

AN ABSTRACT OF THE THESIS OF

Michael A. Castellano for the degree of Doctor of Philosophy in Forest Science presented on December 12, 1988.

Title: The Taxonomy of the Genus *Hysterangium* (Basidiomycotina, Hysterangiaceae) with Notes on its Ecology.

Abstract approved: _____ Signature redacted for privacy.

James M. Trappe

Hysterangium, a genus of hypogeous Basidiomycotina (false truffles) is commonly placed in the Hysterangiaceae and ascribed affinities to the Phallales. It is a large genus among hypogeous taxa and is commonly collected in large numbers in eastern and western North America, Australasia and Europe. Some *Hysterangium* species are dominant components of the below-ground mycorrhizal network of Douglas-fir forests in the Pacific Northwest and *Eucalyptus* forests and plantations in Australia and New Zealand.

Sixty-eight species and nine varietal names have been proposed within *Hysterangium*. This work conserves 25 species names and raises two varieties to species rank. Thirteen species and 7 varietal names are synonymized, and eighteen other species names are transferred to 9 other genera. Placement of an additional 8 species excluded from *Hysterangium* is uncertain. One species was based on nonsporocarpic material, while no specimens of 3 other species could be located. Eleven new species are provisionally proposed.

The scope of this work is worldwide, with a focus on taxonomy and to a limited extent ecology. Due to the pervasiveness of many *Hysterangium* species in a number of forest communities a better understanding of the taxonomy of *Hysterangium* has considerable ecological importance.

The Taxonomy of the Genus
Hysterangium (Basidiomycotina, Hysterangiaceae)
with Notes on its Ecology
by
Michael A. Castellano

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It was the best of times

It was the worst of times

C. Dickens

(Tale of Two Cities)

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The Taxonomy of the Genus *Hysterangium* (Basidiomycotina, Hysterangiaceae) with Notes on its Ecology

INTRODUCTION

Hysterangium, a genus of hypogeous Basidiomycotina (false truffles) is commonly placed in the Hysterangiaceae and, along with several lesser known genera (i.e., *Circulocolumella*, *Clathrogaster*, *Claustula*, *Clavarula*, *Gallacea*, *Gelopellis*, *Hoehneliogaster*, *Jaczewskia*, *Kobaysia*, *Maccagnia*, *Phallobata*, *Phallogaster*, *Protophallus*, *Protuber*, *Protuberella*, and *Rhopalogaster*) has been traditionally ascribed affinities to the Phallales. *Hysterangium* a large genus among hypogeous taxa, is commonly collected in large numbers in eastern and western North America, Australasia and Europe and has often been mistaken for other hypogeous Basidiomycota, e.g., *Rhizopogon*, *Hymenogaster* and occasionally epigeous genera, e.g., *Clathrus* "eggs." Some *Hysterangium* species are a dominant components of the below-ground mycorrhizal network of Douglas-fir forests in the Pacific Northwest (Cromack et al. 1979) and *Eucalyptus* forests and plantations in Australia (Dell and Malajczuk 1985) and New Zealand (Castellano, unpublished data).

Carlo Vittadini (1831) established *Hysterangium* to accommodate three species, *H. clathroides*, *H. membranaceum*, *H. fragile*. He described each as possessing smooth spores and resembling the "egg stage" of many Phallales. Unbeknownst to Vittadini, and to many later workers, spores of all three species possess a fine ornamentation of minute to distinct verrucae (best seen under oil immersion) beneath the loosely to tightly adhering utricle.

In 1843, the Tulasne brothers proposed an additional species (*H.*

stoloniferum) which differed from their interpretation of Vittadini's previously published species. Unfortunately, the Tulasnes did not study Vittadini's material. *Hysterangium stoloniferum*, upon comparison with Vittadini's specimens, proves to be a synonym of *H. fragile* Vitt. The Tulasnes (1851), again without studying material from Vittadini, proposed another new species, *H. pompholyx* and two new varieties of *H. clathroides*: *H. clathroides* var. *cistophilum*; *H. clathroides* var. *crassum*. This marks the beginning of a long history of misinterpreted species concepts that would plague future workers in this genus.

To add to the confusion, other European workers described new species and varieties of *Hysterangium* without studying material of previous workers (Berkeley 1844, Berkeley and Broome 1848, Hesse 1884, 1891, Quélet 1886, Mattiolo 1900, Bucholtz 1908, Patouillard 1914, Soehner 1921, 1949, 1952, Velenovsky 1939, Svrcek 1958). Still others in Europe contributed species that are better placed in other genera (Bresadola 1900, Malençon 1975) or are not even sporocarpic in nature (De Toni 1888).

The year 1881 saw other workers in different parts of the world, especially Australasia, North America and South America begin to publish new *Hysterangium* species, for the most part without studying material of previous authors (Masseé 1881, Speggazzini 1881, Rodway 1898, 1899, Harkness 1899, Masseé 1901, Fischer 1908, 1938, Rodway 1912, 1918, 1920, Fitzpatrick 1913, Patouillard 1915, Lloyd 1921, 1922, Zeller and Dodge 1929, Cunningham 1934, 1938, Ito and Imai 1937, Zeller 1939, 1941, Corner and Hawker 1953, Cribb 1958, Horak 1964, Pacioni 1985).

Zeller and Dodge (1929) were the only workers to study a majority of the available type specimens. Unfortunately they had too little material of several

important and widespread taxa for accurate interpretation e.g., *H. clathroides*, *H. coriaceum*, *H. setchellii*, and *H. crassum*. This confusion caused many workers doing regional surveys in Europe to cite specimens of *H. coriaceum* as *H. clathroides* and workers in western North America to cite specimens of *H. coriaceum* as *H. separabile*, and those of *H. setchellii* as *H. crassum*.

Regional treatments of *Hysterangium* by Soehner (1952) and Gross et al. (1980) for Germany and by Svrcek (1958) for Czechoslovakia lack critical examination of authentic material and rely upon the often misinterpreted species descriptions in the literature.

Although I have examined many hundreds of collections, only a minority of species were represented by fresh material. Examination of fresh material of additional species will sharpen the accuracy of many of the other descriptions. Consequently, this work is preliminary and subject to revision as adequate collections, either in fresh condition or as herbarium specimens with detailed notes, become available.

I have attempted to incorporate every known *Hysterangium* taxon into this monograph. Sometimes the meager amount of available material for some species did not afford enough data to clarify a species concept. In that case I present as much descriptive data as possible.

The scope of this work is worldwide, with a focus on taxonomy and to a limited extent ecology. A better understanding of the taxonomy of *Hysterangium* is of great ecological importance due to the pervasiveness of many *Hysterangium* species in a number of forest communities. I have incorporated in each species discussion all ecological information available for that species.

METHODS

Methods of collection and macroscopic and microscopic approach were generally those of Smith (Smith and Zeller 1966). Herbarium names are abbreviated according to Holmgren and Keuken (1974). Anatomical features were described from fresh material when available or from dried specimens rehydrated in 5% KOH. Simple macrochemical tests (3% iron sulphate (FeSO_4), 95% ethanol (ETOH), and 5% potassium hydroxide (KOH)) were applied to the peridium and/or gleba of fresh specimens. Melzer's reagent was tested extensively on fresh and dried specimens of many of the species but does not react with tissues or spores of *Hysterangium sensu stricto*, so all references to Melzer's reagent have been omitted except for the excluded taxa. Spore dimensions are based on the measurement of at least 50 randomly selected spores from the type collection with all dimensions beyond that range from other collections included in parentheses; spore lengths include sterigmal attachment; spore widths do not include the utricle, except where noted. Measurement of sterile tissues (e.g., peridium) and spores were for the most part from mature sporocarps. Light photomicrographs are from material mounted in 5% KOH or rarely methuian red. Dried herbarium material was prepared for scanning electron microscopy by dusting air-dried spores onto double-sided sticky tape which was mounted on a peg. Fungal material was then covered with approximately 100 Å ($1 \text{ Å} = 0.1 \text{ nm}$) of gold-palladium alloy (60:40), and photographed with an Amray 2000 scanning electron microscope on P/N 55 Polaroid film.

Numbers on the maps correspond to the number of collections examined and are placed according to collection locality (by county or city) when

available.

Many herbarium collections had poor labels containing little, if any, legible information. While it is not critical to have notes on fresh characters of *Hysterangium* species for identification, it is highly desirable to have notes as to collection locality, potential mycorrhizal partners, and time of year. When possible notes on sporocarp and glebal color, bruising reaction, surface texture, characteristics of rhizomorphs and columella, locule size and arrangement, macrochemical reactions of the gleba and peridium are helpful to the monographer when studying the specimens after they have been preserved.

Color names are in general terms of the author or were taken from the original published description or from information available with the collection. Precise color determination is of little value in differentiating species of *Hysterangium*.

Species descriptions are arranged alphabetically by epithet.

HERBARIA

Collections were examined from the following 61 herbaria (in 25 countries and 12 of the United States): Waite Agricultural Institute, Adelaide, South Australia (ADW), Università degli Studi di L'Aquila, Italy (AQUI), Universidad de Buenos Aires, Argentina (BAFC), Hungarian Natural History Museum, Budapest, Hungary (BP), National Fungus Collections, Beltsville, Maryland (BPI), Slovenské Národné Múzeum, Bratislava, Czechoslovakia (BRA), University of Copenhagen, Denmark (C), Centraalbureau voor Schimmelcultures, Baarn, The Netherlands (CBS), Institutul Agronomic "Dr. Petru Groza," Cluj, Romania (CLA), Cornell University, Ithaca, New York (CUP),

Biosystematics Research Institute, Ottawa, Canada (DAOM), Biological and
 Chemical Research Institute, Rydalmere, New South Wales, Australia (DAR),
 Royal Botanic Garden, Edinburgh, Scotland (E), Central Washington State
 College, Ellensburg (ELRG), Field Museum of Natural History, Chicago, Illinois
 (F), Farlow, Harvard University, Boston, Massachusetts (FH), University of
 Florida, Gainesville (FLAS), Northern Arizona University, Flagstaff (FSLF),
 Conservatoire et Jardin Botaniques, Chambésy, Belgium (GKC), University of
 Helsinki, Finland (H), Martin Luther Universität, Halle, East Germany (HAL),
 Universität Hamburg, West Germany (HBG), University of Tasmania, Hobart,
 Australia (HO), Universität Innsbruck, Austria (IB), University of Idaho, Moscow
 (ID), Friedrich Schiller Universität, Jena, East Germany (JE), Royal Botanic
 Gardens, Kew, England (K), Rijksherbarium, Leiden, The Netherlands (L),
 University of Lund, Sweden (LD), V.L. Komarov Botanical Institute of the
 Academy of Sciences, Leningrad, Russia (LE), Université de Liege, Belgium
 (LG), University of Łódź, Poland (LOD), Instituto de Botanica "Spegazzini," La
 Plata, Argentina (LPS), Botanische Staatssammlung, Munich, West Germany
 (M), Instituto Botanico A. J. Cavanilles, Madrid, Spain (MA), Fachbereich
 Biologie der Philipps-Universität, Marburg, West Germany (MB), Jardin
 Botanique National de Belgique, Meise, Belgium (MEISE), University of
 Melbourne, Australia (MELU), University of Michigan, Ann Arbor (MICH), Institut
 de Botanique, Montpellier, France (MPU), University of North Carolina, Chapel
 Hill (NCU), New York Botanical Garden, Bronx (NY), Universitetet i Oslo,
 Norway (O), Oregon State University, Corvallis (OSC), University of Oulu,
 Finland (OULU), Muséum National d'Histoire Naturelle, Paris, France (PC),
 Department of Scientific and Industrial Research, Auckland, New Zealand
 (PDD), Národní Muzeum, Prague, Czechoslovakia (PR), Plant Protection

Research Institute, Pretoria, South Africa (PREM), Città Universitaria, Rome, Italy (RO), Swedish Museum of Natural History, Stockholm, Sweden (S), San Francisco State University, California (SFU), Staatliches Museum für Naturkunde, Ludwigsburg, West Germany (STU), Istituto Botanico della Università, Torino, Italy (TO), University of Toronto, Ontario, Canada (TRTC), University of Turku, Finland (TUR), University of California, Berkeley (UC), University of Uppsala, Sweden (UPS), Naturhistorisches Museum, Wien, Austria (W), University of Washington, Seattle (WTU), Institut für Spezielle Botanik, Zürich, Switzerland (ZT).

ECOLOGY

Various *Hysterangium* species are found in abundance with many different ectomycorrhizal host plants throughout the world (Table 1).

Hysterangium setchellii, *H. coriaceum*, and *H. crassirhachis* are common associates of Douglas-fir in western North America, while *H. gardneri*, *H. inflatum* and *H. affine* are common associates of various *Eucalyptus* spp. throughout the world.

Fogel (1976) found *H. setchellii* (as *H. crassum*) and *H. coriaceum* (as *H. separabile*) to comprise a major portion of the sporocarpic biomass of hypogeous fungi in a western Oregon Douglas-fir stand. *Hysterangium setchellii* and *H. coriaceum* formed up to 8617 and 3139 sporocarps per hectare, respectively, and up to 1206 and 572 grams dry weight per hectare, respectively. These two fungi accounted for over 70% of all hypogeous sporocarps and dry weight produced. In a similar single stand study, Hunt and

Trappe (1987) found *H. setchellii* (as *H. crassum*), and *H. coriaceum* produced up to 3770 and 1833 sporocarps per hectare, and 842 and 204 gr/ha, respectively. Combined this accounted for over 80% of all hypogeous sporocarps found and over 50% of the dry weight produced. In a third study encompassing ten Douglas-fir stands, Luoma (1988) found *H. setchellii* and *H. coriaceum* to constitute only 60 gr/ha and 178 gr/ha, respectively. The Douglas-fir stands studied by Fogel (1976) and Hunt and Trappe (1987) were located at less than 500 m elevation in the Coast Ranges of Oregon while Luoma (1988) studied Douglas-fir stands at 500-1500 m elevation in the western Cascades of Oregon.

In addition to the relative abundance of *Hysterangium setchellii* in the Oregon Coast Ranges, it appears to be an important component of site productivity. perennial hyphal mats formed by *Hysterangium setchellii* in the soils of a 40-65 year-old Douglas-fir stand in Oregon occupied up to 16.7% (mean of 9.6%) of the upper 10 cm of soil (Cromack et al. 1979). *Hysterangium setchellii* exudes large amounts of oxalic acid (Cromack et al. 1979), which is thought to aid in the chemical weathering of clay soils (Graustein et al. 1977, Malajczuk and Cromack 1982). Griffiths et al. (1987) found *H. setchellii* hyphal mats are significantly higher in microbial biomass and respiration rate than adjacent nonmat soil. When comparing respiration rate on a per unit of biomass basis, hyphal mats are over three times more active than nonmat soil. In addition, mat soils have significantly higher (up to 62 times greater) levels of phosphatase, protease and laminarinase than nonmat soils. These enzymes are involved in the breakdown of organic material, especially organic

Table 1. Distribution of *Hysterangium* species.

Species	North America	Europe	Austral- asia	South America	North India	Africa
<i>affine</i>			x	x		
<i>agglutinatum</i>			x			
<i>aggregatum</i>			x			
<i>album</i>	x					
<i>americanum</i>	x					
<i>angustisporum</i>	x					
<i>asperulatum</i>	x					
<i>aureum</i>	x					
<i>calcareum</i>		x				
<i>cistophilum</i>		x			x	
<i>clathroides</i>	x	x				
<i>coriaceum</i>	x	x				
<i>crassirhachis</i>	x					
<i>crassum</i>		x				
<i>epiroticum</i>		x				
<i>fallax</i>	x					
<i>fragile</i>	x	x				
<i>gardneri</i>	x	x	x		x	
<i>gelatinosporum</i>			x			
<i>inflatum</i>	x	x	x		x	
<i>irregulare</i>			x			
<i>malaiense</i>			x			
<i>membranaceum</i>	x	x				x
<i>neotunicatum</i>			x			
<i>nephriticum</i>		x				
<i>occidentale</i>	x					
<i>ochraceogleba</i>	x					
<i>olivaceonigrum</i>			x			
<i>parvisporum</i>			x			
<i>pompholyx</i>		x				
<i>rhodocarpum</i>		x				
<i>rugisporum</i>			x			
<i>salmonaceum</i>			x			
<i>separabile</i>	x					
<i>setchellii</i>	x					
<i>simulans</i>			x			
<i>strobilus</i>	x					
<i>thwaitesii</i>		x				

phosphorus, protein and fungal cell walls. *Hysterangium setchellii* mat soil also has significantly higher levels of total nitrogen, phosphorus, potassium, calcium, magnesium, and various other micronutrients than nonmat soils (Entry et al. 1987). This is probably due to the high levels of oxalic acid produced by the fungus. Oxalic acid forms an insoluble precipitate with calcium, iron and aluminum thereby increasing the concentration of other nutrients in solution (Graustein et al. 1977). *Hysterangium setchellii* hyphal mats also preferentially use organic nitrogen and are more efficient at obtaining and retaining atmospheric nitrogen than adjacent nonmat soil (Griffiths, unpublished data).

Dell and Malajczuk (1987) found *H. inflatum* to form hyphal mats similar to those of *H. setchellii*, occupying up to 10% of the soil surface under *Eucalyptus diversicolor* and *E. marginata* stands in Australia.

Hysterangium is a significant portion of the diet of deer mice (*Peromyscus maniculatus*) in western Oregon (Maser, C. and Maser, Z. 1987); yellow-pine chipmunk (*Eutamias amoenus*) in northeastern Oregon (Maser, Z. and Maser, C. 1987); western red-backed vole (*Clethrionomys californicus*) in southwest Oregon (Hayes et al. 1986); and the northern flying squirrel (*Glaucomys sabrinus*) in northwestern Oregon (Maser et al. 1985).

PHYLOGENY

Hysterangium has traditionally been related to the phalloid fungi due to its resemblance to the Phallales "egg stage," possession of "smooth" spores, and a green tint to the gleba (Beaton et al. 1985, Cunningham 1943, Dodge 1928, Dring 1973, Gross et al. 1980, Fischer 1900, 1933, Hawker 1954, Rehsteiner 1892, Svrcek 1958, Zeller 1939, 1949). This artificial grouping

based on a number of characters, one of which was commonly misinterpreted ("smooth" spores), has led to a polyphyletic origin of the genus *Hysterangium sensu lato*. As can be seen from the excluded taxa list, many mycologists have mistakenly placed new taxa into *Hysterangium*, e.g., *Truncocolumella carneorosea* (Horak) Castellano comb. prov., *Protubera burburiana* (Rodway) Castellano comb. prov., *Chondrogaster pachysporus* Maire, *Phallobata alba* Cunningham among others. Much of the difficulty with species placement can be traced to unfamiliarity with the original concept of the genus and the lack of study of type specimens.

I envision two phylogenetic schemes for derivation of *Hysterangium sensu lato*. Both are based on increase in spore size, progression towards ornamentation, associated hosts, and geographic distribution as determined from available collections.

I assume that the hypogeous habit is an adaptation to environmental pressure and that spore dispersal is by animals. Mycophagy exposes the sporocarpic tissues to digestive acids and enzymes which completely break down the sterile tissue, while the spores pass through the animals digestive tract without apparent morphological change. How the digestive chemicals affect the biochemistry of the spore (especially germinability) is unknown. I propose that this chemical and heat exposure selects in favor of fungal genotypes with either a thicker spore wall, some form of ornamentation (in itself one form of wall thickening) or a loosened utricle (a form of wall protection).

Corner (1972) believes that an advanced hymenium would have crowded spores and increased spore volume through extension along the longitudinal axis e.g., spore length. In the first phylogenetic scheme I propose this would be important since the derived species have larger spores than their

ancestors.

Several studies deal with the specific association of some mycorrhizal fungi with particular hosts (Malajczuk et al 1980, Molina 1981, Molina and Trappe 1983, Trappe 1962). Host specificities also seem to be true for *Hysterangium*: some species are found only in association with *Eucalyptus*, some only with Pinaceae, and still others only with Fagaceae. The associated hosts and their geographic distribution have been reliable characters and helpful in species identification.

In one hypothesis, *Hysterangium sensu lato* is derived from at least four distinct sources within the Phallales. *Hysterangium sensu lato* morphologically resembles many genera of Phallales in several ways. The white, separable peridium of many *Hysterangium* spp. resembles the "volva" in the Phallales. The cord-like basal rhizomorph of some *Hysterangium* spp. approaches in morphology that of some Phallales (Townsend 1954). Several *Hysterangium* spp. develop the characteristic "stinkhorn" smell. In addition, the green gleba which deliquesces at maturity in *Hysterangium* is analogous to the slimy green spore mass of many Phallales.

I use species names as reference only and do not intend to imply direct parentage. If we start (fig. 1) with the Claustulaceae, *Claustula fischeri* (small, smooth spores without a utricle) gives rise to *Hysterangium parvisporum* (small, smooth spores without a utricle), which in turn gives rise to *H. rugisporum* (larger, ornamented spores with a utricle). Next, the Clathraceae gives rise to *Protuberia* (small, smooth spores without a utricle) from which *H. gardneri* and *H. inflatum* (larger, smooth spores with a loosened utricle) are derived. The third line starts through *Phallogaster saccatus* Morgan (1892) which is also derived from the Clathraceae and gives rise to the genus *Trappea* (small,

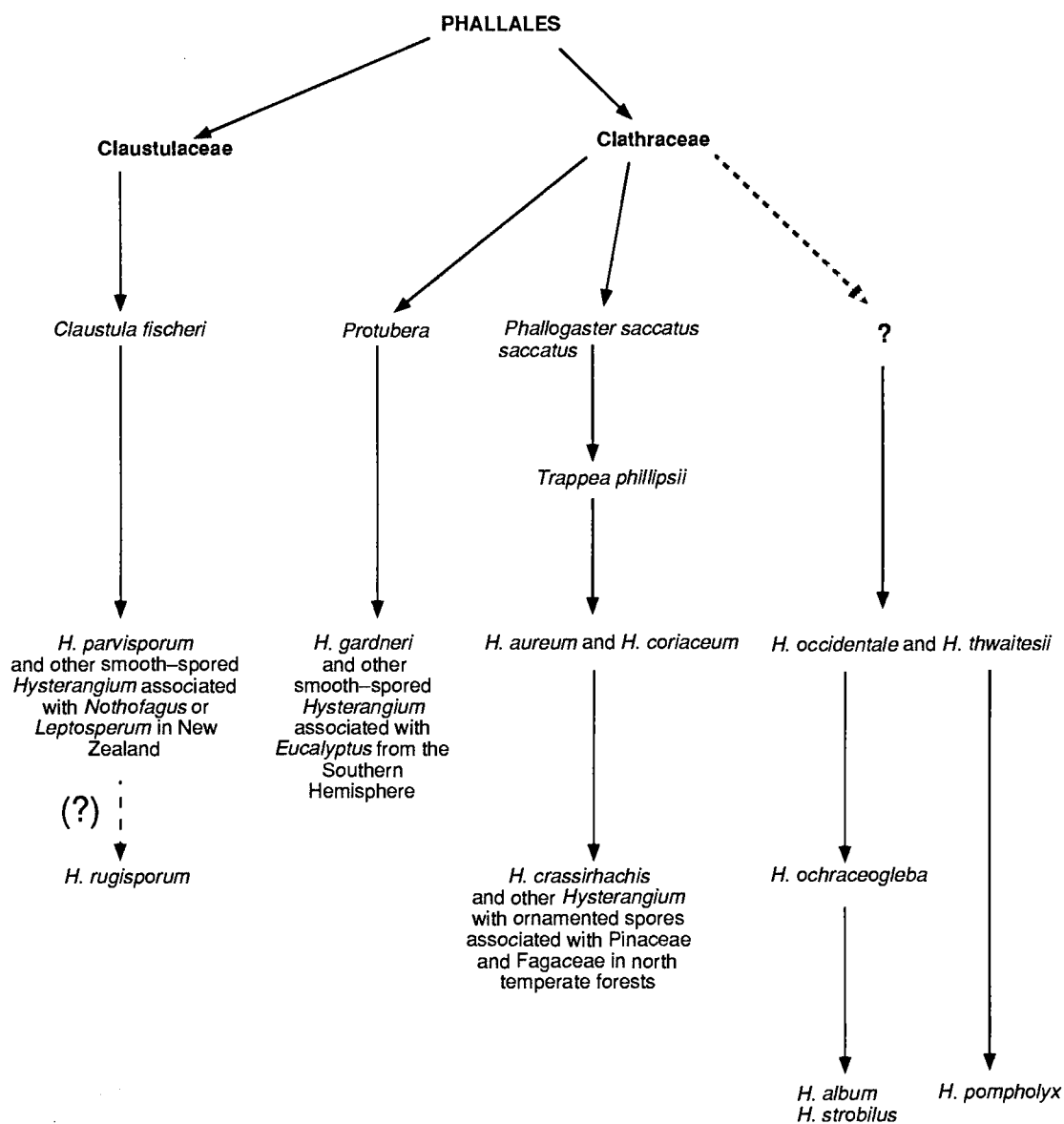


Figure 1. Preliminary phylogenetic derivation of *Hysterangium sensu lato*. Fungal species are listed for reference only, not because of direct parental relationship.

smooth spores without a utricle) which is the predecessor to *H. aureum* and *H. coriaceum* (larger, smooth spores with a utricle) from which *H. crassirhachis* (ornamented spores with a utricle) and a number of other north temperate *Hysterangium* are derived. Finally, I derive would *H. occidentale* and *H. thwaitesii* (smooth spores, without a utricle and with a gleba lacking green tints) in a separate but presently unknown line from the Clathraceae. *Hysterangium occidentale* gives rise to *H. ochraceogleba* from which *H. album* and *H. strobilus* are derived. *H. pompholyx* is derived from *H. thwaitesii*. In all cases small spores precede larger spores, smooth spores precede ornamented spores, and absence of a utricle precedes possession of a distinct utricle.

The other phylogenetic scheme has never been proposed before but deserves further investigation. I envision close similarities of spore shape, color and ornamentation of some genera in the Boletales (e.g. *Austroboletus*, *Boletus*, *Leccinum*, *Pulveroboletus*, and *Tylopilus*) with many species in *Hysterangium sensu lato*. Under this scheme *Hysterangium* is also polyphyletic in origin.

The Boletaceae *sensu* Pegler and Young (1981) possess strongly gelatinized tramal tissue in concordance with the strongly gelatinized tramal tissue of *Hysterangium*. The distinct columella of many *Hysterangium* species is similar to the distinct columella of many *Gautieria* species; *Gautieria* has been aligned with the genus *Boletellus* of the Boletales. Many species of Boletales have an olive or pale brown spore deposit, ellipsoid to subfusiform, smooth to distinctly ornamented spores; some possess a tightly adhering utricle (Pegler and Young 1981, Wolfe 1980).

Many Bolete species could have served as forerunners to species within *Hysterangium sensu lato*. For example, *Boletus chrysenteron* Fries has smooth,

ellipsoid to subcylindric, olive (in mass) spores which measure 12-13.5 x 5-6 μm (Smith and Thiers 1971); these spores are similar to those of *Hysterangium coriaceum* Hesse: 10-14 x 4-5 μm , smooth, and ellipsoid. Another ancestral parent could be *Austroboletus festivus* (Singer) Wolfe from Argentina with narrowly ellipsoid, yellow-cinnamon, punctulate spores that are 13-17 x 5-6.5 μm and possess a closely appressed utricle (Wolfe 1980). This taxon compares well with *Hysterangium angustisporum* Castellano and States nom. prov. from the southwest United States with narrowly ellipsoid, pale green to olive, minutely verrucose spores that are 16-17 x 5 μm with a distinct closely appressed utricle.

Recently, techniques have been developed that allow workers to isolate minute amounts of DNA from preserved specimens (even field dried). This minute amount of DNA, which can be partially degraded, can be reconstituted and amplified hundreds of millions of times to allow the direct sequencing of mitochondrial and genomic DNA. With the simplification of DNA analysis, hypotheses of phylogeny for many fungi can be tested with a powerful new approach. DNA analysis may confirm that *Hysterangium sensu lato* is polyphyletic in origin and is derived at least in part from both the Boletales and Phallales.

TAXONOMY

Hysterangium Vittadini, Monogr. Tuberac. 13-15. 1831.

Basidiomata globose, subglobose or irregular. **Peridium** thin or up to 1 mm thick, white to salmon pink, pale yellow, or pale brown, in many species staining pink to brown where bruised, often readily separable from the gleba, in many species giving rise to numerous hyphae and rhizomorphs on the base and sides of sporocarps or overall. **Gleba** pink to gray, grayish green, olive, or pale brown, with small to prominent, usually labyrinthine locules and a poorly to strongly developed, dendroid, gelatinous to cartilaginous, gray to reddish brown columella. **Odor** not distinctive to fruity, wine-like, or nauseous-sweet.

Basidia in a euhymenium, hyaline to occasionally pale brown, thin-walled, 2-6 spores per basidium. **Subhymenial layer** poorly developed to inconspicuous. **Spores** statismosporic, orthotrophic, smooth to moderately ornamented (verrucure), with or sometimes without a wrinkled to loose utricle. Narrowly ellipsoid or fusoid, sterigmal attachment straight, inconspicuous to truncate-cupped. Hyaline, pale green, pale olive to pale brownish yellow in H₂O or KOH. No distinctive reaction to Melzer's reagent.

DEVELOPMENT: Angiocarpic and hypogaeal.

ETYMOLOGY: Named by Vittadini (1831) from the Greek *hyster-* (womb) and *-angion* (a vessel, a term used by the 19th century mycologists to mean "sporocarp"), hence a "womb-vessel," a redundant way of saying "spore-bearing vessel" or sporocarp.

Type species: *Hysterangium clathroides* Vittadini.

KEY TO HYSTERANGIUM

1. Gleba red or brown, **not** some shade of green.....2
1. Gleba some shade of green or olive..... 1 0

2. Gleba pink when fresh, red brown when dry, spores smooth, 12–16 x 5–7 μm , citriform, distinctly pedicellate, peridium two-layered, epicutis of loosely interwoven to mostly periclinal hyphae, subcutis of interwoven, inflated hyphae, 10–15 x 18–35 μm *H. occidentale* (p. 104)
2. Gleba ochraceous or brown, **without** reddish tints, peridium not as above3

3. Peridium 300–400 μm thick, of hyaline to pale brown, thin-walled, agglutinated, irregularly shaped, compactly interwoven hyphae, 5–8 μm in diam, spores smooth, 12–15 x 5.5–7 μm , broadly ellipsoid, spore wall up to 1 μm thick, thicker at apex, covered with a mucilaginous substance *H. ochraceogleba*
3. Not as above.....4

4. Utricle usually **absent**, when present , slight, wrinkled, adhering to spore5
4. Utricle **present**, usually distinctly rough looking, spores not smooth....6

5. Spores finely verrucose, 17–20 x 6–7 μm , fusiform, utricle sometimes present, peridium 100–200 μm thick, of compact, irregularly shaped, interwoven hyphae, 5–10 μm in diam..... *H. album*
5. Spores smooth, 12–16 x 5–7 μm , citriform, distinctly pedicellate, utricle absent, peridium two-layered, epicutis of loosely interwoven to mostly periclinal hyphae, subcutis of interwoven, inflated hyphae, 10–15 x 18–35 μm *H. occidentale* (p. 104)

6. Peridium **distinctly** two-layered.....7
6. Peridium of more or less one layer with some gradation in tissue size..8

7. Peridium 140–350 μm thick, epicutis 100–250 μm thick, of thick-walled, loosely interwoven to subpericlinal hyphae, 3–4 μm in diam, with abundant crystalline particles adhering to hyphae, subcutis 40–100 μm thick, of thin-walled, irregular to subglobose cells, 5–8 μm in diam, spores smooth at first, finely verrucose at maturity, 13–18 x 4–6 μm ***H. nephriticum*** (p. 101)
7. Peridium 180–260 μm thick, epicutis 100–140 μm thick, of thin-walled, inflated, interwoven hyphae 6–10 x 10–26 μm , subcutis 40–50 μm thick, of interwoven to subpericlinal hyphae, 1–3 μm in diam, spores distinctly verrucose, 13–15 x 6–8 μm ***H. asperulatum*** (p. 43)
8. Peridium 200–250 μm , of dark reddish brown, inflated cells up to 50–70 μm in diam, spores smooth to finely verrucose, 12–16 x 5–7 μm , with a distinct roughened utricle, 1 μm thick, often stuck together in pairs..... ***H. pompholyx*** (p. 113)
8. Not as above, utricle usually 2 μm thick **9**
9. Peridium 100–200 μm , of elongate or irregularly shaped to slightly inflated, capitate, compactly interwoven hyphae, 2–3 μm in diam near gleba and surface, 6–8 μm in diam in the middle, spores coarsely verrucose, 12–17 (-18) x 5–6 μm , broadly fusiform, apex papillate, base slightly appendaged, utricle 2 μm thick, totally enclosing spore, attached at base ***H. strobilus*** (p. 135)
9. Peridium 140–300 μm , of interwoven to subpericlinal, somewhat agglutinated hyphae, 2–4 μm in diam, brown near outside, hyaline within, spores finely verrucose, 12–15 x 6–7.5 μm , apex obtusely blunt, base distinctly pedicellate, utricle 2 μm thick, attached at base..... ***H. gelatinosporum*** (p. 85)
10. Peridium of **one** tissue type which can be variable in cell diameter ... **1 1**
10. Peridium of **two or more** tissue types..... **2 7**
11. Peridium of parenchyma-like cells, not inflated hyphae..... **1 2**
11. Peridium of interwoven or periclinal hyphae, occasionally inflated..... **1 3**

12. Peridium 325–450 μm thick, of a single layer of inflated cells (parenchyma-like), 50–75 μm in diam, spores smooth, 11–12.5 x 4–5 μm , apex acuminate, utricle closely appressed, slightly wrinkled, mostly on young spores *H. aureum* (p. 45)
12. Peridium 100–250 μm thick, a single layer of inflated cells (parenchyma-like), 30–40 x 50–75 μm , spores smooth, 12–15 x 4–5 μm , apex acuminate, utricle thick, irregularly inflated to 1 μm , attached at base of spore *H. affine* (p. 27)
13. Utricle **usually absent** or when present slight 14
13. Utricle **distinct** usually present on all spores..... 19
14. Utricle absent never present..... 15
14. Utricle inconspicuous, usually absent on young spores..... 16
15. Peridium 500–1000 μm thick, of compact, interwoven hyphae, 5–20 μm in diam, spores smooth, 8–12 x 4–5 μm , utricle absent
.....*H. malaiense* (p. 93)
15. Peridium 410–480 μm thick, usually two-layered but sometimes the subcutis is difficult to see, epicutis 400–450 μm thick, of hyaline to pale brown, compact, periclinal hyphae, 4–6 μm in diam, subcutis not easily observed, 10–30 μm thick, of hyaline, clavate shaped inflated cells, 35–55 x 15 μm , spores smooth, 10–12 x 3.5–4.5 μm , utricle absent.....
.....*H. agglutinatum* (p. 31)
16. Sporocarps extremely small, 2–3 (–6) mm in diam, embedded in a mass of soil, roots, and mycelium, peridium 70–90 μm thick, of interwoven hyphae, 3–5 μm in diam, spores 13–17 x 4–7 μm , utricle irregular.....
.....*H. aggregatum* (p. 33)
16. Sporocarps mostly larger than 5 mm, spores not as above 17

17. Peridium 100–200 μm thick, of compact, irregularly shaped, interwoven hyphae, 5–10 μm in diam and up to 20 μm long, spores finely verrucose 17–20 x 6–7 μm , utricle absent or slight, wrinkled, closely adhering to spore *H. album* (p. 36)
17. Spores **equal to or less than** 15 μm long **18**
18. Peridium 400–600 μm thick, of elongate to irregular, gradually inflated hyphae, 3–4 μm in diam near gleba, 9–12 x 30–40 μm near outer edge, spores 9–10 x 3.5–4 μm , utricle absent or when present irregularly inflated *H. gardneri* (p. 81)
18. Peridium 100–200 μm thick, of pale brown, irregularly inflated hyphae, 4–5 μm in diam, up to 15 μm in diam, spores smooth, 10–11 x 5 μm , utricle inconspicuous, usually tightly appressed to spore wall *H. irregulare* (p. 90)
19. Spores finely to coarsely **verrucose** under oil immersion..... **20**
19. Spores **smooth**..... **21**
20. Peridium 100–200 μm , of elongate or irregularly shaped to slightly inflated, capitate, compactly interwoven hyphae, 2–3 μm in diam near gleba and surface, 6–8 μm in diam in the middle, spores coarsely verrucose, 12–17 (–18) x 5–6 μm , broadly fusiform, apex papillate, base slightly appendaged, utricle 2 μm thick, totally enclosing spore, attached at base *H. strobilus* (p. 135)
20. Peridium 100–200 (–350) μm thick, of interwoven hyphae 2–5 (–6) μm in diam, with scattered groups of inflated cells 15–30 μm in diam, spores verrucose, 15–18 x 6–7 μm , fusoid, apex acuminate to papillate, utricle up to 1 μm thick, wrinkled and rough looking *H. membranaceum* (p. 95)

21. Peridium 140–250 μm thick, of irregularly shaped, loosely interwoven hyphae which are occasionally inflated, up to 5 μm in diam near gleba, usually up to 12 x 25 μm in mediostratum, spores smooth, 9–12 x 4–5 μm without utricle, 9–12 x 8–9 μm with utricle, utricle distinct, regularly inflated up to 2.5 μm thick, attached at base and apex of spore to form a cylinder *H. inflatum* (p. 87)
21. Spores and peridium not as above **2 2**
22. Sporocarps extremely small, 2–3 (–6) mm in diam, embedded in a mass of soil, roots, and mycelium, peridium 70–90 μm thick, of interwoven hyphae, 3–5 μm in diam, spores 13–17 x 4–7 μm , utricle irregular.....
.....*H. aggregatum* (p. 33)
22. Sporocarps mostly **greater than 5 mm** in diam, peridium mostly greater than 100 μm thick..... **2 3**
23. Peridium 400–600 μm thick, of elongate to irregular, gradually inflated hyphae, 3–4 μm in diam near gleba, 9–12 x 30–40 μm near outer edge, spores 9–10 x 3.5–4 μm , utricle absent or when present irregularly inflated *H. gardneri* (p. 81)
23. Spores mostly **equal to or greater than** 11 μm long and at least 4 μm wide **2 4**
24. Peridium equal to or less than 200 μm thick and spores equal to or less than 12 μm long **2 5**
24. Peridium thicker than 200 μm and spores usually longer than 12 μm **2 6**

25. Peridium white, unchanging when dried, 100–200 μm thick, of hyaline within, pale brown without, loosely interwoven hyphae, 4–5 μm within, 2–3 μm without, spores smooth, 10–12 x 4 μm , utricle distinct, irregularly inflated, usually not extending beyond spore apex.....
..... ***H. olivaceonigrum*** (p. 109)
25. Peridium mottled white, pale brown and pale orange brown when dried, 50–150 μm thick, of pale golden brown, more or less uniform, compactly interwoven hyphae, 4–7 μm in diam, with much adherent crystalline particles, spores 10–12 x 4–4.5 μm , utricle absent in youth, distinct in age, irregularly inflated up to 2 μm thick..... ***H. simulans*** (p. 133)
26. Peridium easily separable from gleba, 500–600 μm thick, of brownish yellow, periclinal to slightly interwoven hyphae, spores smooth, 11–18 x 4–5 μm , apex acuminate to papillate, utricle thin at first, thickening with age..... ***H. calcareum*** (p. 48)
26. Peridium not easily separable from gleba, up to 600 μm thick, of pale reddish brown, much inflated, agglutinated hyphae, 5–43 μm in diam, spores smooth, 15–20 x 4.5–6 μm , apex acuminate, utricle loosely adherent, to slightly inflated, attached at base of spore
..... ***H. salmonaceum*** (p. 121)
27. Spores smooth, 7–9 x 3–4 μm , apex obtusely blunt, base pedicellate, utricle absent, peridium 575–750 μm thick, epicutis 500–600 μm thick, of inflated cells (parenchyma-like), 25–50 μm in diam, subcutis 75–150 μm thick, of interwoven to subpericlinal hyphae, 1–3 μm in diam.....
..... ***H. parvisporum*** (p. 111)
27. Spores mostly equal to or greater than 10 μm long and 4 μm wide **28**
28. Spores **mostly equal to or greater than** 20 μm long..... **29**
28. Spores not as above..... **30**

29. Peridium 400–600 μm thick, three-layered, epicutis 85–125 μm thick, of pale brown, interwoven hyphae 5–8 μm in diam, mesocutis 200–300 μm thick, of hyaline to pale brown, subglobose to broadly ellipsoid cells (parenchyma-like), 10–35 μm in diam, subcutis 20 μm thick, of pale brown, interwoven hyphae, 1–4 μm in diam, spores verrucose, 18–29 x 5–8 μm *H. epiroticum* (p. 73)
29. Peridium 450–500 μm thick, two-layered, epicutis 350–400 μm thick, of hyaline subglobose cells, 10–25 (–40) μm in diam, subcutis 80–110 μm thick, of hyaline, interwoven hyphae, spores verrucose, 20–24 x 6–7 μm *H. fragile* (p. 78)
30. Peridium of interwoven hyphae, sometimes inflated to some degree. **31**
30. Peridium with a distinct layer of parenchyma-like cells..... **35**
31. Spores **smooth** under oil immersion..... **32**
31. Spores finely **verrucose** under oil immersion **33**
32. Peridium 140–300 μm thick, epicutis 70–150 μm thick, of brown, thick-walled, gelatinized, interwoven hyphae, 2–3 μm in diam, subcutis 70–150 μm thick, of hyaline, interwoven hyphae, 5 μm in diam, spores smooth, 16–19 x 5–7 μm , fusiform, utricle mostly absent, or adhering closely to spore *H. thwaitesii* (p. 138)
32. Peridium 140–350 μm thick, epicutis, 100–250 μm thick, of hyaline thick-walled, loosely interwoven to periclinal hyphae, 3–4 μm in diam, subcutis 40–100 μm thick, of hyaline, irregular to subglobose hyphal cells, 5–8 μm in diam, spores smooth at first, then finely verrucose, 13–18 x 4–6 μm , ellipsoid, utricle to 1 μm in age, spores adhering together in age..... *H. nephriticum* (p. 101)

33. Peridium 420–630 μm thick, epicutis 400–580 μm thick, of hyaline, compact, inflated, interwoven hyphae, 10–15 x 20–30 μm , somewhat smaller near outer edge, subcutis 20–50 μm thick, of hyaline, subpericlinal to interwoven hyphae, 2–4 (–8) μm in diam, spores finely verrucose, 13–15 x 4–5.5 μm , elliptic, utricle loosened in age *H. crassirhachis* (p. 67)
33. Spores mostly **greater than** 5.5 μm wide and 15 μm long **34**
34. Peridium 250–350 μm thick, epicutis 210–290 μm thick, of hyaline to pale yellow, thick-walled, interwoven hyphae, 4–7 μm in diam, subcutis 40–60 μm thick, similar to epicutis but of thin-walled hyphae, spores verrucose, 15–18 x 6–7 μm , fusiform, utricle wrinkled and appressed to spore *H. clathroides* (p. 54)
34. Peridium 200–450 μm thick, epicutis 100–200 μm thick, of hyaline to pale brown, thin-walled, loosely interwoven hyphae, 3–5 μm in diam, subcutis 75–250 μm thick, of hyaline, thin-walled, compact, interwoven hyphae, 2–3 μm in diam. occasionally inflated to 10 μm , spores finely verrucose, 14–19 x 5–6 μm , fusiform, utricle to 1 μm thick, wrinkled *H. setchellii* (p. 128)
35. Peridial **subcutis of inflated cells** (parenchyma-like) **36**
35. Peridial **subcutis of interwoven hyphae** **39**
36. Peridium up to 800 μm thick, epicutis 80–300 μm thick, of hyaline, bead-like hyphae, 2–5 μm in diam, mesocutis 200–400 μm thick, of irregularly shaped, inflated cells (subparenchyma-like), up to 20 μm in diam, subcutis 60–80 μm thick, of collapsed inflate cells (parenchyma-like), spores finely verrucose, 12–16 x 5–6 μm , utricle 1 μm thick, adhering to spore *H. rugisporum* (p. 119)
36. Peridium less than 500 μm thick, **not** three-layered **37**

37. Peridium 410–480 μm thick, epicutis 400–450 μm thick, of hyaline to pale brown, compact, periclinal hyphae, 4–6 μm in diam, subcutis not easily observed, 10–30 μm thick, of hyaline, clavate shaped, inflated cells, 35–55 x 15 μm , spores smooth, 10–12 x 3.5–4.5 μm , utricle absent *H. agglutinatum* (p. 31)
37. Peridium less than 350 μm thick, spores **not** smooth, usually equal to or greater than 13 μm long **38**
38. Peridium 130–290 μm thick, epicutis 30–40 μm thick, of hyaline, loosely interwoven hyphae, 3–8 μm in diam, subcutis 100–250 μm thick, of hyaline, inflated cells (parenchyma-like), 10–20 μm in diam, spores verrucose, 15–17 x 6–7, broadly fusiform, utricle distinct, 1 μm thick, appressed *H. crassum* (p. 71)
38. Peridium 200–220 μm thick, epicutis 20–70 μm thick, of hyaline, loosely interwoven to mostly periclinal hyphae, 2–5 μm in diam, subcutis 150–200 μm thick, of hyaline, irregularly shaped, inflated cells (parenchyma-like), 8–30 μm in diam, spores verrucose, 13–15 x 5–7, broadly fusiform, utricle distinct, appressed to loosened *H. cistophilum* (p. 51)
39. Peridial subcutis **less than** 50 μm thick **40**
39. Peridial subcutis **greater than** 50 μm , usually ca. 100 μm **43**
40. Peridium 420–630 μm thick, epicutis 370–580 μm thick, of hyaline, compact, inflated (subparenchyma-like), interwoven hyphae, 10–15 x 20–30 μm , subcutis 20–50 μm thick, of hyaline, subpericlinal to interwoven hyphae, 2–4 μm in diam, spores finely verrucose, 13–15 x 4–5.5 μm , elliptic, utricle adhering to spore, loosened in age *H. crassirhachis* (p. 67)
40. Epicutis cells **greater than** 30 μm , typically 50–80 μm in diam **41**
41. Spores elliptical or elongate **42**
41. Spores **distinctly** fusiform **45**

42. Peridium 550–600 μm thick, epicutis 500–550 μm thick, of hyaline to brown (outer 50 μm), inflated cells (parenchyma-like), (20–) 40–70 μm in diam, subcutis 30–50 μm thick, of hyaline, interwoven to periclinal hyphae, 2–4 μm in diam, spores verrucose, 16–17 x 5 μm , elongate to narrowly ellipsoid, with closely appressed utricle
 ***H. angustisporum*** (p. 41)
42. Spores 10–15 x 4–5..... **43**
43. Peridium 440–540 μm thick, epicutis 430–500 μm thick, of hyaline within, pale brown without, inflated cells (parenchyma-like), 20–30 x 30–60 μm , subcutis 10–40 μm thick, of hyaline to pale yellow, compact, interwoven hyphae, 3–5 μm in diam, spores smooth, 12–13 x 4.5–5 μm , utricle absent or inconspicuous ***H. rhodocarpum*** (p. 117)
43. Peridium 330–480 μm thick, epicutis 300–450 μm thick, of hyaline, inflated cells (parenchyma-like), 30–75 μm in diam, subcutis 15–25 μm thick, of hyaline, interwoven to subpericlinal hyphae, spores smooth, ellipsoid, 10–14 x 4–5 μm , utricle usually slight, closely adhering to spore
 ***H. coriaceum*** (p. 58)
44. Peridium 390–450 (–850) μm thick, epicutis 350–400 μm thick, of hyaline, inflated cells (parenchyma-like), 50–80 μm in diam, subcutis 40–60 μm thick, of hyaline, interwoven to subpericlinal hyphae, 2–4 μm in diam, clamp connections common, spores 12–17 (–20) x 5–6.5, fusoid, utricle distinct, wrinkled, closely appressed through maturity
 ***H. separabile*** (p. 124)
44. Peridium 500–610 μm thick, epicutis 500–600 μm thick, of hyaline to pale brown inflated cells (parenchyma-like), 30–50 μm in diam, subcutis 10–20 μm thick, of pale brown slightly inflated hyphae, 4–8 μm in diam, clamp connections absent, spores 14–16 (–19) x 6–7 μm , ellipsoid to subfusoid, utricle distinct, wrinkled, closely appressed..... ***H. fallax*** (p. 76)

45. Peridium 350–650 μm thick, epicutis 300–450 μm thick, of irregularly shaped, inflated cells (parenchyma-like), 15–23 x 28–30 μm , subcutis 50–100 (–200) μm thick, of loosely interwoven hyphae 3–4 μm in diam, spores 14–17 x 4–5 μm , ellipsoid, utricle irregular, loosely adhering in age..... ***H. americanum*** (p. 39)
45. Peridium 600–900 μm thick, epicutis 500–700 μm thick, of irregularly shaped, inflated cells (parenchyma-like), 20–65 μm in diam, subcutis 100–200 μm thick, of compact, interwoven hyphae, 3–8 μm in diam, spores 11–14 x 5–6.5 μm , fusiform to broadly fusiform, utricle distinct, irregular, loosely inflated..... ***H. neotunicatum*** (p. 98)

Species Descriptions

Hysterangium affine Massee & Rodway in Massee, Kew Bull. Misc. Info.

1898:127. 1898.

= *Hysterangium affine* var. *irregulare* Massee, Kew Bull. Misc. Info.

1901:158. 1901.

= *Hysterangium affine* var. *tenuispora* Rodway, Paps. & Proc. Roy. Soc.

Tasmania 1911:27. 1912.

Basidiomata 0.5–2 cm in diam, subglobose, lobed or irregular, slightly indented at base, white when fresh, bruising rose, mottled pale brown and white when dry, surface glabrous above. **Gleba** pale green at first, pale gray, olive–green to dark greenish black when dried; locules elongate, empty.

Rhizomorphs single or numerous, stout, attached at base, white at first, concolorous with peridium when dry. **Columella** gelatinous, distinct, dendroid, stout, arising from a sterile base.

Peridium easily separable from gleba, a single layer 100–250 μm thick, of hyaline polyhedral cells (parenchyma–like), 30–40 x 50–75 μm , not underlain by a “tramal peridium” as stated by Zeller & Dodge (1929), crystalline particles adhering to the outer cells, clamp connections absent.

Trama 70–150 μm thick, of hyaline, compact, more or less parallel to interwoven hyphae (3–5 (–7) μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, oblong to subclavate, 8 x 40 μm , (2) 4 spored.

Spores smooth, (11–) 12–15 x 4–5 μm , ellipsoid to oblong; apex acutely blunt, base subsessile to slightly appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** thick, irregularly inflated to 1 μm , attached at base. **Spore color** in KOH hyaline to pale green singly, pale green to green in mass. (Figs. 2 & 3).

ETYMOLOGY: referring to its "affinity" to other *Hysterangium* species.

OTHER REFERENCES: Beaton, Pegler & Young (1985) pp. 442–443, Cunningham (1942) pp. 69–70, Rodway (1912) p. 27, (1924) pp. 154–155, Saccardo & Sydow in Saccardo (1902) p. 246, Zeller & Dodge (1929) pp. 92–93.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Casuarina litteralis*, *Eucalyptus diversicolor*, *E. calophylla*, *E. marginata*, *E. microcorys*, *E. saligna* and *Nothofagus dombeyi*; April through October.

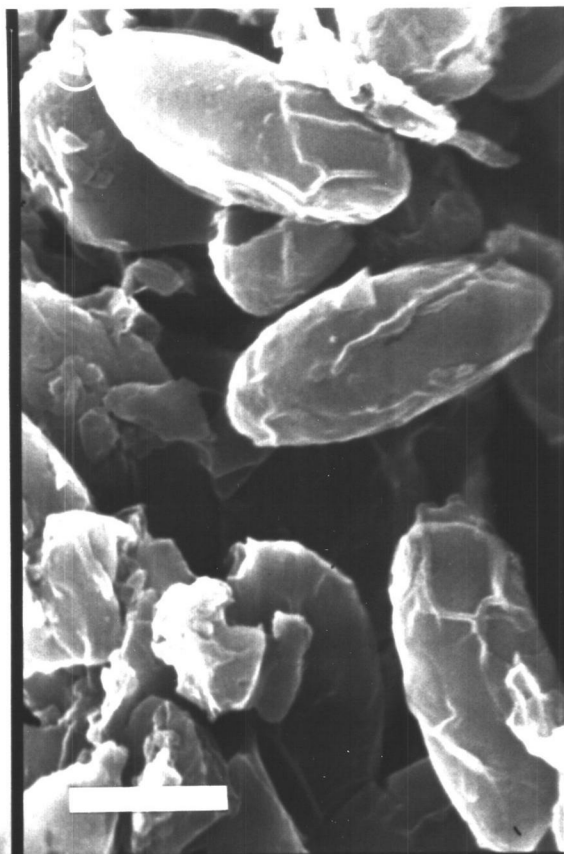
COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, McRobies Gully, leg Rodway 123 (HO 89509), ISOTYPES (K, OSC). **OTHER COLLECTIONS — AUSTRALIA:** New South Wales, leg Walker (DAR 28830). Tasmania, 89507, 89508, 89510, 89511, 89512, 89513, 89524, 89526, 89547 (all HO), (HOLOTYPE of *Hysterangium affine* var. *irregulare* Massee) Rodway 657 (K, HO 89516), Rodway 698 (K, HO 89535), Rodway 1122 (NY). Western Australia, Manjimup, H 111, H 125, H 171, H 176a, H 176b, H 204 (all DAR), HDT 43299 (DAR, SFU), Trappe 6884 (OSC). Dwellingup, H 416 (DAR). Denmark H 426 (DAR). **ARGENTINA:** Buenos Aires, 30372 (BAFC). Neuquen, 23996 (BAFC).

DISCUSSION: This species is a common mycorrhizal associate of *Eucalyptus* in Australia and has been collected under *Nothofagus* spp. in Argentina. Study of type material of *Hysterangium affine* var. *irregulare* reveal it to be within the normal variation of the species and thus it is reduced to a synonym. Although the type of *H. affine* var. *tenuispora* could not be located, all material identified as such by Rodway was found to be identical with the species.

The small spores with an irregularly wrinkled utricle and the peridium which has a single, thin (100–250 μm thick) layer of polyhedral cells separate this species from most *Hysterangium* spp. *Hysterangium affine* resembles *H. aureum* but differs in having a thinner peridium, larger hyphae in the trama, and longer spores with an inflated utricle. *Hysterangium affine* also resembles *H. neotunicatum*, but *H. neotunicatum* has a peridium with a thick subcutis of interwoven hyphae.

Figures 2-5. *Hysterangium* spores. 2. Light micrograph of *H. affine* spores (Holotype, Rodway 123), bar = 10 μm . 3. Scanning electron micrograph (SEM) of *H. affine* spores (Holotype, Rodway 123), bar = 5 μm . 4. SEM of *H. agglutinatum* spores (Holotype, leg Beaton), bar = 5 μm . 5. Light micrograph of *H. agglutinatum* spores (Holotype, leg Beaton), bar = 10 μm .

②

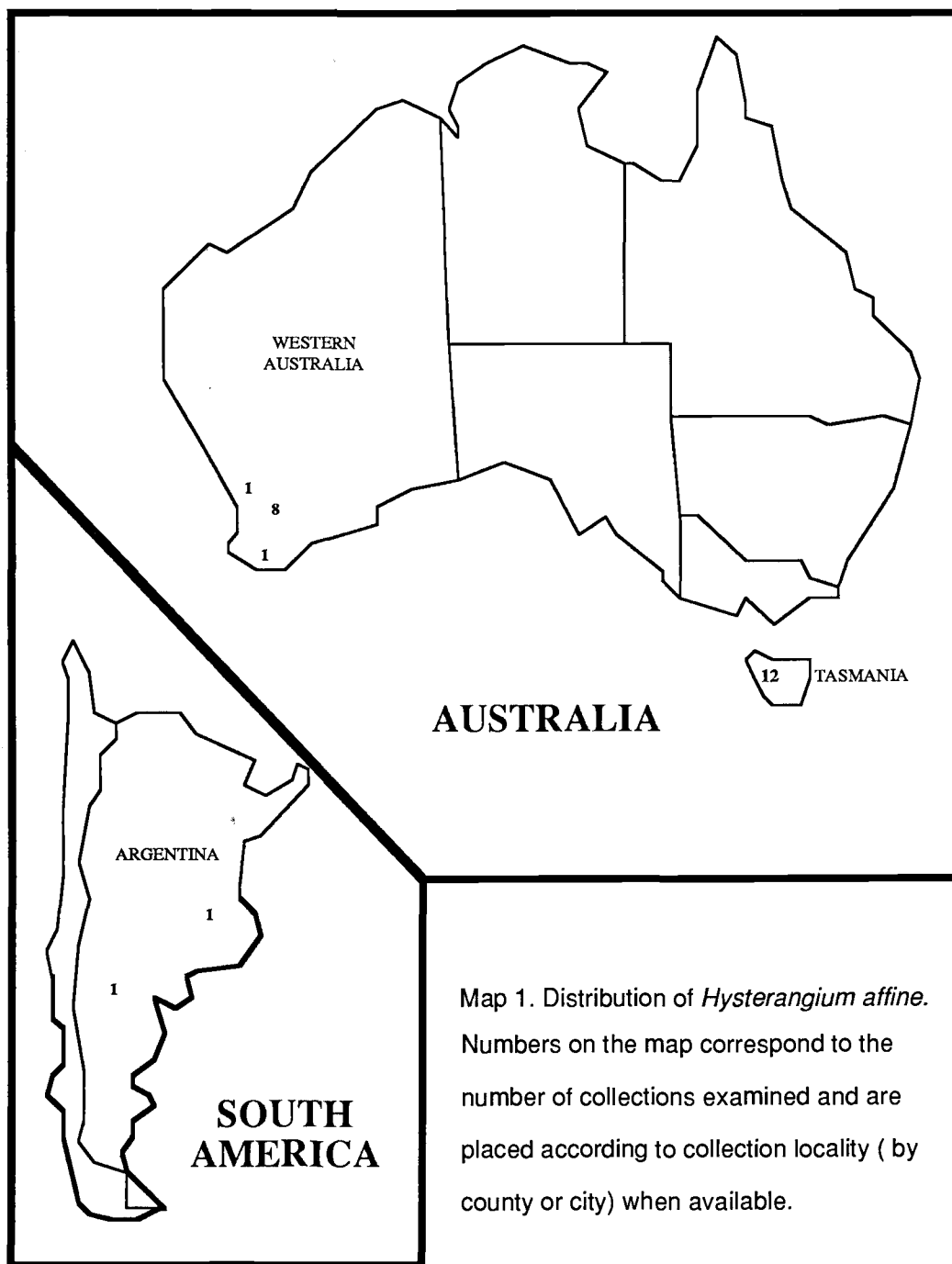


④



⑤





Hysterangium agglutinatum Castellano, nom. prov.

Basidiomata 1–1.5 cm in diam, globose to reniform, mottled pale brown, pale orange brown and pale reddish brown when dried, surface glabrous with some adherent soil particles. **Gleba** olive to dark olive green when dried; locules elongate to irregular, empty to partially filled. **Rhizomorph** single, stout, up to 2 mm wide, concolorous with peridium. **Columella** gelatinous, inconspicuous, arising from a sterile base, dark reddish brown when dried.

Peridium not easily separable from gleba, 410–480 μm thick, two-layered; epicutis 400–450 μm thick, of pale brown to hyaline, thin-walled, agglutinated, compactly periclinal hyphae, 4–6 (–14) μm in diam, numerous crystalline particles in outer 150 μm , clamp connections absent; subcutis (not easily observed) 10–30 μm thick, of hyaline, thin-walled, clavate shaped, inflated cells (parenchyma-like), 35–55 x 15 μm , clamp connections absent.

Trama 50–100 μm thick, of hyaline, compactly interwoven hyphae (3–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, elongate, 40–45 x 5–8 μm , 4 or 6 spored.

Spores smooth, (9–) 10–12 x 3.5–4.5 (–5) μm , ellipsoid; apex blunt, base sessile, occasionally with remnants of the sterigmal attachment. **Spore wall** up to 0.5 μm thick. **Utricle** absent. **Spore color** in KOH pale green singly, brown in mass. (Figs. 4 & 5).

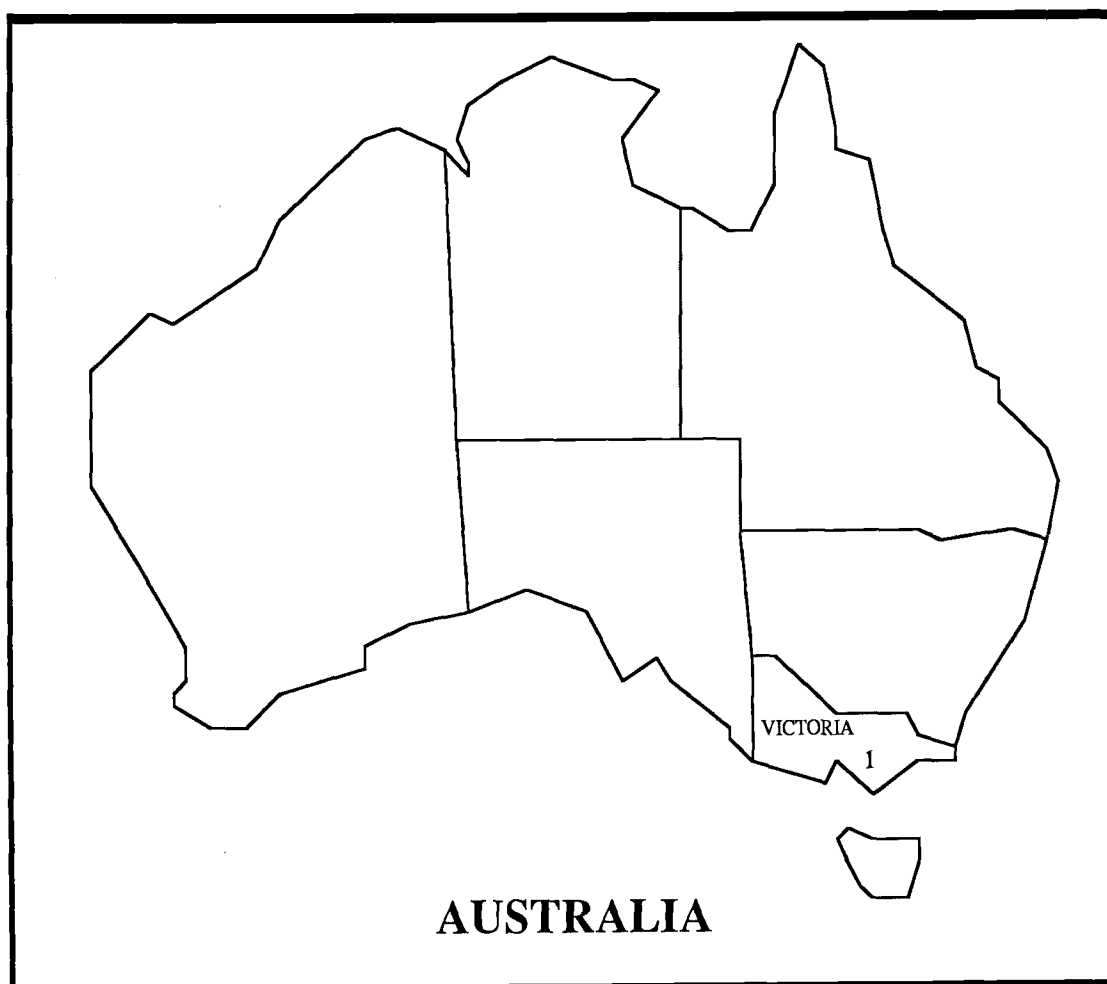
ETYMOLOGY: in reference to the “agglutinated” hyphae in the epicutis.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associate *Eucalyptus* spp.; October.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Victoria, Lorne, Erskine Falls Rd., 23-OCT-1981, leg K. & G. Beaton (K).

DISCUSSION: This species was identified as *Hysterangium affine* Massee & Rodway by Beaton (Beaton et al. 1985). *Hysterangium affine* has more or less larger spores with an irregularly inflated utricle, the smaller spores of *H. agglutinatum* do not have a utricle.

The thick layer of agglutinated, periclinal hyphae of the epicutis in conjunction with the small, smooth spores which lack a utricle separate this species from all others.



Map 2. Distribution of *Hysterangium agglutinatum*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium aggregatum Cribb, Paps. Dept. Bot. Univ. Queensland 3:156. fig. 7. 1958.

Basidiomata 1–3 (–6) mm in diam, more or less subglobose, irregular or lobed, egg white when fresh, unchanging when handled, chalk white when dried, surface tomentose, clustered and imbedded in soil, roots, and profuse white mycelium. **Gleba** green to grayish green when fresh, bright green to olive when dry; locules small, subglobose, nearly filled. **Rhizomorphs** absent. **Columella** absent.

Peridium not separable from gleba, a single layer 70–90 μm thick, of hyaline, thin-walled, compactly interwoven hyphae, 3–5 μm in diam, clamp connections absent.

Trama 25–30 μm thick, of hyaline, interwoven to subparallel hyphae (3–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, sinuous, constricted near the base, 30–40 x 6–10 μm , 2 spored.

Spores smooth, 13–17 x 4–7 μm , ellipsoid to fusiform; apex blunt to acuminate, base sessile to slightly appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** inconspicuous, when present irregular, broken, adhering closely to spore wall. **Spore color** in KOH hyaline to pale green singly, pale green in mass. (Figs. 6-9).

ETYMOLOGY: in reference to the “aggregation” of sporocarps in the soil.

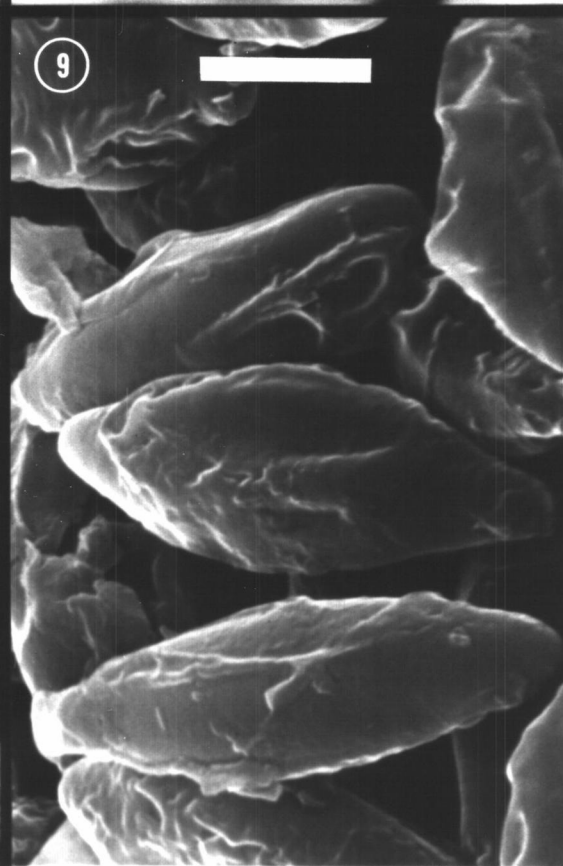
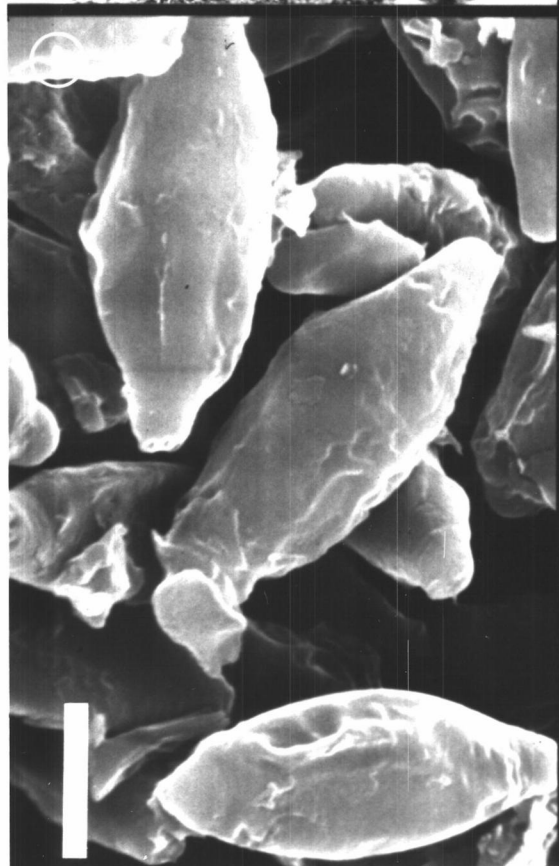
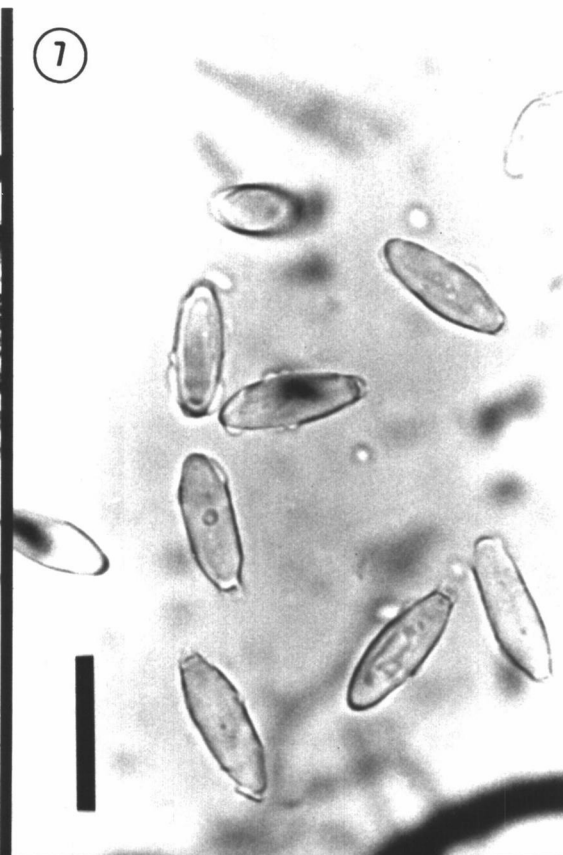
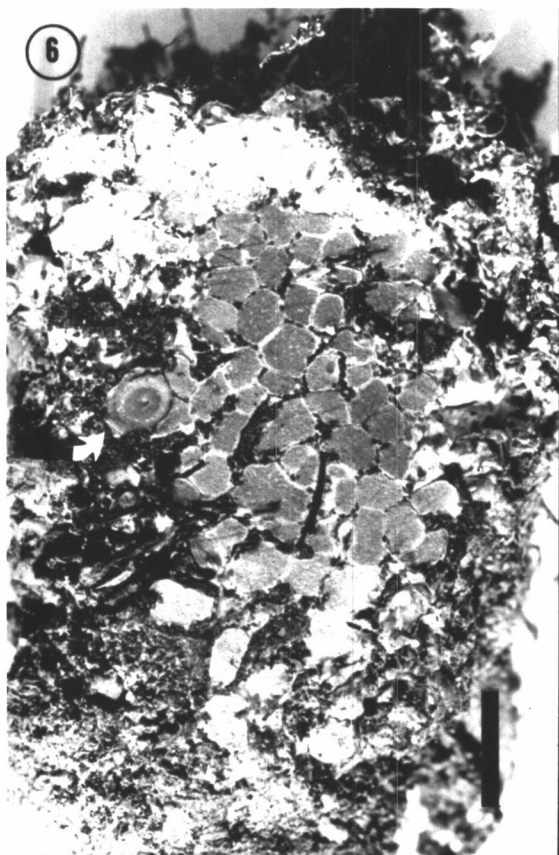
HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Tristania conferta*, *Eucalyptus wandoo* & *E. calophylla*; February, July and September.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Queensland, Cunningham's Gap, 17-FEB-1956, leg Cribb (DAR 21625), ISOTYPES (K, OSC). **OTHER COLLECTIONS — AUSTRALIA:** Western Australia, Glen Eagle State Forest, H 2022, H 2088 (all DAR, OSC), Walyunga National Park (OSC).

DISCUSSION: The extremely small sporocarps which are embedded in clusters in a mass of soil, roots and mycelium distinguish this species from all others. The absence of a columella is peculiar and unexplainable at this time.

The sporocarps of *H. aggregatum* are probably easily overlooked due to their unique habit and extremely small size. The two collections from Western Australia were found in rather loamy soils.

Figures 6-9. *Hysterangium aggregatum*. 6. Sporocarps (H 2022) and *Eucalyptus* roots (arrow) embedded in soil, bar = 10 mm. 7. Light micrograph of spores (Holotype, DAR 21625), bar = 20 μm . 8. SEM of spores (Holotype, DAR 21625), bar = 5 μm . 9. SEM of spores (Holotype, DAR 21625), bar = 5 μm .





Map 3. Distribution of *Hysterangium aggregatum*. Numbers on the map correspond to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium album Zeller & Dodge, Ann. Mo. Bot. Gard. 16:87–88. pl. 1, fig 1, pl. 3, fig. 5. 1929.

Dried **basidiomata** up to 7 mm in diam, globose to subglobose to depressed, pale brown, surface finely pubescent to slightly tomentose, with some adhering soil particles. **Gleba** pale green to pale brown or dark brown; locules empty, round to irregular. **Rhizomorphs** not observed. **Columella** of unknown consistency, narrow, dendroid, translucent.

Peridium easily separable from gleba, a single layer 100–200 μm thick, of irregularly shaped, compactly interwoven hyphae (subparenchyma-like), 5–10 μm in diam, up to 22 μm long, crystalline particles incrusting superficial hyphae, clamp connections absent.

Trama 50–100 μm thick, of hyaline, collapsed, compactly interwoven hyphae (1–2 μm in diam) in a gelatinized matrix, clamp connections absent.

Basidia hyaline, clavate to ovate, $\pm 13 \times 7\text{--}8 \mu\text{m}$, 2 (4) spored.

Spores minutely verrucose, $17\text{--}20 \times 6\text{--}7 \mu\text{m}$, fusiform to broadly fusiform; apex distinctly papillate with wall thickening, base distinctly pedicellate. **Spore wall** less than 0.5 μm thick except near spore apex.

Utricle sometimes absent, when present slight, wrinkled, adhering closely to spore wall. **Spore color** in KOH hyaline to pale brown singly, pale brown in mass. (Fig. 10).

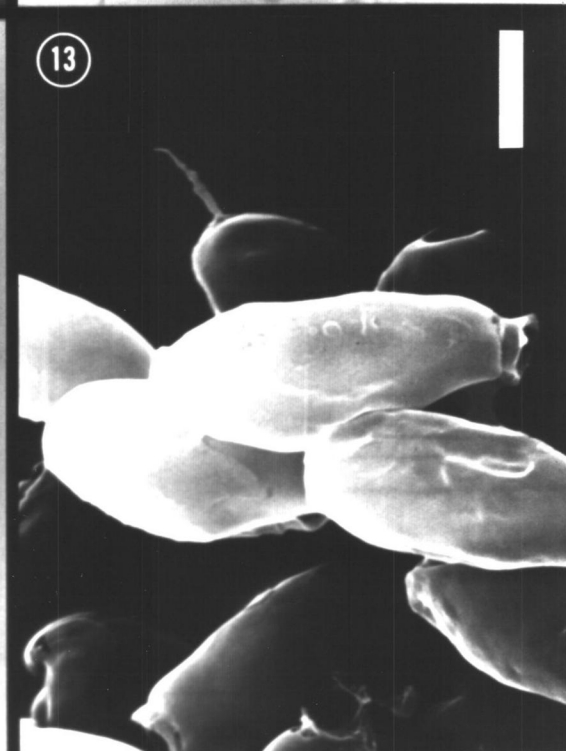
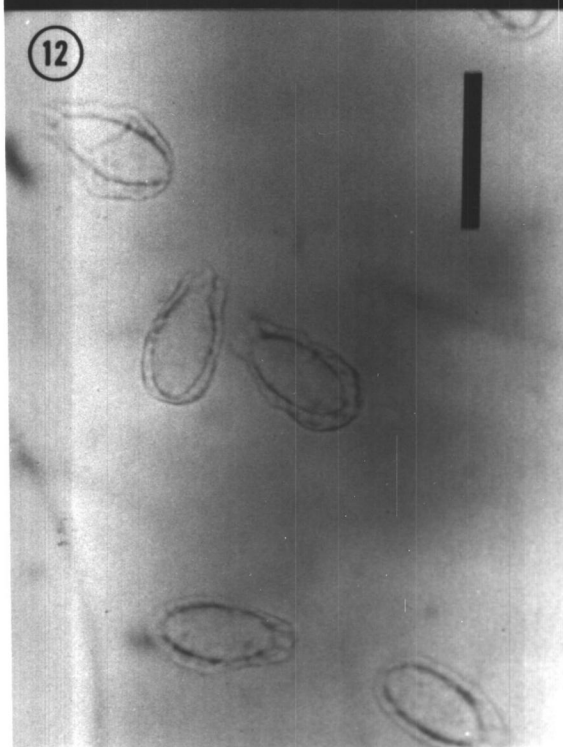
ETYMOLOGY: “white,” in reference to color of the fresh sporocarp.

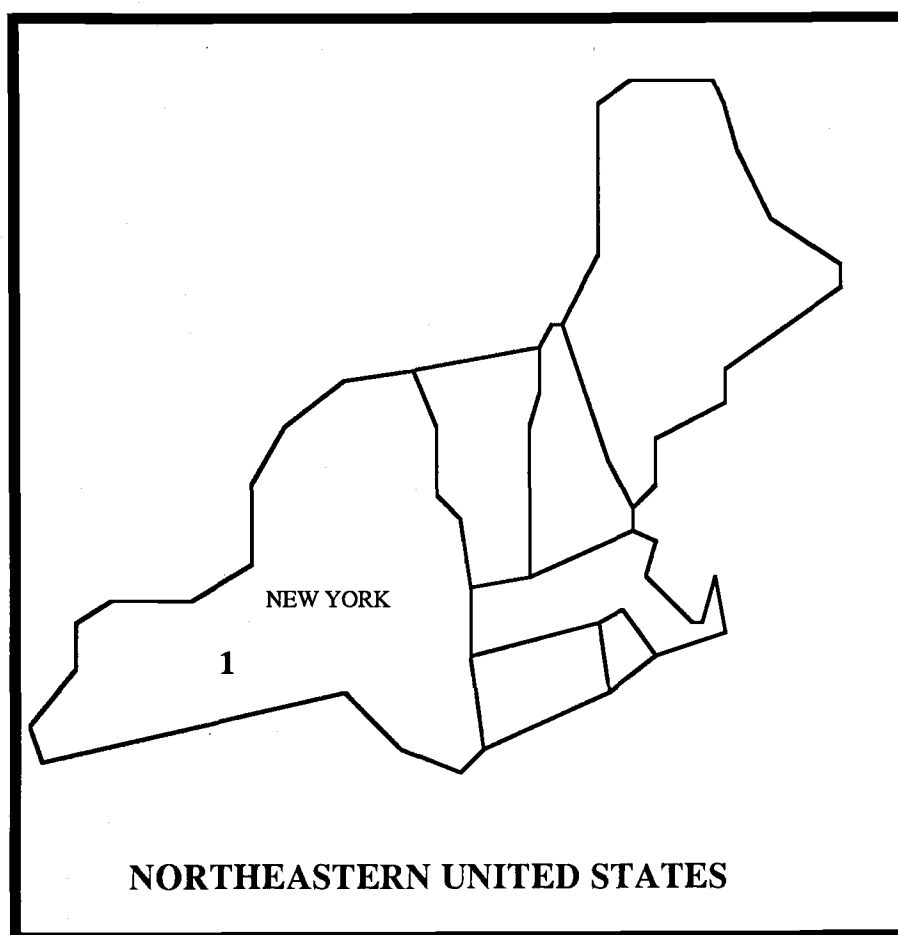
HABIT: Hypogeous.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW YORK:** Ithaca, leg Fitzpatrick 364 (NY), ISOTYPE (FH).

DISCUSSION: The pale brown sporocarps and large, pale brown, fusiform spores separate this *H. album* from all others. This species is tentatively placed in *Hysterangium*, additional fresh collections may shed further light as to placement of this species in a genus other than *Hysterangium*.

Figures 10-13. *Hysterangium* spores. 10. SEM of *H. album* spores (Holotype, Fitzpatrick 364), bar = 5 μm . 11. Light micrograph of *H. angustisporum* spores (Holotype, AHF 249), bar = 10 μm . 12. Light micrograph of *H. asperulatum* spores (Holotype, Couch 7490a), bar = 20 μm . 13. SEM of *H. asperulatum* spores (Holotype, Couch 7490a), bar = 5 μm .





Map 4. Distribution of *Hysterangium album*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium americanum (Fitzpatrick) Castellano stat. prov.

≡ *Hysterangium stoloniferum* var. *americanum* Fitzpatrick, Ann. Mycol. 11:129–135, figs. 2, 6, 10, 20–28. 1913.

Basidiomata 1–2.5 cm in diam, globose, sometimes depressed, slightly indented at base, snow white at first, mottled with brown or reddish brown in age, surface glabrous, ETOH red brown. **Gleba** cartilaginous, olive green, ETOH nonreactive; locules small, irregular, empty. **Rhizomorph** single, thick, cord-like, concolorous with peridium. **Columella** gelatinous, distinct, dendroid, translucent. **Odor** not unpleasant, similar to gasoline.

Peridium easily separable from gleba, 350–650 μm thick, two-layered; epicutis 300–450 μm thick, of hyaline, thin-walled, subglobose to irregularly inflated cells (parenchyma-like), 15–23 x 28–30 μm , some crystalline particles adhering to outer inflated cells, clamp connections absent; subcutis 50–100 (–200) μm thick, of hyaline, thin-walled, loosely interwoven hyphae, 3–4 μm in diam, clamp connections absent.

Trama 50–100 μm thick, of hyaline, collapsed, loosely interwoven hyphae (1–2 μm in diam) in a gelatinized matrix, clamp connections absent.

Basidia reviving poorly, cylindrical, 3 spored.

Spores smooth, (13–) 14–17 x 4–5 (–6) μm , narrowly ellipsoid to slightly fusiform; apex acuminate, base slightly appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** irregularly inflated, loosely adhering in age. **Spore color** in KOH pale green singly, olive green in mass.

ETYMOLOGY: the “American” *Hysterangium*.

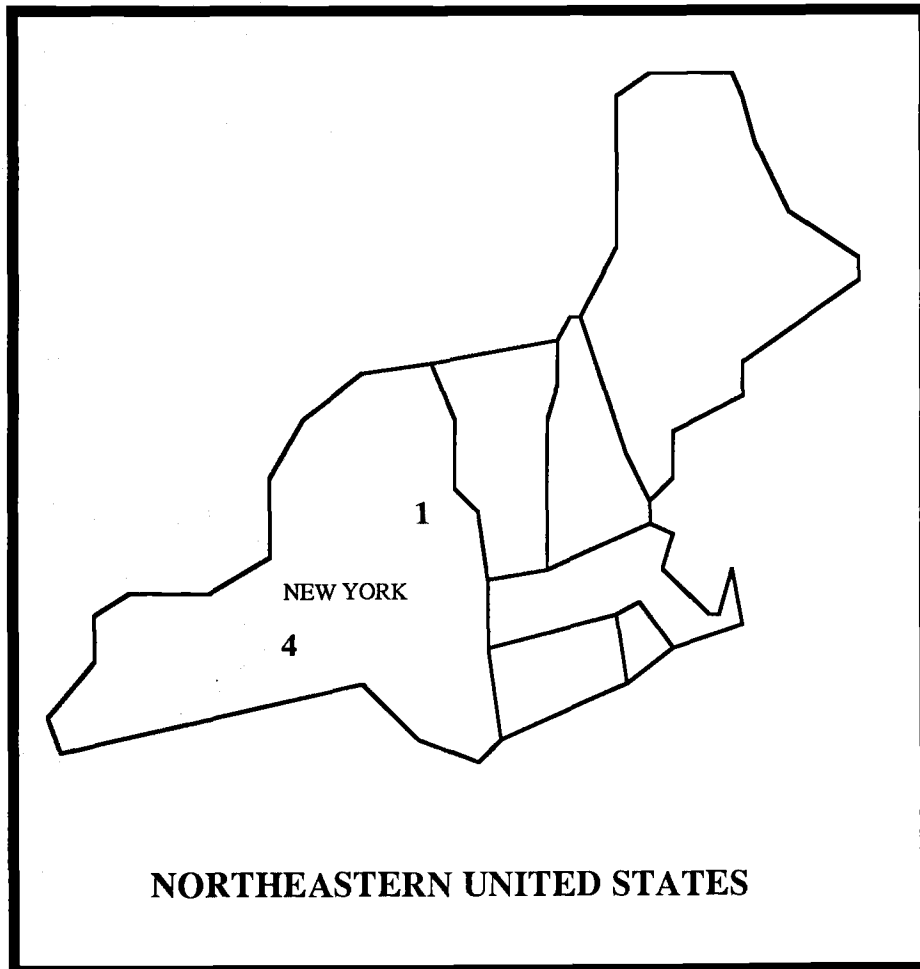
HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associate *Tsuga canadensis*, May and June.

COLLECTIONS EXAMINED: HOLOTYPE: NEW YORK: Tompkins Co., Coy Glen, 27-JUNE-1915, leg Whetzel CUP 8448, dry material (FH), ISOTYPE wet material (FH). **OTHER COLLECTIONS — NEW YORK:** Ticonderoga Co., Trappe 590 (CUP, OSC, WTU). Tompkins Co., 5342, 8269, (all CUP, FH), 9750 (CUP).

DISCUSSION: A thorough search of the Herbarium at Cornell could not locate collection CUP 8448. Hence, the portion of CUP 8448 found at the Farlow Herbarium is designated as the HOLOTYPE.

This species is similar to *H. coriaceum*, *H. fallax*, *H. angustisporum*, *H. separabile* and *H. crassirhachis*. *Hysterangium americanum* differs from them by the combination of the irregularly shaped, inflated cells of the epicutis, thick subcutis of interwoven hyphae, and mostly narrowly ellipsoid, smooth spores.

Fitzpatrick (1913) describes the development of *H. americanum* in detail.



Map 5. Distribution of *Hysterangium americanum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium angustisporum Castellano & States, nom. prov.

Basidiomata 1–1.5 cm in diam, subglobose, mottled white, orange brown and brown when dried, surface glabrous with some adherent soil particles. **Gleba** green to olive when dry; locules irregular to subglobose, mostly empty. **Rhizomorphs** not observed. **Columella** inconspicuous, arising from a sterile base, dark brown when dried.

Peridium not easily separable from gleba, 550–600 μm thick, two-layered; epicutis 500–550 μm thick, of hyaline to brown (outer 50 μm), thin-walled, polyhedral cells, (20–) 40–70 μm in diam, crystalline particles across the brown cells; subcutis 30–50 μm thick, of hyaline, thin-walled, interwoven to mostly periclinal hyphae, 2–4 μm in diam, clamp connections absent.

Trama 100–180 μm thick, of hyaline, interwoven hyphae (4–5 in diam) in a gelatinized matrix, occasional incrustated hyphae scattered throughout trama, clamp connections scattered. **Basidia** hyaline, elongate, 45–47 x 7–10 μm , clamp connection at base, 4 spored.

Spores minutely verrucose, 16–17 x 5 μm , elongate to narrowly ellipsoid; apex blunt to acuminate, base appendiculate. **Spore wall** up to 1 μm thick. **Utricle** distinct, closely appressed, wrinkled. **Spore color** in KOH hyaline to pale green singly, pale green to olive in mass. (Fig. 11).

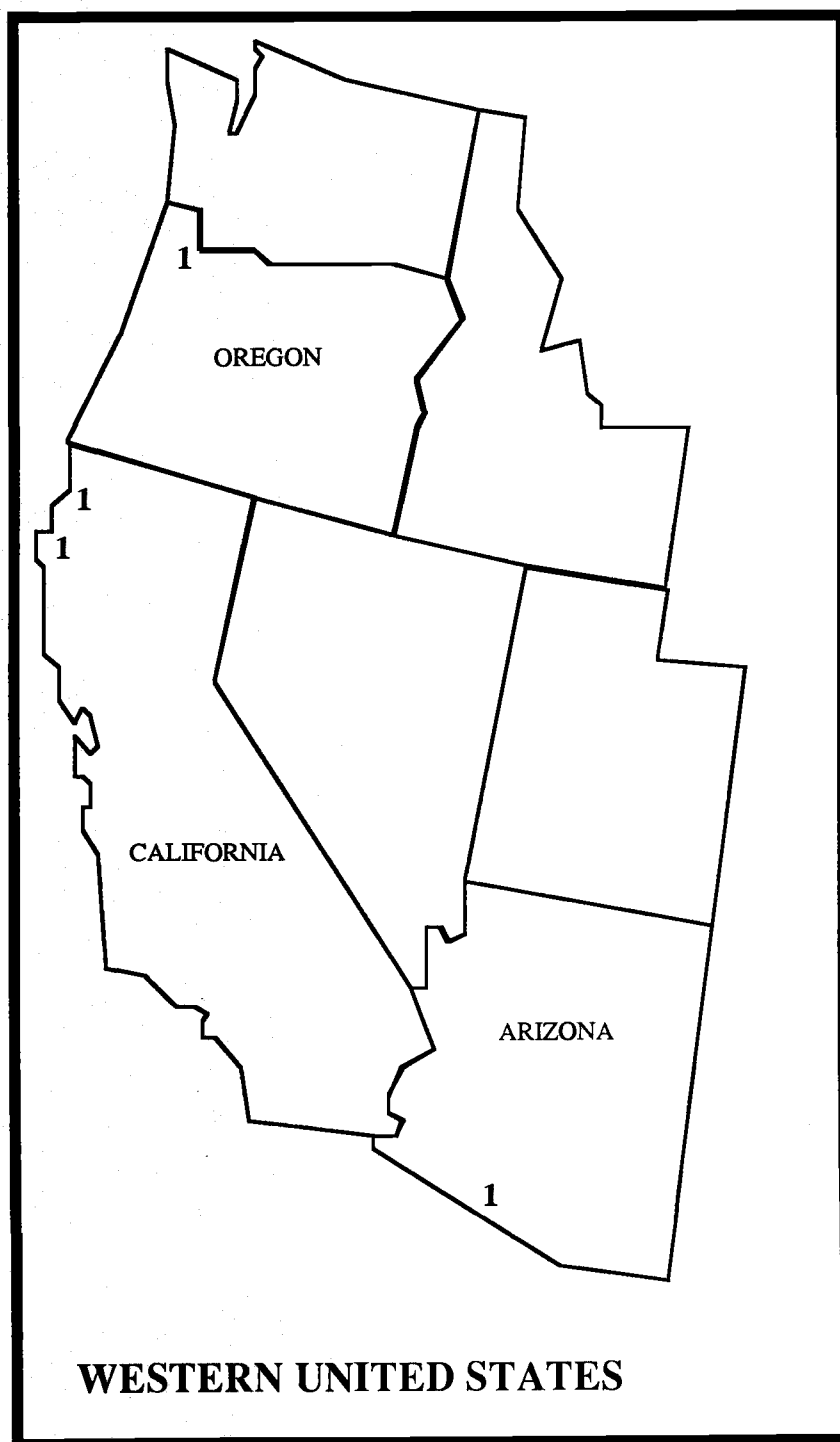
ETYMOLOGY: in reference to the narrowly elongate spores.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associate interior *Pseudotsuga menziesii*; September.

COLLECTIONS EXAMINED: HOLOTYPE: **ARIZONA:** Pima Co., Mt. Lemon, 1-SEPT-1982, leg States AHF 249 (FSLF), ISOTYPE (OSC). **OTHER COLLECTIONS — CALIFORNIA:** El Dorado Co., Trappe 3910 (OSC). Humboldt Co., Trappe 4566 (OSC). **OREGON:** Tillamook Co., Trappe 8509 (OSC).

DISCUSSION: The narrowly ellipsoid to mostly elongate, minutely verrucose spores which have a distinctly wrinkled utricle separate this from all other *Hysterangium* spp.

States (1984) cites AHF 249 as *H. separabile* Zeller.



Map 6. Distribution of *Hysterangium angustisporum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium asperulatum Castellano, nom. prov.

Dried **basidiomata** up to 1.5 cm in diam, subglobose to globose, pale to moderate brown with reddish brown mottling, surface covered with white floccose mycelium with numerous adhering sand particles and organic matter.

Gleba tough and pliable when fresh, pale brown when young, brown at maturity; locules globose to elongate, empty. **Rhizomorphs** numerous, attached to base, less than 0.5 mm in diam, concolorous with peridium.

Columella gelatinous, distinct, irregularly dendroid, arising from a sterile base, translucent.

Peridium not easily separable from gleba, 180–260 μm thick, two-layered; epicutis 100–140 μm thick, of hyaline, thin-walled, elongate to irregularly shaped, inflated, compactly interwoven hyphae, 6–10 x 10–26 μm , outer 20 μm encrusted with numerous crystalline particles, clamp connections absent; subcutis 40–50 μm thick, of hyaline, thin-walled, compactly interwoven to subpericlinal hyphae, 1–3 μm in diam, clamp connections absent.

Trama 40–80 μm thick, of hyaline, subcapitate, interwoven hyphae (2–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, clavate, 16–23 x 6–8 μm , 2 spored.

Spores distinctly verrucose, 13–15 x 6–8 μm , broadly fusoid; apex obtusely blunt, base appendaged (flanged). **Spore wall** $\pm$ 2 μm thick.

Utricle distinct, irregularly roughened, closely appressed to spore wall.

Spore color in KOH pale green singly, golden brown in mass. (Figs. 12 & 13).

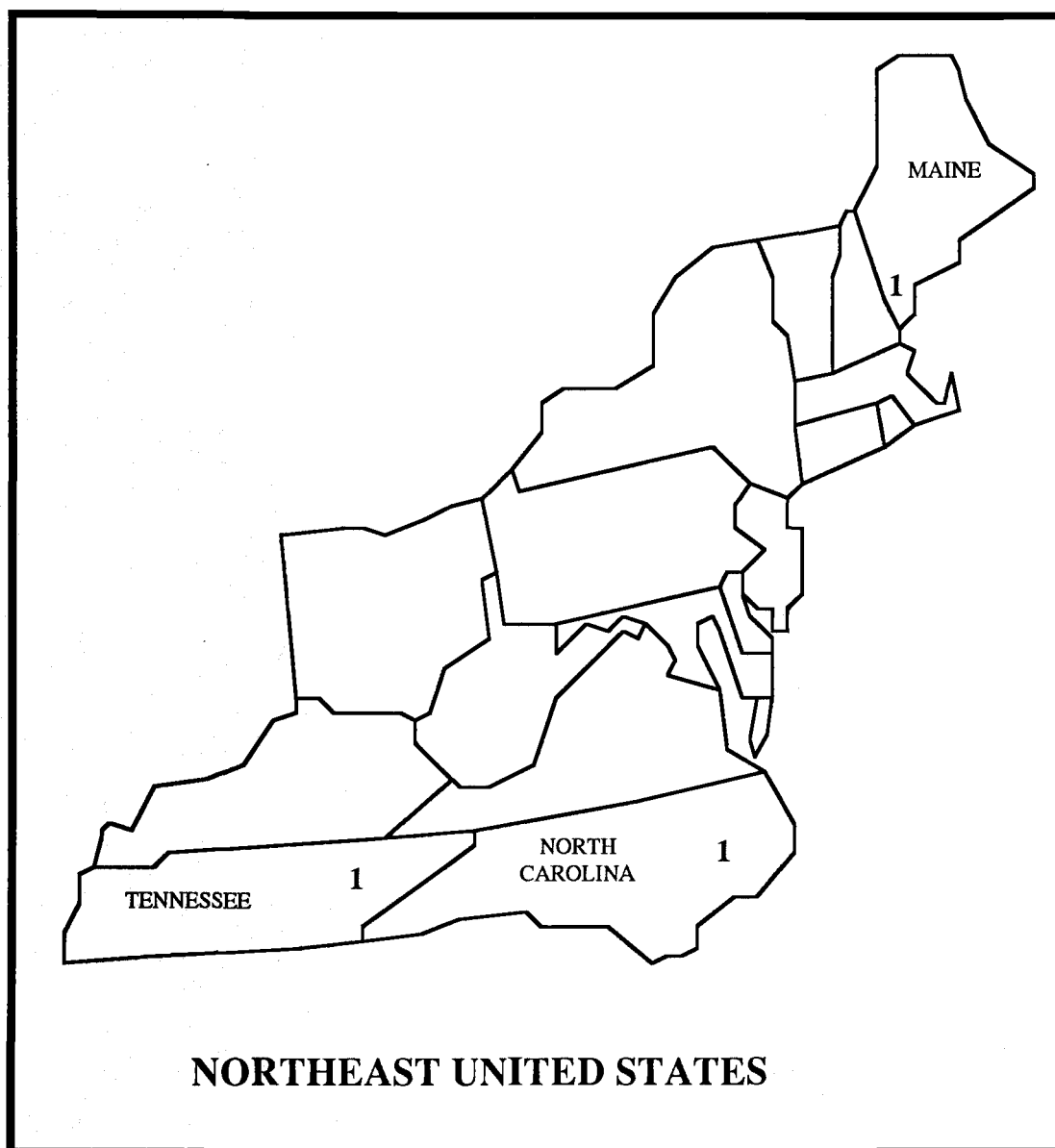
ETYMOLOGY: referring to the “rough or uneven” spore ornamentation.

OTHER REFERENCES: Coker and Couch (1928) pp. 19–20 (as *Hysterangium pompholyx* Tulasne), Zeller & Dodge (1929) pp. 106–107 (as *Hysterangium pompholyx* Tulasne).

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associate *Fagus*; August and September.

COLLECTIONS EXAMINED: HOLOTYPE: **NORTH CAROLINA:** leg Coker, 9–AUG–1924 (NCU 7490 a), ISOTYPE (OSC). **OTHER COLLECTIONS** — **TENNESSEE:** Burbank, Thaxter B3H, 7–AUG–1896 (FH). **MAINE:** York Co., Kittery Point, Thaxter 1902a, 11–SEPT–1902 (FH).

DISCUSSION: The brown gleba and thick-walled, broadly fusiform, distinctly verrucose spores which possess a distinctly inflated utricle distinguish this species from all others except *H. pompholyx*. *Hysterangium asperulatum* has a peridium made up of two distinct layers, the peridium of *H. pompholyx* is of one layer.



Map 7. Distribution of *Hysterangium asperulatum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium aureum Zeller, Mycologia 33:201–202. 1941.

= *Hysterangium stoloniferum* var. *brevisporum* Zeller, Mycologia 39:288. 1947.

= *Hysterangium affine* var. *oreades* Zeller, Mycologia 31:18–19. 1939.

Dried **basidiomata** 1–4 cm in diam, globose, subglobose or irregularly lobed, egg white at first, slowly bruising pale reddish brown, golden brown to dark golden brown when dry, surface more or less glabrous, without adherent soil particles, KOH nonreactive or pale olive yellow, FeSO₄ pale blue green.

Gleba pale green, olive to dark grey green; locules elongate, empty.

Rhizomorphs usually absent, when present numerous, small, attached to base, concolorous with peridium. **Columella** gelatinous, dendroid, narrow, hyaline to opaque. **Odor** fruity.

Peridium not easily separable from gleba, a single layer 325–450 µm thick, of hyaline, thin-walled, polyhedral cells (parenchyma-like), 50–75 µm in diam, no distinct filamentous layer between polyhedral cells and gleba, clamp connections absent.

Trama 150–250 µm, of hyaline, occasionally collapsed, compactly interwoven or occasionally parallel hyphae (1–3 µm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindric, 12–15 x ± 4 µm, 4 or 6 spored.

Spores smooth, 11–12.5 (–15) x 4–5 µm, ellipsoid; apex acuminate, base sometimes slightly pedicellate. **Spore wall** less than 0.5 µm thick.

Utricle closely appressed, slightly wrinkled, mostly on young spores. **Spore color** in KOH hyaline singly, pale green in mass.

ETYMOLOGY: referring to the golden yellow to brown color of the dried sporocarp.

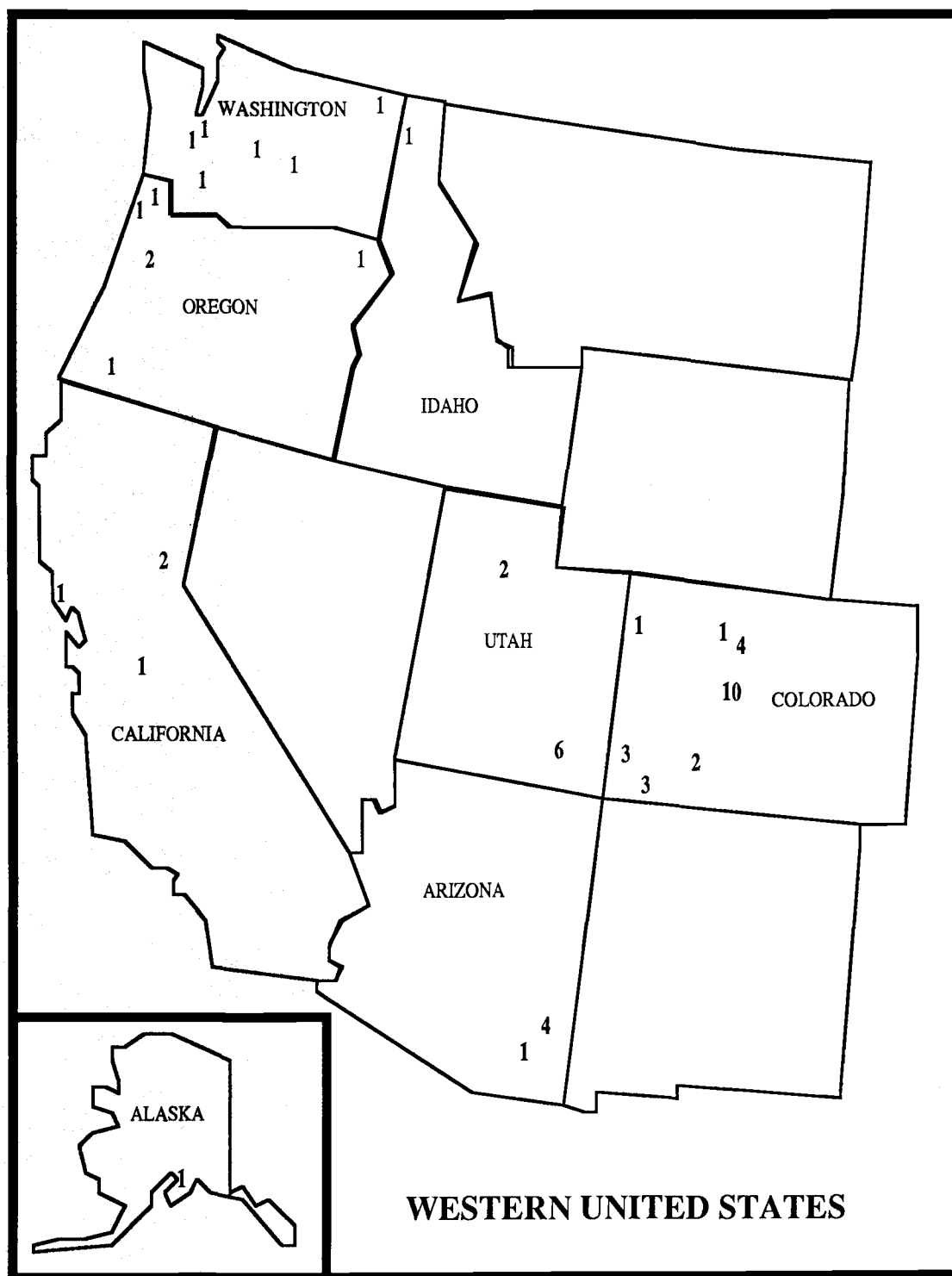
HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Pseudotsuga menziesii*, *Picea engelmannii*, *Tsuga heterophylla*, *Pinus contorta*, *P. monticola*, *P. ponderosa*, or *Abies lasiocarpa*; February to August.

COLLECTIONS EXAMINED: HOLOTYPE: **OREGON:** Linn Co., Trout Creek Recreational Area, Zeller 8480, 21-MAY-1936 (OSC). **OTHER COLLECTIONS — ALASKA :** leg Mowry (OSC). **ARIZONA:** Graham Co., HDT 41260 (SFU). Greenlee Co., HDT 28979, HDT 29427, HDT 29608, HDT 29654 (all SFU). **CALIFORNIA:** Marin Co., Parks 3049 (UC 276314 det. by Zeller as *Hysterangium obtusum* Rodway). Sierra Co., HDT 30015, HDT 47702 (all SFU). Stanislaus Co., HDT 16996 (SFU). **COLORADO:** Boulder Co., F 249, F 264 (in part), F 281 (in part), F 2336 (all MICH). Dolores Co., F 2168, F 2174, F 2712 (all MICH). Grand Co., F 242 (MICH). Lake Co., HDT 26144, HDT 26148, HDT 26154, HDT 26163, HDT 26168, HDT 26263, HDT 26361, HDT 26441, HDT 26446, HDT 26507 (all SFU). La Plata Co., F 2176, F 2177, F 2178 (all MICH). Rio Blanco Co., F 2400 (MICH). Rio Grande Co., HDT 25666, HDT 26622 (all SFU). **IDAHO:** Bonner Co., HDT 11410, HDT 11598 (all SFU). **OREGON:** Columbia Co., Trappe 3032 (OSC). Jackson Co., Trappe 577 (OSC). Linn Co., (TYPE of *Hysterangium stoloniferum* var. *brevisporum* Zeller) leg Zeller (OSC, NY). Tillamook Co., Trappe 2155 (OSC). Wallowa Co., Trappe 1912 (OSC). **UTAH:** Salt Lake Co., (COTYPE of *Hysterangium affine* var. *oreades* Zeller) Darker 5945 (TRTC, FH, S, M, UC 700511, DAOM 70581), Darker 5873 (BPI, FH, DAOM 80189, DAOM 70580,

NY). San Juan Co., F 2152, F 2153, F 2154, F 2155, F 2156, F 2157 (all MICH).

WASHINGTON: Benedict (WTU 20921, OSC). Clallam Co., Trappe 5544 (OSC). Grant Co., Stewart 31 (OSC). Lewis Co., DRH 1185 (ELRG). Oreille Co., HDT 11312 (SFU). Pierce Co., DRH 891 (ELRG). Silver Springs Campground DRH 132 (ELRG). Skamania Co. Trappe 5041 (OSC).

DISCUSSION: *Hysterangium aureum* of North America is similar to *H. affine* of the Southern Hemisphere but differs in its thicker peridium and generally shorter spores which possess a closely appressed utricle. *Hysterangium aureum* is common at higher elevations in the Great Basin area of western North America where it is associated with a number of different species in the Pinaceae.



Map 8. Distribution of *Hysterangium aureum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium calcareum Hesse, Hypog. Deutschl. 1:97. pl. 7, figs. 21, 23, pl. 9, fig. 15. 1891.

Basidiomata up to 2.5 cm, globose to subglobose, grayish white, surface floccose. **Gleba** bluish green to olive green; locules elongate, empty when young, filled at maturity. **Rhizomorphs** numerous, commonly occurring in double strands, concolorous with peridium. **Columella** gelatinous, dendroid, stout, $\pm 1 \mu\text{m}$ thick, translucent when dried.

Peridium easily separable from gleba, a single layer 500–600 μm thick, of brownish yellow to hyaline, thin-walled, periclinal to slightly interwoven hyphae, 7–9 (–17) μm in diam, much smaller near the gleba, abundant crystalline particles in outer portion of peridium, clamp connections absent.

Trama variable in thickness, of hyaline, compactly interwoven hyphae (2–3 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** rehydrating poorly, 2 spored.

Spores smooth, 11–18 x 4–5 μm , broadly ellipsoid; apex acuminate to papillate, base appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** appressed, thin at first, thickening with age. **Spore color** in KOH hyaline singly, gray–green in mass. (Fig. 14).

ETYMOLOGY: probably in reference to the “calcareous” soil in which it is typically found (Hesse 1891).

OTHER REFERENCES: Gross (1980) pp. 68 & 130, Saccardo (1895) p. 168, Zeller & Dodge (1929) p. 119.

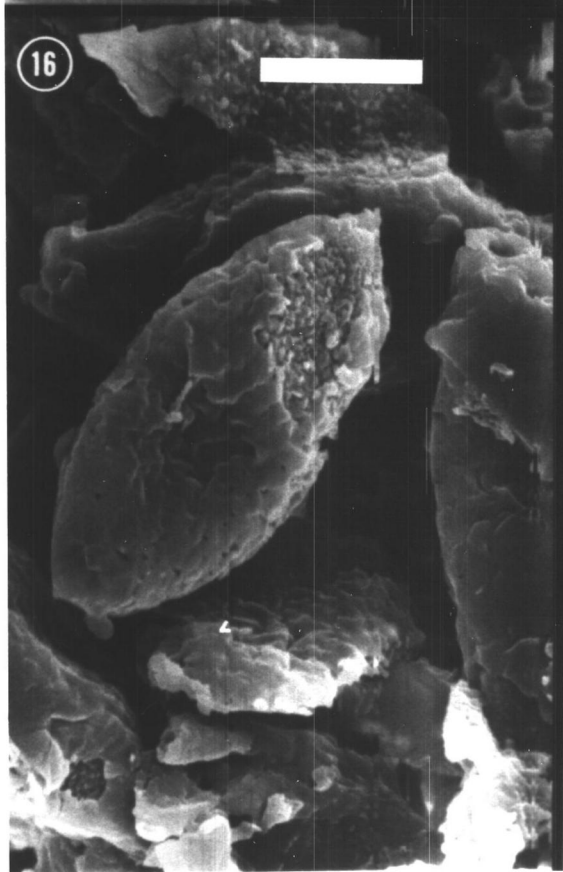
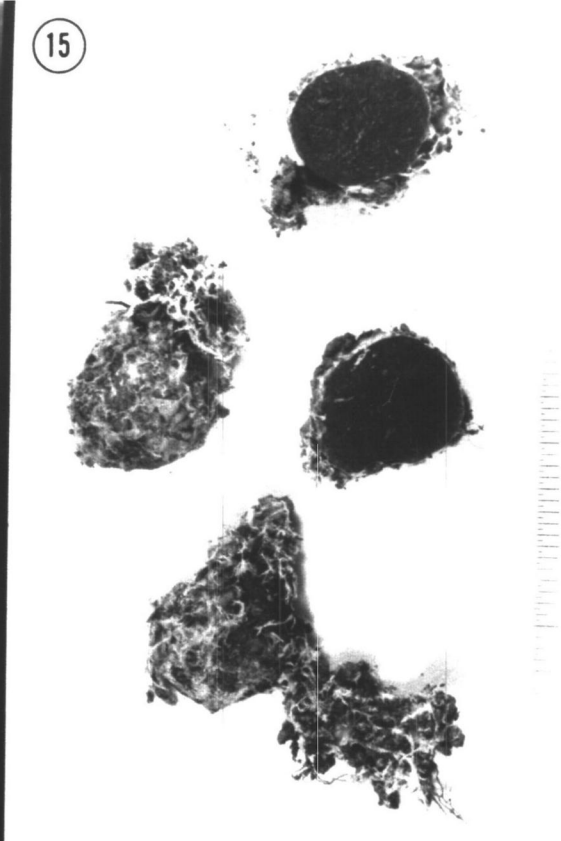
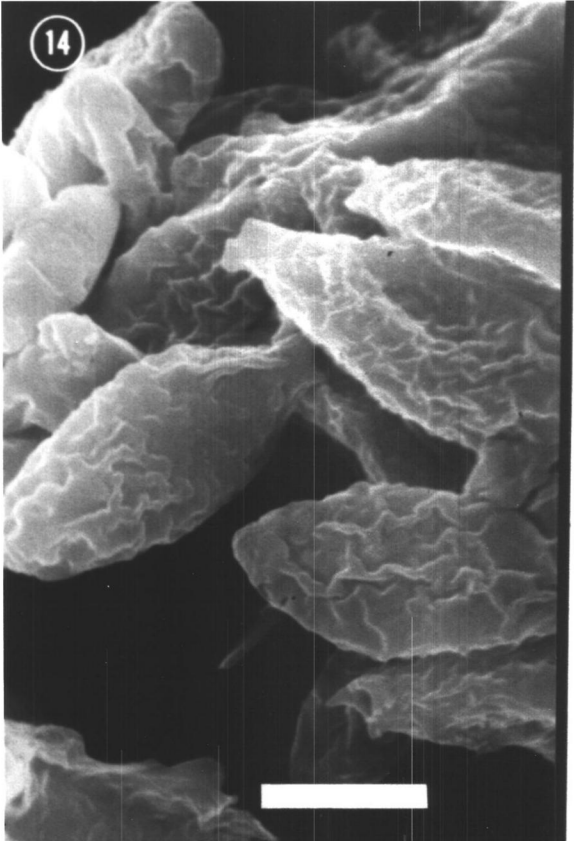
HABIT, HABITAT AND SEASON: Hypogeous, usually in calcareous soil; probable mycorrhizal associates *Betula*, *Corylus*, *Fagus* and *Quercus*; February to November.

COLLECTIONS EXAMINED: LECTOTYPE: **GERMANY (WEST):** Cassel, leg. Hesse, 12-JULY-1881 (MB). **OTHER COLLECTIONS — GERMANY (WEST):** Mahren, Zwittau, leg. Hruby (BPI), Gross 97, Gross, 108, Soehner 466, Soehner 495, Soehner 1431, Soehner 1892, Soehner 1893, Soehner 2102, Soehner 2229 (all M). **ITALY:** Trieste (TO). Reggio Emilia De Vries 1085 (De Vries Herb). **ROMANIA:** Dep. Harghita, pag. Ruganesti, leg Pap, 30-AUG-1973 (CLA).

DISCUSSION: The thick, filamentous peridium covered with floccose mycelium and the smooth, long, narrow spores distinguish this species from all others.

This species is commonly imbedded in white mycelium, soil and roots in calcareous soils under *Fagus* and *Quercus* forests of central Europe.

Figures 14-17. *Hysterangium*. 14. SEM of *H. calcareum* spores (Lectotype, leg Hesse), bar = 5 μ m. 15. Sporocarps of *H. cistophilum* (Trappe 1087), scale in mm. 16. SEM of *H. cistophilum* spores ("olbiae 1845"), bar = 5 μ m. 17. Light micrograph of *H. cistophilum* spores ("olbiae 1845"), bar = 10 μ m.





Map 9. Distribution of *Hysterangium calcareum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium cistophilum (Tulasne & Tulasne) Zeller & Dodge sensu Tulasne & Tulasne, non sensu Zeller & Dodge, Ann. Mo. Bot. Gard. 16:107–109. pl. 2, fig. 2, pl. 3, fig. 22. 1929.

≡ *Hysterangium clathroides* var. *cistophilum* Tulasne & Tulasne, in Durieu de Masion–Neuve, Expl. Sci. de l'Algérie, Bot. 1:395. 1846–1849.

Basidiomata 1–2.5 cm, globose, subglobose to reniform, white when fresh, not staining when cut or handled, surface covered with floccose white mycelium embedded in white rhizomorphs, KOH pale yellow brown to brown, FeSO₄ grayish lilac to bluish black. **Gleba** dark greenish gray to deep olive brown when fresh, becoming dark bluish–green to olive–citrine when dry, KOH dark gray to blackish olive, FeSO₄ black; locules elongate, empty.

Rhizomorphs numerous, appressed and clustered at base, concolorous with peridium. **Columella** gelatinous, inconspicuous or sometimes prominent, dendroid. **Odor** of ether.

Peridium more or less separable, 200–220 µm thick, two-layered; epicutis 20–70 µm thick, of hyaline, thin-walled, loosely interwoven to mostly periclinal hyphae, 2–5 µm thick, overlaid with thin layer of hyphae which are encrusted with crystalline particles, clamp connections common; subcutis 150–200 µm thick, of hyaline, thin-walled, irregularly inflated cells (parenchyma-like), 8–30 (–60) µm in diam, clamp connections absent.

Trama 25–55 µm thick (much thicker when immature), of hyaline, compact, subparallel to interwoven hyphae (3–4 µm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindrical, 30–40 x ± 7 µm, clamped at base, 2 spored.

Spores distinctly verrucose, 13–15 (16) x 5–7 μm , broadly fusiform to citriform; apex blunt to subpapillate, base sessile to subpedicellate. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, wrinkled, closely appressed or sometimes loosely adherent. **Spore color** in KOH hyaline singly, pale olive in mass. (Figs. 15-17).

ETYMOLOGY: the "*Cistus* lover," in reference to an association with *Cistus*.

OTHER REFERENCES: Tulasne & Tulasne, Fung. Hypog. p. 81. 1851.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Carpinus*, *Castanea sativa*, *Cistus monspelliensis*, *Quercus ilex* and other *Quercus* spp.; February through August.

COLLECTIONS EXAMINED: LECTOTYPE: **ALGERIA:** Algiers, 1844, leg Durieu (PC), ISOTYPE (K). **OTHER COLLECTIONS — FRANCE:** Provence, Trappe 4956 (OSC). Packet labelled "ex Tul. Herb." (FH). Packet labelled "Olbiae frequens Hyeme 1847–1848" (PC). Packet labelled "Olbiae 1845" (PC). **CZECHOSLOVAKIA:** Brno, 688260 (PRM). Krnov, 688261 (PRM). Larosice, 619127 (PRM). Ternosice, 619121 (PRM). **ITALY:** Piemonte, Trappe 1087, Trappe 1088 (all OSC).

DISCUSSION: The type collection as cited by Zeller & Dodge (1929) was invalidly selected as it was collected at a vastly different locality (in 1920) then Tulasne & Tulasne ascribe to it. As it turns out the collection designated as the type by Zeller and Dodge (1929) is *H. gardneri*. Material collected by Durieu in 1844 and available from Paris (PC) is selected as the lectotype.

The peridium is covered with floccose white mycelium which does not change color on bruising. The two-layered peridium and broadly fusiform to citriform spores which possess a distinct, closely appressed utricle separate this species from all others.



Map 10. Distribution of *Hysterangium cistophilum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium clathroides Vittadini, Monogr. Tuberac. pp. 13–14. pl. 4, fig. 2. 1831 non sensu auct. pl..

= *Hysterangium siculum* Mattiolo, Malpighia, 14:86. pl. 1. figs. 8–10. 1900.

Dried **basidiomata** up to 0.8 cm in diam, more or less globose with some indentations, reddish brown to brown, surface finely tomentose with adhering sand particles. **Gleba** olive to greenish gray; locules elongate, empty to partially filled. **Rhizomorphs** numerous, usually attached to base, mottled white and brown, occasionally adhering to peridium in more than one spot. **Columella** of unknown consistency, dendroid, narrow, translucent.

Peridium 250–350 μm thick, two-layered; epicutis 190–290 μm thick, of hyaline to pale yellow, thick-walled ($\pm 1 \mu\text{m}$ in diam), compactly interwoven to irregularly subparallel hyphae (4–7 μm thick), some outer hyphae have adherent crystalline particles, clamp connections absent; subcutis 40–60 μm thick, of similar structure as epicutis but of thin-walled hyphal elements, clamp connections absent.

Trama mostly 75–150 (–200) μm thick, of hyaline, interwoven hyphae (3 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** absent.

Spores distinctly verrucose, (14–) 15–18 x (5–) 6–7 μm , fusiform; apex slightly papillate, occasionally blunt, base slightly pedicellate, up to 1 μm long. **Spore wall** up to 1.5 μm thick. **Utricle** distinct, wrinkled and appressed with the texture of a golf ball. **Spore color** in KOH hyaline singly, greenish brown in mass. (Figs. 18 & 19).

ETYMOLOGY: "like *Clathrus*," in reference to the resemblance of the sporocarp to unopened *Clathrus* eggs.

OTHER REFERENCES: De Vries (1977) pp. 9–11, Fischer (1938) p. 104, Tulasne & Tulasne (1851) pp. 80–82.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Quercus garrayana* and other *Quercus* spp.; throughout the year.

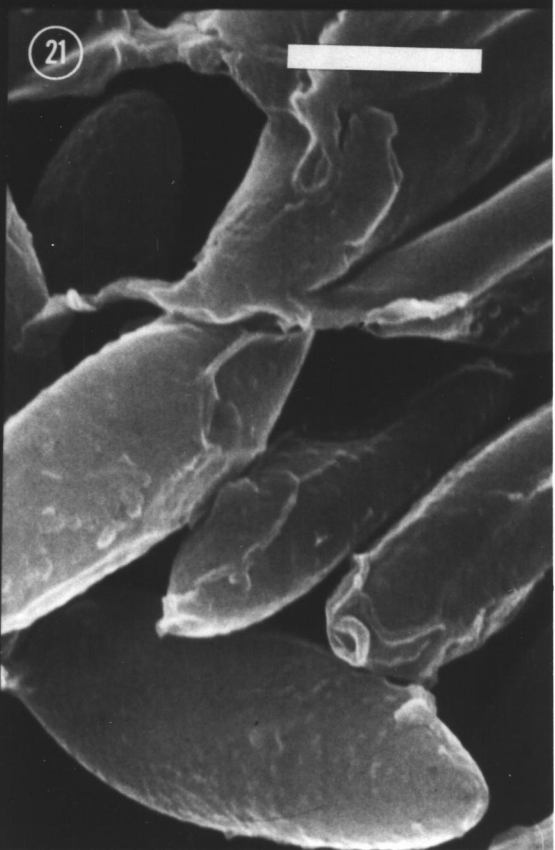
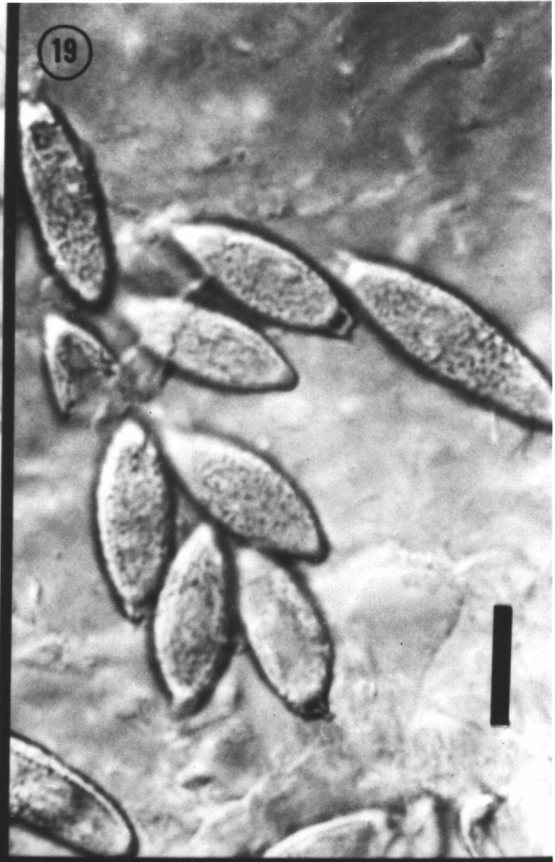
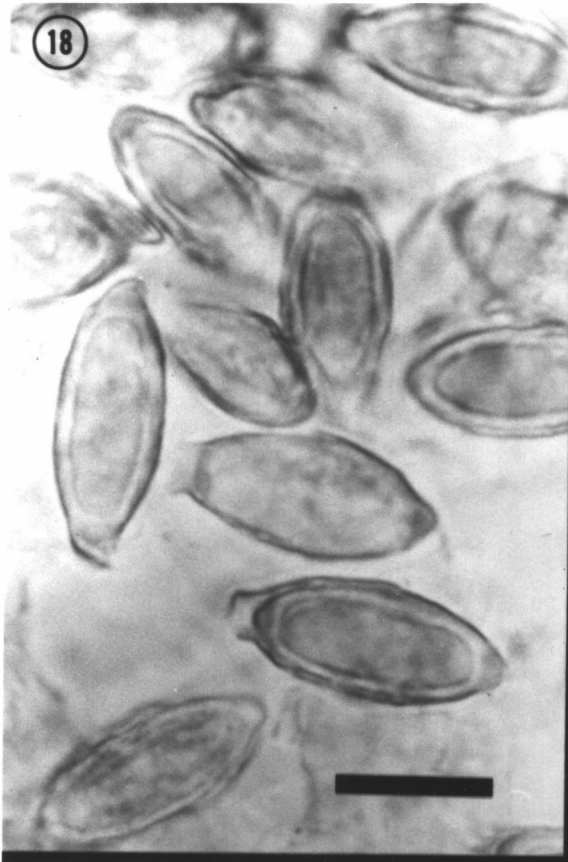
COLLECTIONS EXAMINED: LECTOTYPE: **ITALY:** specimen labelled "Ad ipso Vittadini acceptum" (PC). **OTHER COLLECTIONS — ITALY:** No locality, leg Vittadini (W, TO), packet labelled "TYPE" but no other data (K). Cefalu (ISOTYPE of *Hysterangium siculum* Mattiolo), 3–MAY–1900, leg Mattiolo (AQUI). **FRANCE:** du Poitu, leg Tulasne (PC). Galloprovince, Tulasne 39 (PC). Jurabern, leg Quélet (UPS). **GERMANY (WEST):** Soehner 620, Soehner 883, Soehner 884 (all M). Altmorschen, leg Hesse (UPS). **HUNGARY:** Hárskút, leg Szemere (C). Somogyfajsz, 22232, 22233 (all BP), leg Szemere, 25–JULY–1953 (MPU, BP 22231), leg Szemere, 11–SEPT–1955 (MPU). **OREGON:** Benton Co., Zeller 2581 (OSC).

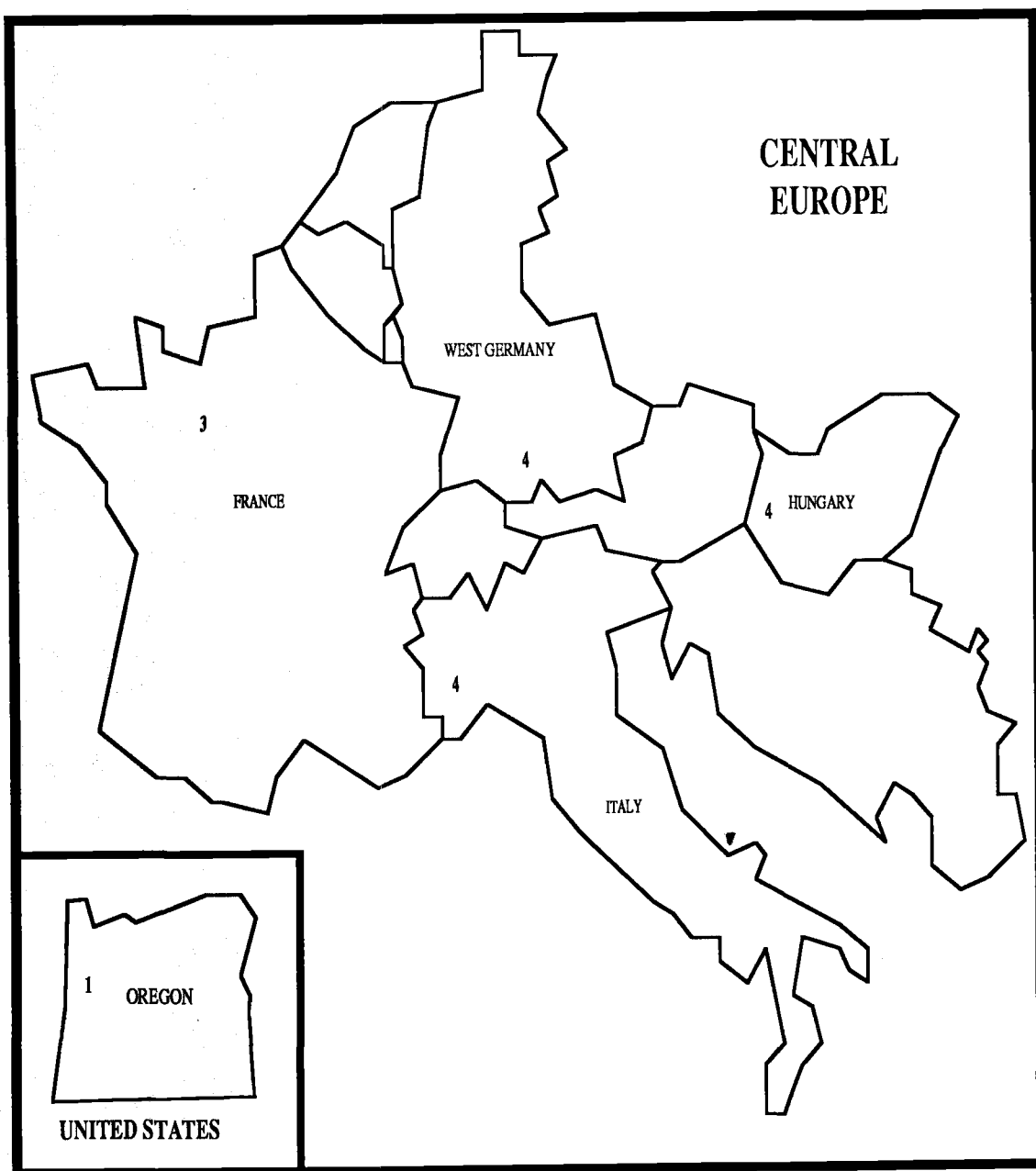
DISCUSSION: I was unable to obtain material from Vittadini's herbarium at Torino, so the above collection is selected as type. The packet of material from Kew labeled "type" had no additional information and has not been designated as such in the published literature, so is not accepted here. *Hysterangium clathroides*, the type species of the genus, has been surrounded by confusion almost from the time of its establishment. Material identified by Vittadini was not studied by subsequent authors up to Fischer (1938). Consequently, specimens of *H. coriaceum* Hesse or other species were misidentified as *H. clathroides* by many workers (Bataille 1923, Bucholtz, 1901,

Coker and Couch 1928, Fries, Th. M. 1909, Gross et al. 1980, Hintz and Winterhoff 1983, Knapp 1958, Lange 1956, Mattiolo 1900, 1922, 1935, Rodway 1924, Schwärzel 1980, 1981, Soehner 1952, Svrcek 1984, Tulasne and Tulasne 1851, Zeller and Dodge 1928).

Hysterangium clathroides differs from other *Hysterangium* species by its two-layered peridium composed of an epicutis of thick-walled hyphae and subcutis of thin-walled hyphae in conjunction with the fusiform, distinctly verrucose spores.

Figures 18-21. *Hysterangium*. 18. Light micrograph of *H. clathroides* spores (Lectotype, leg Vittadini), bar = 10 μm . 19. Light micrograph of *H. clathroides* spores (leg Tulasne (du Poitu)), bar = 10 μm . 20. Sporocarps of *H. coriaceum* spores (Trappe 632), scale in mm. 21. SEM of *H. coriaceum* spores (Trappe 632), bar = 5 μm .





Map 11. Distribution of *Hysterangium clathroides*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium coriaceum Hesse, Hypog. Deutschl. 1:101. pl. 7, fig. 24, pl. 9, fig. 5. 1891.

= *Hysterangium graveolens* Velenovsky, Novitates Mycologicae p. 170. 1939.

= *Hysterangium fuscum* Harkness, Cal. Acad. Sci. Proc. III. 1:257. 1899.

= *Hysterangium hessei* Soehner, Zeitschr. f. Pilzk. 3:29–32. 1949.

= *Hysterangium knappii* Soehner, Sydowia 6:253–254. 1952.

= *Rhizopogon virens* Karsten, Finska Vet.-Soc. Bidrag Natur och Folk 3:354–355. 1876.

= *Rhizopogon virescens* Karsten in Saccardo, Syll. Fung. 9:280. 1891.

Basidiomata 1–2.5 cm in diam, subglobose to convoluted with indented base, white when fresh, rosy brown to flesh red when bruised, nested in dense mycelium in soil which for the most part do not adhere to the sporocarp surface, surface glabrous, ETOH nonreactive, FeSO₄ pale grayish green to bluish gray, KOH yellowish brown to brownish orange, FeCl₃ indigo. **Gleba** cartilaginous, dark greenish gray to greenish olive, FeSO₄ dark greenish gray to dark blue, KOH blackish green, FeCl₃ indigo; locules somewhat rounded to elongate, empty; **Rhizomorphs** single or numerous, stout, up to 1 mm, attached at base, concolorous with peridium. **Columella** gelatinous, distinct, dendroid, gray or translucent. **Odor** faint, fungoid to slightly fruity. **Taste** of peridium, bitter.

Peridium easily separable from gleba, 300–450 μm thick, two-layered; epicutis 280–430 μm thick, of hyaline, inflated cells (parenchyma-like), 10–25 (–40) μm in diam, clamp connections absent; subcutis 20 μm thick, of hyaline, periclinal to interwoven hyphae, 2–4 μm in diam, clamp connections common.

Trama 30–200 μm thick, of hyaline, compactly interwoven hyphae (μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, elongate, 40–50 x 5–8 μm , clamp connection at base, (3-) 4–6 spored.

Spores smooth, 11–14 x 4–5 μm , ellipsoid to elongate; apex acuminate, base slightly appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** slight at first, distinct at maturity, irregularly adhering to spore wall, not inflated.

Spore color in KOH hyaline to pale green singly, pale green in mass. (Figs. 20 & 21).

ETYMOLOGY: in reference to the “leathery” peridium.

OTHER REFERENCES: Bucholtz (as *H. clathroides*) (1901a) p. 7, (1901b) p. 316, (1903) p.171, (1908) p. 467, Lange (1956) pp. 76–77, Rehsteiner (1892) pp.777–787, Saccardo (1895) p. 168, Zeller & Dodge pp. 113–114.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Abies amabilis*, *A. grandis*, *A. lasiocarpa*, *Picea engelmannii*, *P. excelsa*, *Pinus contorta*, *P. flexilis*, *P. lambertiana*, *P. longaeva*, *P. nigra*, *P. ponderosa*, *Pseudotsuga menziesii*, *Tsuga canadensis*, *T. heterophylla* and possibly *Corylus* and *Fagus*; throughout the year, especially spring through autumn, from sea level to subalpine and up to 11200 feet in elevation.

COLLECTIONS EXAMINED: LECTOTYPE: GERMANY (WEST):

Esienkaute, JULY–1891, leg Hesse (MB). **OTHER COLLECTIONS —**

AUSTRIA: leg Hohnel (FH). Wiemerwald, leg Beck (W). Neunkirchner, leg

Moser (IB). **BELGIUM:** Arlon, leg Bourdeau (HBG), leg Rousseau 4684, leg Rousseau APRIL-1902, leg Rousseau SEPT-1907 (all MEISE). **CANADA:** **BRITISH COLUMBIA:** Kamloops, B 104, B 111, B 115, B 116 (all OSC). **CZECHOSLOVAKIA:** Badikov, 153806 (HOLOTYPE of *Hysterangium graveolens* Vel.), 153808 (all PRM). Bezerovice, 604736 (PRM). Bohemia, 688263 (PRM), Klika 5 (W), Bubak 191 (BRA, CUP, E, FH, JE, LD, MICH, S, TUR, W), Bubak 194 (G, MEISE, NY, TUR). Brno, leg Hruby (BP 22223, BRA, HBG, JE, LD, M, MEISE, S). Chrutenice, 619148 (PRM). Havlickuv, 619156 (PRM). Jindrichuv, 619160 (PRM). Kamyk, 600759 (PRM). Karlstejn, 619153 (PRM). Libochovicky, 619159 (PRM). Magurka, 622943 (PRM). Matliary, 709828 (PRM). