AN ALPHA-TAXONOMIC STUDY OF *HYDNELLUM* AND *SARCODON* FOR NORTHERN CALIFORNIA

by

Wilfred A. Franklin

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

December, 1999

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We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Master of Arts.

Approved by the Master's Thesis Committee:

David L. Largent, Major Professor	2 Dec 1999 Date
William L. Bigg, Committee Member	Dec 2, 99 Date
Frank J. Shaughnessy, Committee Member	Dec 2, '99 Date
Jacob P. Varkey, Committee Member	Dec. 2, 1999 Date
Milton J. Boyd, Graduate Coordinator	2 Dec 99 Date
Ronald A. Fritzsche Dean for Research and Graduate Studies	20 Dec 1999 Date

Abstract

Presently, there is no comprehensive study of the species of *Hydnellum* and *Sarcodon* found in California. Previous systematic studies in North America have focused on morphological characters such as color, surface features, spore size and spore ornamentation. This study set out to test the effectiveness of previous classification systems and species concepts to delineate California species, as well as develop a monographic work specific to northern California. One hundred ninety one fresh and herbarium specimens collected in California were characterized by traits obtained from the literature, in addition to new characters developed in this study. Keys and descriptions of Harrison (1961, 1964, 1968, 1971, 1972,1973), Hall (1968), Hall and Stuntz (1971, 1972a, 1972b), and Baird (1986a) were then used to identify taxa based on morphological and anatomical characters. Prior species concepts based primarily on color, pileal surface, spore size and spore ornamentation were effective at identifying most species. Thirteen taxa of *Hydnellum* and eleven taxa of *Sarcodon* have been identified and described in this study and a dichotomous key to these taxa is included. Three of these thirteen *Hydnellum* taxa (*H. geogenium, H. regium and H. subzonatum*) are reported for the first time as occurring in California and one previously undescribed taxa of *Hydnellum* is presented and preliminarily referenced as *H.* WAF131. The systematics of this study differ from the previous studies in North America by emphasizing the presence of swollen and inflated hyphae in members of the genus *Sarcodon* as a character separating it from the genus *Hydnellum*. In addition, spore ornamentation was partitioned into four categories to reflect the diversity observed in taxa of California.

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Introduction

Hydnellum and *Sarcodon* are two closely related genera within *Thelephoraceae* (Basidiomycota) that produce spores born on positively geotropic spines and have a stipitate basidiome (Donk, 1956). Five genera, *Auriscalpium, Bankera, Hericium, Phellodon*, and *Hydnum* also have basidiomes with spines and a stipe. *Hydnellum* and *Sarcodon* are easily differentiated from these five genera on the basis of brown spores that have tuberculate or nodose ornamentation. *Hydnellum* is further characterized by an indeterminate growth habit, a tough or leathery context consistency and basidiomes that often contain thick-walled hyphae. *Sarcodon* is delineated by a determinate growth habit, a fleshy or brittle context consistency and basidiomes that are composed of thin-walled hyphae (Harrison, 1973).

In North America fifty taxa of the genera *Hydnellum* and *Sarcodon* have been reported. Several researchers studying North American, tropical, and European type specimens concluded that many North American species were synonymous with previously described taxa therefore, the actual number of distinct species which occur in North America has, as yet, not been determined (Baird, 1986b).

Previous studies covering *Hydnellum* and *Sarcodon* in the eastern United States were conducted by Banker (1906, 1913 a,b,c), Coker (1919, 1926, 1927, 1939, 1942), Coker and Beers (1951) and Baird (1986a). Studies encompassing western Washington were conducted by Lanphere (1936), Hall (1968), and Hall and Stuntz (1971, 1972a,b). Miller and Bolye (1942) covered Iowa, and Harrison (1961, 1964, 1968, 1971, 1972,1973) included Mid-western regions of the United State and Canada.

A comprehensive study involving the species of *Hydnellum* and *Sarcodon* occurring in California has not been published. However, collections of these fungi exist in several herbaria. The collections of H. D. Thiers in the San Francisco State University Fungal Herbarium (SAFU) date from 1958 and represent central and northern California. The collections of D. L Largent in the Humboldt State University Fungal Herbarium (HSC) date from 1968 and represent north central and northwestern California. In addition, the University of California at Berkeley collections (UC) dates from1938 and represents extensive work for all of California. According to these sources, fourteen taxa of the genus *Hydnellum,* and sixteen taxa of *Sarcodon* have been reported collected in California, (Table 1, original placement, p 13).

Agerer (1991, 1993) identified the two worldwide species *Hydnellum peckii* and *Sarcodon imbricatus* as ectomycorrhizal. To date, this symbiotic relationship has not been proven definitively in any other members of these genera.

The objective of this work is to provide a taxonomic study of the species of *Hydnellum* and *Sarcodon* that occur in northern California. In the process of completing this objective the following question will be answered; can the set of morphological and anatomical features used by previous investigators be used to identify and differentiate the species of *Hydnellum* and *Sarcodon* in northern California. Additionally, a classification system appropriate for northern California will be developed, which includes detailed descriptions of the species with discussions on similar taxa and a dichotomous key to aid in the identification of the taxa.

Methods and Materials

Taxonomic Analysis:

Over the course of three years (1996-1999) specimens were collected from Humboldt, Del Norte, Siskiyou, Mendocino and Trinity counties. I collected in three general topographic areas, coastal, inland and montane forests. Coastal forests were predominately composed of *Picea sitchensis* (Bong.) Carrière, *Tsuga heterophylla* (Raf.) Sarg. and *Sequoia sempervirens* (D. Don) Endl., inland forests were dominated by *Pseudotsuga menziesii* (Mirbel) Franco, *Sequoia sempervirens*, *Lithocarpus densiflora* (Hool. & Arn.) Rehder and *Quercus*, and montane regions were composed of *Abies* and *Pinus*, with *Alnus*, *Salix* and *Acer* in riparian habitats. For each collection I reported as associates all trees visible from the location of the basidiome.

In addition, herbarium specimens from Humboldt State University Fungal Herbarium (HSC), San Francisco State University Fungal Herbarium (SAFU), and the University of California at Berkeley collection (UC) were studied. Specimens observed for each taxon were listed using collectors abbreviations (when available), accession number, and the herbarium. The collector's abbreviations are: DLL (David L. Largent), DED (Dennis E. Desjardin), HDT (Harry D. Thiers) and WAF (Wilfred A. Franklin). In the field, specimens from as many developmental stages as possible were removed and wrapped in aluminum foil or wax paper and notes were taken on habit and habitat. Upon returning from the field, studies of the macromorphologocial features were recorded on a standardized sheet (See appendix A). Additionally, color changes from a 3% potassium hydroxide (KOH) spot test was noted for the context and pellis

tissues of the pileus and stipe. This test was performed on fresh tissue unless otherwise noted in descriptions. Specimens not immediately examined were stored at 5°C in a refrigerator until descriptions were made. For each collection, one mature specimen was prepared to obtain a spore print by removing the pileus from the apex of the stipe, after which the pileus was placed spines down on white paper. The pileus and paper were wrapped in aluminum foil and the package was stored at 5°C for 24 hours or longer until a solid spore deposit was obtained. The remaining samples were dried at 40°C for 24 hours or until no moisture remained in the sample. When dry, specimens were stored in wax paper until micromorphological studies could be recorded.

Color designations were determined from the color standard by Kornerup & Wanscher (1989). Two numbers and a letter (e.g. 7C8) identified color notations. The first number corresponds to the page on which the plate is found, the letter denotes the column of the plate and the second number indicates the row. The corresponding common names were obtained from the charts located in the back of the color standard. In addition, color notations delineated by single quotation marks (i.e., 'Cinnamon Brown') are taken from Ridgeway (1912).

To study micromorphology, dried samples were rehydrated in 70% ethanol for approximately 30 seconds followed by a soaking in water for 1 minute or until thoroughly hydrated. Cross and longitudinal sections of the pileus, stipe and mature spines were mounted in KOH and examined; the results were recorded onto a standardized sheet (See appendix B). Bright-field light microscopy, which was used to examine sporocarps, was conducted with a Zeiss Standard 16 binocular compound

microscope. Line drawings were made with the aid of a Ziess Camera Lucida, model 47 46 05.

The results of all studies of the macro- and micromorphology of all specimens of the same taxa were organized into a single description.

Characters and Character States

Macromorphological Features

The macroscopic features analyzed included: pileus size, shape, surface features and color, pileal context structure, color, taste and odor; stipe size, shape, surface features and color, stipe context structure and color; spine size and color; pileal and stipe reactions with KOH application; spore deposit color. The following abbreviations are used in the discussion of macromorphological characters presented in the species descriptions: M = mean of all collections.

Pileus size was measured in millimeters on fresh specimens or taken from notes provided with herbarium specimens. If no fresh specimens were observed and no notes were provided, pileus size was reported from previous literature sources and differentiated in the descriptions by quotation marks. In specimens that had a fused or concrescent growth habit and the number of basidiomes that were fused together could not be determined, the entire concrescent mass was measured as a single pileus.

With one exception, pileus shape was classified using the standard categories convex, plane, subdepressed, infundibuliform, spathulate, flabellate and rosette (Largent, 1986). The term "rosette" was taken from Harrison (1964) and represents the complex tiers of overlapping pileoli developed by some taxa of *Hydnellum*.

Pileus surface features were classified as glabrous to finely pubescent, areolate to rimose cracked, fibrillose to matted-fibrillose, squamulose, reflexed scaly, wrinkled, scrobiculate, colliculose, tomentose and cottony/wooly (Coker & Beers, 1951; Harrison, 1964; Hall & Stuntz, 1972a, 1972b; Largent, 1986). Pileus color was recorded for young and mature tissue, as well as for the different developmental stages, if several were present in a single collection.

The structure of the pileal context was divided into the three following categories: layered, banded and mottled. A layered context had two distinct periclinal layers and was recorded as duplex. If only one homogenous, non-layered tissue was observed, it was recorded as not duplex (Hall & Stuntz, 1972a, 1972b; Maas Geesteranus, 1975). A banded context had anticlinal dark bands and was recorded as zonate, or azonate if no banding was present (Harrison, 1964; Hall & Stuntz, 1972a; Maas Geesteranus, 1975). A mottled context had small pockets of differently colored tissue scattered throughout and was recorded as possessing mottling or not (Coker & Beers, 1951; Hall & Stuntz, 1972a, 1972b; Maas Geesteranus, 1975). Pileal context color was recorded and coded in the same method as surface color.

The taste and odor of the pileus was recorded on fresh specimens or taken from notes provided with herbarium specimens. If no fresh specimens were observed and no notes were provided, these features were reported from previous literature sources and differentiated in the descriptions by quotation marks.

Stipe and spine features followed conventional terminology (Largent, 1986) or as defined above. The KOH spot test was recorded for pileal and stipe exterior surfaces, as well as the freshly exposed context. The reaction was observed for up to a minute, as

no further changes occur after this time period. The reactions reported are on fresh material unless otherwise noted in species descriptions. A negative reaction was recorded if no color change occurred while a positive reaction was reported as olive, dark green, red then quickly changing to dark green, or yellow. Spore deposit color was recorded as in surface color described above.

Micromorphological Features

Microscopic features observed included: spore length, width, shape, and ornamentation; basidia length, width, and shape; pileipellis and pileus tramal organization, hyphal width and thickness of cell walls; stipitipellis and stipe tramal organization, hyphal width and thickness of cell walls; presence of clamp connections in all tissues. The following abbreviations are used in the discussion of micromorphological characters presented in the species descriptions: M = mean of all collections, Q^m = mean spore length/width ratio. Q = range of spore length/width ratio, N(r) where N = number of collections studied and (r) = the minimum to maximum number of objects measured per collection.

All measurements for spores, basidia, and hyphae are recorded in micrometers (μm). Spore measurements included spore ornamentation. Spore shape was recorded as subglobose to elliptical or elliptical to subcylindric. Basidia shape was divided into three standard character states: cylindrical, subclavate and clavate (Figs. 9-11, p 11) and pellis and tramal hyphae of both the pileus and stipe were characterized as interwoven, highly tangled organization or subparallel, moderately tangled organization.

Spore ornamentation was classified into the following four character states adapted from Largent and Watling (1977): irregularly tuberculate, nodulose, nodose and tuberculate. Irregularly tuberculate was characterized by 9-13, small, rounded, often bifurcating or otherwise irregularly shaped warts per circumference of spore as seen in silhouette from light microscopy (Figs. 1-2, p 10). A range of 7-13 small, rounded warts per circumference of spore characterized nodulose spores (Figs. 3-4, p 10). Nodose spores had 4-6 large, broadly rounded warts per circumference (Figs. 5-6, p 10). Tuberculate was defined as having 5-9 large, angular warts per circumference of spore (Figs. 7-8, p 10).

The hyphal system was characterized as monomitic (Maas Geesteranus 1962, 1963, & 1975). However, the generative hyphae could be thin or thick-walled, swollen or not swollen, inflated or not inflated (Figs. 12-15, p 12-13). Thin-walled hyphae occurred alone or in combination with thick-walled hyphae and each type was characterized as swollen, inflated or simple (not swollen and not inflated).

Hyphal pigmentation is cytoplasmic in species of both *Hydnellum* and *Sarcodon* (Maas Geesteranus, 1962, 1963, & 1975). Granular encrusted pigmentation that dissolves in 3% KOH has been noted in dark violet to blackish blue tissues (Harrison, 1964). Presence of clamp connections in the pellis and tramal tissues were recorded for each collection.

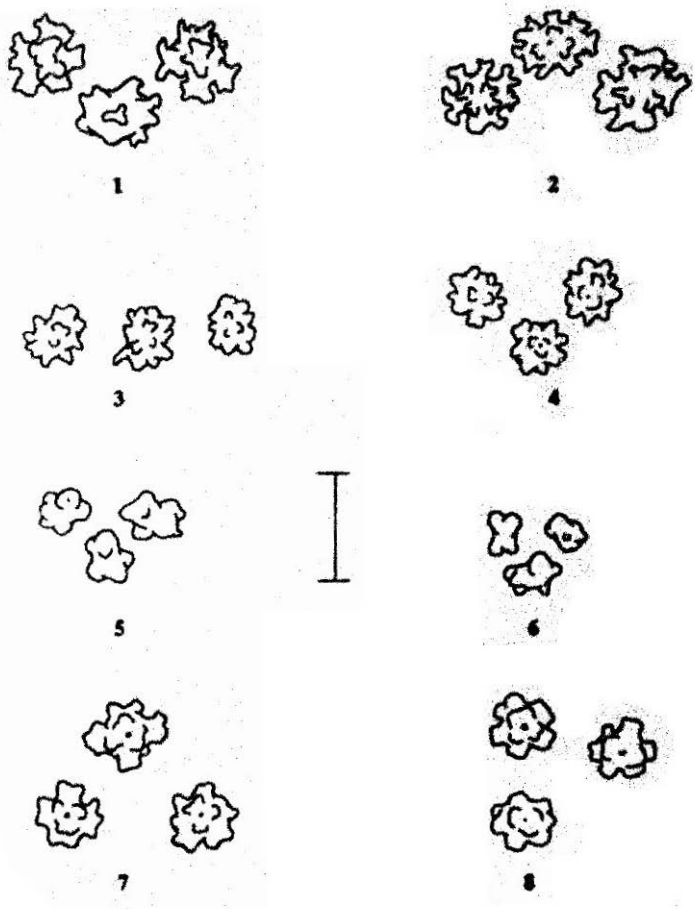


Plate 1

Figures 1-3: Irregularly tuberculate spores. 1: *Sarcodon ustale* (WAF153). 2: *Hydnellum aurantiacum* (HDT 9616). Figs. 3-4: Nodulose spores. 3: *Hydnellum caeruleum* (HDT 14124). 4: *Sarcodon martioflavus* (HDT 36304). Figs. 5-6: Nodose spores. 5: *Sarcodon stereosarcinon* (HDT 17651). 6: *Hydnellum suaveolens* (WAF140). Figs. 7-8: Tuberculate spores. 7: *Sarcodon imbricatus* (HDT 52780). 8: *Hydnellum regium* (WAF135). Scale = 10 µm.

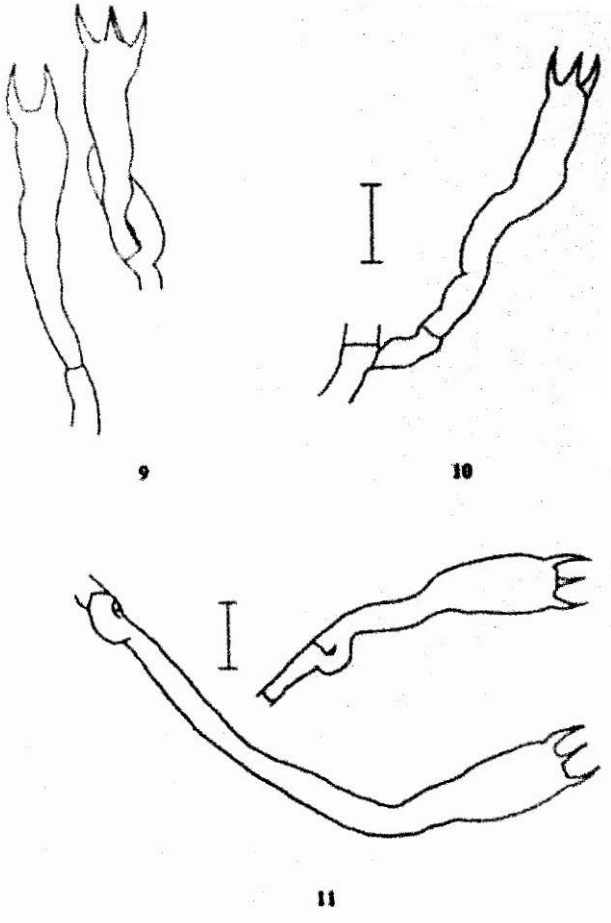
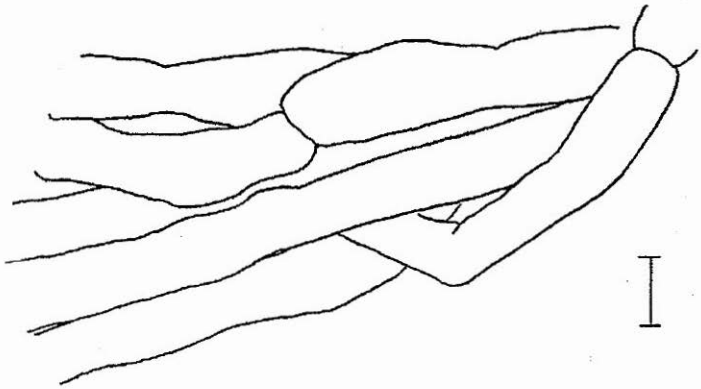


Plate 2

Figures 9-10: *Hydnellum aurantile* (WAF218), 9. subclavate basidia. 10. cylindrical basidium. Fig. 11: *Sarcodon imbricatus* (WAF113), clavate basidia. Scale = 10 µm.



