TAXONOMIC STUDY OF VELUTICEPS (APHYLLOPHORALES)

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ABSTRACT

Veluticeps is emended to include Columnocystis. New combinations of V. fimbriata and V. fusispora are proposed. Descriptions of seven species of Veluticeps are included as well as cultural descriptions of V. abietina and V. fimbriata. Veluticeps fimbriata, common throughout western North America, is a distinct species from V. abietina, which is found primarily in eastern and northwestern North America and Europe. A key to the species of Veluticeps is provided. The Chaetodermataceae is emended to include Veluticeps and Crustoderma.

Key Words: Veluticeps berkeleyi, Columnocystis, Chaetodermataceae, cultural descriptions, brown-rot fungi

Pouzar (1959) discussed the problem of the large, artificial genus Stereum J. Hill ex Pers. and divided it into a number of smaller and more homogeneous genera. One of the new genera Pouzar erected at that time was Columnocystis, to accommodate three species: C. abietina (Pers.: Fr.) Pouzar, the nomenclatural type, C. carpatica (Pilát) Pouzar, and C. ambigua (Peck) Pouzar. Columnocystis remains a small genus that also includes C. africana Boidin et al., and C. pimeriensis Gilbertson.


The striking microscopic similarities between Veluticeps berkeleyi (B. & C.) Cooke and Columnocystis abietina suggested to me that they may be congeneric. Hjortstam and Tellería (1990) arrived at the same conclusion. They transferred C. abietina, C. africana, C. ambigua, and C. pimeriensis into Veluticeps. In addition, cultural studies indicated that specimens called C. abietina in our herbarium included more than one taxon. This study was undertaken to examine the taxonomic relationship between Veluticeps and Columnocystis and to resolve the species complex involving C. abietina.

MATERIALS AND METHODS

Microscopic examination of basidiomata was made from freehand and frozen microtome sections mounted in 2% (w/v) KOH and 1% (w/v) aqueous phloxine or Melzer’s reagent (Hawksworth et al., 1983). Basidiospores were mounted in Melzer’s reagent and measured with a 100x objective under oil immersion. Color designations are from Kornerup and Wanscher (1978): Herbarium abbreviations are from Holmgren et al. (1981). Distribution maps were produced from specimens examined and specimens cited in selected publications; a list is available from the author. All cultures are of polysporous origin unless noted otherwise and are on deposit at the Center for Forest Mycology Research (CFMR). Cultures were grown on 1.5% (w/v) Difco malt extract agar (MEA), 0.5% (w/v) gallic acid agar (GAA), and 0.5% (w/v) tannic acid agar (TAA) in the dark at 25 C (Davidson et al., 1938). Cultures were checked at weekly intervals. Key patterns describing 2-wk-old cultures are based on the system of Davidson et al. (1942), and species codes describing 6-wk-old cultures are based on the system of Nobles (1965) as revised and expanded by Nakasone (1990).
TAXONOMIC TREATMENT

The similarity between Veluticeps and Columnocystis was recognized by Welden (1967), Burdsall (1975: 285), and Hjortstam and Tellería (1990). The type species of each genus has distinctive cystidia, large basidia, and yellowish brown, thick-walled hyphae and hymenia that darken in potassium hydroxide. Both species are associated with brown rot of gymnospermous wood. In addition, basidiomata of both genera may be resupinate, effused-reflexed, or pileate. Although these genera share many significant characters, they differ in one striking character, that is, in the spatial arrangement of the cystidia. The cystidia of Veluticeps are aggregated into fascicles that resemble teeth, while those of Columnocystis occur singly throughout the hymenium. This difference is not considered significant at the generic level by Hjortstam and Tellería (1990) or myself; and Veluticeps and Columnocystis are congeneric.

The structure of the basidiomata of Veluticeps (including Columnocystis) is similar to that of Stereum (Chamuris, 1988: 96). The most elaborate forms have five distinct layers: abhymenial tomentum, cutis, subiculum, subhymenium, and hymenium (Fig. 6a). The simplest forms develop only a subiculum, subhymenium, and hymenium. The abhymenial tomentum and cutis are found only in species that develop an effused-reflexed or pileate habit. The subhymenium thickens during the growing season, and frequently, distinct layers of embedded cystidia can be observed in cross-sections of the context.

The hyphal system of Veluticeps is monomitic. Tissue is composed of thin-walled generative hyphae and thick-walled sclerified generative hyphae. The basic hyphal system consists of hyaline, thin-walled, regularity nodose- or simple-septate, and freely branched hyphae. The sclerified generative hyphal type is slightly modified and is brown, thick-walled, with rare simple septa or clamp connections and scattered adventitious septa, and rarely branched. Sclerified generative hyphae make up most, if not all, of the abhymenial tomentum and cutis. In the subiculum, sclerified and thin-walled generative hyphae occur together. Sclerified generative hyphae also give rise to trama cystidia. Most workers, however, report that Veluticeps is dimitic (Chamuris, 1988; Eriksson and Ryvarden, 1973; Gilbertson, 1974; Hjortstam and Tellería, 1990; Jülich and Stalpers, 1980; Welden, 1967). They describe skeletal hyphae that are brown, thick-walled, aseptate except for adventitious septa, and rarely branched. Superficially, Veluticeps does appear to be dimitic because clamp connections and simple septa are difficult to observe on “skeletal” hyphae. Besides this report, only Reid (1958: 442) describes clamp connections on sclerified generative hyphae of Stereum abietinum although he also states that it is dimitic. The only significant difference between skeletal hyphae and sclerified generative hyphae is the absence or presence, respectively, of clamp connections or simple septa. Donk (1964: 237) noted that because sclerified generative hyphae may be long, straight, and of equal diameter throughout their length, they may resemble skeletal hyphae. Sclerified generative hyphae, however, differ from skeletal hyphae in being septate.

Two basic types of cystidia are found in Veluticeps: trama and hymenial cystidia. Trama cystidia are smaller than hymenial cystidia and are typically embedded, rarely protruding beyond the hymenium. They develop from brown, thick-walled, sclerified generative hyphae of the subiculum and are best described as terminally differentiated sclerified generative hyphae. At first, these hyphae are arranged parallel to the substrate but then curve into the hymenium as they differentiate into trama cystidia. Hymenial cystidia, in contrast, arise from the subhymenium and are similar to trama cystidia except that they are larger and protrude beyond the hymenium. In specimens with a thickening subhymenium, the protruding hymenial cystidia eventually become embedded and turn dark brown. Hymenial cystidia aggregate into fascicles to form protruding toothlike structures observed on the hymenial surface of V. berkeleyi.

Basidiospore size is an important criterion for identification of Veluticeps species, and it is critical to measure mature spores with thin walls and homogeneous contents. Unfortunately, many specimens lack mature basidia and basidiospores. It is also common to find spores embedded in the subhymenium and hymenium. These spores are dark yellow with opaque contents and irregular walls and often appear shriveled.

The nomenclatural problems of Veluticeps are discussed thoroughly by Donk (1957: 122) and Gilbertson et al. (1968). Chaetocarpus P. Karst. is synonymous with Columnocystis (Pouzar,
but is illegitimate as a later homonym of Chaetocarpus Schreb. (Donk, 1957: 24).

VELUTICEPS (Cooke) Pat. emend. Nakas.


