii. The type specimen of Hymenochaete setosa is an amalgam of two or three species; thus, this name should be dropped. Observations on Hymenochaete japonica and Stereum medicum are noted. The genera Veluticeps, Pileodon, and Campylomyces are discussed and compared, and a key to the known species of Veluticeps and related taxa is provided.

Keywords: Basidiomycetes, Boreostereaceae, Campylomyces, Columnocystis, Fomes angularis, Polyporales, Stereum medicum, taxonomy, type studies.

Veluticeps (Cooke) Pat. (Boreostereaceae, Polyporales, Kirk & al. 2001), is a striking and distinctive genus of wood decay fungi that is associated with brown-rotted wood. Previously, Hjortstam and Tellería (1990) expanded the concept of Veluticeps to include Columnocystis Pouzar. Nakasone (1990) accepted this synonymy and included descriptions of seven species of Veluticeps. The disposition of several taxa, however, remained unresolved.

In 1998, an interesting new genus, *Pileodon* P. Roberts & Hjortstam, was proposed to accommodate *P. megasporus* P. Roberts & Hjortstam from Brunei (Hjortstam & al., 1998). *Pileodon* was postulated to be closely related to *Epithele* (Pat.) Pat., for both genera are characterized by hyphal pegs, large basidiospores, and basidia with a distinctly slender stalk. Although not noted previously, the per-

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ennial, brown basidiocarps of *P. megasporus* produce a xanthochroic reaction with potassium hydroxide and display a striking resemblance to some species of *Veluticeps*. Moreover, the hyphal pegs of *P. megasporus* often fuse laterally to form short, thin plates that resemble the extensively developed shallow semireticulum of the morphologically similar taxon, *V. philippinensis* Bresad.

In this study, type specimens of *Pileodon megasporus*, *Veluticeps philippinensis*, *V. pini* Pat., *V. setosa* G. Cunn., *V. tabacinus* (Cooke) Burt, and *Hymenochaete setosa* Berk. & M. A. Curtis were examined. The type specimen of *Veluticeps heimii* Malençon, however, was not available for study. Related taxa such as *Fomes angularis* C. Lloyd, *Hymenochaete boniensis* Yasuda, *Stereum japonicum* Yasuda, and *Stereum medicum* Currey were examined also. *Campylomyces*, a new genus, is proposed to accommodate *V. tabacina* and *V. heimii*. The morphologically similar genera *Veluticeps*, *Pileodon*, and *Campylomyces* are compared and contrasted, and the current status of *Veluticeps* is reviewed. A key to the accepted species of *Veluticeps* and related taxa is provided.

#### Materials and methods

Thin, freehand sections of basidiocarps were mounted in 2% (w/v) KOH and 1% (w/v) aqueous phloxine or Melzer's reagent (Kirk & al., 2001) and examined with an Olympus BH2 compound microscope (Olympus America, Inc., Melville, NY). Drawings were made with a camera lucida attachment, and photographs were taken with an Olympus DP10 or DP12 digital camera system attached to an Olympus SZH zoom stereomicroscope. Color designations are from Kornerup & Wanscher (1978). Herbarium abbreviations are from Holmgren & al. (1990).

Explanation of some terms used in the species descriptions follows. Cystidia are terminal, sterile structures that typically occur singly in the hymenium or subiculum. Although the distinction is not always so clear cut, hymenial cystidia arise from the subhymenium and are part of the hymenium proper whereas tramal cystidia originate in the subiculum. Hymenial cystidia are morphologically differentiated from other sterile hymenial elements such as hyphidia and basidioles. The hyphal system of *Veluticeps* is subject to different interpretations. It has been described as dimitic, composed of generative hyphae and thick-walled skeletal hyphae (Welden, 1967; Hjortstam & Tellería, 1990) and monomitic with sclerified generative hyphae (Nakasone, 1990). Sclerified generative hyphae is a term coined by Donk (1964, p. 237) that refers to hyphae that resemble skeletal hyphae for they are unbranched, thick-walled, 'long, straight, and of equal diameter throughout their length;' however,

scattered clamp connections or simple septa are present. In a typical dimitic system, clamp connections and simple septa are limited to the base of the skeletal or binding hyphae. Hyphal pegs are sterile structures composed of aggregated generative hyphae, skeletal hyphae, or tramal cystidia and may originate in the hymenium, subhymenium, or subiculum. Skeletocystidia as described by Hjortstam & Tellería (1990) are equivalent to tramal cystidia used here.

# Key to the species of Veluticeps, Pileodon, and Campylomyces 2. Basidiocarps dark brown; reported from eastern USA, Europe . . ..... Veluticeps ambigua\* Hymenophore developing hyphal pegs or plates...... 4 Hymenophore smooth, without hyphal pegs..... 4. Hymenophore denticulate or shallowly reticulate; basidiospores 32–41 µm long; reported from the Philippines..... 4. Hymenophore denticulate: basidiospores usually <30 µm long 5 Basidiospores usually 220 µm long..... 6. Basidiocarps effused to effuse-reflexed, basidiospores (10-)12- $14.5(-20) \times 4-6 \,\mu m$ , widely distributed....... V. berkelevi\* 6. Basidiocarps effused, basidiospores 17–21 × 5–6.5(–8) µm; reported from Australia . . . . . . . . . . . . . V. australiensis 7. Basidiocarps effused to effuse-reflexed; generative hyphae not gelatinized; reported from Brunei......... P. megasporus 7. Basidiocarps cupulate or disciform, deeply lobed; generative hyphae gelatinized ...... 8. Basidiospores 20–22× 6–8μm; reported from Spain, Morocco.... ..... Campylomyces heimii 8. Basidiospores 27–33×8–9(–10)µm; reported from Australia ..... 10. Basidiospores 10-13×4-5 um; reported from Europe, North 10. Basidiospores 11.5–15.5×4.5–6µm; reported from western North America . . . . . . V. fimbriata\*

11.	. Basidiospores 5–6.5μm wide; reported from New Zealand
11.	Basidiospores 7–10μm wide; reported from Arizona
	V. pimeriensis
* 0	See Nakasone (1000) for a description and illustration

#### **Taxonomy**

#### Campylomyces Nakasone, gen. nov.

Basidiomata parva, sessilia, gregaria, campanulata, cupulata, extus breviter strigoso-hirsuta, sicca contracta, involuta, ceracea vel cornea, subgelatinosa, uda explanata, molliter elastica. Systema hyphale monomiticum, hyphae fibulatae, gelatinosae. Hymenium numerosa sterilibus clavis. Basidia grandia, clavata, peduculis, tetrasporis. Basidiosporae grandes cylindricae, distinctis obtusis apiculis, tenitunicatis, laevibus, hyalinis, inamyloideis.

Type species. - Aleurodiscus tabacinus Cooke

Etymology. – campylo- (Gr., *campylos* = bent, curved), referring to the incurved margins of the fruitbodies + myces (Gr., *Myces* = mushroom, fungus).