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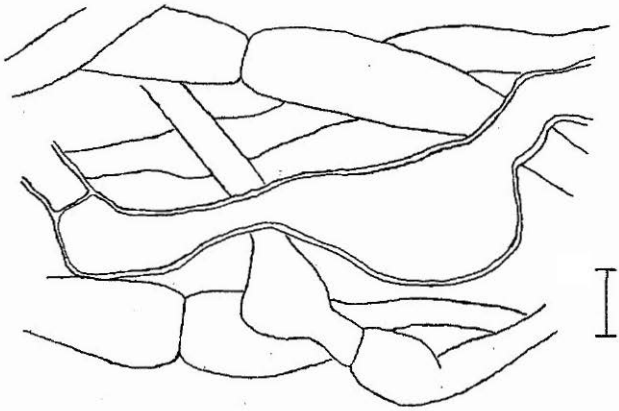

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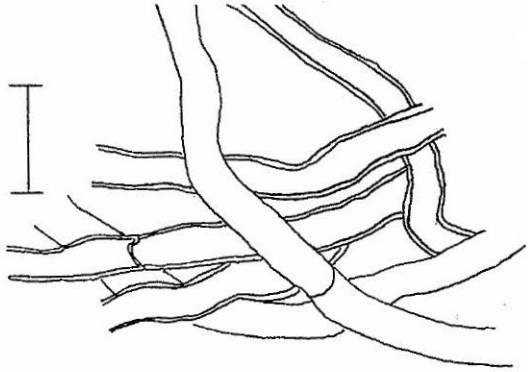
Plate 3

Figure 12: *Sarcodon leucopus* (HDT 52820), swollen hyphae. Figure 13: *Sarcodon stereosarcinon* (WAF190), inflated hyphae. Scale = 10 μm.



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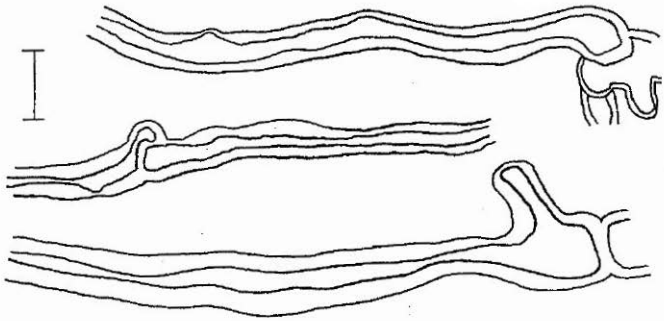

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Plate 4

Figure 14: *Hydnellum scrobiculatum var. scrobiculatum* (WAF176), interwoven simple thin- and thick-walled hyphae. Figure 15: *Hydnellum cyanopodium* (WAF141), thick-walled hyphae of stipe trama. Scale = 10 μm.

Results

Prior to this study, fourteen species of *Hydnellum* and sixteen species of *Sarcodon* were reported for California, Table 1, p13. In the course of this study, four previously unreported taxa of *Hydnellum* were found and identified, eight taxa of *Hydnellum* and *Sarcodon* from herbarium collections are believed to be misidentified and four taxa have been subsequently placed as synonyms of previously published taxa, Table 1. Additional comments on misidentified and conspecific taxa are presented in the remark section of the species descriptions. The synonymy and misidentification reduces the final list of species known to occur in California to thirteen taxa of *Hydnellum* and eleven taxa of *Sarcodon*, Table 2.

TABLE 1: Species of *Hydnellum* and *Sarcodon* reported for California.

ORIGINAL PLACEMENT	PROPOSED PLACEMENT
Hydnellum aurantiacum (Batsch) Karst.	No Change.
H. aurantile. (Britz.) Mass G.	No Change.
H. caeruleum (Hornem. ex Pers.) Karst.	No Change.
H. complectipes var. complectipes Hall and Stuntz.	*H. aurantile*. (Britz.) Maas G. (See Remarks under *H. aurantile*)
H. conigenum Peck.	*H. aurantiacum* (Batsch) Karst. (See Remarks under *H. aurantiacum*)
	H. aurantile. (Britz.) Maas G. (See Remarks under *H. aurantile*)
H. cyanellum Harrison.	*H. cyanopodium* Harrison. (See Remarks under *H. cyanopodium*)
H. cyanopodium Harrison.	No Change.
H. diabolus Banker.	*H. peckii* Banker. (syn: Maas G., 1975)
H. peckii Banker.	No Change.

TABLE 1: CONTINUED

ORIGINAL PLACEMENT	PROPOSED PLACEMENT
H. scrobiculatum var. *scrobiculatum* (Fr) Karst.	No Change.
H. scrobiculatum var. *zonatum* (Batsch ex Fr.) Harrison.	No Change.
H. suaveolens Scopoli. (Scopoli ex Fr.) Karst.	No Change.
H. subsuccosum Harrison.	*H. scrobiculatum* var. *scrobiculatum* (Fr) Karst. (See Remarks under *H. scrobiculatum* var. *scrobiculatum*)
H. zonatum Karst.	*H. scrobiculatum* var. *zonatum* (Batsch ex Fr.) Harrison. (syn: Harrison, 1964)
Sarcodon calvatus Harrison.	*S. leucopus* (Pers.) Maas G. & Nannf. (See Remarks under *S. leucopus*)
S. crassus Harrison.	*S. leucopus* (Pers.) Maas G. & Nannf. (See Remarks under *S. leucopus*)
S. fuligineo-violaceus (Kalchbr. ex Fr.) Pat.	*S. fuscoindicus* Harrison. (See Remarks under *S. fuscoindicus*)
S. fumosus Banker.	*S. atroviridis* (Morgan) Banker. (syn: Baird, 1986b)
S. fuscoindicus Harrison.	No Change
S. glaucopus Maas G. & Nannf.	No Change
S. imbricatus (L. ex Fr.) P. Karst.	No Change
S. laevigatus Fr.	*S. leucopus* (Pers.) Maas G. & Nannf. (syn: Maas G. & Nannf., 1969)
S. leucopus (Pers.) Maas G. & Nannf.	No Change
S. martioflavus Snell and Dick.	No Change
S. rimosus Harrison.	No Change
S. scabrosus (Fr.) Karst.	No Change
S. stereosarcinon Wehmayer.	No Change
S. subfellus Harrison.	*S. leucopus* (Pers.) Maas G. & Nannf. (See Remarks under *S. leucopus*)
S. subincarnatus Harrison.	No Change
S. ustale Harrison.	No Change

TABLE 2: Species of *Hydnellum* and *Sarcodon* reported for California as circumscribed in this study. New reports for California are in bold type.

Hydnellum aurantiacum (Batsch) Karst.
H. aurantile. (Britz.) Maas G.
H. caeruleum (Hornem. ex Pers.) Karst.
H. cyanopodium Harrison.
H. peckii Banker.
***H. geogenium* (Fr.) Banker.**
***H. regium*. Harrison.**
H. scrobiculatum var. *scrobiculatum* (Fr.) Karst.
H. scrobiculatum var. *zonatum* forma *zonatum* (Fr.) Harrison.
H. scrobiculatum var. *zonatum* forma *parvum* (Banker) Hall & Stuntz.
***Hydnellum* WAF131.**
H. suaveolens Scopoli. (Scopoli ex Fr.) Karst.
***H. subzonatum* Harrison.**
Sarcodon atroviridis (Morgan) Banker.
S. fuscoindicus Harrison.
S. glaucopus Maas G. & Nannf.
S. imbricatus (L. ex Fr.) P. Karst.
S. leucopus (Pers.) Maas G. & Nannf.
S. martioflavus Snell and Dick.
S. rimosus Harrison.
S. scabrosus (Fr.) Karst.
S. stereosarcinon Wehmayer.
S. subincarnatus Harrison.
S. ustale Harrison.

Key to Genera of Terrestrial Stipitate Tooth Fungi of North America.

1.) Spores smooth and white in mass.....*Hydnum*

1.) Spores distinctly ornamented and white or brown in mass.....2

2.) Spores echinulate and white in mass.....3

2.) Spores tuberculate, nodose, or nodulose and brown in mass 4

3.) Growth of basidiome determinate. Basidiome consistency fleshy to brittle .....*Bankera*

3.) Growth of basidiome indeterminate. Basidiome consistency tough, leathery or fibrous .....*Phellodon*

4.) Growth of basidiome determinate. Basidiome consistency fleshy to brittle. Width of tramal hyphae highly variable, 4.5 - 30 µm (mean ≥ 9.0 µm) .....***Sarcodon***

4.) Growth of basidiome indeterminate. Basidiome consistency tough to leathery. Width of tramal hyphae uniform, 2.5 – 10 µm (mean ≤ 5.5 µm) ....***Hydnellum***

Hydnellum P. Karst. Medd. Soc. Faun. Fl. Fenn. 5:41. 1879.

Synonym: *Calodon* P. Karst. Rev. Mycol. 3:19-21. 1881.

Hydnum trib. *Mesopus* sect. *Lignosi* Fr. Syst. Mycol. 1:506. 1821.

Type species: *Hydnum suaveolens* Scop. ex Fr.

Diagnostic characters: Growth of basidiome indeterminate. Context consistency tough to leathery. Width of tramal hyphae uniform, 2.5 – 10 µm (mean = 5.5 µm). Generative hyphae becoming thick-walled within older parts of pileus and stipe.

Macroscopic characters: Growth indeterminate; pileus 22 - 155 mm, turbinate when young, sub-depressed to deeply infundibuliform at maturity, rarely rosette; surface felty-tomentose, cottony or strigose, when young, matted-fibrillose, wrinkled scrobiculate or colliculose at maturity; color variable; context consistency tough to leathery, duplex or not, zonate or azonate, with mottling the context or not; color variable; taste and odor variable. Stipe central to eccentric; cylindrical or more often cylindrical but tapered and rooting at base, rarely bulbous at base, or stipe rudimentary; surface glabrous, cottony or matted; color variable; context consistency tough to leathery, typically duplex, zonate or azonate, with mottling the context or not; color often concolorous with pileal context. Spines decurrent, reduced on stipe, typically dense; color variable. KOH reaction variable. Spore deposit light brown (6-7D4).

Microscopic characters: Spores subglobose to elliptical; nodose, nodulose, tuberculate, or irregularly tuberculate. Basidia cylindrical, subclavate or clavate, size variable. Tramal hyphae uniform in width, typically 2.5 – 10 µm and less than 9.0 µm wide, mean width 5.5 µm, thick-walled hyphae common and interwoven with thin-walled hyphae. Pileipellis sub-parallel in young tissue, densely interwoven in age, often indistinguishable from trama, thick-walled hyphae rare. Stipitipellis loosely interwoven, becoming matted and dense in age, typically distinct from trama forming a duplex condition to stipe context, may or may not have thick-walled hyphae. Cytoplasmic

pigmentation in all tissue, incrusted pigmentation only in blackish blue to dark violet tissue.

Habit and habitat: Solitary, scattered or gregarious, some concrescent; terrestrial in coniferous, hardwood or mixed forests.

Key to species of *Hydnellum*

1.) Basidiome with all of the following features: 1.) composed of overlapping, irregularly spathulate or flabellate pileoli, 2.) pileoli grayish violet, and 3.) stipe orange white to light orange.....***H. regium***

1.) Basidiome not as above: composed of turbinate, plane, sub-depressed, or infundibuliform pileoli. Pileoli variously colored. Stipe variously colored.....2

2.) Mature basidiome with pale violet, grayish blue, dark blue, or dark violet pileus and/or stipe.....3

2.) Mature basidiome not as above, yellowish gray, yellowish brown, pale orange, reddish white, orange brown, brown, reddish brown or dark brown.....5

3.) Basidiome entirely pale blue, dull violet, dark blue or dark violet throughout pileus, stipe and context. Surface tomentose soon becoming scrobiculate, also with beads of yellowish and reddish liquid exudate. Purplish gray inclusions mottling the context .....***H. cyanopodium***

3.) Basidiome not blue or violet throughout pileus, stipe and context. Surface tomentose or cottony becoming matted-fibrillose, no liquid exudate present. No inclusions mottling the context.....4

4.) Young pileus whitish, whitish blue, mature pileus blackish blue developing a grayish brown sheen with age. Stipe light to deep orange. Context of pileus zonate, context of stipe orange and zonate. Odor mildly to distinctly farinaceous .....***H. caeruleum***

4.) Young pileus yellowish white to yellowish gray, mature pileus light brown to dark yellowish brown. Stipe grayish violet to dark blue. Context of pileus azonate or only weakly so over stipe, context of stipe dark violet and azonate. Odor distinct, sweetly pungent (=anisealdehyde) .....***H. suaveolens***

5.) Young growing margins of pileus bright yellow becoming dark brown in age. Young and mature surfaces of pileus stains yellow with 3% KOH.....***H. geogenium***

5.) Young margins of pileus whitish, reddish white, or pale orange, becoming grayish yellow, yellowish brown, reddish brown, orange brown, to dark brown in age. Mature surface of pileus stains olive, dark green or with a red flash quickly turning to dark green with 3% KOH.....6

6.) Color of pileus and stipe grayish yellow, yellowish brown or golden brown, darker in age. Pileus context distinctly duplex.....***H. WAF131***

6.) Color of pileus and stipe pale orange white, reddish white, orange brown, reddish brown, light brown, brown, or dark brown. Pileus context not duplex 7

7.) Basidiome pale orange white when young, becoming orange brown to dark brown with age 8

7.) Basidiome reddish white or light brown when young, becoming reddish brown or brown with age 9

8.) Spore mean length less than or equal to 6.0µm; spore ornamentation nodulose to tuberculate. Mean pileus width 5.1 cm (2.4 –7.9 cm). Context azonate .... ***H. aurantile***

8.) Spore mean length greater than 6.0µm; spore ornamentation tuberculate to irregularly tuberculate. Mean pileus width 11.4 cm (3.7-18.5 cm). Context zonate ..... ***H. aurantiacum***

9.) Young growing margin bright yellow, becoming dark brown in age. Surface of pileus stains bright sulfur yellow with 3% KOH..... ***H. geogenium***

9.) Young growing margin whitish or reddish white becoming light brown, brown or reddish brown in age. Surface of pileus negative with 3% KOH or staining olive, dark green, or with a red flash quickly turning to dark green 10

10.) Tramal hyphae of pileus and stipe without clamp connections 11

10.) Tramal hyphae of pileus and stipe with clamp connections.....13

11.) Conspicuous concentric zone lines abundant (equal to or greater than 3) on pileus surface. Pileus often abundantly dotted with small yellowish brown colored pustules conforming to zone lines. Mean pileus width less than or equal to 6.1 cm 12

11.) Concentric zone lines not present on pileus or inconspicuous and few (less than 3). Pileus without pustules or at most with only a few. Mean pileus width greater than 6.1 cm ..... ***H. scrobiculatum* var. *scrobiculatum***

12.) Mean pileus width 3.2 cm (3.0-4.1 cm). Basidiomes commonly concrescent and stipes commonly fused, at least at base .... ***H. scrobiculatum* var. *zonatum* forma *parvum***

12.) Mean pileus width 6.1 cm (3.0-11.1 cm). Basidiomes commonly concrescent, but stipes typically not fused .....

.....***H. scrobiculatum* var. *zonatum* forma *zonatum***

13.) Mean pileus width 7.7 cm (3.5-15.0 cm). Basidiomes typically solitary to scattered, reddish white when young, becoming reddish brown and commonly with prodigious red liquid exudate. Odor aromatic or sweet and hot as in cinnamon candy. Taste distinctly hot or peppery.....***H. peckii***

13.) Mean pileus width 2.5 cm (1.1-3.9 cm). Basidiomes typically concrescent, light brown when young, becoming brown and no exudate present. Odor none to mildly farinaceous. Taste none to mildly farinaceous.....***H. subzonatum***

Hydnellum aurantiacum (Batsch) Karst. Medd. Soc. Fauna Fl. Fenn. 5:41. 1879.

Plate 1, Figure 2.

Basionym: *Calodon aurantiacus* (Batsch) Fries. Syst. Mycol. 1: 403. 1821.

Synonyms: *Hydnum suberosum* var. *aurantiacum* Batsch. El. Fung. Cont. 2: 103. 1789.

Hydnum floriforme Schaef. Fung. Icon. 4: 97. 1774.

Hydnellum floriforme (Schaef.) Banker. Mem. Torr. Bot. Club 12: 159. 1906.

Pileus: 3.7 – 18.5 cm broad, M = 11.4 cm; turbinate to plane when young, sub-depressed to infundibuliform in age, often developing small to large pileoli; surface

matted-fibrillose, wrinkled, ridged, or colliculose; pale orange white (7A2-4) when young, orange brown (7-8A-B7-8) to dark brown (9F5-6) in age; context not duplex, zonate, without mottling, deep orange (6B8) to reddish orange (7B8), zone lines darker in age; taste and odor mildly farinaceous. Stipe: 2.3 – 8.4 x 1.3 – 6.0 cm, M = 5.9 x 3.4 cm; central to eccentric; cylindrical throughout or with bulbous base, occasionally with a tapering and rooting base; deep orange (6B8) when young maturing and bruising dark brown (8F8); context duplex, zonate, without mottling, concolorous with pileus context. Spines: decurrent, up to 8 mm long, pale orange white (5A2) at growing tips, maturing dark brown (9F5). KOH reaction: none to weak reactions on youngest tissue, olive on all other surfaces.

Spores: (4.7)5.7 – 9.0 x (3.9)4.8 – 7.6 µm, M = 7.0 x 5.8 µm, Q^m = 1.19, Q = 1.13 – 1.30, N(r) = 15(15-20); subglobose to elliptical; irregularly tuberculate to nodulose. Basidia: 30 - 65 x 6.0 - 10.0 µm, M = 45 x 7.6 µm, N(r) = 15(10-15), subclavate to clavate; 4-spored with sterigmata up to 6.0 µm. Pileipellis: hyphae 3.0 – 5.0 µm wide, M = 3.9 µm. Pileus trama: hyphae 3.4 – 5.8 µm wide, M = 4.5 µm, thick-walled hyphae present. Stipitipellis: hyphae 2.6 – 4.6 µm wide, M = 3.5 µm, either, thick and loosely interwovern or becoming matted and then thin and densely interwoven, thick-walled hyphae may be present. Stipe trama: hyphae 3.0 – 6.4 µm wide, M = 4.4 µm, thick-walled hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Single, scattered or gregarious; terrestrial in duff and humus; associated with *Picea sitchensis*, *Pseudotsuga menziesii* and mixed *Pseudotsuga menziesii* and *Lithocarpus densiflorus*; occurs predominately in coastal mountains into moderate

elevations of central California and inland in northern California; fruits September through December.