Basidiomata annual or perennial, resupinate, effused-reflexed, pileate, occasionally umbonate or pezizoid, often imbricate, coriaceous to lignaceous, solitary to gregarious, often confluent, darkening permanently in KOH solution (xanthochroic); abhymenial surface tomentose, felty to velvety, sulcate, brown to black; hymenial surface smooth, rugose, warted or hydnaceous, often velutinous from projecting cystidia, some shade of tan, brown, or gray, often with a white bloom from crystalline materials deposited on surface; margins sterile, loosely attached and pulling away from substrate. Context pale brown to dark brown, often with alternating dark and pale brown layers. Up to five layers may be present: abhy-}

menial tomentum, cutis, subiculum, subhymenium (thickening), and hymenium. Hyphal system monomitic; generative hyphae thin-walled and hyaline, often becoming sclerified then thick-walled and yellowish brown, simple- or nodose-septate; cystidia cylindrical to clavate, thin- to thick-walled, simple- or nodose-septate at base, hyaline to yellowish brown, occurring singly or in fascicles, protruding or not, arising from subiculum (trama cystidia) and subhymenium (hymenial cystidia); hyphidia cylindrical to clavate, thin- to thick-walled, abundant to rare or absent. Basidia cylindrical to clavate, attenuated toward base, 60-130 × 6-12 µm, hyaline to yellowish brown, thin- to thick-walled, simple- or nodose-septate at base, 4-sterigmate. Basidiospores ellipsoid to cylindrical, 7-25 × 3.5-8 µm, thin- to slightly thick-walled, hyaline to pale yellow, often darkening to golden yellow with age, smooth; spore walls negative in Melzer’s reagent, acyanophilous. Found on gymnospermous or angiospermous wood and bark; associated with a brown rot.

KEY TO THE SPECIES OF VELUTICEPS

1. Generative hyphae in basidiomata nodose-septate ........................................................... 2
2. Cystidia occurring in fascicles ......................................................... V. berkleyei
3. Cystidia occurring singly ............................................................... 3
4. Basidiospores 5-6.5 µm wide; New Zealand ...................................................... V. fusiforma
5. Basidiospores 7-10 µm wide; Arizona ...................................................... V. pimeriensis
6. Basidiospores 7-13 × (4-)4.3-4.8(-5) µm; Europe, eastern and northwestern North America .............................................. V. abietina
7. Basidiospores 11.9-15.5 × 4.7-5.6(-6) µm; western North America .................................................. V. fimбриata
8. Basidiomata dark brown; eastern United States and eastern Europe .................................................. V. ambigua
9. Basidiomata cream-colored; Gabon ................................................ V. africana

VELUTICEPS ABIELTINA (PERS.: FR.) HJORTSTAM & TELLERIA, Mycotaxon 37: 54. 1990. FIG. 1


Basidiomata annual or perennial, spongy-coriaceous, resupinate to effused-reflexed, imbricate or not, up to 2 mm thick, orbicular at first, then confluent, up to 10 × 5 cm; hymenial surface smooth to tuberculate or rugose, felt, velutinous from protruding cystidia, often cracked, pale yellow (4A3), yellowish white (4A2) to yellowish grey (4B2, 3B2), brownish orange (6C3) to greyish brown (5D3, 6D3), or brownish grey (6C2), rarely dull violet (18E3), turning black in KOH, often with a whitish bloom from crystalline materials deposited on hymenial surface; margins up to 2.5 mm wide, entire to crenate, sterile, loosely attached to substrate and often pulling away, greyish orange (5B4) to brown (6D7-6D6), lackig a bloom; reflexed part, when developed, narrow, 3–20 mm in radius, abhymenial surface dark brown (7F5) to nearly black, sulcate, hard and brittle; context brown, sometimes with alternating dark and light layers.

Hyphal system monomitic. Five distinct layers may be present: 1) abhymenial tomentum 70–400 µm thick; sometimes absent, composed of loosely interwoven hyphae; abhymenial hyphae 3–4.5 µm diam, yellowish brown, thick-walled, with rare clamps and simple septa, sparsely branched; 2) hyphae becoming more compact and dense near the subicular interface to form a dark, nearly black cutis of more or less parallel, horizontally arranged abhymenial hyphae; cutis layer 30–150 µm thick, a textura porrecta; 3) subiculum 150–450 µm thick, a dense textura
intricata to textura porrecta, composed of horizontally arranged agglutinated hyphae; subicular hyphae of two types: a) 2.5–3.5 µm diam, hyaline, thin-walled, nodeose-septate, frequently branched; and b) 2.5–3 µm diam, yellowish brown, thick-walled, nodeose-septate, rarely branched, sometimes differentiating terminally into tramal cystidia; tramal cystidia found scattered in subiculum but often curve toward hymenium to produce a dense palisade of vertical cystidia at the subiculum-subhymenium interface; 4) subhymenium up to 1000 µm thick but sometimes absent in thin specimens, with one or more distinct layers, thickening, composed of vertically arranged, thin-walled, nodeose-septate, 2–3.5 µm diam subicular hyphae, collapsed hymenial elements, and embedded tramal and hymenial cystidia; and 5) hymenial layer up to 130 µm thick, composed of basidia, hyphidia, and tramal or protruding hymenial cystidia. Cystidia of two types: a) hymenial cystidia large, cylindrical to narrowly clavate, 90–300 µm long, 7–12 µm diam at widest, gradually tapering to 2.5–4 µm at base, thin- to slightly thick-walled at apex, walls gradually thickening at mid-section (up to 3 µm thick), then slightly thinner toward base, hyaline or pale yellow at first but turning brown with age, with a basal clamp connection, smooth or encrusted with a thin crystalline coating, protruding up to 100 µm beyond hymenium, arising from subiculum and subhymenium; b) tramal cystidia small, narrowly clavate to cylindrical, up to 160 µm long, 4–5.5(–8) µm diam at widest, tapering to 2–3 µm at base, slightly thick- to thick-walled throughout, often with adventitious septa, sometimes constricted slightly, yellowish brown throughout, occasionally smooth but more often lightly encrusted with granular crystalline materials, typically embedded in subiculum, subhymenium and lower hymenium but occasionally protruding slightly beyond hymenium, arising from subiculum and subhymenium in specimens with thickening subhymenia. Hyphidia cylindrical to narrowly clavate, up to 70 µm long, 3–5 µm wide, thin-walled, with a basal clamp connection, sometimes with adventitious septa, occasionally branched, inconspicuous and scarce in hymenium. Basidia narrowly clavate, with a stalk, 60–90(–108) × 5.7(–8.5) µm, tapering to 2.5–3.5 µm diam at base, thin-walled and hyaline throughout, occasionally becoming slightly thick-walled and pale yellow toward the base, with a basal clamp connection, 4-sterigate; sterigmata 5.5–6.5 × 1.5–2 µm. Basidiospores cylindrical to narrowly elliptical, adaxial side often straight, 10.7–13 × (4–)4.3–4.8(–5) µm, slightly thick-walled, hyaline, smooth; spore walls negative in Melzer’s reagent, acyanophilous; spores embedded in subhymenium and hymenium often pale yellow to light brown with opaque contents.

Habitat: on wood and bark of coniferous logs and stumps, especially Abies and Picea; associated with a brown rot.

Distribution: widespread throughout central and northern Europe, south central U.S.S.R., southeastern and southwestern Canada, northeastern United States and Alaska; rare in Colorado and Utah (Figs. 7 and 8).

CULTURAL MORPHOLOGY: Growth on MEA very slow to slow, (≤ 10%) 15–29 mm diam at 2 wk, 41–90 mm diam at 6 wk. Mats white to light orange (5A4), moderately thick to thick, slightly raised to raised, felty to tomentose around inocula, then becoming thinner towards margins at 2 and 6 wk; margins even, appressed; odor sweet, musty at 2 and 6 wk; agar unchanged at 2 wk, unchanged or orange (6B8) under inocula at 6 wk; not fruiting by 6 wk. Oxidase reactions after 1 wk on GAA negative, growth 0–10 mm diam; on TAA negative, growth none.

MICROSCOPIC CHARACTERISTICS: Marginal hyphae 1.5–3 µm diam, thin-walled, nodose-septate but often clamps not fused, sparsely branched, often branches arising below or from clamp connections. Submerged hyphae 1.5–5.5 µm diam, thin-walled but with scattered irregularly thick-walled sections, clamps often thick-walled, nodose-septate, wider hyphae moderately branched and narrower hyphae frequently branched, sometimes containing dark yellow materials. Aerial hyphae: a) similar to submerged hyphae except developing more irregularly thick-walled hyphae and some hyphal segments heavily encrusted with closely appressed, hyaline, bacilliform crystals; b) fibere-like hyphae 1.5–3 µm diam, slightly thick-walled, smooth but sometimes with roughened walls, hyaline or dark yellow, with a basal clamp connection, with scattered secondary septa, sparsely branched, scarce to abundant at 6 wk. Chlamydospores obovate to obpyriform, 14–18 × 8–12 µm, hyaline, slightly thick- to thick-walled, lateral or terminal, usually simple-septate at base, rare or occasional in aerial mats at 2 and 6 wk.