Basidiocarps perennial or annual, small, sessile, gregarious, campanulate to cupulate, with a hirsute-strigose outer layer, contracting and involute, ceraceous or corneous when dried but expanded, elastic, and subgelatinous when hydrated. – Hymenophore with numerous sterile hyphal pegs not reacting to potassium hydroxide. – Hyphal system monomitic with nodose-septate generative hyphae, walls may be gelatinized. Basidia large, clavate, tapering gradually to a stalk at base, up to  $180\times15~\mu m$ , with a basal clamp connection, bearing four sterigmata. – Basidiospores large, cylindrical, with a distinct, blunt apiculus, walls thin, hyaline, smooth, inamyloid.

This new genus is characterized by small, thin, gregarious, sessile, cupulate basidiocarps with free involute margins and a ceraceous or corneous texture. The basidiocarps readily expand and contract in response to moisture. In addition, *Campylomyces* is characterized by numerous, brown hyphal pegs, generative hyphae with gelatinized walls, large basidia, and large basidiospores with a blunt apiculus. The sterigmata on the basidia often appear pinched together. Although the hymenophore does not change color in potassium hydroxide, the pileus and margin may temporarily blacken.

Campylomyces appears to be closely related to Veluticeps for both genera develop brown hyphal pegs, large basidia, and large basidiospores. However, differences between the two genera are readily apparent in basidiocarp size, thickness, shape, texture, and reaction to KOH. The unique features of A. tabacinus were first

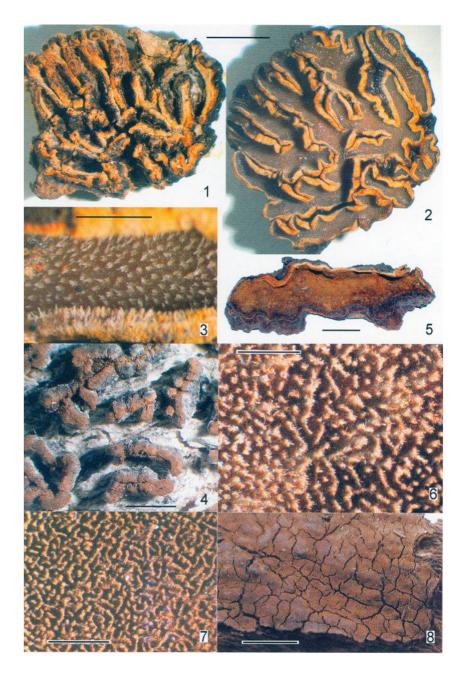
recognized by Cunningham (1963, p. 301) 40 years ago. He wrote that *A. tabacinus* 'could well be made the type of a separate genus' because the only features it shared with *Veluticeps* were the brown hyphal pegs and basidia.

Campylomyces heimii (Malençon) Nakasone, comb. nov., - Figs. 1-3,9.

**■** Veluticeps heimii Malençon, Bull. Trimest. Soc. Mycol. Fr. 55: 42. 1939.

B a s i d i o c a r p probably perennial, pileate, cupulate or disciform, campanulate, sometimes elongate, gregarious, deeply lobed, sessile, attached by a narrowed base, confluent, up to  $30 \times 20$  mm, subgelatinous when fresh then subceraceous to corneous when dried, up to 2 mm thick, brown [6D(7–8)]; pileus surface strigose, tomentose to felty, gray to dark brown to black, temporarily black in KOH; hymenophore denticulate from numerous, tiny, hyphal pegs projecting up to 150 µm, unchanged in KOH; margin free, sulcate, zonate, upturned and involute on drying, lobed, velutinous, sterile, reddish brown, turning black in KOH, then fading to original color; context ceraceous to subceraceous, concolorous with hymenophore, penetrated by dark brown hyphal pegs, unchanged in KOH.

Hypha1 system monomitic, composed of nodose-septate generative hyphae. – Pileus surface composed of a dense, velutinous layer of sclerified hyphae, up to 350 µm thick, arising from a narrow, dense, brown to black, agglutinated cutis layer (about 150-250 µm thick); pileus hyphae 2.2-5.5 µm diam, with rare clamp connections, unbranched, straight, walls thin to 1.5 pm thick, thinning toward apex, yellowish brown to brown, smooth to lightly encrusted. -Subiculum a dense, agglutinated tissue of hyphae arranged parallel to substrate, up to 300 µm thick; subicular hyphae 1.5-6 µm diam, nodose-septate, moderately branched, walls thin to slightly thickened, hyaline to dark yellow, smooth. - Subhymenium up to 500 µm thick, a moderately dense, subceraceous tissue of vertically arranged hyphae; subhymenial hyphae 2–3 µm diam, nodose-septate, moderately branched, walls thin, hyaline, smooth, gelatinous. -Hyphal pegs composed of aggregated, dark yellow to brown tramal cystidia projecting up to 150 µm beyond hymenium, up to 70 µm diam, originating in the subicular-subhymenial interface; tramal cystidia cylindrical to narrowly clavate, sometimes constricted, up to  $230 \times 2.5 - 6 \,\mu\text{m}$ , tapering to  $2 - 4 \,\mu\text{m}$  diam at base, with a basal clamp connection, slightly tapering to an obtuse apex, walls slightly to 1.5 µm thick, often thinning toward base and apex, dark brownish yellow, smooth or encrusted with a thin layer of fine, hyaline crystals, embedded parts often heavily and thoroughly encrusted with hyaline to yellow crystals. – Hymenium up to 150 µm thick, a



Figs. 1–3. Campylomyces heimii (from MA-Fungi 18914). (1.) Dried basidiocarp (scale bar 5 mm). (2.) Hydrated basidiocarp, same sample and magnification as in Fig. 1 (scale bar 5 mm). (3.) Close-up of hydrated hymenophore with hyphal pegs (scale bar 1 mm). Fig. 4. Campylomyces tabacinus (from the holotype, K(M)103894) cluster of dried basidiocarps (scale bar 2 mm). Figs. 5–6. Pileodon megasporus (from the holotype, K(M) 43725. (5.) Dried basidiocarp (scale bar 10 mm). (6.) Close-up of hymenophore with hyphal pegs and plates (scale bar 1 mm). Fig. 7. Pileodon philippinensis (from C. M. Weber 1279 at NY) close-up of semireticulated hymenophore (scale bar 1 mm). Fig. 8. Veluticeps australiensis (from the holotype, PDD 17463) dried basidiocarp with deep cracks (scale bar 10 mm).

