

TAXONOMY OF THE GENUS *RADULODON*^{1,2}

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Abstract. *Radulodon* is emended to include taxa with effuse or effused-reflexed basidiomes, well-developed spines, a dimittic hyphal system, cystidia, globose to subglobose basidiospores, and a thickening subhymenium. Out of eleven species placed in *Radulodon* by various taxonomists, five are accepted: *R. americanus*, *R. calcareus*, *R. casearius*, *R. cirrhatinus*, and *R. erikssonii*. The taxa are described and illustrated, and a key to the species is provided. A comparison of the genera *Radulodon*, *Radulomyces*, *Pseudolagarobasidium*, and *Sarcodontia* is presented. The term "microbinding hyphae" is introduced for the narrow (< 3 µm diam), frequently branched binding-type hyphae found in the subiculum or substrate of corticioid fungi.

Keywords: *Irpex decolorans*, *Irpex modestus*, *Hydnum ayresii*, *Hydnum trechodontium*, *Pseudolagarobasidium*, systematics.

The genus *Radulodon* was erected by Ryvar den (1972) to accommodate three species with well-developed spines and smooth, globose to subglobose basidiospores. The type species, *Radulodon americanus* Ryvar den, occurs on *Populus* in Canada and northern United states. *Radulodon erikssonii* Ryvar den is similar to *R. americanus* but develops cystidia and is found in Europe on woody angiosperms. *Radulodon casearius* (Morgan) Ryvar den is known only from the type specimen from Ohio on *Carya*. Ryvar den (1976) included another species, *R. licentii* (Pilát) Ryvar den from China. Since 1976, seven additional species have been placed in *Radulodon*, namely, *R. calcareus* (Cooke & Masee) Jülich, *R. cirrhatinus* Hjortstam & Spooner, *R. copelandii* (Pat.) N. Maek., *R. pseudomucidus* (Petch) Stalpers, *R. subquercinus* (Henn.) Hjortstam & Ryvar den, *R. subvinosus* (Berk. & Broome) Stalpers, and *R. venustus* Hjortstam & Ryvar den.

The circumscription of *Radulodon* varies among systematists. Hjortstam (1998) and Parmasto (1997) accept five taxa: *R. americanus*, *R. casearius*, *R. cirrhatinus*, *R. erikssonii*, and *R. licentii*. Three other taxa were not accepted and placed in other genera: *R. calcareus* in *Pseudolagarobasidium*, *R.*

copelandii in *Radulomyces*, and *R. subquercinus* in *Phanerochaete*. Stalpers (1998) added two taxa to *Radulodon*, *R. subvinosum* and *R. pseudomucidus*, and placed *R. licentii* in synonymy under *R. copelandii*.

In this study, the genus *Radulodon* is emended and redefined, and five accepted species of *Radulodon* are described and illustrated. A key to the species is presented. In addition, a comparison of the genera *Radulodon*, *Radulomyces*, *Pseudolagarobasidium*, and *Sarcodontia* is presented.

MATERIALS AND METHODS

Thin, freehand sections from the specimens were mounted in a drop of aqueous potassium hydroxide (2% w/v) and aqueous phloxine (1% w/v) or in Melzer's reagent (Hawksworth et al., 1995, p. 437) and examined under an Olympus BH2 compound microscope (Olympus America, Inc., New York). Drawings were made with a camera lucida attachment. An Olympus zoom stereomicroscope, model SZH, with a DP10 digital camera system, was used to take photographs of the hymenophore. Color names are from Kornerup and Wanscher (1978), and herbarium abbreviations are from Holmgren et al. (1990).

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The term "microbinding hyphae" is introduced to refer to narrow (<3 μm diam), frequently branched, often at right angles, aseptate, thin- to thick-walled, nonstaining hyphae arising from generative hyphae and is found typically in the substrate or subiculum of some corticioid fungi. Although similar in origin and branching habit to binding hyphae developed in many polypore fungi, microbinding hyphae are narrower and delicate by comparison. They are exclusively found in the

subiculum and substrate, but their occurrence is variable within a collection and among collections of a species. These hyphae have been described variously as "narrow, much-branched hyphae" in *Phlebia chrysocreas* (Berk. & Curtis) Burds. (Lombard et al., 1975). "binding-type hyphae" in *Hyphoderma leoninum* Burds. & Nakasone (Burdall and Nakasone, 1983), "branched skeletal hyphae" in *Amethicium* (Hjortstam, 1983), and "quasi-binding hyphae" (Wu, 1990).

GENUS DESCRIPTION

Radulodon Ryvarden emended Nakasone

Type species: *Radulodon americanus* Ryvarden.

Basidiome widely effuse or effused-reflexed, hydnaceous, spines conical, cylindrical or flattened, up to 15 \times 0.8 mm, smooth or fimbriate to verruculose, single or fused at the base or throughout length, ceraceous, cartilaginous or soft; not reacting in KOH; hyphal system dimitic with nodose septate generative hyphae and thick-walled, rarely to frequently branched microbinding hyphae or thick-walled skeletal hyphae limited to subiculum and base of spines; subhymenium thickening; hyphidia present or absent; cystidia clavate, obclavate to cylindrical, 25–70(–105) \times 5–10(–15) μm , with a basal clamp connection, embedded in hymenium; basidia clavate, sometimes with a distinct stalk, 15–36 \times 4.5–8.5 μm , with a basal clamp connection, 4-sterigmate; basidiospores

globose, subglobose or ellipsoid, often with a refractive globule, 4–7 \times 3–6 μm , walls thin or slightly thick, hyaline, smooth.

The primary change to the original generic description by Ryvarden (1972) is the addition of the dimitic hyphal system. Microbinding hyphae are present in all species of *Radulodon* except *R. cirrhatinus*, although in some specimens, they are difficult to find. In *Radulodon cirrhatinus*, skeletal hyphae are present in the subiculum and at the base of the spines. Previously, only *R. casearius* was reported to be dimitic (Gilbertson, 1964; Ryvarden, 1972) but Wu (1990) and Stalpers (1998) noted the presence of microbinding hyphae in *R. americanus* and *R. calcareus*. Microbinding hyphae develop only in the subiculum and occasionally at the base of the spines. They are 1.5–3 μm in diameter, rarely to moderately branched, aseptate, with thick, hyaline, smooth walls.

KEY TO THE SPECIES OF *RADULODON*

- 1a. Spines 8–15 mm long 2
 1b. Spines up to 5 mm long 3
 2a. Spines robust; basidiospores 4–7 \times 4.5–6 μm ; fruiting on *Quercus* and *Carpinus* in southern USA *R. casearius*
 2b. Spines slender; basidiospores (4.3–)4.5–5 \times 3.5–4(–4.3) μm ; fruiting on woody angiosperms in Malaysia *R. cirrhatinus*
 3a. Basidiospores usually smaller than 5 \times 4 μm ; texture of basidiomes and spines soft. *R. calcareus*
 3b. Basidiospores usually larger than 5 \times 4 μm ; texture of basidiomes and spines ceraceous to subceraceous . . . 4
 4a. Basidiome up to 2 mm thick excluding spines, 3–4 spines per mm, often without distinct, smooth areas between spines in mature areas; fruiting on *Populus* in Canada and northern USA. *R. americanus*
 4b. Basidiome up to 0.7 mm thick excluding spines, 2–3 spines per mm, typically with distinct, smooth areas between spines in mature areas; fruiting on woody angiosperms in Europe and Asia. *R. erikssonii*

DESCRIPTION OF SPECIES

Radulodon americanus Ryvarden, Canad. J. Bot. 50: 2074. 1972. TYPE: CANADA. British Columbia: Prince George, on (bark of) *P. tremuloides*, 25 August. 1945, *R. F. Foster* V-4015 (Holotype: DAOM 16599!; Isotype: O!). Figs. 1, 2, 6.

Basidiome widely effuse, up to 14 \times 6 cm, up to 2 mm thick excluding spines, ceraceous to subceraceous, hydnaceous to odontoid, distinct smooth areas between spines present only in margins and young developing areas before disappearing as the spines increase in size, on

drying developing deep fissures and forming pyramidal aggregations of spines clustered together, up to 5×5 mm at the base by 5 mm high; cracks few to numerous and deep, exposing a white, fibrillose context; not reacting with KOH; context with a thick, lower, white, membranous layer and narrow, upper, yellow to tan, ceraceous layer; hymenial surface variable, typically composed of cylindrical to conical or flattened spines, $1(-3) \times 0.2-0.3$ mm, 3-4 spines per mm, smooth or with lateral verrucae or acute apices, single or typically fused, tapering to an acute or penicillate, sterile apex, or hymenial surface verruculose from numerous apices formed laterally on spines fused to subiculum and substrate, pale yellow (4A3), light yellow (4A4), light orange (5A4), greyish orange (5B4), yellowish brown [5(D-E)5], light brown (6D6), or brown (6E7) and apices white or lighter; margin up to 1.5 mm wide, closely appressed, abrupt, sterile, with a white, raised, fimbriate to velvety edge.