Keypatterns: A-0-V-1-2-10-16; A-O-S-1-2-10-16. Species codes: 1.3c.8.9.27.34.37.39.47.50. 55.1.3c.9.13.27.34.37.39. 47.50.55.


CULTURAL DESCRIPTION: Boidin (1958: 197) as Stereum abietinum, isolate 426 from France is V. abietina but isolate C.B.S. is probably V. fimbriata.

REMARKS: Veluticeps abietina is common and widely distributed in the mountainous regions of central Europe and throughout northern Europe (Fig. 7). It is reported also from south-central U.S.S.R. in the Altai Mountains (Pilát, 1933) and the Kuznetzk Basin (Killermann, 1943). Veluticeps abietina is uncommon in eastern North America but more common in the northwest, especially in Alaska, and rare in Colorado and Utah (Fig. 8).

Heinrich and Wojewoda (1974) recorded considerable range in basidiospore size of V. abietina from the Polish Carpathian Mountains. The basidiospores from specimens collected in North America and Europe also varied somewhat in size. Statistically, however, there was no significant difference in basidiospore size between specimens from the two continents (Table I).

European mycologists have described and illustrated this taxon many times (Bourdot and Galzin, 1928: 377; Breitenbach and Kranzlin, 1986: 97; Davydkina, 1980: 111–112; Eriksson and Ryvarden, 1973: 251–255; Heinrich and Wojewoda, 1974; Jahn, 1971: 104–106; Pilát, 1930: 75–78; Reid, 1958: 441–442; TortiC, 1978). In addition, photographs of V. abietina can be found in Breitenbach and Kränzlin (1986: 97, Fig. 71), Chamuris (1988: 60, Fig. 17A), and Jahn (1971: 169, Fig. 19).

The species concept of V. abietina held by many North American mycologists is broad and includes V. fimbriata (e.g., Burt, 1920; Chamuris, 1988; Farr et al., 1989; Gilbertson, 1974, 1981; Ginns, 1986; Lentz, 1955; Nobles, 1948; Shaw, 1973). Some workers, however, recognized Stereum rugisporum (Ellis et Everh.) Burt, a synonym of V. fimbriata, as distinct from V. abietina, e.g., Burt, 1920; Cooke, 1943; Overholts, 1929, 1939; Shaw, 1973.

Veluticeps abietina and V. fimbriata are similar.
intricata to textura porrecta, composed of horizontally arranged agglutinated hyphae; subicular hyphae of two types: a) 2.5–3.5 µm diam, hyaline, thin-walled, nodose-septate, frequently branched; and b) 2.5–4 µm diam, yellowish brown, thick-walled, nodose-septate, rarely branched, sometimes differentiating terminally into tramal cystidia; tramal cystidia found scattered in subiculum but often curve toward hymenium to produce a dense palisade of vertical cystidia at the subiculum-subhymenium interface; 4) subhymenium up to 1000 µm thick but sometimes absent in thin specimens, with one or more distinct layers, thickening, composed of vertically arranged, thin-walled, nodose-septate, 2–3.5 µm diam subicular hyphae, collapsed hymenial elements, and embedded tramal and hymenial cystidia; and 5) hymenial layer up to 130 µm thick, composed of basidia, hyphidia, and tramal or protruding hymenial cystidia. Cystidia of two types: a) hymenial cystidia large, cylindrical to narrowly clavate, 90–300 µm long, 7–12 µm diam at widest, gradually tapering to 2.5–4 µm at base, thin- to slightly thick-walled at apex, walls gradually thickening at mid-section (up to 3 µm thick), then slightly thinner toward base, hyaline or pale yellow at first but turning brown with age, with a basal clamp connection, smooth or encrusted with a thin crystalline coating, protruding up to 100 µm beyond hymenium, arising from subiculum and subhymenium; b) tramal cystidia small, narrowly clavate to cylindrical, up to 160 µm long, 4–5.5 (8) µm diam at widest, tapering to 2–3 µm at base, slightly thick- to thick-walled throughout, often with adventitious septa, sometimes constricted slightly, yellowish brown throughout, occasionally smooth but more often lightly encrusted with granular crystalline materials, typically embedded in subiculum, subhymenium and lower hymenium but occasionally protruding slightly beyond hymenium, arising from subiculum and subhymenium in specimens with thickening subhymenium. Hyphidia cylindrical to narrowly clavate, up to 70 µm long, 3–5 µm wide, thin-walled, with a basal clamp connection, sometimes with adventitious septa, occasionally branched, inconspicuous and scarce in hymenium. Basidia narrowly clavate, with a stalk, 60–90 (108) × 5.7 (8.5) µm, tapering to 2.5–3.5 µm diam at base, thin-walled and hyaline throughout, occasionally becoming slightly thick-walled and pale yellow toward the base, with a basal clamp connection, 4-sterigate; sterigmata 5.5–6.5 × 1.5–2 µm. Basidiospores cylindrical to narrowly elliptical, adaxial side often straight, 10.7–13 × (4)–4.3–4.8–5 µm, slightly thick-walled, hyaline, smooth; spore walls negative in Melzer’s reagent, acyanophilous; spores embedded in subhymenium and hymenium often pale yellow to light brown with opaque contents.

HABITAT: on wood and bark of coniferous logs and stumps, especially Abies and Picea; associated with a brown rot.

DISTRIBUTION: widespread throughout central and northern Europe, south central U.S.R., southeastern and northwestern Canada, northeastern United States and Alaska; rare in Colorado and Utah (Figs. 7 and 8).

TABLE I

<p>| Basidiospore size variation in Veluticeps abietina and V. fimbriata |
|-----------------------------|-----------------------------|-----------------------------|</p>
<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Length (µm)</th>
<th>Width (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>V. abietina</td>
<td>North America</td>
<td>11.9 ± 0.7 a²</td>
<td>4.4 ± 0.2 a</td>
</tr>
<tr>
<td></td>
<td>Europe</td>
<td>11.8 ± 0.8 a</td>
<td>4.6 ± 0.2 a</td>
</tr>
<tr>
<td>V. fimbriata</td>
<td>Alaska, Calif., Oreg., Wash., British Columbia</td>
<td>12.6 ± 0.8 a</td>
<td>5.0 ± 0.2 b</td>
</tr>
<tr>
<td></td>
<td>Alberta, Ariz., Colo., Mont., Idaho, Utah, Wyo.</td>
<td>14.5 ± 1.5 b</td>
<td>5.3 ± 0.2 c</td>
</tr>
</tbody>
</table>

a Measurements are based on 375 basidiospores (25 spores from 15 specimens).

b Spore measurements with the same letter are not significantly different at p = 0.01, using Duncan’s multiple range test procedure.

with respect to morphological characters of the basidiomata. The size of the basidiospores, however, can be used to distinguish between these species since spores of V. abietina are shorter and narrower than those of V. fimbriata (TABLE I). In addition, distribution is a useful character although the ranges of V. abietina and V. fimbriata overlap somewhat in western North America (Fig. 8). Veluticeps abietina is relatively rare in North America compared to V. fimbriata, which is quite common.

Cultures of these two species are distinctive (TABLE II). Veluticeps abietina produces rare or scattered chlamydospores, has nodose-septate hyphae in the margin and throughout the mats, and never develops brown spots in malt extract agar. The closely related V. fimbriata, however, produces numerous globose chlamydospores, lacks clamp connections in the marginal hyphae, and often develops brown spots in agar (Fig. 6b). Both species develop fiberlike hyphae in culture; however, because true fiber hyphae are not developed in the basidiomata, these structures probably are best interpreted as cystidia.

Although basidiospore size is critical in distinguishing between V. abietina and V. fimbriata, basidiospores often are rare or completely lacking in many specimens. Additionally, thin specimens may lack the abhymenial tomentum and the subhymenial layers.