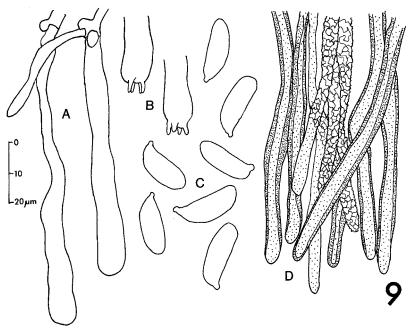


Fig. 9. Microscopic elements of *Cumpylomyces heimii* (from MA-Fungi 18914). (A) Immature basidia; (B) Distal end of basidia with sterigmata; (C) Basidiospores; (D) Hyphal peg composed of yellow to brownish yellow, thick-walled tramal cystidia encrusted with hyaline crystals.

dense palisade of basidia and basidioles developed among projecting hyphal pegs. – Basidioles filiform,  $45-60\times2-3\,\mu m$ , with a basal clamp connection, walls thin, hyaline, smooth. - Basidia clavate,  $80-100\times8-10\,\mu m$ , tapering to  $4-5\,\mu m$  diam stalk, with a basal clamp connection, walls thin, hyaline, smooth, 4-sterigmate, sterigmata up to  $4.5\,\mu m$  long. - Basidiospores cylindrical with a distinct, blunt apiculus,  $(18-)20-22\times6-8\,\mu m$ , walls thin, hyaline, smooth, negative in Melzer's reagent.

Habitat. – On branches of angiospermous wood; associated rot not known.

Distribution. - Morocco, Spain.

Specimens examined. – SPAIN. Santander, Camaleño, Turieno, salida hacia Congarna, 470 m, 30TUN6779, en *Quercus ilex* Linn., 7 Oct. 1986, M. Dueñas, C. Lado & M. T. Tellería, 7705Tell., MA-Fungi 18914 (MA); Potes, Monte Tolibe, 30TUN6878, en *Q. suberi* Linn., 8 Oct. 1986, M. Dueñas, C. Lado & M. T. Tellería, 7712Tell., MA-Fungi 18921 (MA). Jaén, Parque Natural de las Sierras de Cazorla, Segura y Las Villas, La Iruela, junto a1 arroyo Gudahornillos, 30SHW1100, en *Q. rotundifolia* Lam., 1180 m, 13 May 1990, M. T. Tellería, 10565Tell., MA-Fungi37426 (MA).

Campylomyces heimii is characterized by deeply lobed, cupulate basidiocarps, hyphal pegs, basidioles, and large basidiospores. Morphologically, it is most similar to *C. tabacinus*, which has considerably larger basidiospores. The type specimen of *V. heimii* was not available for study; see Malençon (1939) for a detailed description and illustration of the type.

Campylomyces tabacinus (Cooke) Nakasone, comb. nov. - Figs. 4, 10.

- = Aleurodiscus tabacinus Cooke, Grevillea 14: 11. 1885.
- = Veluticeps tabacina (Cooke) Burt, Ann. Mo. Bot. Gard. 6: 261. 1919.

B as i d i o c a r p probably annual, pileate, gregarious, cupulate or disciform, sometimes elongate, up to  $5 \times 5$  mm, involute, sessile or attached by a narrowed base, subceraceous to ceraceous, up to 800 µm thick; pileus surface tomentose to appressed, dark brown to black, black in KOH; hymenophore obscured from involute margins, denticulate from numerous hyphal pegs, pegs about 5 per mm, projecting up to 150 µm, tan-colored to brown [6(E-F)8],unchanging in KOH; margin free, involute, upturned and curving inward on drying, lobed, smooth, sterile, reddish brown, black in KOH; context subceraceous, concolorous with hymenophore, penetrated by darker brown hyphal pegs, unchanged in KOH.

Hyphal system monomitic, composed of nodose-septate generative hyphae. – Pileus surface composed of a dense, velutinous layer of hyphae, up to 150 µm thick, arising from a narrow, dense, brown to black, agglutinated cutis layer (about 100 µm thick); pileus hyphae 3.5-5.5 µm diam, with rare clamp connections, unbranched, straight, sometimes with blue-colored contents, walls thin to thick but thinning toward apex, yellowish or greenish brown, brown or light blue, smooth. - Subiculum 100-200 µm thick, a dense, agglutinated tissue of hyphae arranged parallel to substrate; subicular hyphae 3.5-5.5 µm diam, nodose-septate, sparingly to moderately branched, walls thin to slightly thickened, hyaline, smooth, gelatinous. – Subhymenium 250–300 µm thick, a moderately dense, subceraceous tissue of vertically arranged hyphae and numerous clusters of hyaline crystals; subhymenial hyphae 2-3 µm diam, nodose-septate, sparingly branched, often branching from clamp connections, walls thin, hyaline, smooth, gelatinous. -Hypha1 pegs composed of aggregated, brown tramal cystidia projecting up to 135 µm beyond hymenium, up to 100 µm diam, originating in the subicular-subhymenial interface; tramal cystidia cylindrical to narrowly clavate, sometimes with constrictions, up to 180 × 5.5 µm, tapering to 3-4 µm diam at base, with a basal clamp connection, sometimes with secondary septa, apex obtuse and roun-

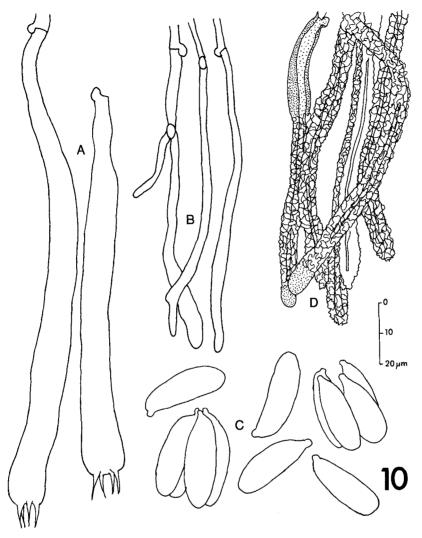


Fig. 10. Microscopic elements of *Campylomyces tabacinus* (from the holotype, K(M)103894). (A) Basidia; (B) Basidioles; (C) Basidiospores; (D) Hyphal peg cornposed of thick-walled trarnal cystidia coated with brown, mucilaginous materials.

ded or slightly tapering, extending up to 100  $\mu$ m beyond hymenium, walls slightly to 3  $\mu$ m thick, often becoming thinner toward base and apex, brownish yellow to dark brown throughout, apical portion encrusted with hyaline crystals or brownish yellow mucilaginous or resinous deposits. – Hymenium up to 150  $\mu$ m thick, a dense palisade of basidia and basidioles developed between projecting hyphal pegs. – Basidioles filiform, often expanding slightly toward apex, up to  $100 \times 3-4 \mu$ m, tapering to 2  $\mu$ m diam at base, with a basal

clamp connection, walls thin, hyaline, smooth. – Basidia clavate,  $125-170 \times 13-15 \,\mu\text{m}$ , tapering to 3–5  $\mu\text{m}$  diam at base, with a basal clamp connection, walls thin, hyaline, smooth, 4-sterigmate, sterigmata up to 8  $\mu\text{m}$  long, often persisting after maturation, collapsed and empty. – Basidiospores cylindrical with a distinct, blunt apiculus,  $27-33 \times 8-9(-10) \mu\text{m}$ , often agglutinated, walls thin, hyaline, smooth, negative in Melzer's reagent.

Habitat. – On angiospermous wood; associated rot not known. Distribution. – Australia.

Specimens examined. - AUSTRALIA. New South Wales, Walcha, Moona, on wood of *Eucalyptus*, Feb. 1885, A. R. Crawford, K(M)103894 (holotype: K; isotype: NY, 00072510). Queensland, Darling Downs, on wood of Eucalyptus, no. 1095, K(M)103895, as *Hydnum delicatulum* (K).

Campylomyces tabacinus is characterized by lobate, cupulate basidiocarps, brown hyphal pegs, basidioles, and large basidiospores. The gelatinous walls of the subicular and subhymenial hyphae and unusual blue walls and contents of the pileus hairs are noteworthy. It is most similar to *C. heimii* in overall morphology. This is a rare species, for only the two collections cited are known. For additional descriptions, see Burt (1919), Cunningham (1963), and Welden (1967).

*Fomes angularis* C. Lloyd, Mycol. Writings 4, Letter 45, p. 6. 1913 (as 'angulus').

= Fomes angularis C. Lloyd, Mycol. Writings 4: 239. 1915.

Basidiocarp about  $40 \times 25$  mm, probably perennial, effuse-reflexed to ungulate, corky-woody, up to 6 mm thick; pileus up to 8 mm wide, greyish brown to brown [7F(3-4)], concentrically zonate; hymenophore denticulate with numerous hyphal pegs, pegs up to 9 per mm, brown (6E5), with obtuse, bristly, fimbriate apices; context stratose, fibrous, light brown (6D7).

Hyphal system monomitic but appearing dimitic, with nodose-septate generative and sclerified hyphae. – Context a dense, nonagglutinated, fibrous tissue composed of regular and sclerified hyphae; subicular hyphae 2–4 μm diam, nodose-septate, moderately branched, walls thin, hyaline to light brown, smooth or encrusted with scattered or numerous, coarse, hyaline crystals; sclerified subicular hyphae 3.5–5.5 μm diam, with clamp connections at the base, often secondarily septate, unbranched, walls thick, brown, smooth or verrucose, sometimes encrusted with coarse, hyaline crystals. – Hyphal pegs an aggregation of tramal cystidia, originating in subhymenium and protruding through hymenium;

tramal cystidia cylindrical to slightly clavate, up to  $140\times6$  µm, with a basal clamp connection, often developing secondary septa, walls thin, hyaline at first, then thick, brown, smooth to lightly encrusted with hyaline crystals. – Hymenium a dense palisade of basidia and sclerified hyphae developed among hyphal pegs. – Basidia narrowly clavate,  $90\times5.5$  µm, with a basal clamp connection, walls thin, hyaline, smooth, 4-sterigmate. – Basidiospores cylindrical often flattened on adaxial side, sometimes tapering slightly toward apiculus,  $10.5\text{--}17\times4\text{--}5.5$  µm, walls thin, hyaline, smooth.

Specimen examined. – JAPAN. Nagoya, growing on *Pasania*, Jintaro Umemura, C. G. Lloyd Cat. No. 16106, US0308310 (holotype: BPI).

Fomes angularis possesses sterile hyphal pegs and is conspecific with Veluticeps berkeleyi (Berk. & M. A. Curtis) Cooke. In 1987, Y. Abe, in notes included in the type collection packet, came to the same conclusion. Lloyd (1913; 1915) inexplicably described F. angularis as having minute pores, and Ryvarden (1989) erroneously reported that the type of F. angularis is a sterile species of Phellinus. Ito (1955) placed F. angularis in synonymy under Veluticeps medica (Currey) Cooke, but the taxa are not conspecific. See description and discussion of Stereum medicum later in this study.

The type specimen of *F. angularis* was fruiting on *Pasania* sp., a hardwood genus related to *Quercus*. This is an unusual substrate for *V. berkeleyi*, which is typically found on coniferous substrates. See Lloyd (1915, Fig. 7586) for an illustration of the type specimen and Welden (1967) for a description.

*Pileodon megasporus* P. Roberts & Hjortstam, Kew Bull. 53: 817. 1998 (as *megaspora*), Figs. 5–6,11.

Basidiocarp perennial, effuse-reflexed, sessile, up to  $7 \times 3.5$  cm, tough, woody, up to 4 mm thick; pileus up to 12 mm wide, hard, dull grayish brown, concentrically zonate; hymenophore with numerous hyphal pegs, pegs 4-6per mm,  $200-250\,\mu\text{m}$  tall, single or laterally fused to form thin plates, with distinct smooth areas between the plates, brown (6E8), dark brown (6F8) to nearly black, black in KOH; margin sterile, up to 1 mm wide, smooth, brownish orange (6C5) to nearly black; context fibrous, dense felty, concolorous with hymenophore, penetrated with numerous dark hyphal pegs that protrude through the hymenium, immediately turning black in KOH.

Hyphal system dimitic with nodose-septate generative and skeletal hyphae. – Pileus hyphae 2.5–3.5 μm diam, rarely branched, walls thin, hyaline, smooth or brown, thick, smooth or

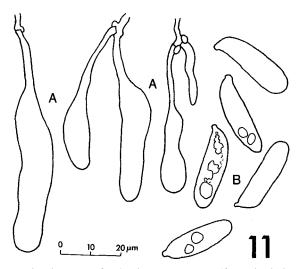


Fig. 11. Microscopic elements of *Pileodon megasporus* (from the holotype, K(M) 43725). (A) Immature, stalked basidia; (B) Basidiospores.

encrusted with hyaline crystals. – Context a dense, compact tissue composed primarily of skeletal hyphae, scattered generative hyphae, and embedded post-mature, brownish vellow basidia and basidiospores; subicular hyphae 1.5-2 µm diam, moderately to sparsely branched, walls thin, hyaline, smooth; skeletal hyphae 2–2.5 µm diam, unbranched, walls thick, brownish yellow, smooth. – Hypha 1 pegs originating deep in context, composed of aggregated terminal skeletal hyphae, slenderly clavate, up to  $200 \times 3.5 - 6.5 \,\mu\text{m}$ , slightly constricted, with rounded apices, walls up to 1 µm thick, thinning toward apex, hyaline to brownish yellow, smooth. - Hymenium developed between sterile hyphal pegs, composed of basidia and hyphidia. – Hyphidia filamentous, about  $100 \times 1.5 - 2 \,\mu m$ , with a basal clamp connection, apex obtuse, walls thin to slightly thickened, hyaline at first, then brownish yellow, smooth. - Basidia rare, cylindrical to clavate with a distinct, slender stalk, up to  $70 \times 11$  µm, at base 2 µm diam, with a basal clamp connection, walls thin, hyaline, smooth, 4-sterigmate; post-mature basidia persisting in context, embedded and brownish vellow. - Basidiospores scattered, cylindrical with a distinct, blunt apiculus,  $26-30 \times 6.5-$ 8.5 µm, often containing several refractive globules, often embedded in context, with walls thin, hyaline at first, then brownish yellow, smooth, negative in Melzer's reagent.