Hyphal system dimitic with nodose septate generative and thick-walled microbinding hyphae. Spines composed of a core of tramal hyphae arranged in parallel and enclosed by subhymenial and hymenial layers, apex sterile, composed of undifferentiated terminal tramal hyphae often with secondary septa; tramal hyphae $2.5-4.5$ μm diam, nodose septate, even, rarely branched, walls thin, hyaline, smooth or occasionally heavily encrusted with closely appressed, small, hyaline crystals. Subiculum thin or up to 1.5 mm thick, consisting of subicular and microbinding hyphae intermixed in a dense to open tissue; subicular hyphae $2-4.5$ μm diam, nodose septate, even, moderately branched, walls thin, hyaline, smooth or encrusted with hyaline crystals; microbinding hyphae $1.5-3$ μm diam, aseptate, lumen narrow or lacking, sparsely to moderately branched, walls up to 1 μm thick, hyaline, smooth. Subhymenium $40-100$ μm thick, consisting of highly branched, short-celled subhymenial hyphae in a dense tissue; subhymenial hyphae $1.8-3$ μm diam, nodose septate, short-celled, walls thin, hyaline, smooth or occasionally encrusted with closely appressed, small hyaline crystals. Hymenium $27-36$ μm thick, a dense palisade of basidia, embedded cystidia and hyphidia. Hyphidia rare, embedded in hymenium, cylindrical, $18-32 \times 2-3.5$ μm , with a basal clamp connection, apex rounded or knobby, walls thin, hyaline, smooth. Cystidia numerous to absent, embedded or slightly pro-

truding (up to 20 μm) beyond hymenium, staining dark pink in phloxine and KOH, broadly cylindrical to clavate, sometimes irregularly constricted, $25-55(-70) \times 6-10$ μm , tapering to $1.5-3$ μm diam at base, with a basal clamp connection, apex rounded, obtuse or papillate, walls thin, hyaline, smooth. Basidia clavate, sometimes curving into hymenium, often stalked, $19-32 \times 5-7$ μm , tapering to $1.5-3.5$ μm diam at base, with a basal clamp connection, 4-sterigmate, walls thin hyaline, smooth. Basidiospores globose to subglobose, with a small but distinct apiculus, $(4.5-5-6(-6.5)) \times 4-5(-5.8)$ μm , often containing a large, refractive globule, walls slightly thickened, hyaline, smooth, negative in Melzer's reagent.

Habit: on wood and bark of *Populus tremuloides* Michx. *P. trichocarpa* Torrey & A. Gray, *P. balsamifera* L., *P. grandidentata* Michx., and *Betula papyrifera* Marsh. (Ginns and Lefebvre, 1993); associated with a stringy or spongy white rot

Distribution: Canada, including Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Northwest Territories, Ontario, Quebec, Saskatchewan (Ginns and Lefebvre, 1993), and United States, including Colorado (Lindsey and Gilbertson, 1978), Idaho, Michigan, Minnesota, Montana, New Hampshire, New York, South Dakota,

Specimens examined: CANADA. Alberta: Kananaskis Experimental Forest, on (decorticate) *P. tremuloides*, 7 July 1962, R. L. Gilbertson 3311 (CFMR). British Columbia: Quesnel, Six Mile Lake, on *P. trichocarpa*, 1 August 1949, W. Ziller (O). Ontario: Temagami Forest Reserve, Lake Temagami, Bear Island, on (wood and bark of) *Populus* sp., 27 August 1935; R. F. Cain US0263289 (BPI). Thunder Bay District, Black Sturgeon Lake, on (bark of) *Populus* sp., 1 August 1965, R. F. Cain US0263291 (BPI). Sudbury District, Renfrew, on *Populus* sp., 28 August 1953, W. Hipwell US0263286 (BPI). Quebec Martin Lake, on *Populus* sp., 12 July 1952, J. A. Stevenson US01106434 (BPI). UNITED STATES. Idaho: Coeur d'Alene, on (bark and wood of) *P. trichocarpa*, 9 September 1919, E. E. Hubert US0263831 (BPI). Lionhead Creek (on bark of) *P. tremuloides*, 29 August 1925, C. R. Stillinger US0263300 (BPI). Michigan: Mackinaw County, S Round Lake, on (bark and wood of) *Populus* sp., 6 September 1969, H. H. Burdsall, Jr. 3206 (CFMR). Minnesota:

Clearwater County, Lake Itasca State Park, on (wood of) *Populus* sp., 31 July 1970, R. L. Gilbertson US0263831 (BPI). Montana: Libby, on (bark of) *P. trichocarpa*, 9 September 1919, E. E. Hubert US0263831 (BPI) and FP6207 (CFMR). Columbia Falls, on (bark of) *Betula* sp., 18 August 1910, C.J. Humphrey FP6207 (CFMR). New Hampshire: North Conway, on fallen *Populus* sp. 1918, L. O. Overholts US0325582 (BPI). New York: Bloomingdale, Saranac River, on *P. grandidentata*, 11 September 1966, R. L. Gilbertson 5454 (CFMR). South Dakota: Custer, on (bark of) *P. tremuloides*, 1 August 1918, J. R. Weir US0263828 (BPI). Washington: Pend Oreille County, Colville National Forest, roadside 2 mi E Sullivan Lake, on (bark of) hardwood, 8 November 1950, W. B. and V. G. Cooke US0263282 (BPI). Wisconsin: Dane County, Blackhawk Ridge Recreation Area, Along Hwy 78, on corticate *P. tremuloides*, 25 September 1993, K. K. Nakasone FP1012614 (CFMR). Wyoming: Contact, on (decorticate) *P. tremuloides*, 29 July 1910, G. G. Hedgcock FP4272 (CFMR).

Radulodon americanus is similar to *R. erikssonii*. Originally, *R. americanus* was described as lacking cystidia and thus was easily distinguished from *R. erikssonii* that produces cystidia. Cystidia, however, are usually present in specimens of *R. americanus* but are overlooked because the hymenial elements are difficult to separate. The most reliable way to distinguish between the taxa is by distribution, for *R. erikssonii* is known from Europe and Asia, whereas *R. americanus* is reported only from Canada and northern United States. Other differences include thicker basidiomes with smaller spines in a denser arrangement (3–4 spines per mm) in *R. americanus* compared with thinner basidiomes, larger spines, and 2–3 spines per mm for *R. erikssonii*. Rattan's (1977) report of *R. americanus* from India is probably *R. erikssonii* although no cystidia were observed. Stralpers (1988) was the first to report the presence of microbinding hyphae in *R. americanus*.

For many years, the name *Hydnum casearium* Morgan was misapplied to *R. americanus* (Ginns and Lefebvre, 1993). Additional basidiocarp descriptions and illustrations are available in Lindsey and Gilbertson (1978), Nikolajeva (1961, as *Radulum casearium*), and Lloyd (1917, fig. 977 as *R. casearium*). Cultural descriptions are available in Stalpers

(1978) and Nakasone (1990). Nobles et al. (1957) reported that *R. americanus* (as *R. casearium*) is heterothallic and bipolar.

Radulodon calcareus (Cooke & Masee) Jülich, Persoonia 9(4): 466. 1978. Figs. 3, 7.

≡ *Hydnum calcareum* Cooke & Masee in Cooke, Grevillea 21(98): 38. 1892

≡ *Irpex calcareus* (Cooke & Masee) Wakef., Bull. Misc. inform. Kew 8: 367. 1915

≡ *Odontia calcarea* (Cooke & Masee) G. Cunn., Trans. Roy. Soc. New Zealand 86: 70. 1959

≡ *Pseudolagarobasidium calcareum* (Cooke & Masee) Sheng-H. Wu, Acta Bot. Fenn. 142: 112. 1990.