Type specimens of Thelephora crispa, Thelephora conchata, and Thelephora striata could not be located for study.

VELUTICEPS AFRICANA (Boidin, Lanquetin, et Gilles) Hjortstam et Telleria, Mycotaxon 37: 54. 1990. Fig. 2


Basidiomata annual, resupinate, 400–700µm thick, orbicular at first then confluent to form patches up to 10 cm long, becoming coarsely to finely cracked in older areas, easily separated from substrate; hymenial surface smooth but velutinous because of protruding cystidia, light brown (6D4, 5D4); immediately turning dark brown in KOH; margins about 0.5 mm wide, sterile, thin, concolorous with hymenium or white, slightly reflexed; context light brown.

Hyphal system monomitic. Four distinct layers may be present: 1) abhymenial tomentum composed of hyphae 3-5 µm wide, pale yellow, slightly thick- to thick-walled, with walls up to

<table>
<thead>
<tr>
<th>Basidiospore size*</th>
<th>V. abietina</th>
<th>V. fimbriata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average length (µm)</td>
<td>11.9 ± 1.1</td>
<td>13.6 ± 1.9</td>
</tr>
<tr>
<td>Average width (µm)</td>
<td>4.5 ± 0.4</td>
<td>5.2 ± 0.5</td>
</tr>
</tbody>
</table>

Cultural characters

<table>
<thead>
<tr>
<th>Character state</th>
<th>V. abietina</th>
<th>V. fimbriata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth on MEA (7d)</td>
<td>15–29 mm diam</td>
<td>(23–)30–52 mm diam</td>
</tr>
<tr>
<td>Marginal hyphae</td>
<td>Nodose-septate</td>
<td>Simple-septate</td>
</tr>
<tr>
<td>Chlamydospores</td>
<td>Rare</td>
<td>Abundant</td>
</tr>
<tr>
<td>Brown spots in agar</td>
<td>None</td>
<td>Often present</td>
</tr>
</tbody>
</table>

* Measurements are based on 750 basidiospores (25 spores from 30 specimens).
FIG. 6. *Veluticeps abietina* and *V. fimbriata* a. Cross-section of *V. abietina* (RLG 5403) basidioma with five distinct layers (×80), b. Six-week-old culture of *V. fimbriata* (DAOM 16093) with characteristic brown spots developed in malt extract agar; the picture shows the bottom of the petri dish (×1).

2 µm thick, aseptate or simple-septate, smooth or with a thin granular coating, grading into subiculum; 2) subiculum 150–350 µm thick, a *textura porrecta*, composed of horizontally arranged hyphae as found in abhymenial tomentum, but some hyphae up to 7 µm diam with walls up to 3 µm thick; hyphae in upper subiculum curving into subhymenium; 3) subhymenium thickening, up to 100 µm thick but absent in thin parts of specimen, composed of: a) compact, vertically arranged hyphae, these 1.5–2.5 µm diam, simple-septate, thin- to slightly thick-walled, hyaline to pale yellow, with smooth walls, frequently branched; b) embedded, clavate cystidia, these 50–70 × 5.5–7 µm, thin- to slightly thick-walled, with secondary septa; and c) embedded, coarse, hyaline crystals; and 4) hymenial layer 60–80 µm thick, composed of basidia and cystidia. Cystidia basically cylindric but with some constrictions, up to 350 × 9–12 µm, tapering to 3 µm diam at base, slightly thick-walled at apex but walls becoming up to 4 µm thick toward base, hyaline at apex but becoming reddish brown toward base, simple-septate at base, smooth, embedded or protruding up to 100 µm above hymenium, arising from subiculum, some arranged parallel to substrate and others curving into hymenium. Basidia narrowly clavate, with a stalk, (35–)55–70 × (4.5–)7–9 µm, tapering to 2–2.5 µm diam at base, thin-walled, hyaline, simple-septate at base, 4-sterigate; sterigmata about 5 × 1.5 µm. Basidiospores narrowly cylindrical, tapered slightly at both ends, (10–)11–13(–16) × 3–4 µm, thin-walled, hyaline to pale yellow, smooth; spore walls negative in Melzer’s reagent, acyanophilous.

HABITAT: on angiospermous wood; associated rot not known.

 DISTRIBUTION: known only from Gabon, Africa.


REMARKS: *Veluticeps aficana* and *V. ambiguа* lack clamp connections throughout the basidiomata, which distinguishes them from the other species of *Veluticeps* treated here. Both *V. aficana* and *V. pimeriensis* have thin basidiomata.
Basidiomata perennial, spongy-coriaceous, broadly effused, 1–2(–3) mm thick, orbicular at first then becoming widely confluent, up to 15 × 5 cm, loosely attached to substrate; hymenial surface smooth to tuberculate, generally following the contour of substrate, velutinous from projecting cystidia, developing deep cracks, yellowish brown (5D8–5E8), light brown to brown (6D4–6E4) or dark brown (6F8–7F8), turning black in KOH, margins 1–2 mm broad, entire to fibrillose, loosely adherent, often detached and pulling away from substrate, slightly reflexed, white to greyish orange (5B4) or yellowish brown (5D6), sterile; context golden brown.

Hyphal system monomitic. Three distinct layers present: 1) subiculum 90–250 µm thick, a loose to dense textura intricata, composed of horizontally arranged subicular hyphae, these 2–4.5 µm diam, hyaline to pale yellow, thin- to slightly thick-walled, simple-septate, freely branched and giving rise to sclerified hyphae, these 2–5 µm diam, yellowish brown to reddish brown, thick-walled, with walls up to 2 µm thick, with rare simple septa, sparsely branched, and gradually turning toward the subhymenium and terminating in upper subiculum to produce a sparse or dense palisade of tramal cystidia; 2) subhymenium up to 600 µm thick, thickening, with one or more layers of vertically arranged, thin-walled hyphae, collapsed basidia, hyphidia, and cystidia; and 3) hymenial layer 70–90 µm thick, composed of basidia, hyphidia, and cystidia. Two kinds of cystidia present: a) hymenial cystidia large, cylindrical to narrowly clavate, 150–250 × 8–14 µm, tapering to 2.5–3.5 µm diam at base, at apex thin- to slightly thick-walled and with hyaline to pale yellow walls, then becoming thick-walled and walls darkening to yellowish brown toward the base (finally turning reddish brown throughout after becoming embedded in subhymenium), with walls up to 6 µm thick, simple-septate at base, with scattered constrictions, infrequently developing adventitious septa, smooth or encrusted with tightly adherent hyaline crystals, arising from subiculum at first then later from subhymenium in specimens with thickening subhymenia, embedded or protruding up to 125 µm beyond hymenium; and b) tramal cystidia smaller, cylindrical, up to 200 µm long × 3-4 µm diam, slightly thick- to thick-walled throughout, often with adventitious septa, yellowish brown throughout, smooth, embedded in subiculum and subhymenium, arising from
Fig. 8. Distribution of Veluticeps abietina, V. ambigua, V. berkeleyi, and V. fimbriata in North and Central America. Veluticeps berkeleyi was described from specimens collected in Cuba but their exact location is not known.

Subiculum and subhymenium, often forming a vertical palisade of cystidia at subiculum-subhymenium interface. Hyphidia cylindrical to narrowly clavate, 30-90 × 3-7 µm, slightly thick-to thick-walled, walls up to 2 µm thick, hyaline to pale yellow at first then turning yellowish brown with age, simple-septate at base, with frequent adventitious septa, smooth, arising from hymenium but becoming embedded as subhymenium thickens. Basidia narrowly clavate, with a stalk, 70-120 × 5-8 µm, tapering to 2-3 µm diam at base, thin-walled and hyaline at first, then walls slightly thickening and turning yellowish brown toward the base, simple-septate at base, sometimes with adventitious septa, 4-sterigmate; sterigmata 4-8 × 1.5-2 µm. Basidio-
sponges cylindrical to narrowly fusoid, 12–16(-21) × (3--)5-4(-5)µm, flattened on adaxial side, thin-walled and hyaline at first, becoming slightly thick-walled and dark yellowish brown with age, smooth; spore walls negative in Melzer’s reagent, acyanophilous.