Habitat. – On rotten log; associated rot not known.

Distribution.-Brunei.

Specimen examined. - BRUNEI. Tamburong District, Sungai Belalong Field Centre, trail to Ashton plot, on rotten log, 25 Mar. 1992, B. M. Spooner B690, K(M)43725 (holotype: K).

*Pileodon megasporus* is characterized by a dark brown, effuse-reflexed basidiocarp, dimitic hyphal system, hyphal pegs, hyphidia, and large basidiospores. It is most similar to *Veluticeps philippinensis*, which has significantly larger basidiospores and a more extensive reticulum than *P. megasporus*.

## Pileodon philippinensis (Bresad.) Nakasone, comb. nov., Figs. 7, 12.

- ≡ Veluticeps philippinensis Bresad., Hedwigia 61: 302. 1915.
- ≡ Hymenochaete philippinensis (Bresad.) Bresad., Syll. Fung. 23: 529. 1925.

Basidiocarp probably perennial, effuse-reflexed, sessile, dimidiate, up to  $6 \times 3.5$  cm, tough and firm, up to 8 mm thick; abhymenial surface tomentose, rugulose, brown [7(E-F)7], concentrically zonate; hymenophore denticulate, daedaloid to semireticulate, developed from hyphal pegs, pegs 4–6per mm,  $100-180 \,\mu m$  high, single or laterally fused to form thin plates with distinct smooth areas between the plates, plates fusing to develop a shallow, daedaloid to semireticulate pattern, light brown [5D(4–5)] to dark brown (6F6), sometimes developing a white bloom over surface (no. 16811 at NY), black in KOH; margin up to 5 mm wide, smooth to furfuraceous, lighter than hymenophore, golden brown (5D6); context with a soft, fibrous texture, brown [6D8; 7(E-F)8], stratose, with a darker cutis next to substrate, numerous dark brown hyphal pegs penetrating the context and hymenium, immediately turning black in KOH.

Hyphal system dimitic with nodose-septate generative and skeletal hyphae. – Abhymenial surface and subiculum not observed. - Context a thickening, loosely defined layer of primarily skeletal and some generative hyphae arranged perpendicular to substrate with embedded, brown-pigmented basidiospores and basidia; subicular hyphae 1.5–2.5 µm diam, nodose-septate, moderately branched, walls thin to slightly thickened, hyaline, smooth; skeletal hyphae 1.8–3 µm diam, straight, unbranched, brittle, walls thick, yellow to brown, smooth or encrusted with hyaline to brownish yellow mucilaginous or resinous deposits. – Hyphal pegs and plates sterile, formed from aggregated skeletal hyphae, originating in subhymenium and subiculum, protruding up to 180 µm beyond hymenium; skeletal hyphae cylindrical to narrowly clavate, up to  $165 \times 3$ -6 μm, often slightly swollen (up to 10 μm diam) in lower half, tapering to 1.5-3 µm diam at base, with a basal clamp connection, sometimes with secondary septa, rarely branched, apex slightly acute or rounded, walls slightly thick or thick, sometimes thinning toward base and apex, yellow or dark brown, often becoming lighter in color

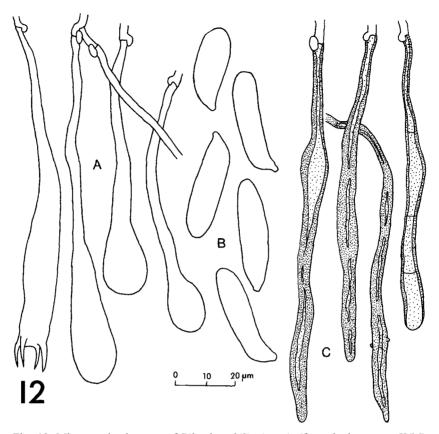


Fig. 12. Microscopic elements of *Pileodon philippinensis* (from the lectotype, K(M) 103896). (A) Mature and immature, stalked basidia; (B) Basidiospores; (C) Skeletal hyphae from hyphal pegs.

toward the apex, smooth or encrusted with hyaline to brownish yellow mucilaginous or resinous deposits at apex. – Hymenium a dense palisade of hyphidia with sparse clusters of basidia developed among hyphal pegs and plates. – Hyphidia similar to skeletal hyphae in hyphal pegs except usually shorter and protruding up to 25 µm beyond hymenium. – Basidia clavate, typically with a distinct, slender stalk,  $67-105\times9-15$  µm, 2-4 µm diam at base, with a basal clamp connection, walls thin, hyaline, smooth, 4-sterigmate, sterigmata up to 8 µm long; post-mature basidia embedded, collapsed with slightly thickened, brownish yellow walls. – Basidiospores rare, cylindrical to fusiform with a distinct, blunt apiculus,  $32-41\times8-12$  µm, often collapsed and embedded in context, walls thin, hyaline at first, then slightly thickened and brownish yellow, smooth, negative in Melzer's reagent.

Habitat. – Probably woody angiosperms; associated rot not known.

Distribution. - Philippines.

Specimens examined. – PHILIPPINES. Luzon, D. Merrill 1279, K(M)103896 (lectotype: K; isolectotype: S); Luzon, Prov. Cagayan, Mar. 1909, H. M. Curran, Forestry Bureau no. 16811 (syntype: NY); Mindanao, Butuan subprovince, Mar.-Jul. 1911, C. M. Weber no. 1279 (NY; BPI: US0277445, US0329931 as *Hymenochaete medica*).

Pileodon philippinensis is a rare and distinctive species characterized by large basidiospores and a shallow, daedaloid to semireticulate hymenophore. It is most closely related to *P. megasporus* for both species develop distinctly stalked basidia and hyphal pegs that fuse laterally to form plates; however, the reticulum is much more extensive in *P. philippinensis* than in *P. megasporus*.

This is the first recorded description of basidia and basidiospores in *P. philippinensis*. Basidia are sparsely distributed and embedded in a dense hymenial layer and are difficult to observe. Thin sections mounted in KOH and phloxine are best for observing basidia and basidiospores. Developing basidia with long, slender stalks are more frequently observed than mature basidia. Basidiospores were uncommon but were observed in all the specimens cited. Other descriptions of this species can be found in Bresadola (1915), Welden (1967), and Hjortstam & Tellería (1990).