Basidiome widely effuse, up to 7 × 3 cm, up to 5 mm thick excluding spines, soft, hydneous with distinct, subceraceous, smooth areas between spines; cracks absent or extensive, then exposing a white fibrous context; not reacting with KOH; hymenial layer flaking off readily to reveal a white, soft, membranous context, context next to substrate white, soft, membranous, and thicker than the yellow to tan-colored, subceraceous, narrower upper layer; hymenial surface composed of well-developed, terete to conical spines, 3–5 spines per mm, up to 3 × 0.2–0.3 mm, smooth, soft brittle, single or fused at base or along entire length, occasionally forming a reticulate pattern, yellowish white (4A2), pale yellow (4A3), to greyish orange (5B4), gradually tapering to an acute or rounded, penicillate, sterile apex, apices white or concolorous with base of spine; margin abrupt or gradually thinning out, up to 2.5 mm wide, appressed, sterile, slightly raised, velvety, white, yellowish white (4A2) to pale yellow (4A3), with a fibrillose edge.

Hyphal system dimitic with nodose septate generative hyphae and thick-walled microbinding hyphae. Spines composed of a core of tramal hyphae arranged in parallel and enclosed by subhymenial and hymenial layers, apex consisting of smooth, undifferentiated tramal hyphae; tramal hyphae 1.5–5 μm diam, nodose septate, even, sparingly branched, walls thin, hyaline, smooth. Subiculum thick, composed of two layers: basal layer next to substrate 100–215 μm thick, a dense tissue of subicular hyphae arranged in parallel, often collapsed, compressed, agglutinated, intermixed with some microbinding hyphae and small, yellowish brown granular material that dissolve in KOH, then hyphae arranged perpendicular to

substrate to form the upper subicular layer, an open, loose tissue composed of subicular and microbinding hyphae; subicular hyphae 1.5-5 μm diam, nodose septate, even, moderately branched, walls thin, hyaline, smooth; microbinding hyphae 0.5-2 μm diam, aseptate, lumen narrow or lacking, sparingly to frequently branched, walls up to 1 μm thick, hyaline, smooth. Subhymenium up to 80 μm thick, consisting of frequently branched, irregular, short-celled subhymenial hyphae in a dense tissue, difficult to separate but not agglutinated; subhymenial hyphae 1.5-3 μm diam, nodose septate, short-celled, walls thin, hyaline, smooth. Hymenium up to 35 μm thick, a dense palisade of basidia and embedded cystidia. Cystidia numerous, arising from upper subiculum, subhymenium, and hymenium, homogeneous contents staining dark pink in KOH and phloxine, broadly cylindrical, clavate, or broadly fusiform, sometimes constricted, often stalked, 25-70(-105) \times 5.5-10 μm , tapering to 2-4.5 μm diam at base, with a basal clamp connection, apex rounded or papillate, embedded or slightly protruding (up to 10 μm), walls thin, hyaline, smooth. Basidia slenderly clavate, sometimes stalked, 15-28 \times 5-6 μm , tapering to 2-2.5 μm diam at base, with a basal clamp connection, 4-sterigmate, walls thin, hyaline, smooth. Basidiospores globose to subglobose with a small but distinct apiculus, 4-5(-5.5) \times 3-3.8 μm , walls thin, hyaline, smooth, negative in Melzer's reagent.

Habitat: on wood and bark of angiosperms.

Distribution: Australia, Malaysia, Sierra Leone, Taiwan.

Specimens examined: AUSTRALIA. New South Wales: Blue Mountains, Katoomba, 1914, *W. N. Cheesman* *K(M) 62576* (K). Victoria, Kangaroo grounds, on fallen rotten trunk, 12 July 1953, *E. M. Davies* 3643, *K(M) 56910* (K). MALAYSIA. Selangor: Kuala Lumpur, Weld Hill, 16 January 1920, *M. Noor* 5576 *K(M) 62577* (K). SIERRA LEONE. Njala, Kori, on dead branch of *Cathormion dinklagei*, Hutch & Dandy, 22 October 1952, *F. C. Deighton* M4898, *IMI 51684*, *K(M)62574* (K). TAIWAN. Nantou, Sun-Moon Lake, alt. 800 m, on branch of *Castanopsis kusanoi* Hayata, 26 October 1988, *S.-H. Wu* 881026-18 (H).

Soft, brittle spines, an easily flaked hymenial layer, and relatively small, thin-walled basidiospores characterize *Radulodon calcareus*. It has a wide distribution from Africa to Australia. Wu (1990) also noted the presence of

microbinding hyphae in *R. calcareus*. Descriptions of this species can be found in Jülich (1978), Reid (1955), Wakefield (1915), and Wu (1990). Cunningham's (1959) report of *O. calcarea* from New Zealand; however, the specimens examined appear to be that of a *Hyphodontia* species somewhat similar to *H. lanata* Burds. & Nakasone.

Radulodon casearius (Morgan) Ryvarden, *Canad. J. Bot.* 50: 2075. 1972. Figs. 4, 8.

\equiv *Hydnum casearium* Morgan, *J. Cincinnati Soc. Nat. Hist.* 10: 11. 1887. TYPE: UNITED STATES. Ohio: Cincinnati, (on *Carya* sp.), *A. P. Morgan, C. G. Lloyd 16737, US0324642* (Holotype of *Hydnum casearium*: BPI!).

\equiv *Radulum casearium* (Morgan) Lloyd, *Mycol. Notes Lloyd Libr. Mus.* 5: *Radulum* p. 8. 1917.

\equiv *Basidioradulum casearium* (Morgan) H. Furuk., *Bull. Gov. Forest Exp. Stn.* 261: 61. 1974.

\equiv *Hydnum trichodontium* Berk. & Ravenel, *Fungi caroliniani exsiccati, Fascicle III*, no. 20. 1855 (*nomen nudum*).

\equiv *Hydnum trechodontium* Berk. in Cooke, *Grevillea* 20(93): 2. 1891 (*nomen nudum*). TYPE: UNITED STATES. South Carolina: on rotten oak log, *H. W. Ravenel 1296, K(M)57154* (Holotype: K!; Isotypes: BPI *US0260556!* and *US0260557!*).

Basidiome widely effuse, rarely effused-reflexed, up to 60 \times 15 cm, up to 1.5(-12) mm thick excluding spines, hydneous often with spines clumping together, smooth between spines, reflexed part up to 4 mm radius; cracks frequent, shallow to deep, breaking into polygons and exposing context; context bilayered, with a thin, beige-colored upper hymenial layer and a thicker, white, lower layer. Hymenial surface of long, slender, terete spines, up to 8 \times 0.5 mm, 2-3(-4) spines per mm, smooth or verrucose, single or fused, gradually tapering to a smooth or penicillate, acute apex, greyish orange [5B(4-5)], brownish orange (5C6), or light brown (5D, 6D6), apices concolorous, lighter in color or white; margin up to 3 mm wide, appressed, with small spines or tubercles, moderately thick to thinning out, appressed, woolly to velvety, pale orange (5A3) to pale yellow (4A3).

Hyphal system dimitic with nodose septate generative and microbinding hyphae. Spines composed of a core of tramal hyphae arranged in parallel and surrounded by thin subhymenial

and hymenial layers; tramal hyphae 1.5-3.5 μm diam, nodose septate, even, rarely branched, walls thin, hyaline, smooth. Subiculum thick, consisting of subicular and microbinding hyphae intermixed in a dense tissue; subicular hyphae 2.5-4.5 μm diam, nodose septate, even or irregular, moderately branched, walls thin, hyaline, smooth or sometimes heavily encrusted with small, hyaline crystals; microbinding hyphae 1-2.5 μm diam, aseptate, lumen lacking, sparingly to frequently branched, scattered in context and base of spines, walls up to 1 μm thick, hyaline, smooth. Subhymenium up to 40 μm thick, consisting of highly branched and short-celled subhymenial hyphae in a dense tissue; subhymenial hyphae 2.2-3 μm diam, nodose septate, frequently branched, walls thin, hyaline, smooth. Hymenium a dense palisade of hyphidia, cystidia, and basidia. Hyphidia rare, embedded in hymenium, narrowly cylindrical, 18-34 \times 2-4 μm with a basal clamp connection, unbranched, occasionally knobby at apex, walls thin, hyaline, smooth. Cystidia scattered to rare, embedded in hymenium, difficult to isolate and often breaking, staining dark pink in KOH and phloxine, broadly cylindrical, clavate, or obclavate, occasionally slightly constricted, 35-70 \times 6-11 μm , tapering to 2.5-4 μm diam at base, often with a short stalk subtended by a basal clamp connection, apex obtuse or with an apical bulb, walls thin, hyaline, smooth. Basidia clavate with a distinct stalk, 22-32 \times 5-8.5 μm , tapering to 3-3.5 μm diam at base, with a basal clamp connection, 4-sterigmate, walls thin, hyaline, smooth. Basidiospores globose to subglobose with a small but distinct apiculus, (4.5-)5-6(-7) \times (4-)4.5-5.5(-6) μm , often containing a large, refractive globule, walls slightly thickened, hyaline, smooth, negative in Melzer's reagent.

Habitat: on wood and bark of *Quercus* and *Carya* logs; associated with a white rot.

Distribution: Florida, Ohio, South Carolina.

Specimens examined: UNITED STATES. Florida: Leesburg, on trunk of *Quercus virginiana* Mill., 8 March 1919, *G. G. Hedgcock* FP32221 (CFMR). Leon County, Tall Timbers Research Station, on *Q. virginiana*, 27 July 1977, *H. H. Burdsall, Jr.*, 9567 (CFMR). Alachua County, 6 mi NW of Gainesville, Devil's Millhopper, on living *Q. laurifolia* Michx., 29 August 1952, *A. S. Rhoads* FP103101 (CFMR). Gainesville, Lake Alice, on bark of *Q. nigra* L., 30 August 1952, *A. S.*

Rhoads FP103134 (CFMR). South Carolina: Mountsville, on down log of *Quercus alba* L., 20 December 1949, *W. A. Campbell* FP94493 (CFMR).

Radulodon casearius was known only from the type for many years. Gilbertson (1964) examined the holotype of *H. casearium* and noted the microbinding hyphae but failed to observe clamp connections on the generative hyphae or cystidia. Although developing large and robust basidiomes, it is relatively rare for only the seven specimens mentioned above are known. Specimen FP32221 is especially thick, up to 12 mm thick, from the incorporation of many layers of spines into the subiculum and suggests that this species is perennial. *Radulodon casearius* is apparently restricted to the southeastern United States. The report by Furukawa (1974) of *Basidiordulium casearium* from Japan probably presents a misidentification of *R. erikssonii*, which is known from that geographical region.

Hydnum casearium is the first validly published name for this species. Berkeley and Ravenel's name, *H. trichodontium*, is earlier but invalid because they failed to provide a description or diagnosis. The name *Hydnum casearium* was misapplied for many years to the species now known as *R. americanus* (Gilbertson, 1964; Ginns and Lefebvre, 1993). *Radulodon casearius*, however, has a larger basidiome with more robust spines and different distribution and substrate preferences than *R. americanus*. See Lloyd (1917) for a description and photograph of *R. casearius*.

Radulodon cirrhatinus Hjortstam & Spooner, Kew Bull. 45(2): 312. 1990. TYPE: MALAYSIA. Sabah: Danum Valley, elev. 400 ft, on fallen log, 30 November 1985, *B. M. Spooner* 295, *K(M)62575* (Holotype: K!). Figs. 5, 9, 11.

Basidiome effused-reflexed, up to 7 \times 8 cm, up to 1 mm thick between spines, subceraceous, hydnceous with distinct smooth areas between spines, pileus up to 20 mm diam and up to 1 mm thick, smooth with slightly raised, radial ridges, light orange to greyish orange [5A(4-5)]; not reacting to KOH; cracks absent; context dense, compact, fibrous, white; hymenial surface composed of long, slender, terete to flattened spines, 1-10(-15) \times 0.3-0.8 mm, 1-3 spines per mm, smooth, brittle, single but occasionally fused at the base, tapering to an acute, entire apex, orange white (5A2) at base, then gradually turning darker toward

apex, apices smooth, entire, greyish orange (5B5) or brownish orange (5C5), with distinct smooth, orange white (5A2) fertile areas between spines; margin distinct, abrupt, crenulate, loosely attached to substrate, white to orange white (5A2), with sterile edges.

Hyphal system dimitic with nodose septate generative and thick-walled skeletal hyphae. Spines composed of a core of tramal hyphae arranged in parallel and surrounded by subhymenial and hymenial layers, apices sterile, consisting of agglutinated, smooth, undifferentiated terminal hyphae, occasionally with a few skeletal hyphae in the base of spines; tramal hyphae 3-5.5 μm diam, nodose septate, even, rarely branched, walls thin to slightly thick, hyaline, smooth. Subiculum about 1 mm thick, consisting of subicular and skeletal hyphae intermixed in a dense tissue; subicular hyphae 2-5.5 μm diam, nodose septate, even, moderately branched, walls thin to slightly thick, hyaline, smooth; skeletal hyphae 2.5-5.5 μm diam, aseptate, lumen narrow or lacking, rarely branched, walls up to 1.5 μm thick, hyaline, smooth. Subhymenium up to 100 μm thick, consisting of frequently branched, short-celled subhymenial hyphae in a dense tissue; subhymenial hyphae 2-3 μm diam, nodose septate, short-celled, walls thin, hyaline, smooth. Hymenium 25-36 μm thick, consisting of basidia, embedded cystidia and hyphidia. Hyphidia rare, embedded in hymenium, cylindrical, 28-32 \times 2.5-3.5 μm , tapering to 2-2.5 μm diam at base, with a basal clamp connection, walls thin, hyaline, smooth. Cystidia scattered to numerous, embedded, arising from subhymenium or hymenium, staining dark pink in KOH and phloxine, broadly cylindrical, fusoid, or clavate, 25-45 \times 8-15 μm , tapering to 3-3.5 μm diam at base, with a basal clamp connection, apex rounded, obtuse or papillate, walls thin, hyaline, smooth. Basidia clavate, 25-30 \times 4.5-5.5 μm , tapering to 2 μm diam at base, with a basal clamp, 4-sterigmate, walls thin, hyaline, smooth. Basidiospores subglobose to ovoid, with a small but distinct apiculus, (4-)4.5-5 \times 3.5-4(-4.5) μm , often with a large, refractive globule, walls slightly thick, hyaline, smooth, negative in Melzer's reagent.

Habitat: on bark of hardwood log.

Distribution: Malaysia.

This is a striking, robust species with long, brittle, slender spines. The subhymenium is quite dense and is responsible for the subceraceous texture; however, the hyphae are not

agglutinated. *Radulodon cirrhatinus* also develops skeletal hyphae that are unique in the genus.

Radulodon erikssonii Ryvarden, *Canad. J. Bot.* 50: 2075. 1972. TYPE: NORWAY. Oslo, Sørkedalen, Molliksåsen, on dead *Populus tremula*, 24 October 1968, L. Ryvarden 72845 (Holotype: O!; Isotype: DAOM 138851!). Figs. 10, 12, 13.

Basidiome effuse, up to 10 \times 6 cm, up to 0.7 mm thick excluding spines, ceraceous to subceraceous, hydneous with distinct smooth areas between spines, on drying sometimes cracking into polygons and spines clustering together, orange yellow (5A4), yellowish brown (5D5-8), greyish orange (5B5), or brownish orange (5C5); not reacting in KOH; cracks absent or numerous and deep, exposing a white, fibrillose context; context with a thicker, membranous, white basal layer and narrower, ceraceous, yellow to tan upper layer; hymenial surface composed of narrowly cylindrical to conical spines, 1-4 \times 0.3 mm, 2-3(-4) spines per mm, smooth or occasionally with smaller lateral apices, single or fused, tapering to an acute, occasionally penicillate, sterile apex, apices white or paler than base of spines; margin up to 1.5 mm wide, closely appressed, abrupt or gradually thinning out, sterile, with a white, slightly raised, fibrillose edge.

Hyphal system dimitic with., nodose septate generative and thick-walled microbinding hyphae. Spines composed of a core of tramal hyphae arranged in parallel and surrounded by subhymenial and hymenial layers, apex sterile, consisting of smooth, undifferentiated terminal hyphae often with secondary septa; tramal hyphae 2.5-5 μm diam, nodose septate, even, rarely branched, walls thin, hyaline, smooth or occasionally encrusted with closely appressed, small, hyaline crystals. Subiculum thin to thick, 250-700 μm thick, consisting of subicular and microbinding hyphae intermixed in a dense to open tissue; subicular hyphae 3-5 μm diam, occasionally inflated up to 14 μm diam, nodose septate, even or irregular in shape, moderately branched, walls thin, hyaline, smooth; microbinding hyphae 0.5-2.5 μm diam, aseptate, lumen very narrow or lacking, sparsely to moderately branched, walls up to 1 μm thick, hyaline, smooth. Subhymenium 20-70 μm thick, consisting of highly branched and short-celled subhymenial hyphae in a dense tissue;

subhymenial hyphae 2-3 μm diam, nodose septate, short-celled, walls thin, hyaline, smooth or occasionally encrusted with closely appressed, small, hyaline crystals. Hymenium up to 30-40 μm thick, consisting of basidia, embedded cystidia, and occasional hyphidia. Hyphidia rare, embedded in hymenium, cylindrical, 18-26 \times 2-3.5 μm , with a basal clamp connection, unbranched, walls thin, hyaline, smooth. Cystidia abundant to rare, embedded or slightly protruding (up to 10 μm) beyond hymenium, staining dark pink in KOH and phloxine, broadly cylindrical, clavate, or obclavate, sometimes constricted, often stalked, 25-45(-80): \times 6-10 μm , tapering to 2-3 μm diam at base, with a basal clamp connection, apex obtuse or papillate, walls thin, hyaline, smooth. Basidia clavate, (18-)25-36 \times 5-7 μm , tapering to 1.5-3 μm diam at base, with a basal clamp connection, 4-sterigmate, walls thin, hyaline, smooth. Basidiospores subglobose to broadly ellipsoid, with a small but distinct apiculus, 5-6(-6.5) \times (3.5-)4-5 μm , often with a large, refractive globule, walls slightly thickened, hyaline, smooth, negative in Melzer's reagent.

Habitat: on wood and bark of *Populus* sp., especially *P. tremula* L.

Distribution: Norway, Sweden, Finland, Switzerland, Italy, India (Rattan, 1977).

Specimens examined: INDIA. Mahasu, Narkanda, on (decorticate) angiospermous log, 17 October 1967, *H. S. Khara* 4223 (O). ITALY. Südtirol: Ubersch, on *Quercus* (?), 1966, *J. Poelt* 3043 (GB). FINLAND. Karelia borealis: Pielisjärvi, Koli, on (decorticate) *P. tremula*, 28 August 1956, *V. Kujala*, GB 9786 (GB). Mustiala, on bark and wood of *P. tremula*, September 1895, *PA. Karsten*, GB 9783 Rabenhorst-Pazschke: *Fungi europaei et extra europaei Nr. 4343, ut Hydnum fallax* (GB). NORWAY. Buskerud: Ringerike, 400 m. alt., on lautre, 24 May 1995, *G. Gaarder* 879 (O). Østfold: Hvaler, Ladalen, on *P. tremula*, 25 May 1993, *L. Ryvarden* 32987 (O; ARIZ: AN028321). Vestfold: Larvik, Jordstogy, on dead *P. tremula*, 14 May 1995, *H. Andersen* (O). SWEDEN. Uppland: Bondkyrka sn, Nosten, nara Predikstolen, shat S om Uppsala, on *P. tremula*, 20 September 1928, *S. Lundell* 225, GB 9759 (GB). Hälsingland: Bjuråker par., along river Svågan c. 8 km NNO of Brännås, on old fallen aspen, 13 August 1980, *R. Moberg* 4952 (GB). SWITZERLAND.

Golino, on branch of corticated *Populus*, 6 December 1986, *E. Martini* 1513 (GB). Losone, Maia, on (bark and wood of) *P. tremula*, February 1988, *E. Martini* 1544, 1546, 1547, 1548 (GB).

Cystidia are rare or absent in some specimens of *Radulodon erikssonii*, thus these specimens may be difficult to distinguish from *R. americanus*. However, *R. erikssonii* typically has thinner basidiomes with distinct smooth areas between the spines and larger, smoother spines than *R. americanus*. Because their distribution does not overlap, they can be distinguished by geographic location. *Radulodon erikssonii* probably occurs in eastern Russia as evidenced from the description of *Radulum casearium* from the Volga-Don region provided by Nikolajeva (1961) resembles that of *R. erikssonii*. Similarly, the report of *Basidioradulum casearium* from Japan by Furukawa (1974) should be referred to *R. erikssonii*.

EXCLUDED TAXA

Irpex decolorans Cooke, *Grevillea* 19: 109. 1891. TYPE: CUBA. On rotting logs, Herb. Berk. 1879, No. 835, *K(M)62571* (Holotype: K!).

The holotype specimen has brown, terete or laterally fused, flattened spines up to 2.5 mm long, a monomitic hyphal system with nodose septate generative hyphae, a thickening subhymenium (up to 36 μm thick), no cystidia, indistinct, collapsed basidia, and slightly thick-walled, broadly ellipsoid basidiospores (4-5 \times 2.8-3.5 μm). Hjortstam and Larsson (1995, p. 53) suggested that *I. decolorans* is a species of *Radulodon*. Since it lacks cystidia and microbinding hyphae, *I. decolorans* is not accepted in *Radulodon*. Instead, *I. decolorans* may be related to *Pseudolagarobasidium subvinosum*.

Radulodon copelandii (Pat.) N. Maek., Rep. Tottori Mycol. Inst. 31: 93. 1993. TYPE: PHILIPPINES. *E. B. Copeland*, *C. G. Lloyd* 36682, *US0324650* (Isotype: BPI!).

\equiv *Hydnum copelandii* Pat., *Leafl. Philipp. Bot.* 6(104): 2251. 1914.

\equiv *Oxydontia copelandii* (Pat.) S. Ito, *Mycol. fl. Japan* 2(4): 189. 1955.

\equiv *Sarcodontia copelandii* (Pat.) Imazeki, *Col. illustr. fungi Japan* 2: 127. 1965.

\equiv *Mycoacia copelandii* (Pat.) Aoshima & H. Furuk., *Trans. Mycol. Soc. Japan* 7(2-3): 136. 1966.

≡ *Radulomyces copelandii* (Pat.) Hjortstam & Spooner, Kew Bull. 45(2): 314. 1990.

Specimens examined: JAPAN. Hokkaido, Sapporo, on *Abies sachaliensis* (F. Schmidt) Mast., 21 October 1919, T. Hemmi, C. G. Lloyd 26558, US0324649 (BPI). KOREA. Gyungsangnam-do, Mt. Goya, between Haein Temple and Maaebul, on *Prunus* branch, 16 August 1991, Hack Sung Jung, SNU 910816-56 (CFMR).

Radulodon copelandii is characterized by long, slender spines, a monomitic hyphal system with nodose septate generative hyphae, hyphidia, and slightly thick-walled, globose to subglobose basidiospores. This combination of characters indicates that this species is properly placed in *Radulomyces*. Because *R. copelandii* has a monomitic hyphal system, it is not accepted in *Radulodon*. See Hjortstam et al. (1990) and Maekawa (1993) for a description and illustration of *R. copelandii*.

Radulodon licentii (Pilát) Ryvarden, Česká Mykol. 30(1): 40. 1976. TYPE: CHINA. Chansi: Yao Chan, (on corticated branch of angiosperm), 31 August 1935, E. Licent 4390, PRM169105 (Lectotype: PRM!).

≡ *Acia licentii* Pilát, Ann. Mycol. 38(1): 66. 1940.

≡ *Radulum licentii* (Pilát) Nikol., Flora pl. cryptog. URSS. 6(2): 98. 1961.

≡ *Radulomyces licentii* (Pilát) Parmasto, Consp. syst. cortic. p. 111. 1968.

The lectotype specimen is in good condition with numerous, globose basidiospores (5.5-6 × 5-6 µm). I agree with Stalpers (1998) who considered *R. licentii* a synonym of *Radulomyces copelandii*. Ryvarden (1976) provides a good description of the lectotype specimen, and Nikolajeva (1961) describes and illustrates this species as well.

Radulodon pseudomucidus (Petch) Stalpers, Folia Cryptog. Estonica 33: 137. 1998. TYPE: CEYLON (SRI LANKA). Hakgala, April 1919, Petch 5962, K(M) 56913 (Neotype: K!).

≡ *Hydnum pseudomucidum* Petch, Ann. Roy. Bot. Gard. (Peradeniya) 6: 156. 1916.

≡ *Radulomyces pseudomucidus* (Petch) Jülich, Persoonia 10(3): 334. 1979.

≡ *Cerocorticium pseudomucidum* (Petch) Jülich, Persoonia 11(4): 427. 1982.

The neotype specimen is in fairly good condition although it is covered by a hyphomycete.