HABITAT: on gymnospermous wood, especially *Picea* and *Abies*; associated with a brown rot.

DISTRIBUTION: eastern United States, southeastern Canada, east-central Europe, and eastern U.S.S.R. (Figs. 7, 8), not common.


REMARKS: Veluticeps ambigua is distinct because of its dark brown color and lack of clamp connections. In addition, it lacks an abhymenial tomentum and cutis found in other species of *Veluticeps*. *Veluticeps ambigua* is uncommon throughout its range. It is known from eastern United States and Canada and eastern and southern central Europe where it is sympatric with *V. abietina* (Figs. 7, 8). Although simple-septate generative hyphae are found also in *V. africana*, this species is light brown in color and is restricted to Africa.

I agree with Jahn (1971, p. 107) and notes left by George P. Chamuris and Ždeněk Pouzar with the syntype of *Stereum carpaticum* that it is synonymous with *V. ambigua*. Additional descriptions and illustrations of *V. ambigua* can be found in Breitenbach and Kranzlin (1986, p. 97), Burd (1920, pp. 190-191), Chamuris (1988, pp. 58-59), Davydová (1980, pp. 112-113), and Pištálek (1930, pp. 78-80). For photographs of basidiomata, see Breitenbach and Kranzlin (1986, p. 97, Fig. 72) and Chamuris (1988, p. 61, Fig. 18).

VELUTICEPS BERKELEYI (Berl. & Curtis) Cooke, Grevillea 8: 149. 1880. FIG. 4


Basidiomata perennial, firm to tough, coriaceous, resupinate, effused-reflexed or apllanate, occasionally unulate, imbricate, up to 3 mm thick, confluent, up to 15 × 5 cm; hymenial surface smooth or warted, sometimes deeply cracked, light brown (6D4) to greyish brown (6D3) or brownish grey (6C2), often with a pale white bloom, covered with abundant, small teeth with fibrillose apices that protrude about 250 µm; margins up to 3 mm wide, entire to crenate, sterile, closely attached to substrate but often pulling away slightly when dried, concolorous with hymenium but often with a yellowish tint (greyish orange (5B4) or light brown (6D7-6D6)); reflexed or pileate portion 3-25 mm in radius, occasionally comprise, abhymenial surface feeble to hard and brittle, concentrically sulcate, brown (7E4) to dark brown (7F4), margins often turning upward; context bicolor, with a dark-brown layer next to substrate and a lighter brown hymenial layer.

Hyphal system monomitic. Five distinct layers and cutis found in other species of *Veluticeps*. *Veluticeps ambigua* is uncommon throughout its range. It is known from eastern United States and Canada and central and southern United States and Canada and eastern and southern central Europe where it is sympatric with *V. abietina* (Figs. 7, 8). Although simple-septate generative hyphae are found also in *V. africana*, this
walls up to 3 \(\mu\)m thick, with rare clamp connections and adventitious septa, sparsely branched; and b) generative hyphae 2–3.5\(\mu\)m diam, hyaline to yellowish brown, thin- to slightly thick-walled, nodose-septate, freely branched; 2) abhymenial hyphae becoming more compact and dense at the subicular interface to form a dark, nearly black cutis, cutis 50–130 \(\mu\)m thick, composed of more or less parallel, horizontally arranged hyphae, lacking in some specimens; 3) subiculum 350–650(–1000)\(\mu\)m thick, a dense textura intricata to textura porrecta, composed of two kinds of subicular hyphae: a) generative hyphae 1.5–5.5 \(\mu\)m diam, hyaline, thin- to slightly thick-walled, nodose-septate with abundant adventitious septa, yellowish brown, thin- to slightly thick-walled, nodose-septate, freely branched, somewhat agglutinated; and b) sclerified generative hyphae 2–5.5 \(\mu\)m diam, brown, thick-walled, nodose-septate with abundant adventitious septa, freely branched, subicular hyphae horizontally arranged next to cutis or abhymenial tomentum then gradually turning into subhymenium with the brown pigmented hyphae forming a palisade of vertically arranged tramal cystidia; 4) subhymenium thickening, 140–700\(\mu\)m thick in well-developed specimens, 15–50\(\mu\)m thick in young specimens, sometimes appearing homogeneous but often with one or more distinct layers, these layers composed of vertically arranged, thin-walled, nodose-septate hyphae that are 2–3.5 \(\mu\)m diam, collapsed hymenial elements and fascicles of cystidia; and 5) hymenium 70–100 \(\mu\)m thick, composed of basidia and fascicles of cystidia. Cystidia of two types: a) some limited to subiculum, these smaller, narrowly clavate to cylindrical, often constricted slightly, up to 350 \(\mu\)m long, 3.5–7 \(\mu\)m diam at widest, slightly thick-walled throughout, with walls up to 2.5 \(\mu\)m thick, with a basal clamp connection, often with adventitious septa, yellowish brown throughout, smooth or coated with granular substances, arising from horizontal subicular hyphae then curving toward hymenium and becoming embedded in upper subiculum to form a dense palisade; b) others found in fascicles, these larger, narrowly clavate to cylindrical, often constricted, 170–250(–300)\(\mu\)m long, 7.5–9\(\mu\)m diam at widest then gradually tapering to 2–3.5\(\mu\)m diam at base, with a basal clamp connection, often with a thin, granular coating, those protruding from hymenium hyaline, smooth, thin-walled at apex and walls gradually thickening toward the base but with age becoming thicker, pale yellow, eventually yellowish brown and encrusted with granular or crystalline materials, aggregating into toothlike fascicles, at first arising from subiculum and later from hyaline subhymenial hyphae in the thickening subhymenium, finally becoming embedded and becoming brown and thick-walled throughout. Basidia narrowly clavate, stalked, 65–100(–150) × 7–8(–10)\(\mu\)m, tapering to 2–3 \(\mu\)m diam at base, thin-walled and hyaline, occasionally becoming slightly thick-walled and yellowish brown toward the base, with a basal clamp connection, 4-sterigmate; sterigmata 8–11 × 1.5–2 \(\mu\)m. Basidiospores cylindrical, (10–12–14.5 × 4–5\(\mu\)m, adaxial side slightly convex, slightly thick-walled, hyaline, smooth; spore walls negative in Melzer’s reagent, acyanophilous.

HABITAT: causes a heart rot of living gymnospermous trees, also found on decorticated wood, especially Pinus ponderosa Laws., in western United States; associated with a brown rot.

 DISTRIBUTION: western U.S.A., Mexico, Cuba, Guatemala, Taiwan, and Japan (FIG. 8).

Veluticeps fimbriata (Ellis et Everh.) Nakas.,

**Remarks:** Veluticeps berkeleyi is well-characterized by a perennial basidiomata and projecting fascicles of cystidia. It is common in Arizona on ponderosa pine and associated with a brown cubical rot (Gilbertson et al., 1968; Martin and Gilbertson, 1973). In Taiwan and Japan, it is associated with a brown cubical rot of yellow cypress, Chamaecyparis obtusa var. formosana (Hayata) Rehd. (Chen, 1973; Davidson and Chen, 1976; Yamamoto and Ito, 1936). I concur with Gilbertson et al. (1968) and place V. fusca in synonymy with V. berkeleyi. Welden (1967) and Gilbertson et al. (1968: 36) suggest that V. pini Pat., from Indochina, also may be synonymous with V. berkeleyi.

Cultural morphology of V. berkeleyi is described by Gilbertson et al. (1968). Martin and Gilbertson (1973) report that V. berkeleyi has a tetrapolar (or bifactorial) incompatibility system.

**Veluticeps fimbriata** (Ellis et Everh.) Nakas.,

**Fig. 5**

- **Hymenochaete fimbriata** Ellis et Everh., J. Mycol. 1: 149. 1885.