There is some confusion concerning the specimens that Bresadola cited. In 1914, Bresadola & Sydow (1914) first mentioned V. philippinensis and cited the collection 'Mindanao, Butuan Subprovince, C. M. Weber 1279, March-July, 1911.' However, a year later when Bresadola (1915) validly described the species, he mentioned two specimens 'Luzon, D. Merrill 1279, Forestry Bureau 16811.' The question is whether Weber 1279 and Merrill 1279 are from the same gathering. After examining three collections of V. philippinensis, C. M. Weber 1279 and two of D. Merrill 1279, I believe it is likely that they are all from the same gathering. However, since the protologue mentions D. Merrill as the collector, the K and the S collections are the best candidates for lectotype designation. Hjortstam & Tellería (1990) choose the specimen at Kew as the holotype. This is a particularly small specimen, only 9 × 9 mm. The specimen of V. philippinensis deposited at S, however, would have been a better choice as lectotype because it is a larger collection and the original packet has a description of the fungus written in Bresadola's hand.

#### Veluticeps australiensis Nakasone, nom. nov., Figs. 8, 13.

<sup>=</sup> Veluticeps setosa G. Cunn., N. Z. Dep. Sci. Ind. Res. Bull. 145: 332. 1963; non V. setosa (Berk. & M. A. Curtis) Cooke, Grevillea 8: 149. 1880.

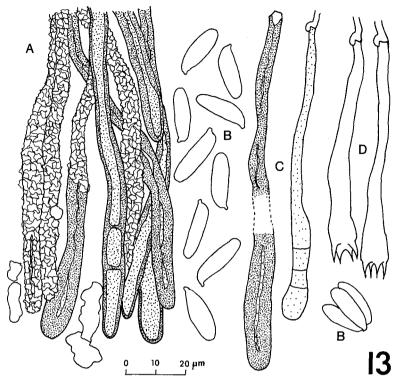


Fig. 13. Microscopic elements of *Veluticeps australiensis* (from the holotype, PDD 17463). (A) Hyphal peg composed of encrusted, thick-walled tramal cystidia encrusted with crystals; (B) Basidiospores; (C) Tramal cystidia; (D) Basidia.

Basidiocarp resupinate, effuse, up to  $5 \times 3.5$  cm, dense, firm, up to 1.5 mm thick, rimose; hymenophore denticulate from numerous, tiny, projecting hyphal pegs, brown [6(E-F)7], black in KOH; hyphal pegs about 7 per mm, projecting up to 180  $\mu$ m, apices penicillate to bristly; margin thinning, felty, fibrous, smooth, lacking hyphal pegs, concolorous with hymenium, black in KOH; context a dense, reddish brown fibrous tissue penetrated by dark brown to black hyphal pegs, black in KOH.

Hyphal system monomitic although appearing dimitic, with nodose-septate generative and sclerified hyphae. – Subiculum up to 700 μm thick, a dense, fibrous tissue of primarily sclerified hyphae arranged parallel to substrate and curving into and terminating in lower subhymenium; subicular hyphae sclerified, 2.5–4 μm diam, with rare clamp connections, rarely branched, slightly enlarged at apex, walls thick, light to dark brown, smooth, occasionally developing small, hyaline pegs or warts, or encrusted with small, hyaline

granules or dark brown, mucilaginous deposits. - Subhymenium thickening up to 750 um thick, a dense, fibrous layer of vertically arranged sclerified hyphae and embedded hyphal pegs: subhymenial hyphae sclerified, 2-4 um diam, with rare clamp connections, rarely branched walls thick light to dark brown, smooth - H v p h a l pegs an aggregation of tramal cystidia projecting up to 180 um beyond hymenium, up to 75 um diam, originating in the subjcularsubhymenial interface: tramal cystidia long clavate to cylindrical, un to  $180 \times 5 - 12 \,\mathrm{um}$ , tapering to  $2 - 4 \,\mathrm{um}$  diam at base, with a basal clamp connection, sometimes with secondary septa, apex obtuse and rounded or slightly tapering, walls thin at first, then up to 5 um thick, brownish vellow to dark brown throughout, often encrusted with hyaline, granular crystals or with brownish vellow mucilaginous or resinous materials. – Hymenium up to 100 um thick, a layer of indistinct, collapsed, thin-walled basidia and large, embedded, hyaline crystals interspersed with hyphal pegs. - Basidia clavate.  $70-75 \times 8-9$  µm. gradually tapering into a stalk 2 µm diam. with a basal clamp connection, walls thin, light brown, smooth, 4-sterigmate, sterigmata usually collapsed. - Basidiospores allantoid to cylindrical with a distinct, blunt apiculus,  $17-21 \times 5-6.5(-8) \mu m$ , often embedded in subhymenium and hymenium, often agglutinated. walls thin, hyaline to light brown, smooth, negative in Melzer's reagent.

Habitat. – On angiospermous wood.

Distribution. – Australia.

Specimen examined. – AUSTRALIA. Queensland, Cunningham's Gap, on *Tristania conferta* R. Br., 1 Nov. 1953. J. Gresty, PDD 17463 (holotype: PDD).

The new name *V. australiensis* is proposed for *V. setosa* G. Cunn., which is illegitimate as pointed out by Parmasto (1998). Veluticeps australiensis is characterized by resupinate basidiocarps with deep and numerous cracks, hyphal pegs, and large basidiospores. Its resupinate, effuse habit and slightly larger basidiospores distinguish it from *V. berkeleyi*. The tramal cystidia of the hyphal pegs are slightly larger and darker than the sclerified hyphae found embedded in the subiculum and subhymenium. For additional descriptions and illustrations see Cunningham (1963) and Welden (1967).

Veluticeps pini Pat., Bull. Trimest. Soc. Mycol. Fr. 22: 72. 1907.

≡ Hymenochaete pini (Pat.) Sacc. & A. Trotter, Syll. Fung. 21: 404. 1912.

Specimen consists of several large pieces (33–40×12–33 mm) and about six smaller pieces, up to 1 mm thick, sessile, pileate to effuse-reflexed, umbonate, imbricate, complicate, confluent, some-

times pileus attenuate and attached by a point; pileus concentrically sulcate, black to reddish brown (8F8), a hard, felty, matted tissue with deposits of acerose, shiny crystals; hymenophore denticulate from numerous, acicular hyphal pegs, pegs 8–10 per mm, yellowish brown [5D(4–6)], immediately turning black in KOH, then fading to brown; context stratose with columns of brown hyphal pegs, fibrous, black in KOH at first, then fading to brown.

Hyphal system monomitic although appearing dimitic, with nodose-septate generative and sclerified hyphae. - Pileus trama composed of sclerified generative hyphae arranged in parallel, these 3.5-6.5 µm diam, with occasional single clamp connections, unbranched, walls thick, dark brown, smooth. – Subiculum composed of sclerified and regular hyphae arranged in parallel then turning into hymenium, stratose; subicular hyphae 2–4 µm diam, nodose-septate, frequently branched, walls thin, hyaline, smooth; sclerified subicular hyphae 3.5-5 um diam, with rare clamps, unbranched, straight, curving into hymenium, often embedded, walls thick, brownish yellow to golden yellow, smooth or encrusted with fine granular material. – Subhymenium up to 600 µm thick. – Hyphal pegs sterile, composed of aggregated tramal cystidia, originating in subhymenium and subicular-subhymenial interface then protruding through hymenium; tramal cystidia slenderly clavate, 3-8 um diam, clamped at base, unbranched, walls up to 2 um thick, hyaline to brownish yellow, smooth or encrusted with fine, granular, hyaline material. – Hymenium about 150 µm thick, composed of basidia and tramal cystidia developed among hyphal pegs. - Basidia clavate,  $81-84 \times 7-8 \,\mu\text{m}$ , tapering to  $2.5-3 \,\mu\text{m}$  diam at base, clamped at base, walls thin, hyaline, smooth, 4-sterigmate. - Basidiospores cylindrical, sometimes tapering slightly toward apiculus,  $13-15 \times 5-$ 6 µm, walls thin, hyaline, smooth, negative in Melzer's reagent.

Specimen examined. – [VIETNAM], Tonkin, sur *Pinus taeda* L., Eberhardt LBA, no. 93 (lectotype: FH)

Veluticeps pini is conspecific with V. berkeleyi. Welden (1967) and Gilbertson & al. (1968) noted similarities between V. pini and V. berkeleyi but were reluctant to consider them conspecific because of slight differences in basidiospore width and wall thickness of the hyphal peg elements.

#### Notes and observations on related taxa

*Hymenochaete japonica* Yasuda in C. Lloyd, Mycol. Writings 5, Letter No. 65, p. 8. 1917.

Specimen examined. – JAPAN. Inyo, Sendai, 16 Aug. 1916, A. Yasuda, Lloyd No. 29719, US0330142, as *H. medica* (BPI).

Although the basidiocarp is a little unusual (effused with a dark brown hymenophore), the microscopic features are consistent with *V. berkeleyi. The* basidiospores,  $12-21 \times 4.5-6.3 \, \mu m$ , are within the range for *V. berkeleyi*, although some spores are longer than usual. The name *H. japonica* was not validly published, but it has appeared in the literature. In Note 542, Lloyd (1917, p. 8) first used this name to refer to a specimen (US0330142) received from A. Yasuda from Japan. Although Lloyd states that 'The Japanese plant was sent under the name *Hymenochaete japonica* by Yasuda,' it appears that the specimen was originally named *Stereum japonicum* as evidenced by a small, hand-written label included in the specimen box. Lloyd believed that this specimen was identical to *Hymenochaete medica*, and this is the name on the specimen box label. There is at least one other reference of *H. japonica* by Ito (1930) who listed it as a synonym of *H. medica*.

#### Hymenochaete setosa Berk. & M. A. Curtis, Grevillea 1: 165. 1873.

= *Hymenochaete* [subg. *Veluticeps*] setosa Berk. & M. A. Curtis in Cooke, Grevillea 8: 149. 1880.

Basidiocarp effuse, closely appressed, thin; hymenophore varied, composed of slender spines up to 200  $\mu$ m long, about 9 spines per mm, attenuated, pale in color at apex, sometimes spines fusing laterally to form irregular pits, brown (6E6), not changing color in KOH, or hymenophore smooth to tuberculate, degraded, rimose, ceraceous, light brown to brown [6D(6–8)],black in KOH then fading to reddish brown; no margin observed. Three hyphal types observed: (1) hyphal fragments with clamp connections, with thin, hyaline walls; (2) straight, rigid hyphae, 2  $\mu$ m diam, aseptate, with brown, thick walls; (3) *Scytinostroma*-like fiber hyphae. Set a e fusiform, with or without a sheath, single or clustered and agglutinated, walls brown and thick. Basidia not observed. Basidiospores abundant, broadly ellipsoid, flattened slightly on the adaxial side,  $7 \times 4.5 \mu$ m, walls brown, thick, smooth.

Specimen examined. – UNITED STATES. Alabama, ad lign. Querc., Peters (599), no. 4547 (holotype: K, K(M)103897; isotype: FH).

The specimen at FH consists of two small, rectangular pieces,  $20 \times 14$  and  $16 \times 6$  mm, and the packet has information on the collector and numbers found in the protologue that are lacking in the Kew specimen. Both specimens, however, appear to be an amalgam of two or three different species. The presence of setae indicates that one of the elements is probably a *Hymenochaete* species. The fiber hyphae are suggestive of a *Scytinostroma* species, whereas the observed basidiospores are similar to those found in *Leucogyr*-

ophana. Hymenochaete setosa is, therefore, an untenable name, a nomen confusum. Earlier, Burt (1918) reported that the holotype was a hyphomycete.

Stereum medicum Currey, Trans. Linn. Soc. London, Bot. II, 1(3): 127. 1876.

- ≡ Porostereum medicum (Currey) Hjortstam & Ryv., Synopsis Fungorum 4: 37.1990.
- ≡ *Hymenochaete medica* (Currey) C. Lloyd, Mycol. Writings 5, Letter No. 65, p. 8. 1917.
- ≡ Lloydella medica (Currey) Rick, Broteria Ser. Trimest. Cienc. Nat. 3(1): 33.
  1934.

Basidiocarp resupinate, effuse, up to 1 cm thick, stratose, soft but with a firm and fibrous texture; hymenophore smooth with scattered tubercules, with a short-velutinous surface, brown (6E7), turning black in KOH; margin felty to fibrous. Hyphal system monomitic but appearing dimitic, with nodose-septate generative and sclerified hyphae. Subjected hyphae of two types: generative hyphae (only fragments observed) 1.8-3 µm diam, nodoseseptate, walls thin; sclerified hyphae 3-5.5 um diam, with a basal clamp connection, unbranched, walls up to 2 µm thick, brownish vellow, smooth, swelling in KOH. Subhymenium and hymenium not observed. Cystidia cylindrical, up to 150  $\mu$ m  $\times$  2–4  $\mu$ m, with a basal clamp connection, often with secondary septa, apex obtuse, sometimes slightly expanded, walls up to 2 µm thick, dark yellow in KOH, brownish yellow in Melzer's reagent, smooth or encrusted with fine granular material at apex, swelling in KOH but not in Melzer's reagent or water. Basidia and basidiospores not observed.

Specimens examined. – INDIA. Sikkim, Oct. 1868, F. Currey 2582, K(M)107271 (holotype: K); Lloyd Cat. No. 29750, US0329930, as *Hymenochaete medica* (BPI).

The holotype specimen is a small fragment,  $20 \times 20$  mm, that is sterile. A smaller specimen,  $12 \times 8$  mm, labeled 'authentic' in the Lloyd Herbarium at BPI is morphologically similar to the holotype specimen and may represent an isotype; this specimen is sterile also. See Hjortstam & Ryvarden (1990) for a description and illustration of *S. medicum*. Although lacking a fertile hymenium, *S. medicum* does not belong in *Veluticeps* as suggested by Lloyd (1917) because it lacks hyphal pegs and has a soft basidiocarp texture. Hjortstam & Ryvarden (1990) postulated that *S. medicum* is congeneric with *Porostereum*. The specimen from Japan identified as *H. medica* by Lloyd (1917) in Note 542 is *V. berkeleyi*; see discussion under *Stereum japonica*.

Tab. 1. - Comparison of critical characters differentiating *Campylomyces, Pileodon*, and *Veluticeps*.

Taxon	Hyphal system	Sclerified hyphae/ tramal cystidia	Gelatinized hyphae	Hyphal pegs	Basidia with a distinct stalk	Hymeno- phore turn- ing black in KOH
Campylo- myces	Monomitic	Present	Present	Present	None	No
Pileodon	Dimitic	None	None	Present	Present	Yes
Veluticeps sensu stricto*	Monomitic	Present	None	Present	None	Yes
Veluticeps sensu lato**	Monomitic	Present	None	None	None	Yes

<sup>\*</sup> Includes Veluticeps berkeleyi and V. australiensis.

#### Discussion

Eight species of *Veluticeps*, two of *Pileodon*, and two of *Campylomyces* are recognized worldwide. These distinctive genera are characterized by a smooth, tuberculate, denticulate, or reticulate hymenophore, large, brown-pigmented cystidia, and large basidiospores. Six species develop hyphal pegs, namely, *V. australiensis*, *V. berkeleyi*, *C. heimii*, *C. tabacinus*, *P. megasporus*, and *P. philippinensis*. Hyphal pegs are composed of skeletal or sclerified generative hyphae that appear as tramal cystidia. In addition, the hyphal pegs in *P. philippinensis* and *P. megasporus* often fuse together to form thin plates. Table I summarizes the distinguishing features of *Campylomyces*, *Pileodon*, and *Veluticeps*.

Most of the species studied herein have a restricted geographical range and are quite rare except for *V. berkeleyi*, which is reported from Europe, North America, Central America, and eastern Asia. For example, *P. philippinensis* is known only from the Philippines and is represented by five specimens. Similarly, there are only two specimens of *C. tabacinus* from Australia; *V. australiensis* from Australia and *P. megasporus* from Brunei are known only from the type collections.

Hjortstam & Tellería (1990) proposed a broad definition of *Veluticeps* that discounted the significance of hyphal pegs and instead stressed the similarities in basidia and basidiospore shape and size when they placed *Columnocystis* in synonymy with *Veluticeps*. They also noted that species of *Veluticeps* and *Columnocystis* 

<sup>\*\*</sup> Includes Veluticeps fusispora and taxa formerly placed in Columnocystis, i.e., V. abietina, V. africana, V. ambigua, V. fimbriata, and V. pimeriensis.

were associated with a brown-rot decay. Nakasone (1990) accepted this broad, inclusive definition of Veluticeps. Morphological studies of taxa described in this paper, however, demonstrate that the genus Veluticeps as presently defined is too broad. Thus, *Veluticeps philippinensis* is transferred to *Pileodon*, and the new genus *Campylomyces* is proposed to accommodate *Veluticeps* species with hyphal pegs but cupulate, ceraceous basidiocarps and gelatinized hyphae (Tab.I).

The new genus Campylomyces is proposed for Veluticeps heimii and V. tabacina. Although developing hyphal pegs and large basidiospores, they are quite distinct from other Veluticeps species in other features. The basidiocarps of *Campylomyces* are small, thin, cupulate or disciform with involute, free margins and a ceraceous or corneous texture. In contrast, the basidiocarps of Veluticeps and Pileodon are large, thick, pileate to effuse-reflexed, tough, and firm or woody. All tissues of Veluticeps and Pileodon produce a xanthochroic reaction but in *Campylomyces* the reaction is temporary and limited to the pileus and incurled margins. Furthermore, the hymenophore in Campylomyces does not blacken in KOH, and gelatinized hyphae are present. The gelatinized subhymenial and subicular hyphae are probably responsible for the ability of the basidiocarps to contract and expand in response to moisture conditions. The basidiocarps of C. heimii and C. tabacina are reminiscent of some Aleurodiscus species such as A. amorphus (Pers.: Fr.) Schröter and A. oakesii (Berk. & M. A. Curtis) Pat. that develop cupulate basidiocarps that also contract and expand in response to moisture conditions.

The dark brown, tough and woody basidiocarps of *Pileodon* are similar to those of *V. berkeleyi. Pileodon* is further characterized by a dimitic hyphal system, numerous hyphidia in the hymenium, distinctly stalked basidia, and hyphal pegs formed from skeletal hyphae. The construction of the hyphal pegs in *Pileodon* is quite different from those in *Veluticeps* and *Campylomyces* that are composed of tramal cystidia. In addition, the hyphal pegs in *Pileodon* often fuse laterally to form thin plates. These sterile plates often continue fusing to develop a semireticulate or daedaloid pattern. The distinctly stalked basidia of *Pileodon*, resembling those developed in *Epithele typhae* (Fr.) Pat., are different from the clavate basidia with gradually tapering stalks found in *Veluticeps* and *Campylomyces*.

Eight species remain in *Veluticeps* with the transfer of *V. philippinensis*, *V. tabacina*, and *V. heimii* to *Pileodon* and *Campylomyces*. Of the remaining taxa, only *V. berkeleyi*, the type species, and *V. australiensis* develop hyphal pegs. In recent phylogenetic studies by Kim & Jung (2000) and Lim (2001) on the relationship of corticioid fungi and other Homobasidiomycetes using sequences of the

nuclear small subunit ribosomal RNA gene, *V. berkeleyi* and *Gloeophyllum sepiarium* (Fr.) P. Karsten clustered together in a separate clade from *V. abietina* and *V. ambigua*. If this division in *Veluticeps* is confirmed by other phylogenetic studies, it will be necessary to reinstate the genus *Columnocystis*. For now, however, it seems prudent to keep the genus *Veluticeps* intact, recognizing two groups based on the presence or absence of hyphal pegs. *Veluticeps sensu stricto* is limited to taxa with hyphal pegs, namely, *V. berkeleyi* and *V. australiensis*. *Veluticeps sensu lato*, essentially equivalent to the genus *Columnocystis*, includes taxa that lack hyphal pegs, namely, *Veluticeps abietina* (Pers.: Fr.) Hjortstam & Tellería, *V. africana* (Boidin, Lanquetin & Gilles) Hjortstam & Tellería, *V. ambigua* (Peck) Hjortstam & Tellería, *V. fimbriata* (Ell. & Ev.) Nakasone, *V. fusispora* (G. Cunn.) Hjortstam & Ryv., and *V. pimeriensis* (Gilbertson) Hjortstam & Tellería.

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