Materials studied:

Del Norte Co.: (WAF182); Humboldt Co.: (WAF154, 160, 173, 174, HDT 38282), DLL 1341, 3724, 5210, 7356, 7360, 7138, 7470, 7875, 11132; Mendocino Co.: (WAF217, HDT 9616, 9719, 14118, 54229, 35478), DLL 3440, 4245; Siskiyou Co.: (WAF148, HDT 39136, 46472); Trinity Co.: (DLL 8553).

Remarks:

Hydnellum aurantiacum can be identified by an orange to orange brown basidiome, a similarly colored context with distinct dark zone lines and large irregularly tuberculate to nodulose spores. It is the largest of the orange colored *Hydnellum* taxa. *Hydnellum caeruleum* can be as large, but is orange only over its stipe and has a whitish blue, blackish blue to grayish blue pileus. A mature *H. aurantile* has a similar size to an immature specimen of *H. aurantiacum*, but the former has a context that does not develop distinct zone lines, a typically thinner flesh and it has spores that are smaller (M = 5.4 x 4.5 µm) and nodulose.

Hydnellum aurantiacum develops a variety of forms. Hall and Stuntz (1972b) described two varieties of *H. aurantiacum*, var. *colliculosum* and var. *bulbopodium*, characterized by pronounced radiating ridges on the pileus surface, which is evidently lacking in var. *aurantiacum*. Furthermore, var. *bulbopodium* has a thinner pileal flesh, more developed and imbricate pileoli and a stipe base abruptly widening and becoming bulbous; all of which may develop in the other varieties, but are not as pronounced (Hall & Stuntz 1972b, p577, p580). In collections of *H. aurantiacum* made during fall,

1996 and 1997, specimens of the same population exhibited a continuum of these features. The surface of the pilei were glabrous to ridged from agglutinated and collapsed tomentum and some small, rounded warts had spines developing, such that it could not be certain if the surface was colliculose or had small pileoli, or both. Moreover, the stipes varied from cylindrical with rooting bases to cylindrical with slightly bulbous bases, which seemed to depend on the condition of the soil and duff. If the basidiome developed around coarse woody or rocky debris the stipes tended to be rooting, and in thick needle-duff without obstructions they tended to be bulbous at the base. These trends are based only on casual observations made in the field. Nevertheless, the varieties described by Hall and Stuntz appear to be questionable. Formal synonymy awaits a study of the type collections.

The collection HDT54229 is an orange species of *Hydnellum* with spores 5.6 – 8.5 x 4.9 – 6.5 µm. It was reported as *H. conigenum*, but this species is described as growing on pinecones and has a pileus up to 2 cm broad. The collection HDT54229 was terrestrial and had a preserved pileus diameter over 6 cm. Based on the spore size, and macromorphological features of this specimen, I believe it is actually a *H. aurantiacum*.

Hydnellum aurantile (Britz.) Maas G., Persoonia I: 111. 1959.

Plate 2, Figure 9-10.

Synonym: *Hydnum aurantile* Britz., Hym. Sudbayern 8:14. 1891.

Pileus: 2.4 – 7.9 cm broad, M = 5.1 cm; plane when young, sub-depressed to infundibuliform or with imbricate pileoli in age; surface matted-fibrillose, wrinkled or ridged, occasionally with concentric zone lines; pale orange white (7A2-4) when young, orange brown (7-8A-B7-8) to dark brown (9F5-6) in age; context not duplex, azonate or only weakly zonate, no mottling, deep orange (6B8) to reddish orange (7B8), zone lines darker if present; taste and odor mildly farinaceous. Stipe: 1.3 – 3.7 x 0.4 – 1.2 cm, M = 2.4 x 0.7 cm, central to eccentric; terete, slightly tapering at base; deep orange (6B8) when young, maturing and bruising dark brown (8F8); context duplex, azonate, no mottling, concolorous with pileus trama. Spines: decurrent, up to 5 mm long; white to orange white (7A2) at growing tips, dark brown (9F6) at maturity. KOH reaction: none to weak reactions on youngest tissue, olive on all other surfaces.

Spores: (3.8)4.6 – 6.1(6.6) x 3.6 – 5.4 µm, M = 5.4 x 4.5 µm, Q^m = 1.19, Q = 1.15 – 1.24, N(r) = 8(15-20); subglobose to elliptical; nodulose. Basidia: 26 – 51 x 5 - 8 µm, M = 35 x 6.0 µm, N(r) = 8(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.0 µm. Pileipellis: hyphae 3.2 – 6.0 µm wide, M = 4.4 µm. Pileus trama: hyphae 3.5 – 5.9 µm wide, M = 4.5 µm, thick-walled hyphae present. Stipitipellis: absent or thin and then pigmented slightly darker than trama, hyphae 2.8 – 5.1 µm, M = 3.9 µm wide, thick-walled hyphae present. Stipe trama: hyphae 3.2 – 5.8 µm wide, M = 4.2 µm, thick-walled hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Single to scattered; terrestrial in duff and humus; associated with *Pseudotsuga menziesii* and mixed *Pseudotsuga menziesii* and *Lithocarpus densiflorus*; occurs

predominately in coastal mountains into moderate elevations of central California and inland in northern California; fruits September through December

Materials studied:

Humboldt Co.: (WAF163), DLL 1359, 7701; Mendocino Co.: (WAF218, 222, HDT 21767), Selva 25 (HSC); Trinity Co.: (WAF196, 201, 207, 208,) DLL 8552, DLL 9089.

Remarks:

Hydnellum aurantile can be recognized by an orange to orange brown basidiome, a similarly colored context without zone lines or with faint and poorly developed zone lines, and nodulose spores. It is the smallest of the orange-colored *Hydnellum* taxa. A discussion of the other orange colored species of *Hydnellum* can be found in the remark section of *H. aurantiacum*.

Hydnellum aurantile exhibits a gradient of pileus forms. At one extreme, the pileus is sub-depressed to infundibuliform. At the other, it develops a complicated rosette of two to three overlapping or imbricate pileoli. However, there are intermediate forms with one, dominate pileus and only rudimentary pileoli. *Hydnellum complectipes* is an orange to orange brown taxon that has an imbricate pileus, has larger spores (6.0-7.0 X 5.0-6.0 µm) and a zoned context. It is distinguished from *Hydnellum aurantiacum* by the mass of fused pilei arising from its many, fused stipes.

The collection DLL8552 was reported as *Hydnellum complectipes* var. *complectipes*, but has spores outside the range (4.5-5.5 X 3.8-4.4 µm) of that species and does not have fused stipes. *Hydnellum complectipes* could represent an intermediate between the small, thin-fleshed *H. aurantile* with small spores and the larger, thick-

fleshed *H. aurantiacum* with larger spores. Until more specimens of these taxa can be studied, I believe DLL 8552 is more appropriately placed in the species *H. aurantile*.

Specimen SFSU 2176, reported as *H. conigenum*, I believe is misidentified. *Hydnellum conigenum* is small and orange; however, it is described as growing on pinecones and has a pileus up to 2 cm broad. The collection SFSU 2176 was noted as terrestrial and had a preserved pileus diameter of nearly 5 cm. I believe *H. aurantile* to be the proper placement of SFSU 2176 on account of the microscopic features are consistent and it visually looks identical to preserved specimens of that taxon.

Hydnellum caeruleum (Hornem. ex Pers.) Karst., Medd. Soc. Fauna Fl. Fenn. 5:41. 1879.

Plate 1, Figure 3.

Basionym: *Hydnum caeruleum* Hornemann. Fl. Dan. VIII, Fasc. 23:7 1808.

Synonyms: *Hydnum suaveolens* var. *caeruleum* Fries. Syst. Mycol. I: 402. 1821.

Hydnum cyaneotinctum Peck. Bull. Torr. Bot. Club 30: 98. 1903.

Hydnellum cyaneotinctum (Peck) Banker. Mem. Torr. Bot. Club 12: 164. 1906.

Pileus: 8.0 – 15.5 cm broad, M = 13.4 cm; turbinate when young, plane or sub-depressed in age; surface tomentose to cottony when young, matted-fibrillose and colliculose in age; young growth white soon becoming grayish blue (19-20B2-4), developing a grayish brown (7-8D-E3) sheen in age, bruising blackish blue; context not

duplex, zonate, without mottling, grayish blue (19-20B2-4) to dark blue (19E4) at margins becoming grayish brown (8D-E3) over stipe; taste and odor mildly to distinctly farinaceous. Stipe: 4.5 – 6.5 x 1.5 – 3.9 cm, M = 5.2 x 2.9 cm; central to eccentric; cylindrical to contorted and irregular; light orange (5-6A2-4) when young, light orange to deep orange (7-8A-B8) in age; context duplex, zonate, without mottling, concolorous with surface. Spines: decurrent, up to 7 mm long; grayish red (8B4), grayish brown (8D-E3) to dark brown (9F4). KOH reaction: green on pileus, olive on stipe.

Spores: 4.2 – 6.7 x 3.0 –5.6 µm, M = 5.4 x 4.1µm, Q^m = 1.31, Q = 1.21 – 1.42, N(r) = 12(15-20); elliptical; nodulose. Basidia: 25 – 55 x 4.0 – 7.5 µm, M = 37.3 x 5.7 µm, N(r) = 12(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.0 µm. Pileipellis: hyphae 3.2 – 5.4 µm wide, M = 4.2 µm. Pileus trama: hyphae 3.6 – 5.9 µm wide, M = 4.6 µm, thick-walled hyphae present. Stipitipellis: hyphae 3.1 – 4.8 µm wide, M = 3.8 µm, thick-walled hyphae present. Stipe trama: hyphae 3.5 – 8.0 µm wide, M = 4.9 µm, thick-walled hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Single, scattered or gregarious; terrestrial in duff and humus; associated with *Picea sitchensis*, *Tsuga heterophylla*, *Sequoia sempervirens*, *Pseudotsuga menziesii*, *Pinus* and *Quercus*; occurs in mixed *Sequoia sempervirens*/*Picea sitchensis* forests and mixed *Pseudotsuga menziesii*/*Pinus*/*Quercus* woodlands: fruits September through December.

Materials studied:

Humboldt Co.: (WAF180, 205, HSS 3697), DD 17, 276 (HSC), DLL 3655, 8012, 8084; Mendocino Co.: (WAF221, HDT 11099, 14124, 38397); San Mateo Co.:

(Keller 728(SFSU), V. Pando(SFSU), HDT 35395); Sierra Co.: (M.Boom(SFSU)), Sonoma Co.: (HDT 30784), DLL 5549.

Remarks:

Hydnellum caeruleum can be recognized by its bluish pileus, orange stipe and nodulose spores. At times *H. caeruleum* has a blue pileus reminiscent of *H. cyanopodium*, but the latter species typically produces liquid exudate on its pileus, has a grayish violet to dark blue stipe and nodose spores. In addition, *H. caeruleum* does not have clamp connections, where as *H. cyanopodium* has large, abundant clamp connections.

Hydnellum cyanopodium K. Harrison. Can. Jour. Bot. 42:1221. 1964.

Plate 4, Figure 15.

Pileus: 4.7 – 19.0 cm broad, M = 10 cm; turbinate when young, remaining so or becoming plane to sub-depressed in age; surface tomentose when young, soon becoming scrobiculate, and developing abundant golden to red, watery exudate; pale violet (18-19A3) when young, grayish violet (19E3) to dark blue (19E4) in age; context blackish blue (19F6) with purplish gray (14D-E2) mottling, not duplex, azonate; taste pungent to acerbic; odor uniquely sweet and pungent (=anisealdehyde). Stipe: 1.5 – 3.8 x 0.6 – 2.3 cm, M = 3.1 x 1.2 cm; central to eccentric; irregularly cylindrical and contorted; grayish violet (19E3), or dark blue (19E4); context concolorous with pileus context, not duplex, azonate, with mottling as in pileus context. Spines: decurrent, up to 5 mm long; pale violet (18-19A3) at growing tips, dark blue (19E4) to blackish blue (19F6). KOH: green on all surfaces.

Spores: 3.6 – 6.0 x 2.8 – 5.3 µm, M = 4.8 x 4.1 µm, Q^m = 1.17, Q = 1.14 – 1.21, N(r) = 7(15-20); subglobose to elliptical; nodose. Basidia: 20 – 52 x 4 - 7 µm, M = 36.0 x 5.0 µm, N(r) = 7(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 3.7 – 6.2 µm wide, M = 4.7 µm. Pileus trama: hyphae 3.1 – 6.6 µm, M = 4.7 µm in diameter, thick-walled hyphae present. Stipitipellis: hyphae 2.6 – 5.5 µm wide, M = 4.0 µm, thick-walled hyphae rare. Stipe trama: hyphae 3.5 – 25.0 µm wide, M = 4.8 µm, thick-walled hyphae abundant. Clamps: present at base of basidia and abundant on all hyphae throughout basidiome.

Habit, habitat, distribution and fruiting season:

Single to scattered; terrestrial in duff and humus; common and abundant associated with *Picea sitchensis* and *Tsuga heterophylla*; occurs predominately in coastal northern California; fruits (June) July through December.

Materials studied:

Humboldt Co.: (WAF100, 106, 141, 146, 166, 185, HDT 49470). DD 20, 289 (HSC), DLL, 1357, 5441.

Remarks:

Hydnellum cyanopodium can be recognized by its violet and blue colors, turbinate to sub-depressed pileus that exudes abundant golden to red watery exudate that beads up in the highly pitted surface, concolorous stipe, sweet, pungent odor and small, nodose spores. *Hydnellum suaveolens*, which smells similarly and has a violet stipe, can be separated from *H. cyanopodium* by the white to pale brown pileus of the former, which contrasts to the violet to dark blue pileus of the latter. *Hydnellum scleropodium* and *H. cruentum*, two taxa from eastern and mid-western North America,

are reported to have the same distinct odor. *Hydnellum scleropodium* is scrobiculate with red liquid exudate, "fawn color" to "wood brown", with a bluish tinge in the context next to the teeth and has a "slate gray" dried context mottled with "vinaceous fawn". It can be recognized by a very large stipe (3-9 X 2-4 cm), which has a rooting base that is swollen and hard, like a sclerotium (Harrison, 1964). *Hydnellum cruentum* is pale brown to darker, scrobiculate, producing red juice, and having a pale gray context with tints of lilac that has bluish zone lines in the stipe (Harrison, 1961). It can be distinguished from *H. cyanopodium* and *H. suaveolens* by the surface colors of the pileus and from *H. scleropodium* by the lack of sclerotium-like stipe.

The sweetly pungent odor of *H. cyanopodium*, *H. suaveolens*, *H. scleropodium* and *H. cruentum* is unique and has been called "medicinal" by Harrison (1961). Wood et al. (1988) identified anisealdehyde as the chemical responsible for the odor in *H. suaveolens*. Since *H. cyanopodium*, *H. suaveolens*, *H. scleropodium* and *H. cruentum* all have nodose spores in the 4-5 X 3.5-4.5 µm range, blue and violet hues somewhere in the basidiome and the same unique odor, it seems they form a taxonomically distinct group.

At times *H. caeruleum* has a blue pileus reminiscent of *H. cyanopodium*. A discussion of the differences of these two species can be found in the remark section of *H. caeruleum*.

Collection DD 289, reported as *Hydnellum cyanellum*, is of questionable identity. Harrison (1964) describes *H. cyanellum* as a violet-colored, fleshy and brittle species, with a smooth to appressed-scaly pileus surface and without thick-walled hyphae. The species *H. cyanopodium* is violet-colored, but has a tough and pliable

texture, a distinctly scrobiculate pileus surface and has abundant thick-walled hyphae. The specimen of collection DD 289 has a scrobiculate pileus surface, abundant thick-walled hyphae and is otherwise consistent with *H. cyanopodium*. Therefore, I believe *H. cyanopodium* to be the proper placement of DD 289.

Hydnellum geogenium (Fr.) Banker. Mycologia 5:204. 1913.

Synonym: *Hydnum geogenium* Fries. Vet. Akad. Förh. 131. 1852.

Pileus: 3.0 – 10.0(25) cm broad, M = 6.0 cm; concrescent and then forming a pileal mass up to 25 cm with the individual pilei up to 7.0 cm; plane or sub-depressed; surface tomentose to cottony when young, then matted-fibrillose in age; young growth yellow (1-2A3-4) soon becoming violet brown (11F4-5) to dark brown (9F5-6); context not duplex, azonate, concolorous; taste and odor none to mildly farinaceous. Stipe: up to 3.0 cm; often lacking, if present then poorly developed and fused, branched and rooting; dark brown (9F5-6); context not duplex, azonate, no mottling, concolorous with pileus. Spines: decurrent, up to 3 mm long; young growth yellow (1-2A3-4) soon becoming violet brown (11F4-5) to dark brown (9F5-6). KOH reaction: yellow on all surfaces.

Spores: 4.5 – 5.7 x 3.5 – 5.7 µm, M = 5.2 x 4.6µm, Q^m = 1.13, Q = 1.08 – 1.31, N(r) = 1(25); subglobose; nodose to tuberculate. Basidia: 34 – 59 x 4.5 – 8.0 µm, M = 45.8 x 6.8 µm, N(r) = 1(15); subclavate to clavate; 4-spored with sterigmata up to 5.0 µm. Pileipellis: hyphae 2.8 – 5.0 µm wide, M = 4.1 µm. Pileus trama: hyphae 2.8 – 5.5 µm wide, M = 4.0 µm, thick-walled present. Stipitipellis: loosely interwoven hyphae

indistinguishable from trama. Stipe trama: hyphae 2.3 – 4.7 µm wide, M = 3.2 µm, thick-walled hyphae present. Clamps: present in all tissues.

Habit, habitat, distribution and fruiting season:

Gregarious to concrescent, terrestrial in duff and humus; associated with *Picea sitchensis*, *Tsuga heterophylla* and *Sequoia sempervirens* occurs in mixed *Picea sitchensis*, *Tsuga heterophylla* and *Sequoia sempervirens* forest; fruits August through December.

Materials studied:

Humboldt Co.: (WAF112).