Basidiomata perennial, spongy-coriaceous, resupinate, effused-reflexed or planar; resupinate forms 0.4 to 2 mm thick, orbicular at first, coalescing, often becoming oblong in shape, 5 × 5 to 120 × 50 mm in size but sometimes larger, hymenial surface smooth, wrinkled or warted, often cracked, velutinous from projecting cystidia, greyish brown (5D3) to grey (5D1), brownish orange (6D3) or light brown (6D4), bruised areas turning dark brown (6F7), turning black in KOH, often with a pale white bloom from crystalline materials deposited on hymenial surface; margins 0.5 to 3 mm wide, sterile, uneven and fimbriate to crenate and smooth, sometimes apressed and closely attached but often loosely attached and pulling away from substrate, lacking a bloom and darker than hymenium, golden brown (5D7), light brown (6D6), or brown (6E8). Effused-reflexed forms 0.5-3 mm thick, often oblong to linear, commonly 15 × 10 to 100 × 40 mm in size but sometimes larger, becoming imbricate, hymenial surface smooth to warted, slightly to extensively cracked, greyish orange (5B4), light brown (6D5-6D4) to brownish grey (6D2), or brown (7E4), sometimes with a white bloom; margins crenate and smooth, sterile, pale yellow (4A3) to brown (6E7), loosely attached to substrate and pulling away, reflected pileus 3- to 7-mm radius; abhymenial surface felty, light brown (6D6) to brown (6E7). Pileate forms 1-4 mm thick, up to 30-mm radius, imbricate, hard and brittle, hymenial surface as described above; margins often lobed and occasionally turning upward, sterile; abhymenial surface zonate, felty, sulcate, greyish brown (9E3) or brown (6E8-6E4), sometimes bleached; context brown, sometimes with alternating dark- and pale-brown layers.

Hyphal system monomitic. Five distinct layers may be present: 1) abhymenial tomentum 0.18-2 mm thick, a dense textura intricata, composed of two kinds of abhymenial hyphae: a) generative hyphae (2–)3.5–7µm diam, hyaline or yellowish brown, with scattered clamp connections and adventitious septa, rarely branched; and b) sclerified generative hyphae 1.5-3 µm diam, slightly thick- to thick-walled with rare clamp connections and scattered adventitious septa; 2) mycelia becoming denser at the subicular interface to form a dark, nearly black cutis that is 20–150µm thick; 3) subiculum 150-800µm thick, a dense textura intricata to textura porrecta, composed of horizontally arranged and agglutinated hyphae of two types: a) some 2–3µm diam, hyaline, thin-walled, nodose-septate, freely branched and b) others 3–6.5 µm diam, yellowish brown, thick-walled, nodose-septate, rarely branched, these pigmented subicular hyphae give rise to trimal cystidia found scattered throughout subiculum and also curving toward hymenium to form a dense palisade of vertically arranged cystidia; 4) subhymenium thickening, up to 450 µm thick but sometimes absent in thin specimens, with one or often with several distinct layers of vertically arranged, thin-walled, nodose-septate hyphae, collapsed hymenial elements and thick-walled, yellowish brown trama and hymenial cystidia, some specimens with numerous, small clusters of agglutinated basidiospores embedded in subhymenium, these basidiospores dark yellow, cylindrical but irregular in outline; and 5) hymenial layer.
100–130 µm thick, composed of basidia, hyphidia, embedded trama cylindrica and protruding hymenial cystidia. Cystidia of two types: a) hymenial cystidia large, cylindrical to narrowly clavate, 145-350 µm long, (3.5–)5.5–(7.5–)10 µm at widest, then tapering to 3.5–3.5 µm diam at base, at apex walls thin to slightly thick and gradually thickening to mid-section then thinning slightly toward base, walls up to 2-3 µm thick, hyaline or pale yellow at apex then darkening to yellowish brown toward the base, with a basal clamp connection, smooth or encrusted with hyaline, granular materials, extended 35–80 µm beyond hymenium but eventually embedded and becoming dark brown in specimens with thickening subhymenium, arising from subhymenium and upper subiculum; and b) trama cylindrica small, clavate to cylindrical, up to 180 µm long, (4–)6–10 µm wide at apex then tapering to 3.5–3.5 µm at base, slightly thick- or thick-walled throughout, often with adventitious septa, sometimes constricted slightly and occasionally moniloid in part, yellowish brown throughout, smooth or encrusted with granular materials, embedded in subhymenium and lower hymenium but occasionally protruding up to 30 µm beyond hymenium, arising from subiculum and later from subhymenium in specimens with thickening subhymenium. Hyphidia cylindrical to narrowly clavate, up to 80 µm long, 4.5–5 µm diam, thin- to slightly thick-walled, hyaline to pale yellow, often with adventitious septa, with a basal clamp connection, rare and inconspicuous. Basidia narrowly clavate, attenuated toward base, (66–)85–100–(130) × 5.8–(10) µm, tapering to 2.3.5 µm diam at base, thin-walled and hyaline throughout or limited to apex, then becoming slightly thick-walled and pale yellow toward base, occasionally with adventitious septa, with a basal clamp connection, 4-sterigmate; sterigmata 7–9 × 1.5–2.5 µm. Basidiospores ellipsoid to cylindrical, adaxial side straight to slightly convex, 11.9–15.5 × 4.7–5.6 (–6) µm, slightly thick-walled, hyaline but occasionally pale yellow, smooth, sometimes in clusters, often embedded in subhymenium; spore walls negative in Melzer’s reagent, acyanophilous.

Habitat: on decorticate coniferous logs, especially Abies and Picea; associated with a brown rot.

Distribution: western North America from Alaska, British Columbia and Alberta south to Arizona and east to Colorado (Fig. 8); common.


Cultural morphology: Growth on MEA slow to moderately slow, (23–)30–52 µm diam at 2 wk, >90 mm diam at 6 wk. Mats white, thin, appressed and subfelty or raised, downy to submentose around inocula, then becoming thinner toward margins at 2 wk, by 6 wk mats similar except becoming moderately thin to moderately thick and some isolates developing numerous, small to large brown spots in agar (Fig. 6b); margins even, appressed; odor sweet.
and fruity at 2 and 6 wk; agar unchanged at 2 wk, darkening to reddish brown (8E8) under inocula at 6 wk; not fruiting by 6 wk. Oxidase reactions after 1 wk on GAA negative, growth 0–10 mm diam; on TAA negative or faint brown stain, growth none.

**Microscopic characters:** Marginal hyphae 2–3 µm diam, thin-walled, simple-septate, sparsely to moderately branched, branches often short and arising at right angles from main hyphae. Submerged hyphae 1.5–6–8.5 µm diam, thin-walled but wider hyphae sometimes irregularly thick-walled, simple-septate with scattered single clamp connections and pseudo-clamps, moderately to frequently branched, sometimes developing opaque, dark yellow or brown contents or walls. Surface and aerial hyphae: a) similar to submerged hyphae; or b) fiberlike hyphae 2.5–4 µm diam, slightly thick-walled, pale yellowish brown, with a basal clamp connection and occasional adventitious septa, scattered to abundant at 2 and 6 wk. Chlamydo­spores globose to oblong, 6–15 × 4.5–15 µm, hyaline, thin- to slightly thick-walled at first then becoming thick-walled with age, usually borne terminally on a stalk but occasionally intercalary, often developed in clusters (best seen in 2-wk-old cultures), abundant throughout surface and aerial mats at 2 and 6 wk. Brown spots in agar composed of yellowish brown to reddish brown amorphous materials and large, coarse, hyaline crystals. Clusters of thin, platelike crystals scattered throughout aerial mat at 2 wk.

**Key patterns:** A-P-S-1-2-10-16; A-P-S-1-2-10; B-P-S-1-2-10.

**Species codes:** 2.3r.8.9.31c.34.37.39.46.50. 55. 2.3r.9.13.31c.34.37.39.46.50. 55. 1.3.4.5.7.8.34.37.39.47.53. 55. (Nobles 1965: 1100, as Stereum abietinum)

**CULTURES STUDIED:** CANADA—BRITISH COLUMBIA—DAOM 16039 (V1488) and 16093, rot cultures from *Picea sitchensis*, DAOM 16603, rot culture from *Abies sp.* or *Tsuga heterophylla*, UNITED STATES—CALIFORNIA—JLL 10628, on conifer; OREGON—DAOM 11792 (FP 66264), rot culture from *Tsuga sp.*

**Cultural descriptions:** Nobles (1948: 397) as *Stereum abietinum* Pers.; Boidin (1958: 197) as *S. abietinum*, the isolate from C.B.S. (which was received from M. K. Nobles in Canada) is probably *V. fimбриata*.