The hymenium is well preserved with abundant, globose, thin-walled basidiospores (6-7.5 × 5.5-6.5 µm). Its monomitic hyphal system excludes *H. pseudomucidum* from *Radulodon*. Hjortstam et al. (1990) placed *H. pseudomucidum* in synonymy with *R. copelandii*, and I concur.

Radulodon subquercinus (Henn.) Hjortstam & Ryvarden, Mycotaxon 10(2): 285. 1980.

≡ *Radulum subquercinum* Henn. in O. Warburg, Monsunia I. Fungi 2: 46. 1899.

≡ *Phanerochaete subquercina* (Henn.) Hjortstam, Windahlia 17: 58. 1987.

≡ *Odontia subirpicoidea* Rick, Iheringia, Bot. 5: 162. 1959.

≡ *Phanerochaete radulans* Hallenb., Iranian J. Pl. Pathol. 14: 67. 1978.

The synonymy presented is from Hjortstam (1987) and Hjortstam and Ryvarden (1982) who considered *Radulodon subquercinus* a species of *Phanerochaete*. This species is characterized by a monomitic hyphal system of simple-septate generative hyphae and thin-walled, ellipsoid basidiospores, thus, is not accepted in *Radulodon*.

Radulodon subvinosus (Berk. & Broome) Stalpers, Folia Cryptog. Estonica 33: 137. 1998.

≡ *Hydnum subvinosum* Berk. & Broome, J. Linn. Soc., Bot. 14: 60. 1995. TYPE: CEYLON. Herb. Bresadola, US0269529 (Isotype: BPI!).

≡ *Irpex subvinosum* (Berk. & Broome) Petch, Dis. tea bush 173. 1923.

≡ *Pirex subvinosus* (Berk. & Broome) Hjortstam, Windahlia 17: 58. 1987.

≡ *Pseudolagarobasidium subvinosum* (Berk. & Broome) Sheng-H. Wu, Acta Bot. Fenn. 142: 113. 1990.

≡ *Hydnum ayresii* Berk. in Cooke, Grevillea 20(93): 2. 1891. TYPE: MAURITIUS. (on bark), K(M)64594 (Holotype: K!).

My observations of the isotype specimen agree with Mass Geesteranus' (1974, p. 459) description. The monomitic hyphal system, thin subiculum, and thin-walled basidiospores indicate that *Hydnum subvinosum* is not a *Radulodon*. The most appropriate generic placement for this taxon at this time is in *Pseudolagarobasidium*. See Wu (1990) for a description and illustration of *P. subvinosum*.

Hjortstam and Larsson (1995) synonymized *Hydnum ayresii* with *H. subvinosum*, and I concur. Wu (1990) placed *Pseudolagarobasidium*

leguminicola J. C. Jang & T. Chen in synonymy under *P. subvinosum*. I am unable to confirm this synonymy since I was not able to borrow the type specimen. *Irpex modestus* Berk. in Cooke was placed in synonymy with *Hydnum ayresii* by van der Byl (1934) and Maas Geesteranus (1974, p. 488). The holotype specimen of *Irpex modestus* (Mauritius, hills above Port Louis, on bark, April 1857, Ayres K(M) 77598, from K) bears a striking resemblance to *H. ayresii* but lacks basidiospores.

Radulodon venustus Hjortstam & Ryvardeen, Mycotaxon 74(1): 250. 2000. TYPE: BRAZIL. Sao Paulo: Cananeia, Ilha do Cardoso, on bark of palm, 2 February 1987, D. N. Pegler, K. Hjortstam, and L. Ryvardeen, Hjortstam 16838, K(M) 77909 (Holotype: K!).

The holotype specimen is characterized by a thin, membranous basidiome with terete spines, a monomitic hyphal system of nodose-septate, generative hyphae, broadly ellipsoid, thin-walled basidiospores [(4.5-)5-5.5 × 3.2-3.5 μm], and numerous, fusiform to clavate cystidia. No basidia were observed, however. The gross morphology of *Radulodon venustus* is reminiscent of some *Radulodon* species. However, it is not accepted in *Radulodon* because it lacks a dimitic hyphal system. *Radulodon venustus* may be related to *Pseudolagarobasidium subvinosum* for they have similar microscopic features including basidiospores, hyphal system, and cystidia.

DISCUSSION

Radulodon is defined as a genus with a hyd-naceous hymenophore, dimitic hyphal system, thickening subhymenium, embedded cystidia, and globose to subglobose basidiospores. The five species accepted in the genus represents a closely related group of taxa. The microbinding hyphae, found only in the subiculum or at the base of the spines and often overlooked, is a significant trait of the genus. Previously, only *Radulodon casearius*, *R. calcareus*, and *R. americanus* were reported to be dimitic (Gilbertson,

1964; Ryvardeen, 1972; Stalpers, 1998; Wu, 1990). However, microbinding hyphae are present in four species of *Radulodon* accepted here. *Radulodon cirrhatinus* develops skeletal hyphae instead of microbinding hyphae. *Radulodon calcareus* is the most divergent member of the genus because it lacks hyphidia and has small, thin-walled basidiospores.

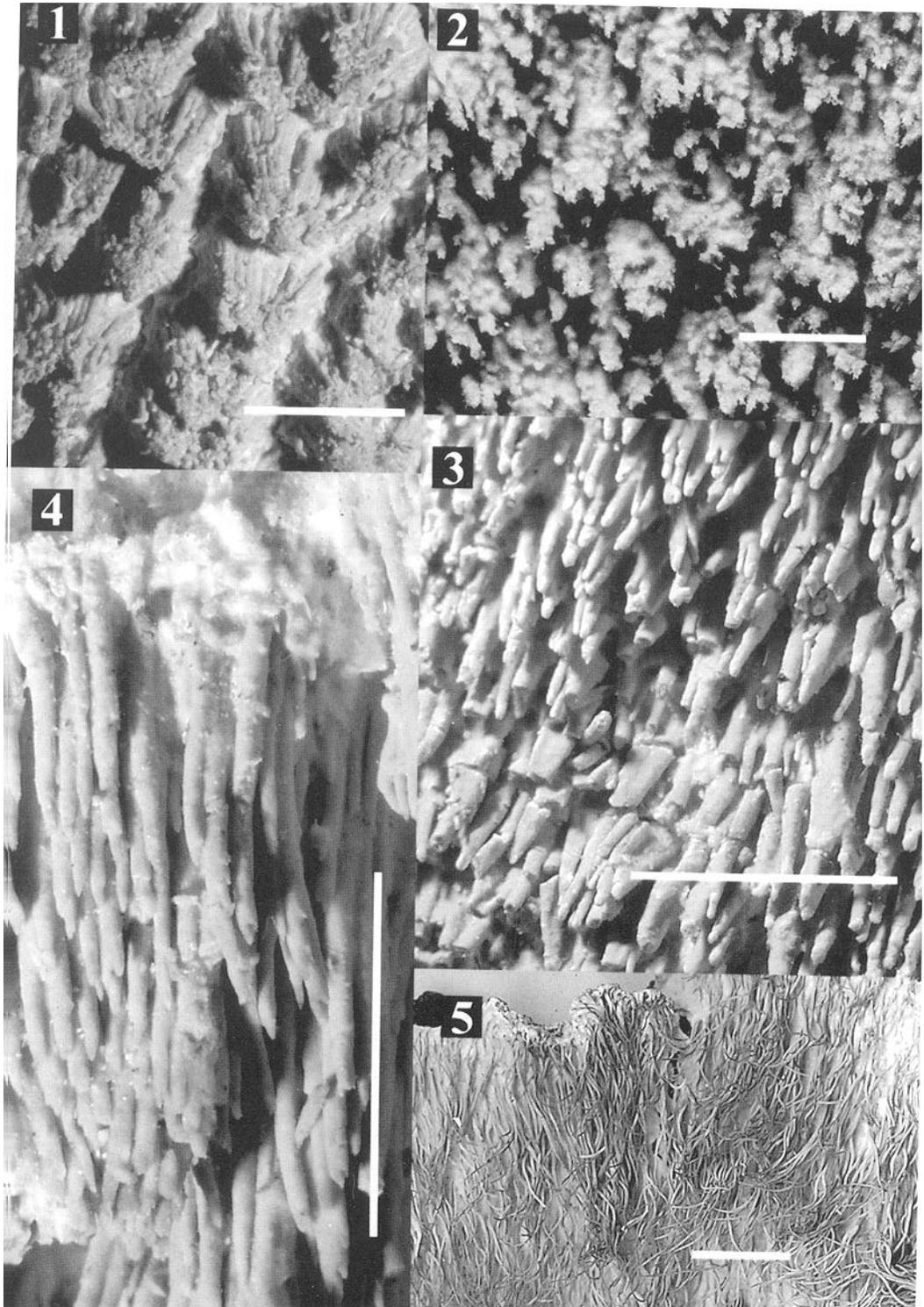
Further study and additional collections from southeast Asia and neotropics are needed to resolve the taxonomy of *Pseudolagarobasidium subvinosum* and related taxa such as *Irpex modestus*, *Hydnum ayresii*, and *Irpex decolorans*.

There is a lot of confusion among the hyd-naceous genera of *Radulodon*, *Radulomyces* M. P. Christ., *Pseudolagarobasidium*, and *Sarcodontia* Schulzer. Table 1 summarizes the salient features of these genera. The core taxa of *Radulodon*, *R. americanus*, *R. erikssonii*, and *R. casearius*, have not changed since the genus was first proposed. Other species, however, were placed in *Radulodon* and *Pseudolagarobasidium* (e.g., *R. calcareus* and *P. subvinosum*) or *Radulodon* and *Radulomyces* (e.g., *R. licentii*). Recently, Stalpers (1998) proposed to synonymize *Pseudolagarobasidium* and *Radulodon*. Further morphological and phylogenetic studies of these genera are needed to fully resolve their circumscription.

The relationship of *Radulodon* to other corticioid genera is not known. Ryvardeen (1972) suggested a possible relationship to *Mycoacia* Donk, *Hypochnicium* J. Erikss., *Hyphoderma* Wallr. emend. Donk, *Radulomyces*, and *Basidioradulum* Nobles. Jülich (1981) placed *Radulodon* in the Phlebiaceae Jülich with *Mycoacia*, *Mycoaciella* J. Erikss. & Ryvardeen, *Phlebia* Fr., *Resinicium* Parmasto, and *Sarcodontia*. Parmasto (1986), however, placed *Radulodon* along with *Sarcodontia* and *Iriciporus* Murrill in the subfamily Hyphodermoideae and *Phlebia*, *Resinicium*, and *Mycoacia* in the Phlebioideae. The application of molecular phylogenetic methods may be able to resolve the relationships of these genera.

TABLE 1. Morphological features to differentiate *Radulodon*, *Radulomyces*, *Pseudolagarobasidium*, and *Sarcodontia*.

GENERA	HYPHAL SYSTEM	SUBHYMENIUM	BASIDIOSPORES WALLS	CYSTIDIA
<i>Radulodon</i>	dimitic	thickening	slightly thick or thin	present
<i>Radulomyces</i>	monomitic	not thickening	slightly thick	absent
<i>Pseudolagarobasidium</i>	monomitic	not thickening	thin	present
<i>Sarcodontia</i>	monomitic	thickening	slightly thick	absent



FIGURES 1-5. 1. *Radulodon americanus*. Basidiome with clumping spines. From G. G. Hedgcock FP4272 (CFMR). Bar = 5 mm. 2. *Radulodon americanus*. Basidiome showing spines with fimbriate apices. From C. J. Humphrey FP6207 (CFMR). Bar = 1 mm. 3. *Radulodon calcareus*. Basidiome showing brittle spines. F. C. Deighton M4898 (K). Bar = 5 mm. 4. *Radulodon casearius*. Basidiome close-up of spines. W. A. Campbell FP94493 (CFMR). Bar = 5 mm. 5. *Radulodon cirrhatinus*. Basidiome bearing long, slender spines. From B. M. Spooner 295 (K). Bar = 10 mm.

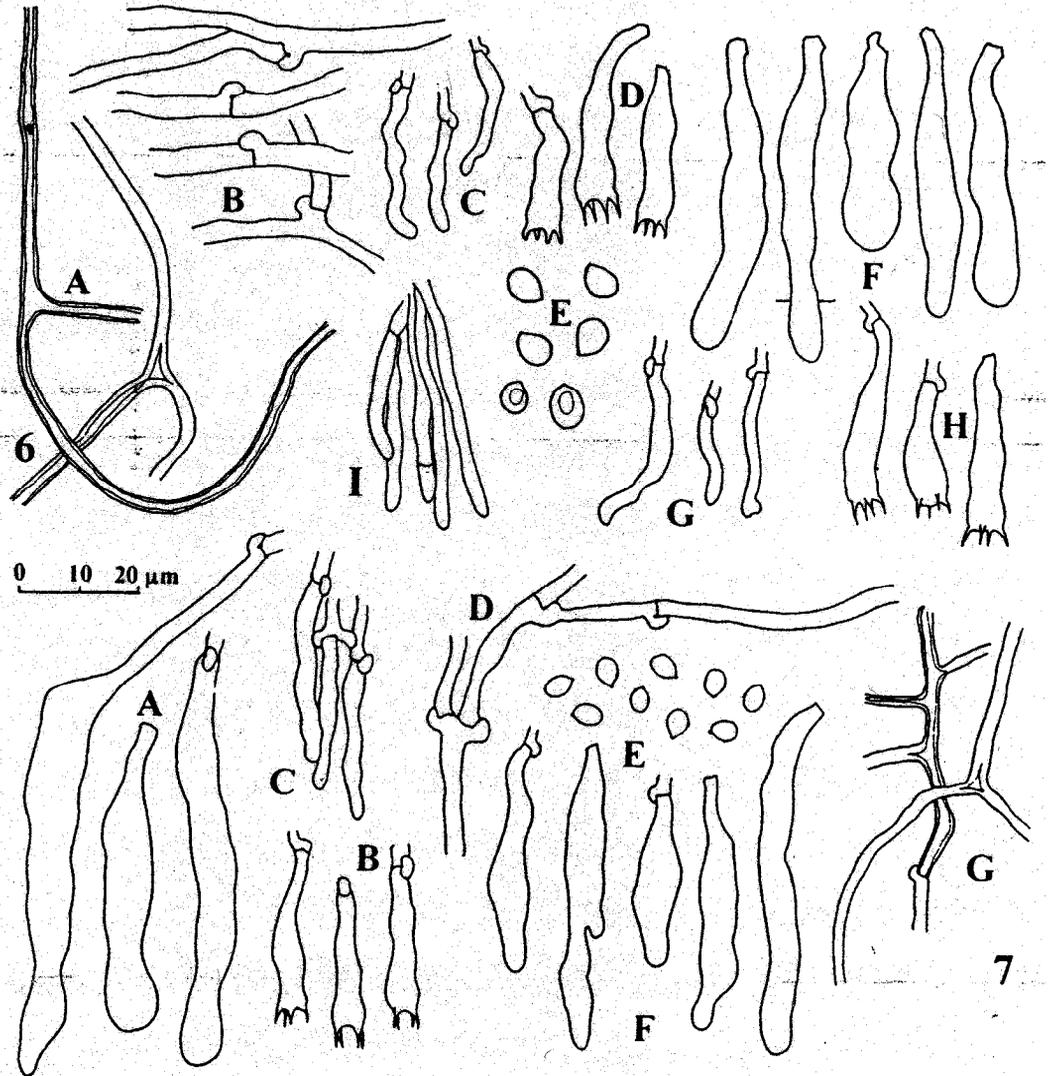


FIGURE 6. A-I. *Radulodon americanus*: A, microbinding hyphae from subiculum; B, tramal hyphae from spines; C and G, hyphidia; D and H, basidia; E, basidiospores; F, cystidia; I, hyphae from apex of spine. A-E from *R. F. Foster V-4015* (DAOM); F-I from *R. F. Cain US0263289* (BPI).

FIGURE 7. A-G. *Radulodon calcareus*: A and F, cystidia; B, basidia; C, hyphae from apex of spine; D, subicular hyphae; E, basidiospores; G, microbinding hyphae. A-B from *W. N. Cheesman K(M)62576* (K). C from *S. H. Wu 881026-18* (H). D-G from *F. C. Deighton K(M)62574*.

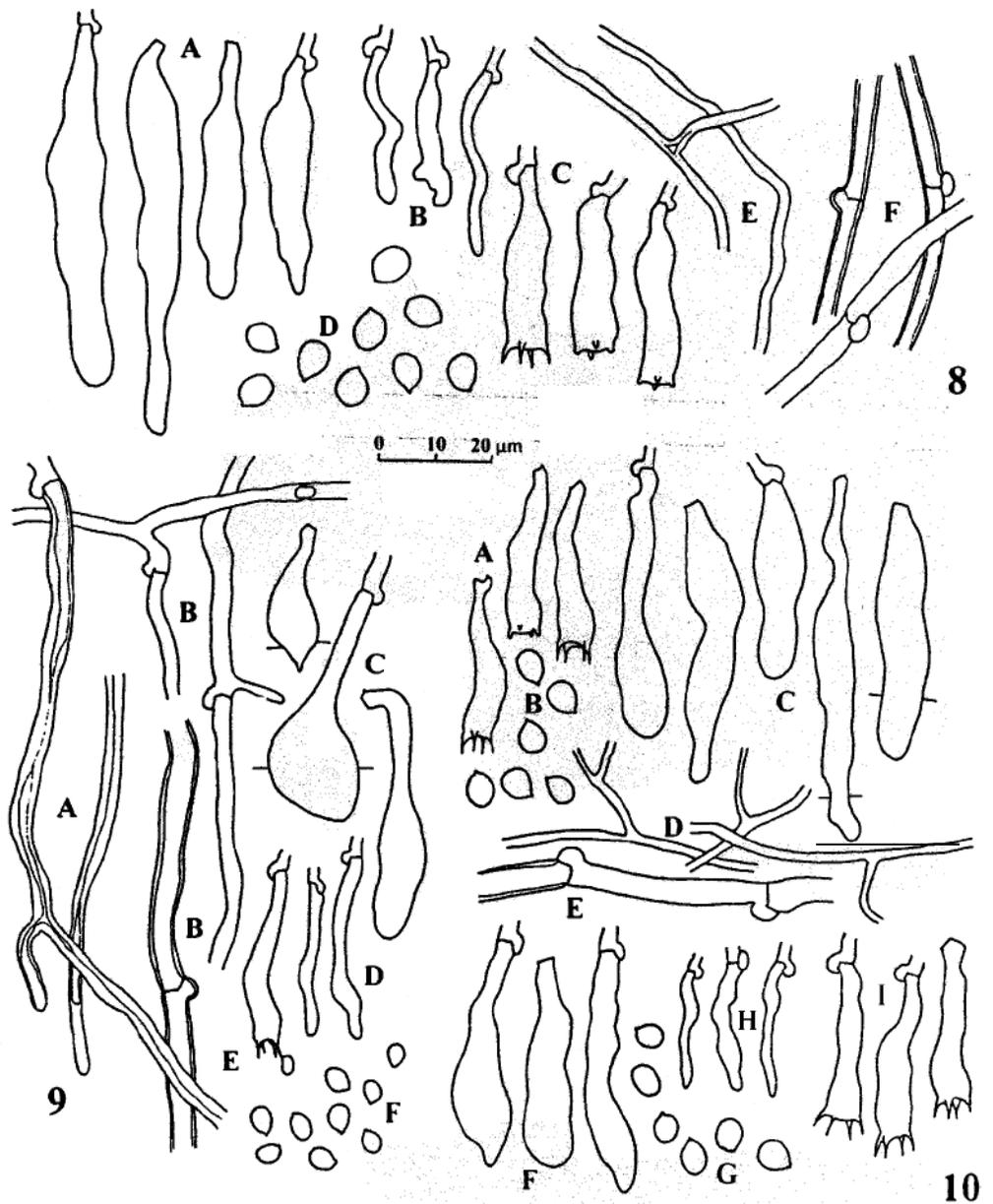


FIGURE 8. A-F. *Radulodon casearius*: A, cystidia; B, hyphidia; C, basidia; D, basidiospores; E, microbinding hyphae; F, tramal hyphae from spines. From H. H. Burdsall, Jr. 9567 (CFMR).

FIGURE 9. A-F. *Radulodon cirrhatinus*: A, skeletal hyphae; B, subicular hyphae; C, cystidia; D, hyphidia; E, basidium; F, basidiospores. From B. M. Spooner 295 (K).

FIGURE 10. A-I. *Radulodon erikssonii*: A and I, basidia; B and G, basidiospores; C and F, cystidia; D, microbinding hyphae; E, subicular hyphae; H, hyphidia. A-E from L. Ryvardeen 32987 (ARIZ); F-I from L. Ryvardeen 72845, DOAM 138851 (DAOM).

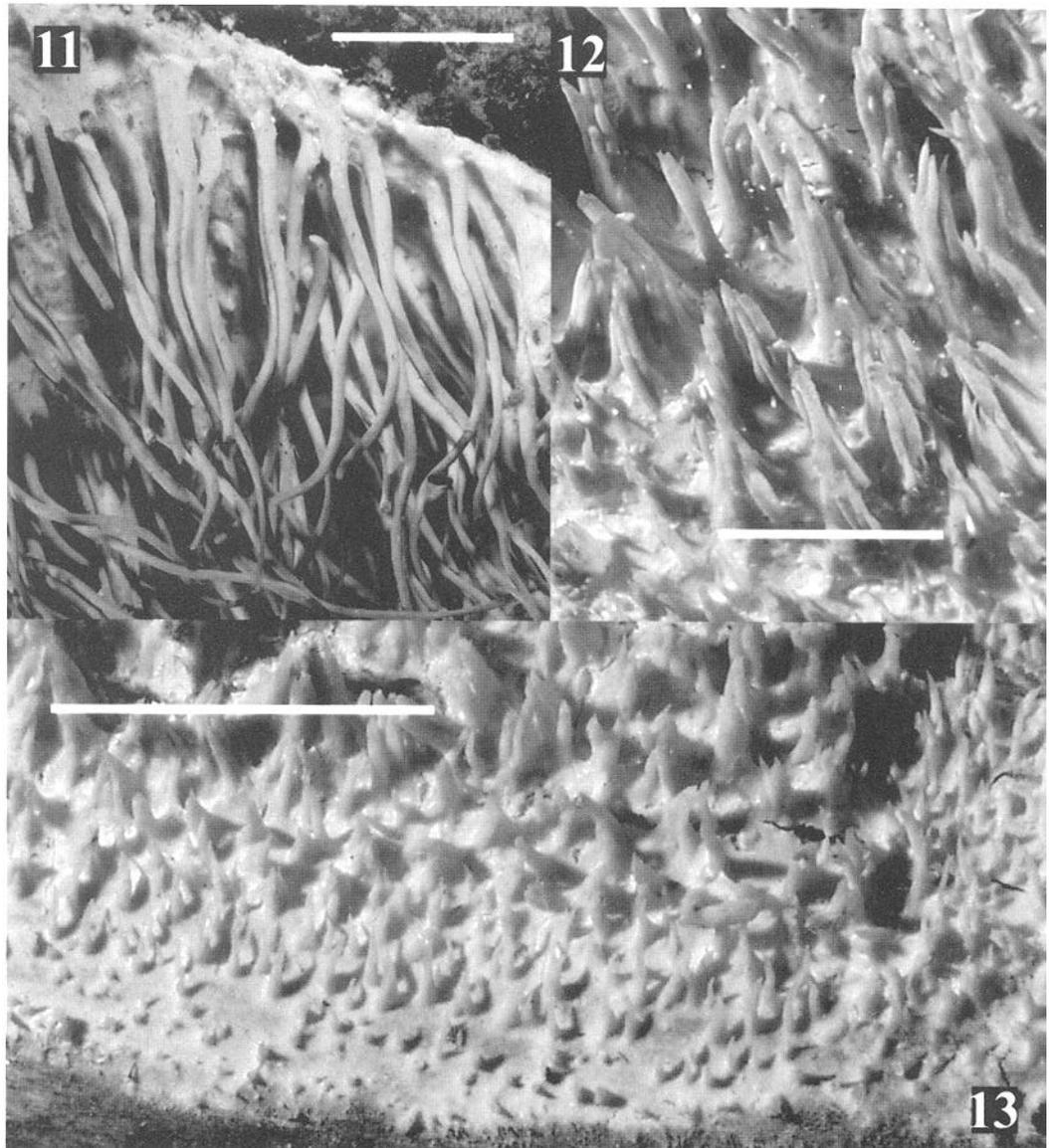


FIGURE 11. *Radulodon cirrhatinus*. Basidiome close-up of spines. From *B. M. Spooner 295 (K)*. Bar = 5 mm.

FIGURE 12. *Radulodon erikssonii*. Basidiome close-up of clumping spines. From *E. Martini 1547 (GB)*. Bar = 5 mm.

FIGURE 13. *Radulodon erikssonii*. Basidiome showing margin and developing spines. From *V. Kujala, GB 9786 (GB)*. Bar = 5 mm.

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