Remarks:

This species is remarkable in its bright, yellow actively growing tissue. In age it becomes brown and resembles the *H. scrobiculatum* complex, but it can be distinguished by the yellow KOH reaction on all surfaces and by the presence of clamps. The KOH reaction is red, quickly turning to dark green and clamps are absent in the *H. scrobiculatum* group.

The collection studied consisted of two basidiomes. However, the larger developed from what seemed to be the fusion of two originally separate individuals. This specimen had no noticeable stipe, while the other single specimen only had a poorly developed loosely arranged mass of hyphae leading to the pileus. Maas Geesteranus (1975) described the stipe as at times hardly developed, while Harrison (1964) stated the basidiome appears to be sessile.

Hydnellum peckii Banker. Mycologia 5: 203. 1913.

Synonym: *Calodon peckii* (Banker) Snell & Dick. in Snell et al. Lloydia 19: 163. 1956.

Hydnellum diabolus Banker. Mycologia 5: 194. 1913.

Pileus: 3.5 – 15.0 cm broad, M = 7.7 cm; turbinate to plane when young, sub-depressed to infundibuliform in age; tomentose to strigose hairy when young, matted-fibrillose to weakly scrobiculate in age, often with red watery exudate; growing tissue reddish or pinkish white (8-9A2), maturing grayish orange brown (6-7B4) to reddish brown (8-9D-E4-6), dark brown (7-9F6-8) when bruised; context not duplex, zonate, dotted with small, black mottling, grayish red (9B3), grayish orange brown (6-7B4) to reddish brown (8-9D-E4-6), dark brown (7-9F6-8) when bruised; taste peppery hot, acerbic; odor aromatic or sweetly hot, as in hot, cinnamon candy. Stipe: 2.0 – 12.1 x 0.9 – 5.3 cm, M = 3.8 x 1.7 cm; central to eccentric; irregularly cylindrical, often contorted; grayish orange brown (6-7B4) to reddish brown (8-9D-E4-6), dark brown (7-9F6-8) when bruised; context duplex, zonate or azonate, often with small, black mottling, inner region reddish brown (8-9D-E4-6) to dark brown (7-9F6-8), outer region grayish red (9B3) to dark brown (9F6-8) when matted and bruised. Spines: decurrent, up to 6 mm long; white to pale pinkish white (8-9A2) at growing tips, grayish brown to reddish brown(6-8D-E4), finally dark brown (9F5). KOH reaction: green to olive on pileus and stipe, olive on context.

Spores: 4.1 – 7.3 x 3.2 – 6.1 µm, M = 5.8 x 4.6µm, Q^m = 1.26, Q = 1.11 – 1.40, N(r) = 20(15-20); subglobose to elliptical; nodulose to tuberculate. Basidia: 24 - 56 x 4

–8.5 µm, M = 38.0 x 6.3 µm, N(r) = 20(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 3.4 – 6.1 µm wide, M = 4.6 µm. Pileus trama: hyphae 2.8 – 6.3 µm wide, M = 4.3 µm, thick-walled hyphae present. Stipitipellis: hyphae, 3.0 – 5.6 µm wide, M = 4.2 µm, thick-walled hyphae rare. Stipe trama: hyphae 3.3 – 6.7 µm wide, M = 4.8 µm, thick-walled abundant. Clamps: abundant in stipe trama, scattered elsewhere.

Habit, habitat, distribution and fruiting season:

Scattered to gregarious; terrestrial in duff and humus; common and abundant; associated with *Picea sitchensis*, *Tsuga heterophylla* and *Pinus*; occurs in coastal forests of *Picea sitchensis* and *Tsuga heterophylla* and in inland and montane forests of predominately *Pinus*; fruits September through December.

Materials studied:

Del Norte Co.: (HDT 28459), DLL 5225; Humboldt Co.: (WAF128, 129, 139, 147, HDT 21472, 23032), DLL 2887, 5342, 7469, 7137, 81221,8475, DD 107(HSC); Mendocino Co.: (WAF219, HDT 8343, 9615, 10650, 14116, 21397, 21578, 21780, 24426, 38452, 43947, Halling 982(SFSU), Molla 132(SFSU)), DLL 4250; Siskiyou Co.: (WAF150).

Remarks:

Hydnellum peckii is easily distinguished from the other reddish brown *Hydnellum* taxa by its hot peppery taste and sweetly hot odor. Additionally, it can be separated by the presence of clamps, abundant in the stipe context but scattered elsewhere.

Maas Geesteranus (1975) examined the type specimens of *H. peckii* and *H. diabolus* and placed *H. diabolus* in synonymy under *H. peckii*. Harrison (1968) believes the two species are unique, separating the two on odor and pileal surface features. Baird (1986b) concurred with Harrison and concluded that *H. diabolus* has an aromatic odor and a strigose hairy pileus surface, while *H. peckii* has a weakly fragrant odor and a tomentose pileus surface. In addition, the distribution of *H. peckii* is purported to be in the northeastern and western United States, contrasting to the eastern United States range of *H. diabolus*. On this basis I have called all the collections in this study *H. peckii*. Yet, several specimens in these collections have a strigose to hairy pileal surface and might be better placed in *H. diabolus* (WAF147, HDT 38452, Halling 982). However, I could make out no difference in the odor, therefore, until I collect more material and study the type specimens I will defer to the species concept of Maas Geesteranus (1975).

Hydnellum regium K. Harrison. Can. Jour. Bot. 42: 1231. 1964.

Plate 1, Figure 8.

Pileus: 4.3 – 9.0 cm broad, M = 6.8 cm; infundibuliform or forming a complex rosette of many overlapping pileoli and then up to 5.0 cm tall; pileoli spathulate, flabellate or irregularly lobed and with eroded margins; surface glabrous to pubescent, matted-fibrillose in age; grayish violet (19B3-4), patches darker (19B-C6), aging and bruising reddish gray to brownish orange (7B-C3-4); context not duplex, azonate or

with faint zone lines over stipe only, no mottling, concolorous with surface; taste and odor mildly acerbic to farinaceous. Stipe: 2.4 – 4.1 x 0.7 – 2.2 cm, M = 3.1 x 1.5 cm, central to eccentric; cylindrical, bulbous, or branching, orange white to light orange (5-6A2-4); context not duplex, azonate or with faint zone lines near pileus, no mottling, concolorous with stipe surface. Spines: decurrent, up to 5 mm long; young and growing tips pale violet to violet white (19A1-2), older spines dark blue, blackish blue (19E-F6-7) to violet brown (11F4-6). KOH reaction: green on pileus, no reaction to olive on stipe.

Spores: 5.0 – 7.2 x 4.7 – 6.7 µm, M = 6.5 x 6.0 µm, Q^m = 1.10, Q = 1.05 – 1.21, N(r) = 2(20-25); globose to subglobose; tuberculate. Basidia: 30 – 56 x 6 - 8 µm, M = 39.4 x 6.9 µm, N(r) = 2(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.0 µm. Pileipellis: hyphae 2.3 – 4.7 µm wide, M = 3.1 µm. Pileus trama: hyphae 2.5 – 9.9 µm wide, M = 4.2 µm, some hyphae moniliform and then M = 8.8 µm, thick-walled hyphae also present, moniliform or not. Stipitipellis: hyphae 2.2 – 9.1 µm wide, M = 4.9 µm, nearly indistinguishable from trama, thick-walled hyphae present. Stipe trama: hyphae 4.1 – 18.2 µm wide, M = 9.3 µm, generative and thick-walled hyphae present, both can be inflated or simple. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Single to scattered; terrestrial in duff and humus; rare; associated with *Picea sitchensis*, and *Tsuga heterophylla*; occurs in coastal northern California; fruits September through December.

Materials studied:

Humboldt Co.: (WAF135, 301).

Remarks:

Hydnellum regium is unique because of its pileus composed of a complex rosette of overlapping pileoli, its light orange stipe contrasting with its grayish violet pileus and the presence of inflated hyphae in the tramal tissue of the stipe. This combination of characters makes it hard to confuse with any of the other violet to bluish colored species of *Hydnellum*. *Hydnellum caeruleum* is a species with a bluish cast to its pileus and a brownish orange stipe, however, the pileus is white to grayish blue soon becoming grayish brown and the stipe is a rusty, orange-brown, not a light orange to orange white as in *H. regium*. Furthermore, *H. caeruleum* is a much larger and robust species and never develops imbricate pileoli. *Hydnellum cyanopodium* is distinctly scrobiculate, exudes watery juices, has an aromatic odor and is entirely dark violet to blackish blue throughout its basidiome. The remaining violet to bluish species of *Hydnellum* do not occur in California, however, a discussion of their diagnostic features is presented in the remarks section of *H. cyanopodium*.

The inflated hyphae of *H. regium*, confers a fleshy to brittle consistency to the context of the stipe that is more similar to that of *Sarcodon* taxa than species of *Hydnellum*. Although it shares this feature with species of *Sarcodon*, the basidiome has a distinct indeterminate growth habit, evidenced by the imbricate pilei, and therefore, is better delineated as a species of *Hydnellum*.

Hydnellum scrobiculatum var. ***scrobiculatum*** (Fr) Karst. Medd. Soc. Fauna Fl. Fenn. 5: 41. 1879.

Plate 4, Figure 14.

Basionym: *Hydnum scrobiculatum* Fries. Obs. Mycol. 1: 143. 1815.

Synonyms: *Hydnum cyathiforme* Bull ex Fries. Syst. Myc. I: 405. 1821; non *H. cyathiforme* Schaeff. 1774.

Hydnum concrescens Pers. Mycol. Europ. 2: 164. 1825.

Hydnum queletii Fries. in Quélet. Mem. Soc. Emul. Montbelbliard II 5: 293. 1872.

Calodon scrobiculatus (Fr.) Karst. Bidr. Kann. Finl. Nat. Folk 37: 108. 1882.

Calodon zonatus var. *scrobiculatus* (Fr.) Quélet. Ench. Fung. 190. 1886.

Phaeodon scrobiculatus (Fr.) Henn. Nat. Pfl. Fam. 1(1): 148. 1898.

Hydnellum velutinum var. *scrobiculatum* (Fr.) Maas G. Fungus 27: 63. 1957.

Hydnellum queletii (Fr.) Karst. Medd. Soc. Fauna Fl. Fenn. 5: 41. 1879.

Calodon zonatus var. *queletii* (Fr.) Quélet. Ench. Fung. 191. 1886.

Hydnellum zonatum var. *queletii* (Fr. in Quélet) Cost. and Duffour. Nouv. Fl. Champ. 160. 1891.

Phaeodon queletii (Fr. in Quélet) Henn. Nat. Pfl. Fam. 1(1): 149. 1898.

Pileus: 4.9 – 12.5 cm broad, M = 6.7 cm; plane when young, sub-depressed to infundibuliform in age; rarely concrescent; glabrous to tomentose when young, becoming weakly scrobiculate, matted-fibrillose and often developing small to large imbricate pileoli; often with red watery exudate; pileal surface infrequently developing grayish brown (8-9E4) tiny pustules scattered along concentric zone lines; growing margins reddish or pinkish white (8-9A2), maturing grayish orange-brown (6-7B4) to reddish brown (8-9D-E4-6), dark brown (7-9F6-8) when bruised; context not duplex, azonate or weakly zonate; dark brown (7-9F6-8), dotted with small grayish brown (8-9E4) mottling, taste mildly acerbic; odor mildly farinaceous to farinaceous. Stipe: 2.0 – 7.1 x 0.8 – 2.6 cm, M = 4.5 x 1.8 cm; central to eccentric; irregularly terete and contorted; grayish red brown (7-8B3-4) to reddish brown (8-9D-E4-6) when young, dark brown (7-9F6-8) in age; context duplex, inner region reddish brown (8-9D-E4-6) to dark brown (7-9F6-8) with small, grayish brown (8-9E4) mottling, outer region grayish red (9B3) to dark brown (9F6-8) when matted and bruised, azonate or weakly zonate. Spines: decurrent, up to 6 mm long; white to pale pinkish white (8-9A2) at growing tips, grayish brown to reddish brown (6-8D-E4), finally dark brown (9F5). KOH reaction: Observed best on pileus surface; all mature surfaces instantly red often so rapid as to be missed; promptly changing to dark green.

Spores: 4.0 – 6.5 x 3.4 – 5.5 µm, M = 5.3 x 4.3µm, Q^m = 1.22, Q = 1.16 – 1.28, N(r) =9(15-20); subglobose to elliptical; nodulose to tuberculate. Basidia: 20.0 – 55.0 x 4.5 –8.0 µm, M = 36.1 x 6.1 µm, N(r) = 9(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 3.4 – 5.8 µm wide, M = 4.6 µm, thick-

pileus. It also has the least concrescent growth habit, where as forma *zonatum* and forma *parvum* commonly have fused pilei. Although the pileus size overlaps in var. *scrobiculatum* and var. *zonatum* forma *zonatum*, the average width of the stipe is greater than 1.4 cm in var. *scrobiculatum* and less than 1.4 cm in var. *zonatum*. This gives var. *scrobiculatum* a more robust look as compared to var. *zonatum*. Variety *zonatum* forma *zonatum*, as its name suggests, develops the most conspicuous zone lines of all varieties, is intermediate in pileal width (4.5 and 6.0 cm) and rarely produces watery exudate. Forma *parvum* is the smallest, typically less than 4.5 cm in width and can be distinguished from forma *zonatum* only with difficulty; however, because of the small pileus width and highly concrescent habit of forma *parvum*, it typically has stipes that are fused, at least at their base.

Collection HDT21657 was reported as a specimen of *Hydnellum subsuccosum*, but the macro- and microfeatures are more consistent with *H. scrobiculatum* var. *scrobiculatum*. Harrison (1964) writes "this species [*H. subsuccosum*] resembles *H. scrobiculatum*, but is much more irregular in growth and has a vellutinous appearance when dried". On visual inspection HDT 21657 does not appear vellutinous, in fact it looks like all other collections of *H. scrobiculatum*. Furthermore, HDT 21657 does not have a cclliculose pileus surface or ridged and irregular margins as reported in the description of *H. subsuccosum* by Harrison (1964). Therefore, I consider *H. scrobiculatum* var. *scrobiculatum* a more appropriate placement of this collection.

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Hydnellum scrobiculatum (Fr. ex Secr.) Karst. var. ***zonatum*** (Batsch ex Fr.) K Harrison forma ***zonatum*** Hall & Stuntz. Mycologia 64 (3): 584. 1972.

Basionym: *Hydnum zonatum* Batsch ex Fr. Epicr. Syst. Myc. p. 509. 1836 – 1838.

Synonyms: *Hydnum cyathiforme* Fries. Syst. Myc. I: 405. 1821; non *H. cyathiforme* Schaeff. 1774.

Hydnellum zonatum Karst. Medd. Soc. Fauna Fl. Fenn. 5: 41. 1879.

Hydnellum velutinum var. *zonatum* (Fr.) Maas G. Fungus 27: 64. 1957.

Pileus: 3.0 – 11.1 cm broad, M = 6.1 cm; plane when young, remaining so, or becoming sub-depressed, rarely infundibuliform; frequently concrescent; glabrous to tomentose when young, becoming weakly scrobiculate, matted-fibrillose and some developing small imbricate pileoli, red watery exudate rare; pileal surface typically covered with grayish brown (8-9E4) tiny pustules scattered along concentric zone lines, growing margins reddish or pinkish white (8-9A2), maturing grayish orange brown (6-7B4) to reddish brown (8-9D-E4-6), dark brown (7-9F6-8) when bruised; context not duplex, weakly zonate, dark brown (7-9F6-8), dotted with small grayish brown (8-9E4) mottling, taste mildly acerbic; odor mildly farinaceous to farinaceous. Stipe: 1.1 – 6.0 x 0.5 – 2.2 cm, M = 3.4 x 1.0 cm; central to eccentric; irregularly terete and contorted; grayish red brown (7-8B3-4) to reddish brown (8-9D-E4-6) when young, dark brown (7-9F6-8) in age; context duplex, inner region reddish brown (8-9D-E4-6) to dark

brown (7-9F6-8) with small, grayish brown (8-9E4) mottling, outer region grayish red (9B3) to dark brown (9F6-8) when matted and bruised, azonate or weakly zonate. Spines: decurrent, up to 5 mm long, white to pale pinkish white (8-9A2) at growing tips, grayish brown to reddish brown (6-8D-E4), finally dark brown (9F5). KOH reaction: Observed best on pileus surface; all mature surfaces instantly red often so rapid as to be missed; promptly changing to dark green.

Spores: 4.1 – 6.4 x 3.0 – 5.6 µm, M = 5.2 x 4.2 µm, Q^m = 1.24, Q = 1.16 – 1.35, N(r) = 9(15-20); subglobose to elliptical; nodulose to tuberculate. Basidia: 23.0 – 45.0 x 5.0 – 7.5 µm, M = 31.8 x 6.0 µm, N(r) = 9(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 3.1 – 6.2 µm wide, M = 4.6 µm, thick-walled hyphae rare. Pileus trama: hyphae 3.2 – 6.0 µm wide, M = 4.4 µm, thick-walled hyphae present. Stipitipellis: 2.6 – 4.7 µm wide, M = 3.6 µm, thick-walled hyphae rare. Stipe trama: hyphae 3.0 – 5.8 µm wide, M = 4.7 µm, thick-walled abundant. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Gregarious to highly concrescent, terrestrial in duff and humus; associated with *Picea sitchensis*, and *Tsuga heterophylla*, also found in mixed conifer and hardwood forests dominated by *Pseudotsuga menziesii* and *Lithocarpus denisflorus*; occurs in coastal and inland forests of central and northern California; fruits August through December.

Materials studied:

Humboldt Co.: (WAF183, 186, 188, 203, 210, HDT 38288), DLL 7136, 7358, 7472, 7512; Mendocino Co.: (WAF225, HDT 30861, 21775).

Remarks:

Hydnellum scrobiculatum var. *zonatum* forma *zonatum* is characterized by its reddish brown basidiome, which commonly develops grayish brown, tiny pustules along very distinct concentric zone lines and its typically concrescent growth habit. See remarks under *H. scrobiculatum* var. *scrobiculatum* for a discussion on differentiating the varieties of *H. scrobiculatum*.

Hydnellum scrobiculatum (Fr. ex Secr.) Karst. var. ***zonatum*** (Batsch ex Fr.) K. Harrison. forma ***parvum*** (Banker) Hall & Stuntz. Mycologia 64 (3): 584. 1972.

Basionym: *Hydnellum parvum* Banker. Mycologia. 5: 200. 1913.

Pileus: 3.0 – 4.1 cm broad, M = 3.2 cm; plane when young, remaining so, or becoming sub-depressed; frequently concrescent; glabrous to tomentose when young, becoming weakly scrobiculate, matted-fibrillose and some developing small imbricate pileoli, red watery exudate rare; pileal surface typically covered with grayish brown (8-9E4), tiny pustules scattered along concentric zone lines, growing margins reddish or pinkish white (8-9A2), maturing grayish orange brown (6-7B4) to reddish brown (8-9D-E4-6), dark brown (7-9F6-8) when bruised; context not duplex, weakly zonate, dark brown (7-9F6-8), dotted with small grayish brown (8-9E4) mottling, taste mildly acerbic; odor mildly farinaceous to farinaceous. Stipe: 0.3 – 7.1 x 0.2 – 1.2 cm, M = 2.4 x 0.65 cm; central to eccentric; irregularly terete and contorted, commonly fused with

nearby stipes of basidiomes growing concrescently, some free or only fused at the bases; grayish red brown (7-8B3-4) to reddish brown (8-9D-E4-6) when young, dark brown (7-9F6-8) in age; context duplex, inner region reddish brown (8-9D-E4-6) to dark brown (7-9F6-8) with small, grayish brown (8-9E4) mottling, outer layer grayish red (9B3) to dark brown (9F6-8) when matted and bruised, azonate. Spines: decurrent. up to 4.5 mm long; white to pale pinkish white (8-9A2) at growing tips, grayish brown to reddish brown (6-8D-E4), finally dark brown (9F5). KOH reaction: Observed best on pileus surface; all mature surfaces instantly red often so rapid as to be missed; promptly changing to dark green.

Spores: 4.1 – 6.4 x 3.3 – 5.3 µm, M = 5.2 x 4.1 µm, Q^m = 1.24, Q = 1.19 – 1.28, N(r) = 8(15-20); subglobose to elliptical; nodulose to tuberculate. Basidia: 24.0 – 67.0 x 5.0 – 7.0 µm, M = 33.5 x 5.6 µm, N(r) = 8(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 2.9 – 6.0 µm wide, M = 4.3 µm, thick-walled hyphae rare. Pileus trama: hyphae 2.7 – 6.0 µm wide, M = 4.4 µm, thick-walled hyphae present. Stipitipellis: hyphae 2.1 – 3.8 µm wide, M = 2.9 µm, nearly indistinguishable from trama, thick-walled hyphae rare. Stipe trama: hyphae 2.5 – 5.9 µm wide, M = 4.2 µm, thick-walled abundant. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Gregarious to highly concrescent, terrestrial in duff and humus; associated with *Picea sitchensis*, and *Tsuga heterophylla*, but predominately found in mixed conifer and hardwood forests dominated by *Pseudotsuga menziesii* and *Lithocarpus densiflorus*; occurs in coastal and inland forests of central and northern California; fruits August through December.

Materials studied:

Humboldt Co.: (DLL 8025); Mendocino Co.: (WAF224); Trinity Co.: (WAF197, 198, 199, 212, 214, 215, 216), DLL 8525.

Remarks:

Hydnellum scrobiculatum var. *zonatum* forma *parvum* is characterized by reddish brown, concrescent basidiomes that commonly develop grayish brown tiny pustules along very distinct concentric zone lines. It is a consistently small form of var. *zonatum*, in which the stipes tend to be fused, at least at the base, because of the close proximity of the many developing concrescent basidiomes. For a complete discussion on differentiating the varieties of *H. scrobiculatum* see remarks under *H. scrobiculatum* var. *scrobiculatum*.

Hydnellum suaveolens (Scopoli ex Fr.) Karst. Medd. Soc. Fauna Fl. Fenn. 5: 41. 1879.

Plate 1, Figure 6.

Basionym: *Hydnum suaveolens* Scopoli. Fl. Carniol. 2:472. 1772.

Synonym: *Calodon suaveolens* Scopoli (Fr.) Karst. Revus Mycol. 3(9): 20. 1881.

Pileus: 2 - 16 cm broad, M = 9 cm; turbinate when young, plane to sub-depressed in age, occasionally developing imbricate pileoli; surface tomentose to cottony when young, matted-fibrillose in age; white, yellowish gray (4A-B2-3) to light brown (6D-E4-5) when young, dark yellowish brown (5F5-6) in age and when bruised,

disc over stipe may become dull violet (18D3); context not duplex, azonate or only weakly so over stipe, no mottling, yellowish gray (4A-B2-3) becoming dull violet (18D3) to dark violet (18F7) over stipe; taste pungent to acerbic; odor aromatic, uniquely sweet and pungent. Stipe: 1.0 – 6.6 x 0.7 – 2.3 cm, M = 4.0 x 1.5 cm; central to eccentric; cylindrical occasionally with sub-bulbous base; light violet (19A4) when young, grayish violet (19E3) or dark blue (19E4) in age; context duplex, azonate to weakly so near pileus, no mottling, concolorous with stipe surface. Spines: decurrent, up to 10 mm long; white to pale orange white (5A2) at growing tips, light brown to grayish brown (6-8D-E4), finally dark brown (9F5). KOH reaction: none on young tissue, olive on mature pileus, green on stipe.

Spores: 3.1 – 5.4 x 2.1 – 4.6 µm, M = 4.3 x 3.1 µm, Q^m = 1.37, Q = 1.23 – 1.46, N(r) = 9(15-20); subglobose to elliptical; nodose. Basidia: 25 - 50 x 4 -7 µm, M = 34 x 5.7 µm, N(r) = 9(10-15), subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 3.4 – 6.2 µm wide, M = 4.7 µm. Pileus trama: hyphae 3.4 – 6.6 µm wide, M = 4.9 µm, thick-walled present. Stipitipellis: hyphae 3.2 – 6.0 µm wide, M = 4.4 µm, thick-walled hyphae rare. Stipe trama: hyphae 3.2 – 6.9 µm wide, M = 4.6 µm, thick-walled hyphae present. Clamps: present at base of basidia and abundant on all hyphae throughout basidiome.

Habit, habitat, distribution and fruiting season:

Single to scattered; terrestrial in duff and humus; common and abundant; associated with *Picea sitchensis* and *Tsuga heterophylla*; occurs predominately in coastal northern California; fruits September through December.

Materials studied:

Humboldt Co.: (WAF104, 137, 140, 187, HDT 23031, 38319, Edelbrook 96(SFSU), Gerry 158(SFSU)), DLL 3668, 7357, 7471, 7902; Del Norte Co.: (HDT 45246).

Remarks:

Hydnellum suaveolens can be recognized by its pale yellowish brown to dark brown pileus that is in contrast to its violet to dark blue stipe, its sweet and pungent odor and its small, nodose spores. The brown pileus separates it from *H. cyanopodium*, which also has a dark violet stipe and sweet pungent odor. *Sarcodon stereosarcinon* has a similar color pileus, but lacks the fragrance, dark violet stipe and is glabrous versus cottony to matted-fibrillose as in *H. suaveolens*.

Hydnellum subzonatum K. Harrison. Can. Dept. Agr. Publ. 1099:37. 1961.

Pileus: 1.1 – 3.9 cm broad, M = 2.5 cm; plane when young, remaining so or becoming plane to sub-depressed; scrobiculate over stipe, matted-fibrillose elsewhere; orange white (6A2) when young, brown (5-7D-E6-8), grayish brown (7D3) to dark brown (7F6-8) in age; context not duplex, azonate, no mottling, orange gray (6B3); taste and odor none to mildly farinaceous. Stipe: 0.4 – 2.2 x 0.1 – 0.5 cm, M = 1.3 x 0.2 cm; central to sub-eccentric; irregularly terete; concolorous with pileus; context not duplex or only weakly so; concolorous with pileal context. Spines: sub-decurrent, typically with an abrupt stop on apex of stipe, up to 2.5 mm long; white to pale orange white (5A2) at growing tips, orange gray (5-6B2) to grayish brown (6-8D-E4) at maturity,

bruising dark brown (9F5). KOH reaction: green on pileus, olive context, and olive to green on stipe.

Spores: 3.3 – 5.0(5.9) x 2.5 – 4.6µm, M = 4.3 x 3.3µm, Q^m = 1.28, Q= 1.20 – 1.34, N(r) = 4(15-20); subglobose to elliptical; nodose. Basidia: 20 - 41 x 4.5 -6 µm, M = 30.3 x 5.4 µm, N(r) = 4(10-15); subclavate to clavate; 4-spored with sterigmata up to 4.0 µm. Pileipellis: hyphae 3.2 – 6.2 µm wide, M = 4.2 µm, thick-walled hyphae uncommon. Pileus trama: hyphae 2.8 – 6.4 µm wide, M = 4.3 µm, thick-walled hyphae present. Stipitipellis: hyphae 2.8 – 5.7 µm wide, M = 4.1 µm, nearly indistinguishable from trama, thick-walled hyphae present. Stipe trama: hyphae 2.7– 6.2 µm wide, M = 4.3 µm, thick-walled hyphae present. Clamps: present at base of basidia and abundant on all hyphae throughout basidiome.

Habit, habitat, distribution and fruiting season:

Typically concrescent, rarely gregarious; terrestrial in duff and humus; rare to uncommon; associated with mixed *Sequoia sempervirens*, *Picea sitchensis* and *Tsuga heterophylla*; occurs in coastal northern California; fruits September through December.

Materials studied:

Humboldt Co.: (WAF114, 136, 158, DLL 8719).

Remarks:

Hydnellum subzonatum is delineated by its small, brown to grayish brown, concrescent basidiomes that posses abundant clamps and produce small, nodose spores. It resembles *H. scrobiculatum* var. *zonatum* forma *parvum*, but *H. scrobiculatum* var. *zonatum* forma *parvum* lacks clamps and produces larger (M = 5.2 x 4.1 µm), tuberculate spores. In the field *H. subzonatum* is distinguished from *H. scrobiculatum*

var. *zonatum* forma *parvum* in having a much lighter, grayish brown hue. which is always reddish brown in *H. scrobiculatum* var. *zonatum* forma *parvum*. However, *H. subzonatum* takes on a reddish brown color when wet, and then can only be separated by the microscopic features of spore size and presence of clamp connections.

***Hydnellum* WAF131**

Pileus: 3.0 – 7.2 cm broad, M = 4.3 cm; turbinate when young, then convex to sub-depressed; surface thickly tomentose to vellutinous, when young, then matted-fibrillose; young growth whitish to orange white (4-5A2-3), soon becoming yellowish brown (5-6D-E4-5) and finally reddish golden (6C7) to brown (6D-E7) over the stipe; context duplex, zonate, pale orange (5A3) to grayish orange (5B3), zone lines darker, no mottling, taste mildly acerbic to farinaceous; odor mildly farinaceous. Stipe: 2.8 – 4.0 x 0.9 – 2.0 cm, M = 5.9 x 4.7 cm, irregularly cylindrical, often with bulbous base; thickly vellutinous to cottony, concolorous with pileus; context duplex, zonate, no mottling, concolorous with pileus context. Spines: decurrent, up to 5 mm long; orange white (4-5A2-3), then brown (6D-E7) to dark brown (9F5-6). KOH reaction: none in young tissue, olive on all mature surfaces.

Spores: 4.8 – 6.8(7.5) x (3.8)4.5 – 5.7 µm, M = 5.9 x 4.7µm, Q^m = 1.23, Q = 1.20 – 1.24, N(r) = 3(15-20); subglobose to elliptical; nodulose. Basidia: 35 – 51 x 5.5 – 8.0 µm, M = 42 x 6.7 µm, N(r) = 3(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.0 µm. Pileipellis: hyphae 3.2 – 6.0 µm wide, M = 4.4 µm. Pileus trama: hyphae 3.3 – 5.7 µm wide, M = 4.4 µm. Stipitipellis: 2.5 – 4.9µm wide, M = 3.8

µm. Stipe trama: hyphae 4.7 – 13.4 µm wide, M = 6.9 µm, generative hyphae rarely inflated, thick-walled hyphae rare. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Single, scattered or gregarious; terrestrial in duff and humus; associated with *Picea*, *Pinus*, *Abies*, *Alnus* and *Salix*; found in mixed conifer and hardwood montane forests of northern California; fruits September through December.

Materials studied:

Siskiyou Co.: (WAF131, 133, 300).

Remarks:

Hydnellum WAF131 can be recognized by the golden to honey to yellow brown basidiome that is thickly velutinous on pileus, especially so when young and thickly cottony on the stipe. It resembles *H. peckii* in shape and surface features, but *H. peckii* has a reddish brown pileus and has a hot, peppery taste.

Hydnellum WAF131 is very close to *H. ferrugineum* and *H. spongiosipes*, both of which are found in the eastern U.S. The specimens described above do not fit perfectly in either *H. spongiosipes* or *H. ferrugineum*. The basidiome color and spore characteristics resemble those of *H. spongiosipes*, however, this species occurs in hardwood forests and does not develop zone lines in the context of the pileus. *Hydnellum ferrugineum*, on the other hand, has zone lines and occurs in coniferous forest, but the color of the basidiome is darker and the spores are smaller (M = 5.2 X 4.4 µm) than *Hydnellum* WAF131. Furthermore, Harrison (1964) described a new species, *H. chrysinum*, which fits fairly well with the specimens described above, except for the lack of orange shades in the spines that are diagnostic for *H. chrysium*. All collections

of *Hydnellum* WAF131 were young and this may be the reason for the ambiguities. However, until I collect more specimens and study the type collections of all relevant taxa I will defer actual placement of *Hydnellum* WAF131 into a previously published species.

Sarcodon (L. ex Fr.) Karsten. Rev. Mycol. 3 (9):20. 1881.

Synonym: *Hydnum* Banker. Bull. Torrey bot. Cl. 29: 442, 448. 1902.

Type species: *Hydnum imbricatum* L. ex Fr.

Diagnostic characters: Growth of basidiome determinate. Context consistency fleshy to brittle. Width of tramal hyphae highly variable, 4.5 - 30 µm (mean ≥ 9.0 µm). Thick-walled hyphae uncommon.

Macroscopic characters: Growth determinate; pileus 29 – 200 mm, convex to plane; surface variable, typically glabrous marginally and squamulose to scaly over disc; color variable, context consistency fleshy to brittle, not duplex, azonate, no mottling, color variable; taste variable, typically none or bitter, odor none to farinaceous. Stipe central to eccentric; typically cylindrical, some tapered, others bulbous at base; concolorous with pileus or lighter; context consistency fleshy to brittle, not duplex, azonate, no mottling, concolorous with pileal context. Spines typically decurrent and reduced on stipe, diffusely spaced, not dense; color variable. KOH reaction variable, typically green on pileus. Spores pale brown in deposit (6D4).

Microscopic characters: Spores subglobose to elliptical; nodose, nodulose, tuberculate or irregularly warty. Basidia size variable, subclavate to clavate. Tramal hyphae highly variable in width, typically greater than 9.0 µm wide, swollen and or inflated often present and then up to 40 µm in width, rarely thick-walled and then sparsely interwoven with generative hyphae. Pileipellis hyphae typically not swollen or inflated, generally more uniform and narrow in width then tramal hyphae. Stipitipellis poorly developed, typically indistinguishable from tramal hyphae. Cytoplasmic pigmentation in all tissue, incrusted pigmentation only in blackish blue to dark violet tissue and then dissolving in 3% KOH.

Habit and habitat:

Solitary, gregarious or caespitose; terrestrial in coniferous, hardwood or mixed forests.

Key to species of *Sarcodon*

1.) Pileus and stipe entirely orange, brownish orange to brown .....***S. martioflavus***

1.) Pileus and stipe variously colored, if orange or brownish orange, then only in part or in patches, never entirely so 2

2.) Pileus and stipe pale green to olive entirely or in part, may become light brown, dark brown or brownish orange with lilac tints in part. Context soon becoming entirely olive .....***S. atroviridis***

2.) Pileus and stipe variously colored, never pale green to olive. Context yellowish white, grayish pink, orange white, grayish orange, dark violet or blackish blue. if olive, then only in localized regions (See *S. scabrosus, S. glaucopus & S. leucopus*) 3

3.) Context and surface of the pileus and stipe entirely dark violet to blackish blue .....***S. fuscoindicus***

3.) Context and surface of the pileus and stipe not as above.....4

4.) Pileus surface grayish violet to blackish blue or with tints of pinkish white or grayish red colors. Stipe at first grayish orange, then brownish orange, and finally concolorous with pileus .....***S. rimosus***

4.) Pileus and stipe surface not as above. Pileus and stipe pale orange white, yellowish brown, reddish brown, violet brown, light brown, brown, or dark brown, if grayish violet, purplish gray or reddish gray, then only in part or in patches 5

5.) Surface and context of stipe base olive to gray-green 6

5.) Surface of stipe base variously colored. Context of stipe base whitish, grayish white, or pinkish white, with or without pinkish or violet tints, not olive to gray-green 7

6.) Pileus yellow-brown with a vinaceous to purplish brown cast, surface matted-tomentose and only rarely squamulose at margins, areolate over disc, frequently with yellowish excreted dots on surface.....***S. glaucopus***

6.) Pileus reddish brown, dark brown to violet brown, surface appressed scaly, if glabrous, then only when young or distally at margins, never with yellowish excreted dots on surface.....***S. scabrosus***

7.) Basidiome glabrous to finely pubescent often with small, scattered wart-like pustules. Pileus plane to sub-depressed; pileal margins undulating and often eroded .....*S. stereosarcinon*

7.) Basidiome areolate, appressed scaly or reflexed scaly, if glabrous, then only when young or distally at margins and with no wart-like pustules. Pileus convex to plane; pileal margins slightly enrolled 8

8.) Basidiome light brown, brown to dark brown, with flushes of reddish gray, pinkish white, or purplish gray tints between scales or in a mosaic pattern. Clamps absent .....*S. subincarnatus*

8.) Basidiome variously colored, but not flushed with tints of pinkish white, reddish gray, or purplish gray between scales or not in a mosaic pattern. Clamps present 9

9.) Pileus glabrous from collapsed felt becoming areolate over disc; if scaly, then scales are small and tightly appressed .....*S. leucopus*

9.) Pileus entirely and distinctly scaly 10

10.) Pileus with tightly appressed scales. Spores irregularly tuberculate.....*S. ustale*

10.) Pileus with large scales, typically reflexed at tips. Spore tuberculate .....

.....*S. imbricatus*

Sarcodon atroviridis (Morgan) Banker. Mem. Torrey Bot. Club 12: 148. 1906.

Basionyms: *Hydnum atroviride* Morgan. Jour. Concinn. Soc. Nat. Hist. 18: 38. 1895.

Synonyms: *Phaeodon atroviridis* (Morgan) Earle *in* Mohr. Pl. Life Alabama, 205. 1901.

Hydnum blackfordae Peck. Bull. Torrey Bot. Club 33: 218. 1906.

Sarcodon blackfordae (Peck) Banker. Mem. Torrey Bot. Club 12: 142. 1906.

Sarcodon fumosus Banker. Mycologia 5: 16. 1913.

Hydnum fumosum (Banker) Trotter. Syll. Fung. 23: 468.; [*non Hydnum fumosum* (Banker) Pouzar. Mykol. 10: 68. 1956.; *non Hydnum fumosum* (Banker) Hall and Stuntz. Mycologia 64: 36. 1972. *nom. illeg.* (homonym)]

Hydnum bambusinum Baker and Dale. Mycol. Pap. No. 33: 36. 1951.

Sarcodon bambusinum (Baker and Dale) Maas G. Proc. K. Ned. Akad. Wet. (Ser. C) 77: 221. 1974.

"Pileus up to 11.0 cm broad, convex to plane, pubescent to glabrous, smooth, pale green (30A3), lilac (16B3) tints, dark brown (9F-3) or light brown (7C3), later olive (2E4) to brownish orange (7C4) or blackish in the glabrous areas; context not duplex, azonate, brittle, whitish (4A1), soon becoming lilac (16B3) to bluish gray (20F3), later olive (2E4) when dry; taste bitter; odor none to slight when fresh, soon

having a smell of a strong acid. Stipe up to 11.5 x 4.0 cm, usually central or rarely sub-eccentric, terete, to attenuate below, pubescent to glabrous or smooth, usually filled, rarely hollow, grayish brown (10D3) to violet brown (10F4), rosewood (9C5) to bluish gray (20F3) at the base, later concolorous with pileus when dry; context not duplex, azonate, lilac (16B3) to dark violet (17F4), later concolorous with pileus flesh when dry. Spines up to 6.0 mm long, not decurrent, sub-crowded, easily breaking off at the base, whitish (4A1), yellowish white (4A2) to light brown (7D4) or olive (2E4), olive when dry." – (Baird, p89, 1986a). KOH reaction: On preserved material, dark green on pileal surface, olive elsewhere.

Spores: 6.4 – 10.7 x 5.7 – 8.7(10.5) µm, M = 8.6 x 7.2 µm, Q^m = 1.20, Q = 1.1 – 1.26, N(r) = 4(20-25); subglobose; tuberculate. Basidia: 39.0 – 64.0 x 6.6 – 11.0 µm, M = 51.4 x 8.8 µm, N(r) = 4(10-15); subclavate to clavate; 4-spored with sterigmata up to 6.0 µm. Pileipellis: hyphae 5.0 – 15.7 µm wide, M = 7.7 µm. Pileus trama: hyphae 4.4 – 18.6 µm wide, M = 8.3, swollen hyphae abundant. Stipitipellis: hyphae 4.0 – 10.8 µm, M = 8.1 µm. Stipe trama: hyphae 4.2 – 19.2 µm wide, M = 10.4 µm, swollen hyphae abundant. Clamps: present.

Habit, habitat, distribution and fruiting season:

"Single to gregarious, found in coniferous woods, October to December." – (Baird, p90, 1986a).

Materials studied:

Calavaras Co.: (HDT 16633); Sierra Co.: (HDT 45012, 52608,); Siskiyou Co.: (Sommer 301(HSC)).

Remarks:

Sarcodon atroviridis can be recognized by a pileus with a pubescent to glabrous surface and olive green colors with lilac tints. No other *Sarcodon* has such a distinctively green pileus and stipe. Also, the spores are the largest observed for any *Sarcodon* or *Hydnellum* taxa.

Collection HDT52608 was reported as *Sarcodon calvatus*, but its spores measured 7.8-9.8 X 6.5-8.2 µm, which were well out of the reported size range of 4-5.5 X 3.5-5 µm for *S. calvatus*. As the preserved basidiomes of this collection had green and olive tone consistent with *Sarcodon atroviridis* and the spore measurements fit within the range reported for *Sarcodon atroviridis*, I believe the SAFU collection HDT 52608 should be transferred to this taxon.

Sarcodon fuscoindicus Harrison. Can. Jour. Bot. 42:1213. 1964.

Pileus: 4.0 – 17.0 cm broad, M = 8.8 cm; convex to plane; pubescent to glabrous when young, squamulose in age, occasionally splitting and cracking radially into deep scales; grayish violet (18E4) to blackish blue (19F4) with tints of pinkish white (9-10A2) and grayish red (9B3); context dark violet to dark blue (18-19E-F4-6); taste absent to mildly farinaceous; odor absent to weakly farinaceous. Stipe: 2.0 – 8.0 x 0.8 – 1.9 cm, M = 4.6 x 1.9 cm; central to slightly eccentric; cylindrical; concolorous with pileus; context concolorous with pileus context. Spines: decurrent, up to 7 mm; pinkish white, grayish red to grayish violet (16-17C2-3), finally violet brown (10-12F7-8). KOH reaction: dark green on all surfaces.

Spores: 4.2 – 7.5 x 3.1 – 5.9 µm, M = 5.7 x 4.7 µm, Q^m = 1.20, Q = 1.15 – 1.28, N(r) = 6(15-20); subglobose to elliptical; nodulose. Basidia: 29.0 –55.0 x 6.5 – 9.5 µm, M = 41.2 x 7.3 µm, N(r) = 6(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 2.9 – 15.1 µm wide, M = 6.9 µm. Pileus trama: hyphae 4.8 – 23.5 µm wide, M = 9.7 µm, swollen and inflated hyphae present. Stipitipellis: hyphae 3.1 – 18.0 µm wide, M = 8.8 µm. Stipe trama: hyphae 4.1 – 18.0 µm wide, M = 10.5 µm, swollen and inflated hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Single to scattered to gregarious; terrestrial in duff and humus; found associated with mixed *Pseudotsuga menziesii* and hardwood forest; occurs predominately in inland regions of central and northern California; fruits October through December.

Materials studied:

Humboldt Co.: (DLL 7703); Mendocino Co.: (HS 3800(HSC)), DLL 4249; Trinity Co.: (WAF115, 124b, 191, 204, 209), DLL 8549, 9273. No local: DLL 847.

Remarks:

Sarcodon fuscoindicus can be recognized by a squamulose to radially cracked, dark violet pileus and nodulose spores. It may be confused with *S. rimosus* and *S. subincarnatus*. In *S. rimosus* the basidiome is a mosaic of colors including grayish orange to brownish orange, grayish violet and blackish blue with tints of pinkish white and grayish red. Also, it has an orange white context with violet white and pinkish white flushes, compared to the dark blue to dark violet context of *S. fuscoindicus*. In *S. subincarnatus* the pileus is brown on the surface with some violet, pink and lilac tints. In addition, the context is grayish orange with violet white and pinkish white flushes.

The collection DLL 847 had no herbarium notes on location or fresh morphology and therefore was not included in the numerical analysis. It was reported as *Sarcodon fuligineo-violaceus*, which is similar to *Sarcodon fuscoindicus* in stature and color; however, it has a pale purple to violet blue pileus context, red in the stipe with a green stipe base (Maas Geesteranus, 1975). *Sarcodon fuscoindicus* has a pileus and stipe context that is entirely dark violet to dark blue (18-19E-F4-6) throughout. Additionally, Harrison (1964) describes *S. fuligineo-violaceus* as vinaceous brown, while *S. fuscoindicus* is entirely dark violet to dark blue. As the micromorphological features of DLL 847 were consistent with *S. fuscoindicus* and it has an entirely dark violet context, I believe this to be a more appropriate placement.

Sarcodon glaucopus Maas G. & Nannf. *in* Svensk Bot. Tiskr. 63: 64. 1969.

Synonyms: *Sarcodon amarescens* (Quél.) Quél. sensu Maas G. *in* Fungus 26: 47. 1956.

"Pileus up to 110 cm broad, plano-convex or sub-depressed, at first tomentose, then matted forming a cuticle that breaks up into scales near margin, into areoles in center; scales adhering to appressed, yellow-brown with vinaceous shade or pale to dark purplish brown, occasionally locally violet-gray, at times very dark brown in center, contrasting with dingy yellowish ground color, not infrequently covered with yellowish dots of excreted matter when dried. Stipe 2.7 – 7.5 x 1.0 – 4.0 cm, cylindrical, tapering below or somewhat broadened below, tomentose, fibrillose, covered with adnate fibrillose squamules or partly matted, dingy whitish, soon pinkish brown to purplish

brown above, gray-green below, with pointed whitish base. Spines up to 5 mm long, whitish, finally purplish brown. Context whitish to somewhat yellowish in pileus, sometimes suffused with reddish tint, gray-green in base of stipe. Taste bitterish. Odor farinaceous." – (Maas Geesteranus, p105, 1975). KOH reaction: On preserved material, dark green on pileal surface, olive elsewhere.

Spores: 5.1 – 6.3 x 4.1 – 5.4 µm, M = 5.6 x 4.8 µm, Q^m = 1.18, Q = 1.11 – 1.21, N(r) = 1(25); subglobose; nodulose. Basidia: 30.0 – 40.0 x 5.0 – 7.0 µm, M = 36.2 x 6.4 µm, N(r) = 1(15); subclavate to clavate; 4-spored with sterigmata up to 6.0 µm. Pileipellis: hyphae 3.2 – 9.3 µm wide, M = 6.7 µm. Pileus trama: hyphae 6.4 – 21.6 µm wide, M = 11.3 µm swollen hyphae abundant. Stipitipellis: hyphae 7.4 – 21.2 µm wide, M = 10.7 µm. Stipe trama: hyphae 7.1 – 22.8 µm wide, M = 10.8 µm, swollen hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

"Single or caespitose, in coniferous woods." – (Maas Geesteranus, p105, 1975).

Materials studied:

Shasta Co.: (HDT 47913).

Remarks:

Sarcodon glaucopus can be recognized by its yellowish brown to purplish brown basidiome, a pileal surface that is frequently covered with yellowish excreted dots and is matted-tomentose to scaly near the margins while areolate over the disc and its pale gray-green stipe base. *Sarcodon scabrosus* is a similar species with a gray-green stipe base, but it has a reddish brown, dark brown to violet brown pileus that has distinct appressed scales and it never has yellowish excreted dots. Furthermore, the gray-green

color can run partly up the lower half of the stipe in *S. scabrosus*, whereas, this color is confined to the extreme base of the stipe in *S. glaucopus*.

Sarcodon imbricatus (L. ex Fr.) P. Karst. Rev. Mycol. 3 (9):20. 1881.

Plate 1, Figure 7, Plate 2, Figure11.

Basionym: *Hydnum imbricatum* (Lin.) Fr. Syst. Mycol. I:398. 1821.

Synonyms: *Hydnum badium* Persoon. Mycol. Europ. 2:155. 1825.

Sarcodon adpressum Lloyd. Myc. Notes 552. 1916.

Pileus: 5 – 25.4 (47) cm broad, M = 18 cm; convex to plane, then finally with central depression extending into stipe; scaly, the scales over disc typically large and erect, imbricate with reflexed tips toward margin, and appressed at young growing margins; light brown (6-7C-D4-5), grayish brown (9-10B-D3), to reddish brown (9E3) or violet brown (10-11E-F4-5), bruising dark brown (9F4-6) especially at scale tips; context pallid grayish white (9B2) to grayish light brown (10D3); taste mildly bitter or lacking; odor absent to weakly pungent. Stipe: 5 – 14 x 1.6 – 7.5 cm, M = 8.8 x 3.8 cm; central to slightly eccentric; terete, typically with swollen to bulbous base, reddish gray (7B2), brownish gray (7C2-3), bruising dark brown (7-9F4-8); context concolorous with pileus context. Spines: decurrent, up to 1 cm long; orange gray (6B2) to flesh (6B3) when young, later darker to brownish orange (7C3), bruising to dark brown or liver brown (8F7). KOH reaction: green on pileus, context weak to olive, olive on stipe.

Spores: 5.5 – 9.8 (10.4) x 4.4 – 7.7 (8.7) µm, M = 7.0 x 5.8 µm, Q^m = 1.20, Q = 1.12 – 1.33, N(r) = 14(15-20); subglobose to elliptical; tuberculate with large angular

warts. Basidia: 28 –70 x 5.5 –9.5 µm, M = 44.3 x 7.2 µm, N(r) = 14(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm, rarely 2-spored and then with sterigmata up to 10 µm. Pileipellis: hyphae 3.7 – 28.1 µm wide, M = 9.1 µm. Pileus trama: hyphae 2.6 –30.0 µm wide, M = 9.3 µm, swollen and inflated hyphae present. Stipitipellis: apex of stipe with vestigial hymenial elements, lower portion with hyphae 2.7 – 20.5 µm wide, M = 7.5 µm. Stipe trama: hyphae 3.5 – 25.0 µm, M = 9.6 um, swollen and inflated hyphae abundant. Clamps: present at base of basidia and abundant on all hyphae throughout basidiome.

Habit, habitat, distribution and fruiting season:

Single to scattered to gregarious, occasionally caespitose; terrestrial in duff and humus; common and abundant with *Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Abies*, and *Pinus*; fruits September through December.

Materials studied:

Del Norte Co.: Kettenhorn 35(HSC); Humboldt Co.: (WAF113, 179); Siskiyou Co.: (WAF132, 152, 159, HDT 46767); Mendocino Co.: (HDT 10651, 1106, Sunberg 398(SFSU)); Tehama Co.: (HDT 36475, 36614, 52780); Tuolumme Co.: (HDT 13328); Sierra Co.: (FO 23(SFSU))

Remarks:

Sarcodon imbricatus is easily recognized by its tuberculate spores and its pileus that has imbricate scales and is convex to plane at first and then deeply depressed over the stipe. *Sarcodon scabrosus* is a scaly brown species that resembles *S. imbricatus*, but *S. scabrosus* can be distinguished by its pileus with appressed scales rather than imbricate scales and is at most sub-depressed over its stipe. In addition, *S. scabrosus*

does not develop clamp connections in the tramal hyphae. Furthermore, *S. scabrosus* has a grayish green stipe base, which is absent in *S. imbricatus*. *Sarcodon ustale* is another taxon with a scaly brown pileus but it differs from *S. imbricatus* by having no depression in the pileus and possessing spores that are irregularly tuberculate. *Sarcodon leucopus* is similar in basidiome size and color and spore size and ornamentation. However, *S. leucopus* can be distinguished from *S. imbricatus* based on the smoother pileal surface that may develop small to medium appressed scales but these scales never become reflexed at the tips as they do in *S. imbricatus*. In addition, *S. leucopus* has a convex to plane pileus and never develops a deep depression over the stipe that is typical of *S. imbricatus*.

Hall (1972a) recognized two varieties of *S. imbricatus*, var. *imbricatus* and var. *monticola*. The two can be distinguished by pileus and scale color. Variety *imbricatus* has chocolate brown (6F4) or negro (6F3) scales and is 'Light Ochraceous-Buff' to 'Warm Buff' between the scales. Variety *monticola* has 'Aniline Black' to 'Burnt Umber' scales and is 'Vinaceous Russet' to 'Terra Cotta' between scales and near margins.

In collections made during fall 1996 and 1997, I observed some color variation, but this depended on the age and whether or not the pileus surface was water-logged. Older and water-logged specimens were violet brown (10-11E-F4-5) over pileus surface, while younger and dryer specimens had a pileus that was light brown (6-7C-D4-5) with darker scales. Until I study the type collections I have to postpone recognizing the varieties erected by Hall and Stuntz.

Sarcodon leucopus (Pers.) Maas G. & Nannf. *in* Svensk Bot. Tiskr. 63: 415. 1969.

Plate 3, Figure 12.

Synonym: *Hydnum laevigatum* Fr. Syst. Mycol. 1: 399. 1821.

Hydnum leucopus Pers. Mycol. Europ. 2:158. 1825.

Hydnum curtisii Berkeley. Grevillea 1: 71. 1872.

Hydnum colosseum Bres. *in* Atti Accad. Agiati III 8 130. 1902.

Sarcodon colosseus (Bres.) Bat. *in* Bull. Trimest. Soc. Mycol. 39: 207. 1924.

"Pileus: up to 200 mm across, plano-convex to plane or slightly depressed, without concentric or radiate markings, at first finely felted then felt collapsed to form smooth, more or less shiny, innately-scaly cuticle, breaking up into areoles in center, pale purplish brown on yellowish drab ground color or a rich purplish brown to dark brown, context whitish, suffused with purplish brown to violet tints, after some time pale greenish, taste bitter after some time, odor commonly experienced as disagreeable. Stipe: 40 – 80 x 20 – 60 mm, cylindrical to ventricose, finely tomentose, later with smooth or innately-scaly cuticle, concolorous with pileus or paler, whitish below. Spines: decurrent, up to 15 mm, whitish, finally purplish brown" - (Maas Geesteranus, p103,1975). KOH reaction: On preserved material, green, olive or no reaction on pileus, olive on stipe; context no reaction or pale olive.

Spores: 5.0 – 8.9 x 4.0 – 7.0 µm, M = 6.7 x 5.6 µm, Q^m = 1.21, Q = 1.16 – 1.26, N(r) = 15(15-20); subglobose to elliptical; tuberculate with large angular warts. Basidia: 29.0 –65.0 x 6.0 –9.0 µm, M = 45.1 x 7.4 µm, N(r) = 15(10-15); subclavate to clavate;

4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 4.2 – 12.8 µm wide, M = 7.1 µm. Pileus trama: hyphae 4.7 –19.0 µm wide, M = 9.5 µm, inflated hyphae common. Stipitipellis: apex of stipe with vestigial hymenial elements, hyphae 1.9 – 34.7 µm wide, M = 7.2 µm. Stipe trama: hyphae 3.4 – 34.6 µm wide, M = 9.6 um, swollen and inflated hyphae abundant. Clamps: present at base of basidia and abundant on all hyphae throughout basidiome.

Habit, habitat, distribution and fruiting season:

"Occurring singly, in coniferous forest." - (Maas Geesteranus, p103, 1975).

Materials studied:

Humboldt Co.: (DLL 5464, 7291); Mendocino Co.: (Miller 1295(UC), Calhoun 306(SFSU)); Nevada Co.: (HDT 48001); Sierra Co.: (HDT 52188, 52731, 53154, 52820, HS 2006(SFSU)); Sonoma Co.: (11/12/38(UC), 11/24/40(UC)); Tuolumme Co.: (HDT 46943, 47634); Trinity Co.: (DLL 8592); Yuba Co.: (HDT 45344).

Remarks:

Sarcodon leucopus can be recognized by its smooth to innately-scaly, purplish brown pileus that may become areolate-cracked in age and its large tuberculate spores. *Sarcodon imbricatus* is similar in basidiome size and color and spore size and ornamentation. However, *S. leucopus* can be distinguished from *S. imbricatus* based on the smoother pileal surface that may develop small to medium appressed scales but these scales never become reflexed at the tips as they do in *S. imbricatus*. In addition, *S. leucopus* does not develop a deep depression over the stipe that is typical of *S. imbricatus*.

Collections HS2006, HDT52188, HDT53154, HDT46943, HDT45344, DLL5464, HDT48001, HDT47634 and DLL7291, all seem to be of dubious placement. *S. leucopus*. The collection HS2006 was identified as *S. glaucopus,* but has abundant clamp connections and therefore can not be *S. glaucopus* as this species does not produce clamp connection. The species *S. leucopus* does have abundant clamps and fits HS2006 in all other regards. Therefore, I consider the HS2006 collection conspecific with *S. leucopus*. The collections HDT46943, HDT52188, and HDT53154 were identified as *S. calvatus*. However, all have spores outside the size range for that species and fit well with the size range of the species *S. leucopus*. The remaining collections HDT45344 (*S. crassum*), HDT47634 (*S. crassum*), DLL 5464 (*S. subfellum*), DLL 7291 (*S. subfellum*), HDT48001 (*S. subfellum*), were more consistent with *S. leucopus*. Upon visual inspection these preserved specimens look identical to those of *S. leucopus* and have matching micromorphological features. Thus, I consider these collections to be specimens of *S. leucopus*.

Sarcodon martioflavus Snell and Dick. Llyodia 25: 161. 1962.

Plate 1, Figure 4.

"Pileus 4.0 – 15.0 cm broad, convex to plane, tomentose to matted, glabrous in spots, red hair (6C4), titian red (7D6) to dark brown (7F5); cuticle becoming subareolate with a few appressed scales; margin thin, lobed by fused pilei; context not duplex, orange white (6A2) to orange gray (6B2); taste farinaceous; odor strongly farinaceous to sweetish farinaceous. Stipe 2.5 – 7.0 x 0.7 – 3.0 cm, often fused with

others at base, occasionally with aborted spines, 'Cinnamon Brown' to 'Hazel' or 'Cinnamon-Rufous', with patches of 'Mars Yellow' at base, when young 'Mars Yellow'; context tinged brownish, more or less orange towards subsurface layer, base often lighter brown. Spines 2.0 – 6.0 mm long, 'Capucine Yellow' to 'Mars Yellow' or 'Zinc Orange', later 'Sanford's Brown' or 'Auburn'; seen sideways 'Orange Buff', 'Ochraceous Salmon', 'Ochraceous Orange' or 'Zinc Orange'". – (Baird, p50, 1986b).

KOH reaction: On preserved material, olive on pileus, stipe and context.

Spores: 5.2 – 6.8 x 4.1 – 5.4 µm, M = 5.9 x 4.8 µm, Q^m = 1.22, Q = 1.15 – 1.26, N(r) = 3(20-25); subglobose; nodulose. Basidia: 34.0 – 50.0 x 6.0 – 7.5 µm, M = 41.2 x 6.5 µm, N(r) = 3(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.0 µm. Pileipellis: hyphae 2.7 – 7.1 µm wide, M = 4.6 µm. Pileus trama: hyphae 3.8 – 31.2 µm wide, M = 9.0 µm, swollen and inflated hyphae abundant. Stipitipellis: hyphae 2.1 – 5.5 µm wide, M = 3.3 µm. Stipe trama: hyphae 4.7 – 25.8 µm wide, M = 11.6 µm, swollen and inflated hyphae abundant. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Solitary under *Abies*; occurs near timberline; fruits summer and early fall.

Materials studied:

Siskiyou Co.: (HDT 36304, WBC-638059(UC), WBC-1463205(UC)).

Remarks:

Sarcodon martioflavus can be recognized by its tomentose-matted to sub-areolate pileus with a few appressed scales and its orange, brownish orange to dark brown color. It is the only species of *Sarcodon* that is brownish orange over the entire basidiome and from the field notes included with the herbaria specimens, it occurs in

California only above 5,000 ft. *Sarcodon martioflavus* may be confused with the orange *Hydnellum* taxa. However, it has a sub-areolate, tomentose to matted pileus that is glabrous in spots and a fleshy to brittle context consistency, whereas the basidiomes of *Hydnellum* taxa have an entirely matted-fibrillose pileus that is never areolate and a tough to leathery context consistency. Additionally, the presence of inflated and swollen hyphae in the pileal trama can be used to separate *Sarcodon* from *Hydnellum*.

Sarcodon rimosus Harrison. Can. Jour. Bot. 42:1212. 1964.

Pileus: 5.0 – 12.8 cm broad, M = 8.6 cm; convex to plane; glabrous to finely pubescent, often splitting and cracking radially into a scale-like pattern; grayish orange (6B3-4) to brownish orange (7C3-4) at margins, grayish violet (18E4) to blackish blue (19F4) with tints of pinkish white (9-10A2) and grayish red (9B3) toward disc, colors very patchy and mosaic-like in composition, violet and blue hues dominate; context orange white (6A2) to grayish orange (7B2) with tints of pinkish white (7A2); taste absent to mildly farinaceous; odor absent to weakly farinaceous. Stipe: 3.5 – 5.7 x 2.2 – 3.3 cm, M = 4.8 x 2.8 cm; central to slightly eccentric; cylindrical; grayish orange (6B3-4) then brownish orange (7C3-4), finally concolorous with pileus and having the same patchy composition; context orange white (6A2) to grayish orange (6-7B-C2-3) with tints of pinkish white (7A2). Spines: decurrent, up to 7 mm long; grayish orange (6B3-4) then brownish orange (7C3-4), occasionally dark brown (9F8) in extreme age. KOH reaction: dark green on pileal surface, no reaction to olive elsewhere.

Spores: 4.5 – 6.7 x 3.5 – 5.6 µm, M = 5.6 x 4.6 µm, Q^m = 1.22, Q = 1.14 – 1.27, N(r) = 3(15-20); subglobose to elliptical; nodulose. Basidia: 36.8 – 50.0 x 6.0 – 9.0 µm, M = 38.3 x 7.1 µm, N(r) = 3(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 2.5 – 1.1 µm wide, M = 5.2 µm. Pileus trama: hyphae 4.4 – 25.9(44.2) µm wide, M = 6.7 µm, swollen and inflated hyphae present. Stipitipellis: hyphae 3.6 – 14.5 µm wide, M = 8.0 µm. Stipe trama: hyphae 4.2 – 14.6 µm, M = 8.9 µm, swollen and inflated hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Solitary to scattered to gregarious; terrestrial in duff and humus; associated with mixed *Pseudotsuga menziesii* and hardwood forest; fruits October through December.

Materials studied:

Del Norte Co.: (WAF181); Humboldt Co.: (WAF167); Trinity Co.: (DLL 2249).

Remarks:

Sarcodon rimosus can be recognized by its patchy composition of grayish orange, brownish orange, grayish violet to dark violet colors, its glabrous to areolate or radially cracked pileal surface and its nodulose spores. A discussion of the differences between *S. rimosus*, *S. subincarnatus* and *S. fuscoindicus* will be found in the remark section under *S. fuscoindicus*.

Sarcodon scabrosus (Fr.) Karst. Revue Mycol. 3(9): 20. 1881.

Basionym: *Hydnum scabrosum* Fries. Anteckn. Sverige Vax. Atl. Svamp. 62. 1836.

Synonym: *Phaeodon scabrosus* (Fr.) Hennigs. Nat. Pfl. Fam. 1: 149. 1898.

"Pileus: up to 8.5 cm broad, convex to plane or sub-depressed, fibrillose to squamulose at margin, appressed scales to larger in size and with raised tips at disc, pinkish brown to reddish brown (9E4), later dark brown (7F4-6) to violet brown (10-11E-F4-7), margin rarely slightly lobed, context not duplex, azonate, orange white (5A2) often damaged by insects; taste bitter; odor none. Stipe: up to 9.0 x 2.0 cm; central to eccentric; attenuate below to a radicating base, scabrous from abortive spines, pubescent to fibrillose, later glabrous, white tomentum at the base soon collapsing exposing a greenish black to black area, above concolorous with the pileus; context not duplex, azonate, cream buff (4A4) to pale vinaceous drab (14D3) with blackish or greenish base. Spines: up to 6 mm, decurrent, crowded, Sahara (6C5), reddish brown (8E4) to somalis (7E5)." – (Baird, p107, 1986a). KOH reaction: On preserved material, dark green on pileal surface, no reaction or olive to rusty, reddish orange colors elsewhere.

Spores: 5.1 – 7.6(8.6) x 4.4 – 6.4(7.4) µm, M = 6.7 x 5.7 µm, Q^m = 1.17, Q = 1.12 – 1.18, N(r) = 5(15-20); subglobose; nodulose. Basidia: 30.0 – 58.0 x 5.0 – 10.0 µm, M = 42.5 x 7.6 µm, N(r) = 5(10-15); subclavate to clavate; 4-spored with sterigmata up to 6.0 µm. Pileipellis: hyphae 5.3 – 26.4(38.4) µm wide, M = 10.9 µm. Pileus trama: hyphae 5.7 – 36.8 µm wide, M = 13.3 µm, swollen hyphae present. Stipitipellis: hyphae 2.6 – 14.5(21.1) µm wide, M = 7.3 µm. Stipe trama: hyphae 4.3 – 38.6 µm wide, M = 10.6 µm, swollen hyphae abundant. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Solitary to gregarious; terrestrial in duff and humus; found in coniferous forests; fruits October through December.

Materials studied:

Humboldt Co.: (Baroni 31(HSU), DLL 3728, 4929); Mendocino Co.: DLL 4256; San Mateo Co.: (HS 3837(SFSU)); Trinity Co.: (DLL 8293, 1167412).

Remarks:

Sarcodon scabrosus can be recognized by the conspicuously scaly, dark violet-brown pileus, the stipe with a distinct gray-green to greenish black base and the nodulose spores. *Sarcodon ustale* is a scaly, violet-brown species, but it does not develop a gray-green stipe base, it possesses clamp connections and its spores are irregularly tuberculate. In addition, the pileal surface of *S. ustale* becomes areolate to rimose-crack at the disc where as the pileal disc is squamulose to scaly in *S. scabrosus*. A discussion on differentiating *S. scabrosus*, *S. ustale*, *S. imbricatus* and *S. leucopus* will be found in the remark section under *S. imbricatus*.

Sarcodon stereosarcinon Wehmayer. Can. Jour. Bot. Res. 18:102. 1940.

Plate 1, Figure 5. Plate 3, Figure 13.

Synonym: *Hydnum stereosarcinon* (Wehmeyer) K. Harrison. Can. Dept. Agric. Publ.1099: 30. 1961.

Hydnum brevipes Coker. Jour. Elisha Mitch. Sci. Soc. 55: 375. 1939.

Sarcodon brevipes (Coker) Snell. Mycologia 37: 88. 1945.

Pileus: 3.0 – 8.6 cm broad, M = 5.0 cm; plane when young, sub-depressed or infundibuliform in age; glabrous to finely pubescent, surface often diffusely scattered with tiny warts; margins undulate and eroded; pale orange white (5A3) when young, yellowish golden brown (5D-E5-8), light brown (6-7C-D4-5) to dark brown (9F4) in age; context not duplex, azonate to weakly zonate near margin, yellowish white (4A2), yellowish gray (4B2) to orange gray (5A-B2); taste absent to mildly pungent; odor absent to weakly pungent or farinaceous. Stipe: 3.1 – 9.0 x 0.8 – 1.7 cm, M = 3.4 x 1.2 cm; central to slightly eccentric; terete, typically rooting, concolorous with pileus surface; context not duplex, azonate, concolorous with pileus context. Spines: decurrent, up to 7 mm long; orange white (5A2) to orange gray (6B2) when young, becoming light brown (6 D-4-6) to dark brown (6-7F7). KOH reaction: green on darkest surfaces, olive or no reaction elsewhere, olive or no reaction on stipe, context olive or no reaction.

Spores: 3.5 – 6.1 x 2.8 – 5.2 µm, M = 4.9 x 3.9 µm, Q^m = 1.28, Q = 1.20 – 1.35, N(r) = 12(15-20); elliptical; nodose. Basidia: 26.0 –54.0 x 4.0 – 8.0 µm, M = 35.0 x 5.6 µm, N(r) = 12(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 2.4 – 18.9 µm wide, M = 5.1 µm. Pileus trama: hyphae 2.5 – 29.0 µm wide, M = 7.3 µm, inflated hyphae common, thick-walled hyphae rare. Stipitipellis: hyphae 1.5 – 22.8 µm wide, M = 6.0 µm. Stipe trama: hyphae 1.5 – 23.0 µm wide, M = 6.0 µm, both thin- and thick-walled hyphae swollen and inflated. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Solitary to scattered to gregarious; terrestrial in duff and humus; associated with *Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*; fruits September through December.

Materials studied:

Del Norte Co.: (HDT 21351, 45247), DLL, 7135; Humboldt Co.: (WAF111, 121, 134, 138, 190, HDT 40368, 21461, 38301, 17651, Perez 191(SFSU)), DLL 4489, 7468, 7562, VW 7 (HSC).

Remarks:

Sarcodon stereosarcinon can be recognized by its glabrous, light brown pileus and small nodose spores (M = 4.9 x 3.9 µm). *Sarcodon stereosarcinon* is unique because of the poor indeterminate growth and the presence and abundance of thick-walled hyphae in the trama. Since these features are more characteristic of *Hydnellum*, there appears to be some question on generic disposition for this taxon. However, *S. stereosarcinon* has distinctly swollen and inflated hyphae, a feature typically found in taxa of *Sarcodon*. Since this character seems highly correlated to the fleshy to brittle context consistency and determinate growth observed in species of *Sarcodon*, I believe this to be the most suitable generic disposition for *stereosarcinon*. A discussion of differentiating *S. stereosarcinon* from *Hydnellum suaveolens* will be found in the remark section under *H. suaveolens*.

Sarcodon subincarnatus Harrison. Can. Jour. Bot. 42:1216. 1964.

Pileus: 7.1 – 25.0 cm broad, M = 15.5 cm; convex to plane; glabrous to finely pubescent, surface becoming squamulose to appressed scaly; light brown (7D-E4), brown (7-8E6), to dark brown (8-9F4-6) in overall appearance at arms length, but very faintly reddish gray (8-9B-C2), pinkish white (13-15A2), or purplish gray (14-15B2-3)

between squamules/scales or colors occasionally patchy and mosaic-like in composition, brown to dark brown hues dominate; context off white, yellowish white (4A2), orange white (6A2) to grayish orange (7B2) with flushes of pinkish white (7A2), reddish gray (12C2) or purplish gray (13C2) when cut or around worm holes; taste absent to mildly farinaceous; odor absent to weakly farinaceous. Stipe: 3.6 – 8.4 x 1.6 – 5.5 cm, M = 5.4 x 5.0 cm; central to slightly eccentric; cylindrical; grayish orange (6B4-5) then brownish orange (6-7C3-4), light brown (6D4-5), finally concolorous with pileus surface composition; context orange white (6A2) to grayish orange (6-7B-C2-3) with tints of pinkish white (7A2). Spines: decurrent, up to 7 mm long, whitish orange (6A2), and brownish orange (7C3-4), grayish brown (6-7C3) then dark brown (9F8). KOH reaction: dark green on pileal surface, no reaction to olive elsewhere.

Spores: 4.5 – 6.9(8.3) x 3.6 – 6.3 µm, M = 5.7 x 5.0 µm, Q^m = 1.15, Q = 1.10 – 1.21, N(r) = 15(15-20); subglobose to elliptical; resembling nodulose spores with small rounded warts, however they are tuberculate because of small, angular warts. Basidia: 28.0 – 60.0 x 5.0 – 8.0 µm, M = 41.0 x 6.2 µm, N(r) = 15(10-15); subclavate to clavate; 4-spored with sterigmata up to 5.5 µm. Pileipellis: hyphae 2.0 – 20.4(33.5) µm wide, M = 6.6 µm. Pileus trama: hyphae 3.7 – 44.0 µm wide, M = 11.5 µm, swollen and inflated hyphae present. Stipitipellis: hyphae 2.1 – 16.5 µm wide, M = 5.8 µm. Stipe trama: hyphae 3.7 – 36.6 µm wide, M = 11.1 µm, swollen and inflated hyphae present. Clamps: absent.

Habit, habitat, distribution and fruiting season:

Solitary to scattered to gregarious; terrestrial in duff and humus; associated with *Pseudotsuga menziesii* in mixed hardwood forest and *Pinus contorta* and *Picea sitchensis* in coastal dune forests; fruits October through December.

Materials studied:

Humboldt Co.: (WAF192, 195, DLL 7699), Sweet 224, 370(HSC); Mendocino Co.: (HDT 30777, 18515, 30775); Sonoma Co.: (HDT 21891); Trinity Co.: (WAF126, 193, 206, 213, DLL 7789, 7699), DLL 8293.

Remarks:

Sarcodon subincarnatus can be recognized by its grayish orange, brownish gray to mostly dark brown pileus with faint tints of pink and purplish gray between squamules and/or scales, its glabrous, squamulose, areolate or radially cracked pileal surface and its tuberculate spores. These spores resemble nodulose spores at low magnification, but have small, angular warts, which categorizes them as tuberculate, rather than nodulose spores that have small, rounded warts. A discussion of the differences between *S. rimosus*, *S. subincarnatus* and *S. fuscoindicus* will be found in the remark section under *S. fuscoindicus*.

Sarcodon ustale Harrison. Can. Jour. Bot. 42:1215. 1964.

Plate 1, Figure 1.

Pileus: 7.0 – 14.1 cm broad, M = 11.0 cm; convex to plane; margin glabrous to squamulose; disc typically and distinctly scaly, often areolate cracked; scales tightly

appressed; grayish orange (5-7B3-4), light brown (7D4), scales grayish brown (7F3) to dark brown (7F4-6); context yellowish white (4A2) with tints of orange gray (5B2); taste absent to mildly farinaceous; odor absent to weakly farinaceous. Stipe: 2.5 – 5.8 x 2.1 – 3.3 cm, M = 4.2 x 2.7 cm; central to slightly eccentric; cylindrical; grayish orange (6B3-4) then brownish gray (6-7B2), bruising dark brown (7F4-5); context concolorous with pileal context. Spines: decurrent, up to 7 mm long; grayish red (7-8B2) to reddish gray (7-8B-C2). KOH reaction: dark green on pileal surface, no reaction to olive elsewhere.

Spores: 5.8 – 8.7 x 4.7 – 7.5 µm, M = 7.1 x 6.0 µm, Q^m = 1.20, Q= 1.17 – 1.23, N(r) = 2(15-20); subglobose to elliptical; irregularly tuberculate. Basidia: 33.0 – 46.0 x 6.0 – 10.0 µm, M = 38.8 x 7.3 µm, N(r) = 2(10-15); clavate rarely subclavate; 4-spored with sterigmata up to 6.0 µm. Pileipellis: hyphae 4.0 – 14.0 µm wide, M = 7.2 µm. Pileus trama: hyphae 5.8 – 19.1 µm wide, M = 8.3 µm, swollen and inflated hyphae present. Stipitipellis: hyphae 2.6 – 5.8 µm wide, M = 3.8 µm. Stipe trama: hyphae 5.0 – 17.8 µm wide, M = 9.3 µm, swollen and inflated present. Clamps: present in all tissue.

Habit, habitat, distribution and fruiting season:

Solitary to scattered to gregarious, terrestrial in duff and humus; associated with *Picea*, *Abies*, and *Pinus*; occurs in montane coniferous forests; fruits October through December.

Materials studied:

Siskiyou Co.: (WAF151, 153), DLL 9331.

Remarks:

Sarcodon ustale can be recognized by its squamulose pileus margin, scaly to areolate-cracked pileal disc, its dark brown pileus with light brown stipe and its irregularly tuberculate spores. Although this taxon can be confused with several other dark brown, scaly-capped *Sarcodon* species, it can be easily distinguished by the irregularly tuberculate spores. The warts, which Harrison (1964) described as "compound tuberculate", are similar to large rounded-spines that can be bent, contorted or branched. A discussion on differentiating *S. scabrosus*, *S. ustale*, *S. imbricatus* and *S. leucopus* will be found in the remark section under *S. imbricatus*.

Discussion

The efficacy of classification systems and species concepts from previous literature was assessed by the degree to which they could identify species found in California. Independently, none of the previous studies from around North America could identify all taxa found in California. However, a compilation of the traits gleaned from these sources was useful in identifying most species.

Macromorphological Characters of Taxonomic Significance

The size of the pileus is highly variable in taxa of *Hydnellum* and *Sarcodon*. This variation is compounded by indeterminate growth patterns exhibited by species of *Hydnellum*. In any given fruiting of a member of *Hydnellum*, individuals have the ability to grow as long as the environmental conditions remain favorable. In addition, many taxa can fluctuate between active growth and dormancy, stopping growth and then re-starting. The range of pileus diameter in species of *Hydnellum* is 22 - 155 mm. *Hydnellum subzonatum* can develop a pileus 22 – 27 mm broad, while *H. caeruleum* can grow as broad as 112 – 155 mm. With the exception of *Sarcodon stereosarcinon*, members of the genus *Sarcodon* have a determinate growth pattern. The pileus of members of *Sarcodon* range from 29 – 200 mm in width. *Sarcodon stereosarcinon* exhibits an intermediate growth pattern between indeterminate and determinate as the pileus occasionally develops new girth beyond original expansion. The lightly pigmented, uneven and undulating margin of *S. stereosarcinon*, seems to be the result of this intermediate growth habit.

The shape of the pileus can aid in delimiting most species of *Hydnellum* from species of *Sarcodon*. The majority of *Hydnellum* taxa are turbinate when young and soon becomes sub-depressed to deeply infundibuliform. However, *H. regium* forms a complex rosette of imbricate pilei with one pileus growing from the top of a lower pileus. On the other hand, species of *Sarcodon* have a pileus that is typically convex when young that either remains convex or becomes plane, although, in *S. imbricatus* the pileus usually is deeply umbilicate and in *S. stereosarcinon* the pileus is sub-depressed to infundibuliform.

Pileal surface features are distinct between species of *Hydnellum* and *Sarcodon*. In members of *Hydnellum* the pileus surface is felty-tomentose to densely cottony when young and matted-fibrillose, wrinkled, scrobiculate, or colliculose in age. The rounded, raised bumps of the colliculose surface may or may not become tiny pileoli, like those that can develop in *Hydnellum aurantiacum*. Species of *Sarcodon*, on the other hand, typically have a glabrous pileus surface when young that either remains glabrous or becomes rimose-cracked, areolate, squamulose or reflexed scaly at maturity. However, *S. martioflavus* is reported as having a tomentose surface when young, but becomes matted, glabrous and sub-areolate with a few appressed scales. Pileal surface characteristics are highly variable in taxa of *Sarcodon*. Within one collection and even on one individual, there may develop several distinct features. The margins may be glabrous or finely squamulose, while the apex of the pileus may be areolate to scaly, as in *S. martioflavus, S. leucopus, S. rimosus, S. subincarnatus*, and *S. fuscoindicus*.

Color can be used to separate taxa into smaller color groups as well as be used to distinguish between some closely related species. Overall color of basidiomes split

members of *Hydnellum* into three groups: red-browns, orange-browns, and purple-blues. It split members of *Sarcodon* into four groups: browns, oranges, purples-blues and olive-greens. At the species level, *Hydnellum suaveolens* and *H. cyanopodium* have the same stature, size, odor, and taste, but *H. cyanopodium* is violet throughout its basidiome, while *H. suaveolens* has a cream to light brown colored pileus and a violet colored stipe. Additionally, the color of the pileus in members of the genus *Hydnellum* can vary with the age of the tissue. Most taxa have actively growing margins that are light pink, cream or off-white. However, *Hydnellum geogineum* has sulfur yellow growing margins that contrast distinctly with the reddish brown mature tissue. In members of the genus *Sarcodon* the pileus and stipe can have a subtle, patchy-mosaic pattern as in *S. subincarnatus, S. fuscoindicus* and *S. rimosus,* all of which have various shades of violet, pink and brown, but to different degrees.

The layered, banded and mottled structure of the pileus and stipe context are valuable aids for generic and specific differentiation. A layered context has two distinct periclinal layers demarcated by a faint zone line at the interface of the regions. A banded context has anticlinal dark bands, while a mottled context has small pockets of differently colored tissue scattered throughout the flesh of the basidiome. At the generic level, only members of *Hydnellum* develop clearly layered, banded or mottled context features, with the exception of *Sarcodon stereosarcinon*, which may develop faint zone lines from adding girth to the pileus beyond initial extension. At the specific level, specimens of the collection WAF131 are distinctly duplex and zonate in the pileus and stipe, but not mottled. A diagnostic feature of members of the *Hydnellum scrobiculatum* group is their light, grayish-brown pockets mottling the context of both

the pileus and stipe. Similarly, *H. cyanopodium* develops purplish-gray mottling in its context and *H. peckii* develops small, black mottling.

The size and shape of the stipe is too variable to be of taxonomic importance for species of *Hydnellum*, but these features are important in circumscribing species of *Sarcodon*. On one extreme *S. scabrosus* can develop a long, narrow and tapered stipe, while on the other, *S. atroviridis* typically develops a short broad stipe. Stipe color varies in taxa of both *Hydnellum* and *Sarcodon* and is useful in making some specific determinations, such as distinguishing *H. caeruleum* with an orange stipe from *H. cyanopodium*, which has a violet stipe.

Typically, the spines are confluent over the underside of the pileus and partially cover the stipe apex in species of both *Hydnellum* and *Sarcodon*. At the stipe apex the spines gradually abort and disperse. Members of *Hydnellum* develop spines that are typically terete, thin and dense, such that no intervening flesh is visible on the hymenophore. The spines are also terete and narrow in *Sarcodon*, but they are more dispersed on the underside of the pileus, such that an intervening, smooth hymenophore can be seen. The length of mature spines range from 1 mm in *H. subzonatum* to 20 mm in *S. imbricatus*.

For species of *Hydnellum* and *Sarcodon*, both taste and odor of basidiomes can be used to identify species or to differentiate closely related species. There are several red-brown taxa of *Hydnellum* that can exude red liquid from the pileus, but only *H. peckii* has a peppery hot taste and an odor reminiscent of radishes. *Sarcodon scabrosus* can be distinguished from the similar looking *S. imbricatus* by the distinct and immediate bitter taste of the former and the slowly bitter or mild taste of the latter.

The KOH chemical spot test is essential in differentiating taxa within the two genera. Macroscopically, old specimens of *Hydnellum geogenium* cannot be readily separated from specimens of the *H. scrobiculatum* group, but specimens of the former produce a distinctive yellow reaction with the application of KOH, whereas specimens of the latter group produce a dark violet reaction that quickly turns dark green. Most species of *Sarcodon* have an olive green reaction on the pileus surface, but *S. crassus* is reported as turning dark green (Harrison, 1961).

Spore deposit color was an invariable light brown (6-7D4) and is presented in the generic descriptions.

All members of the two genera are terrestrial with the majority found solitary to scattered in habit. However, *H. geogenium*, *H. scrobiculatum* var. *zonatum* forma *zonatum*, *H. scrobiculatum* var. *zonatum* forma *parvum*, and *H. subzonatum* typically develop fused pilei. This concrescent habit can occur with or without fused stipes. In contrast, members of *Sarcodon* do not fuse along the pileus, but *S. imbricatus* will occasionally develop a caespitose habit, with slight fusion at the stipe bases.

Micromorphological Characters of Taxonomic Significance

Spore characteristics are essential in circumscribing taxa of *Hydnellum* and *Sarcodon*. Although spore shape is too variable, with a continuum of spore shapes typically observed in a single specimen and further obscured by the large and abundant spore ornamentation, spore size and ornamentation is often a diagnostic character of a taxon. For example, nodose spores, smaller than 6 X 5 µm are typical of only *Hydnellum cyanopodium* and *Sarcodon stereosarcinon*. Similarly, irregularly

tuberculate spores occasionally develop in *Hydnellum aurantiacum*, but are diagnostic for *Sarcodon ustale*. Size is also useful for generic differentiation, with most species of *Hydnellum* producing spores less than or equal to 6.0 X 4.5 µm and most members of *Sarcodon* developing spores greater than or equal to 6.0 X 4.5 µm. The exceptions are *Hydnellum aurantiacum* producing spores as large as 9.0 X 7.6 µm and *Sarcodon stereosarcinon* producing spores as small as 3.5 X 2.8 µm.

The size of basidia in species of *Hydnellum* and *Sarcodon* is highly variable with a range of 25 – 60 X 4.5 – 8.5 µm. Even within a taxon the size is highly variable. For example, *H. regium* has basidia ranging from 30 – 60 µm in length. No correlation analysis was employed, but empirical evidence suggests the position of the basidia on the spine relative to the base or tip may be related to its final size and shape. Typically, all three shapes occur as mature basidia on a single spine. At the base of the spine, nearest the pileus, clavate basidia are most common, Fig. 12, p 34. Near the tip of the spine, cylindrical basidia (Fig. 11, p 34) are most common and subclavate basidia (Fig. 10, p 34) are the most abundant and are located throughout the length of the spine.

Pellis and tramal organization is relatively invariable. However, the width of the hyphae and the thickness of the hyphal walls are useful characters for generic differentiation. Members of *Hydnellum* are characterized by simple, uniformly narrow, thin-walled hyphae that become gradually thick-walled as the tissue ages. Therefore, young tissue at the actively growing margins of the pileus are comprised solely of simple, thin-walled hyphae, while older tissues deep in the context of the pileus or stipe contain both thin and thick-walled hyphae. In extreme cases, the majority of old stipe tissue can be comprised of thick-walled hyphae in which the wall thickenings nearly

obliterate the hyphal lumen, Fig. 16, p 36. In species of *Hydnellum*, the width of the tramal hyphae is uniform, only fluctuating between 2.5 – 10.0 µm with a mean of 5.5 µm.

In contrast, members of *Sarcodon* are characterized by swollen and or inflated, thin-walled hyphae. The width of tramal hyphae in *Sarcodon* is highly variable, ranging from 4.5 – 30 µm and the mean width is consistently greater than 9.0 µm. One exception is *Sarcodon stereosarcinon*, in which thick-walled hyphae can develop in swollen or inflated hyphae, Fig. 14, p 35. In short, there seems to be a genus specific, hyphal syndrome. In species of *Hydnellum*, the hyphae are uniformly narrow and are thin and thick-walled, whereas swollen and inflated, thin-walled hyphae are typical of members of *Sarcodon*. These typical hyphal syndromes are what I hypothesize to be conferring the tough, leathery consistency to species of *Hydnellum* and the fleshy, brittle consistency to members of *Sarcodon*. However, *S. stereosarcinon* is a species that has both thick-walled and inflated hyphae and is therefore intermediate between *Sarcodon* and *Hydnellum*. Additionally, *H. regium* Harrison and *H. spongiosipes* (Peck) Harrison have scattered inflated hyphae in their stipe trama. Therefore separation of the two genera should be based primarily on the presence or absence of swollen and inflated hyphae in the pileus trama.

Pileipellis and stipitipellis characteristics are invariable at the species level, but are useful for generic differentiation. In members of *Hydnellum*, the pileipellis develops more cytoplasmic pigmentation than tramal hyphae, but is otherwise indistinguishable from the trama. The stipitipellis can have more or less pigmentation, but is composed of very loosely interwoven hyphae with many large interstitial spaces. In comparison, the

trama in members of *Hydnellum* is densely interwoven with few interstitial spaces. These characters are observed best in young specimens as the stipitipellis can become matted and compacted with age.

On the other hand, taxa of *Sarcodon* typically develop a distinct pileipellis consisting of hyphae smaller, more uniform in width and darker in pigmentation relative to the tramal hyphae. The stipitipellis of members of *Sarcodon* is commonly undistinguishable in size, shape and color from the tramal hyphae.

Presence of clamp connection varies among all taxa of *Hydnellum* and *Sarcodon*. *Sarcodon scabrosus* is readily distinguished from other scaly capped members, such as *S. imbricatus* and *S. ustale*, by the absence of clamp connections. *Hydnellum peckii* is macroscopically very similar to *H. scrobiculatum* var. *scrobiculatum*, but unlike the latter, possesses large clamp connections.

Ecological Characteristics of Taxonomic Significance

Tree associations, geographical distribution and life span characteristics often can be useful in identifying species, especially if one or more of these characters are unique. This study was primarily concerned with morphological characters; however, in several taxa there were unique ecological characteristics that were important to their taxonomic placement.

Agerer, (1991, 1993) definitively proved that *Hydnellum peckii* and *Sarcodon imbricatus* both were mycorrhizal with Norway Spruce (*Picea abies*). As this host species of tree does not occur in California these fungal species must have a more general host range. It seems likely that *S. imbricatus* can associate with hosts of other

genera based on the fact that it can be found in California in locations where no *Picea* sp. are present. The tree associations of this and other species in this study remains speculative, nevertheless, trees found in the vicinity of basidiomes are listed in the species descriptions.

The geographic distribution of species in the genera *Hydnellum* and *Sarcodon* is generally unknown. There are two factors confounding research in this regard. First, the study of this group has been carried out by a myriad of researchers covering disparate geographical areas (Baird, 1986a). Second, most of the species are uncommon and have a very patchy distribution when they do occur. This could be related to any number of factors including host distribution (if the species are mycorrhizal), seasonal cycles influencing fruiting, and the inherent nature of the species' natural history. Two exceptions are *Hydnellum peckii* and *Sarcodon imbricatus*, which are known to have a worldwide distribution (Maas Geesteranus, 1975), and to have distinct mycorrhizal hosts. Both of these occur abundantly in California from late summer through winter and are associated with *Picea* and *Tsuga* on the coast and *Pinus*, *Abies* and *Pseudotsuga* in montane and inland forests. *Sarcodon martioflavus* is another species that has a distinct distribution. This species has been collected only in montane regions above 5,000 ft. and is associated with *Abies* sp.

Although the nature of collecting over a wide geographical area did not permit the detailed study of life spans, personal observations on the life span of members of *Hydnellum* and *Sarcodon* suggest that some species develop long lasting basidiomes. No species encountered in this study were perennial. However, because of the indeterminate growth habit of species of *Hydnellum*, the life span could start, stop and

re-start several times as long as conditions remained favorable. For example, I witnessed a basidiome of *Hydnellum cyanopodium* develop in a coastal *Picea sitchensis* and *Tsuga heterophylla* dominated forest from late June 1996 through October, 1996, but was unable to pin-point when it finally deteriorated. The following year in the same location a basidiome of *H. cyanopodium* started in early July 1997, but deteriorated by early September. Likewise, I witnessed basidiomes of *H. scrobiculatum* var. *scrobiculatum* that had life spans of at least two months.

Species of *Sarcodon* do not exhibit indeterminate growth and thus have much shorter life spans. Nevertheless, they have longer life spans than typical agaricoid fungi. I have observed mature basidiomes of *Sarcodon imbricatus* last over two weeks. It is my opinion that they had began fruiting at least a week before and may have persisted one or two more weeks, which would put a conservative estimate on the life span of *Sarcodon imbricatus* at one month.

Indeterminate growth and long life spans in general raises the question of whether or not environmental conditions can affect shape and overall size proportions of morphological characters. The allometric changes in morphologic features will need to be addressed in future studies.

Conclusion

A taxonomic study of the genera *Hydnellum* and *Sarcodon* for northern California is presented. The results of this study are the culmination of three years of collecting by the author throughout northern California. In addition, over 200 herbarium collections have been examined from three different sources (SAFU, UC, & HSC). Macro- and microscopic descriptions are included for each taxon along with a dichotomous key to allow for identification of fresh specimens.

Thirteen taxa of *Hydnellum* and eleven taxa of *Sarcodon* are presented in this study: *Hydnellum aurantiacum, H. aurantile, H. caeruleum, H. cyanopodium, H. geogenium, H. peckii, H. regium, H. scrobiculatum* var. *scrobiculatum, H. scrobiculatum* var. *zonatum* forma *zonatum, H. scrobiculatum* var. *zonatum* forma *parvum, H. suaveolens, H. subzonatum, Hydnellum* WAF131, *Sarcodon atroviridis, S. fuscoindicus, S. glaucopus, S. imbricatus, S. leucopus, S. martioflavus, S. rimosus, S. scabrosus, S. stereosarcinon, S. subincarnatus* and *S. ustale.* Four of these taxa, indicated by an underline, are reported in this study for the first time as occurring in California. *Hydnellum* WAF131 may be a new species.

The classification system of this study differs from previous studies in several important ways. First, it emphasizes the presence of swollen and inflated hyphae in members of the genus *Sarcodon* as a character separating it from the genus *Hydnellum.* Second, two new character states for spore ornamentation were added to more accurately describe the diversity exhibited in the taxa of California. Lastly, this study is the first taxonomic study of the genera *Hydnellum* and *Sarcodon* for California and brings the completion of a North American monograph one step closer.

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