**Remarks:** The variable morphology of *V. fimбриata* is remarkable and is contrasted with the consistent micromorphology of the hymenial elements. A maximum of five distinct layers may be observed in sections of the basidiomata; however, some specimens may lack a distinct sub-hymenium or abhymenial tomentum. Embedded spore clusters also may or may not be present. The basidiospores of *V. fimбриata* vary significantly in size (TABLE I). Specimens from the west coast, namely Alaska, California, Oregon, Washington, and British Columbia, typically have smaller basidiospores than those from non-coastal states and provinces.

Although Burt (1920, p. 189) recognized the similarity between *Hymenochaete fimбриata* and *H. rugispora*, he was hesitant to consider them conspecific because *H. fimбриata* is resupinate, and *H. rugispora* is effused-reflexed to pileate. In addition, *H. fimбриata* lacked embedded clusters of basidiospores that were present in *H. rugispora*. After examining the type specimens of these taxa, it is clear that they are conspecific. Although the name *H. fimбриata* was rarely used, *Stereum rugisporum* was in common usage (e.g., Cooke, 1943; Overholts, 1929; Seaver and Shope, 1935; Shaw, 1973).

*Veluticeps fimбриata* is a distinct taxon from the closely related species *V. abietina*; they are further discussed under *V. abietina*. TABLE II summarizes the characters that can be used to distinguish these two species. The fiberlike hyphae developed in culture also may be interpreted as cystidia.

Other descriptions of *V. fimбриata* are available from Burt (1920: 188–189) and Overholts (1929: 283–285) as *Stereum rugisporum* and from Gilbertson (1974: 168) as *Columnycystis abietina*. Photographs of this species can be found in Seaver and Shope (1935: 645) and Chamuris (1988: 60, Fig. 17B).

**Veluticeps fusispora** (G. H. Cunn.) Nakas., comb. nov. —Fig. 9


Basidiomata perennial, membranous, broadly effused, 300–600 µm thick, orbicular at first then becoming widely confluent, up to 60 × 30 mm, closely attached to substrate; hymenial surface smooth, following contours of substrate and
therefore sometimes irregular, velutinous, sometimes developing deep cracks and breaking into polygons, light brown (6D5) to brown (6D6, 6D8, 6E7), turning black in KOH; margin ≤0.5 mm broad, entire, loosely adherent, often detached and pulling away from substrate, concolorous or paler than hymenium, greyish orange (6B4–6B3), sterile; context brown.

Hyphal system monomitic. Three distinct layers may be present: 1) subiculum 200–450 µm thick, a loose or dense textura porrecta, composed of two types of hyphae arranged parallel to substrate: a) generative hyphae 2.5–4.5 µm diam, hyaline, thin- to thick-walled, with scattered clamp connections and adventitious septa, sparsely branched; and b) sclerified generative hyphae 3–4.5 µm diam, yellowish brown to brown, slightly thick- to thick-walled, with scattered clamp connections and adventitious septa, sparsely branched, sometimes encrusted with small, hyaline crystals, some of these pigmented hyphae terminating into cylindrical to slightly clavate tramac cystidia that form a dense palisade at the subicular-subhymenial interface; 2) subhymenium 70 µm thick, absent in the type specimen, composed of hyphae 2–3 µm diam, hyaline, thin-walled, nodose-septate with adventitious septa, sparsely branched, often irregular in outline, sometimes lightly encrusted with hyaline crystals, in some specimens with thickening subhymenia also with hyphidia, cystidia, and basidia; and 3) hymenium 80 µm thick, composed of hyphidia, cystidia, and basidia. Hyphidia more or less cylindrical with constrictions and knobs, sometimes contorted, 50–85 × 2.5–4 µm, hyaline, thin-walled, with a basal clamp connection but sometimes also with scattered clamps along its length, sometimes branched, abundant in specimen no. 7065 but infrequent in the other two specimens. Cystidia of two types: a) some cylindrical to narrowly clavate, 100–185 × 7–9.5 µm, tapering to 2–3.5 µm diam at base, hyaline or pale yellow, thick-walled, walls up to 2–2.5 µm thick then becoming thinner toward base and apex, with a basal clamp connection, with or without adventitious septa, smooth or lightly encrusted with small, hyaline crystals, arising from subhymenium or subiculum, extending up to 50 µm beyond hymenium, but eventually becoming embedded in subhymenium; and b) others clavate, 60–80 × 6–8 µm, tapering to 3 µm at base, hyaline, thin- to slightly thick-walled, with a basal clamp connection and one or more adventitious septa, smooth, enclosed within hymenium and therefore difficult to see, arising from hymenium, eventually becoming embedded in subhymenium. Basidia clavate, 50–90(–107) × 9–11 µm, tapering to 3 µm diam at base, hyaline, thin-walled, with a basal clamp connection, becoming embedded in subhymenium and then developing adventitious septa, mature basidia typically with apex collapsed, 4-sterigmate; sterigmata 7–10 × 2–3 µm. Basidiospores cylindrical to slightly fusiform, (17–)19–21(–23.5) × (5–)5.5–6.5 µm, hyaline, thin-walled; spore walls negative in Melzer’s reagent, acyanophilous.

Habitat: on bark of dead Phyllocladus; associated rot not known.

Distribution: known only from New Zealand.

**Remarks:** Because of its large basidiospores and restricted distribution, *V. fusispora* is readily distinguished from other species in the genus. Although it is similar to *V. abietina* in structure and morphology, *V. fusispora* lacks an abhymenial tomentum and cutis. The type specimen of *D. fusispora* (G.H.C. 4981) is not as well developed as the other two specimens because it lacks a subhymenial layer and the larger cystidial type is not well formed. The basidia I observed were considerably larger, [50-90(-107) × 9-11 µm], than of those reported by Cunningham (35-40 × 8-10µm).

**Veluticeps pimeriensis** (Gilbertson) Hjortstam et Telleria, *Mycotaxon* 37: 54. 1990. **Fig. 10**


Basidiomata annual, membranous, resupinate to effused-reflexed, up to 0.5 mm thick, beginning as small orbicular structures that coalesce to produce linear patches up to 30 × 10 mm; hymenial surface smooth to slightly rugose, becoming deeply rimose in older sections, greyish brown (7D3, 8D3–8E3), turning dark brown to black in KOH, with a scant white bloom from crystalline materials deposited on surface; margins narrow, entire to crenate, sterile, yellowish brown (5D5–5D6) to light brown (6D5), loosely attached to substrate and often pulling away, lacking a bloom; reflexed portion narrow, up to 0.5 mm wide, abhymenial surface light brown, sulcate; context light brown.

Hyphal system monomitic. Three layers present: 1) subiculum up to 300 µm thick, a loose to compact *textura intricata*, composed of subicular hyphae, these 2–3.5µm diam, hyaline to yellowish brown, thin- to slightly thick-walled, occasionally thick-walled, and nodose-septate but also with adventitious septa; 2) subhymenium thickening, up to 300µm thick, absent in thinner parts of specimens, with one or more distinct layers of vertically arranged, brown cystidia, collapsed basidia, and thin-walled, nodose-septate hyphae; and 3) hymenium composed of basidia and cystidia. Cystidia cylindrical to narrowly clavate, 50–90(–140) × 4.5–7 µm, thin- to thick-walled, hyaline to yellowish brown, torulose or not, often with adventitious septa, with a basal clamp connection, smooth, embedded but occasionally protruding up to 90 µm beyond hymenium, arising from subiculum and later from subhymenium in thicke areas. Basidia clavate with a basal stalk, 80–95 × 11–12µm, tapering to 34 µm diam at base, thin-walled, hyaline, with a basal clamp connection, 4-sterigmate; sterigmata up to 17 × 4 µm. Basidiospores ellipsoid to cylindrical, (18–)20–26 × 7–11 µm, adaxial side straight to slightly convex, slightly thick-walled, hyaline, smooth; spore walls negative in Melzer’s reagent, acyanophilous.

**Habitat:** on *Pinus ponderosa*; probably associated with a brown rot.

**Distribution:** known only from type locality—Santa Catalina Mountains, Tucson, Arizona.

**Specimen examined:** UNITED STATES—ARIZONA: Pima County, Coronado National Forest, Santa Catalina Mountains, General Hitchcock Picnic Area, on *Pinus ponderosa*, 30.IV.69, R. L. Gilbertson 9120 (HOLOTYPE BPI, ISOTYPE ARIZ).

**Remarks:** *Veluticeps pimeriensis* has the largest basidiospores and the thinnest basidiomata of the species discussed in this work.

**Discussion**

*Veluticeps berkeleyi*, the type of *Veluticeps*, and *Columnocystis abietina*, the type of *Columnocystis*, are closely related species that differ only...
by minor characters. The similarities between these two species are overwhelming and include the structure of the basidiomata and morphology of the microscopic elements and cultures. In addition, both species are associated with brown-rot decay and exhibit xanthochroic tissues. These species differ slightly in form because the basidiomata of *V. berkeleyi* are planate or occasionally ungulate, and those of *C. abietina* are never applanate although effused-reflexed forms do occur. The most striking difference, however, is in the spatial arrangement of the cystidia. In *V. berkeleyi*, the cystidia occur in fascicles and those of *C. abietina* occur singly. Since these are relatively minor differences, I agree with Hjortstam and Tellería (1990) and consider *Veluticeps* and *Columnocystis* congeneric.

The description of *Veluticeps* presented by Hjortstam and Tellería (1990) is in general agreement with that included here. However, I disagree with their description in two areas. First, they state that the hyphal system is dimitic. I believe that it is monomitic and earlier discussed my reasons for reaching this conclusion. Second, they describe the basidia as possessing basal clamp connections. This is probably an oversight since several species have simple-septate generative hyphae, and therefore, the basidia lack clamps.

If *V. berkeleyi* and *V. abietina* are considered typical representatives of the genus, then it is relatively easy to relate the other species to them. For example, *V. fimbriata* appears to be intermediate to these two species since it can be planate in form like *V. berkeleyi* and its cystidia are macroscopically and microscopically similar. The remaining taxa, *V. africana*, *V. fusispora*, and *V. pimeriensis* may represent derived species as they develop a trend toward thin basidiomata and restricted distributions. In addition, *V. africana* and *V. fusispora* are found on angiospermous wood and bark. The distribution of the species treated here is noteworthy. *Veluticeps berkeleyi* ranges from Washington and South Dakota to Cuba and Central America in the Western Hemisphere and across the Pacific Ocean to Japan and Taiwan. *Veluticeps fimbriata*, however, is restricted to western North America and is quite common throughout its range; in the United States its distribution overlaps that of *V. berkeleyi*. *Veluticeps abietina* and *V. ambigua* are sympatric in North America; Europe, and probably Asia although records are spotty. *Veluticeps abietina* is common and widely distributed in Europe but is uncommon in North America, where it is limited to northeastern and northwestern sections of the continent with rare occurrences in Colorado and Utah. *Veluticeps ambigua* is an uncommon species found in eastern North America, eastern Europe, and eastern U.S.S.R. The remaining species, *V. africana*, *V. fusispora*, and *V. pimeriensis*, are limited to the area whence they were first described, that is, Gabon, New Zealand, and Arizona, respectively.

Other species probably belong in *Veluticeps* and deserve further study, such as *Veluticeps pini* Pat., *V. heimii* Malençon, *V. setosa* G. H. Cumn., *V. tabacina* (Cooke). Burt, and *V. philippiniensis* Bres. Most of these species, however, are known only from type material (Welden, 1967).

The relationship of *Veluticeps* to other genera in the Aphyllophorales is subject to different interpretations. I believe that *Veluticeps* (inclusive of *Columnocystis*), *Chaetoderma*, and *Crustoderma* belong together in a single family. This proposal, however, does not agree with the views of other taxonomists working in the Aphyllophorales. Oftentimes these genera are placed in different and unrelated families or orders. Donk (1964: 294) placed *Veluticeps* and *Columnocystis* in the Stereaceae Pilát. Parmasto (1968) proposed the genera *Chaetoderma* and *Crustoderma* and placed them together in the Corticiaceae and placed *Columnocystis* in the Stereaceae. Talbot (1973) and Gilbertson (1974, 1981) followed the classification systems of Donk (1964) and Parmasto (1968). Although Eriksson and Ryvarden (1975: 314) do not believe that *Chaetoderma* and *Crustoderma* are closely related, they place both genera and *Columnocystis* (Eriksson and Ryvarden, 1973: 250) together in the Corticiaceae sensu lato. Jülich (1981: 139, 197, 201) proposed a complex classification of the four genera. In Jülich’s scheme, *Crustoderma* (of the Peniophoraceae Maire) and *Veluticeps* (of the Duportellaceae Jülich) are placed in the Stereales Jülich, and *Chaetoderma* and *Columnocystis* (of the Chaetodermataceae Jülich) are placed in the Cylnindrobasidiales Jülich. Recently, Rauschert (1988) proposed the new name *Chaetodermella* for *Chaetoderma* Parm., which is a later homonym of *Chaetoderma* Kutzing, a genus of red algae.
Veluticeps (inclusive of Columnocystis), Chaetodermella, and Crustoderma share significant basidioma and cultural characters and therefore should be placed together in a single family distinct from the Corticiaceae and Stereaceae. The characters they share include thickening subhymenia, hymenia that darken in KOH, stalked or elongate basidia, large cylindrical cystidia, and association with brown rots. In culture, they produce irregularly thick-walled hyphae and chlamydospores. The Chaetodermataceae Jülich, which presently includes Chaetodermella and Columnocystis, is the most appropriate family but is too narrowly delimited (Jülich, 1981: 138) and must be broadened to include Veluticeps and Crustoderma. Although the Chaetodermataceae is placed in the Cylindrobasidiales Jülich, it may not be related to the other families in the order, because they are all white-rot fungi. It is not clear as to what group of brown-rot basidiomycetes the Chaetodermataceae is related, but its closest relative might be Gloeophyllum P. Karst.

CHAETODERMATACEAE Jülich emend. Nakas.

Basidiomata annual or perennial, resupinate, pulvinate or effused-reflexed, occasionally pileate or ungulate, often imbricate, membranaceous, crustose, coriaceous, or ceraceous. Hyphal system monomitic but superficially dimitic. Generative hyphae hyaline or brown, thin- to thick-walled, rarely irregularly thick-walled, narrow, even, clamps present or absent, contents homogeneous. Subhymenium distinctly thickened. Cystidia cylindrical or clavate, hyaline, yellow or brown, thin- or thick-walled, with or without adventitious septa, basal clamp present or absent, enclosed or more often projecting, smooth or lightly encrusted with granular or crystalline materials, contents homogeneous, scattered to numerous, single or in fascicles, originating from subiculum, subhymenium, or hymenium. Basidioles cylindric or clavate, short to very long (25-130 µm long), hyaline or slightly brownish, often with a stalk, thin- or slightly thick-walled, smooth, with or without adventitious septa, basal clamp connection present or absent, contents homogeneous, with four sterigmata. Basidiospores hyaline to yellowish, ellipsoid to cylindrical or fusiform, thin- to slightly thick-walled, smooth, with small and distinct apiculus, contents homogeneous, spore walls inamyloid, acyanophilous. Saprophytic on wood or bark; associated with a brown rot. Genera accepted: Chaetodermella, Crustoderma, Veluticeps.

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LITERATURE CITED


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Donk, M. A. 1937. The generic names proposed for Hymenomycetes-VII. Taxon 6: 17–28; 106–123.


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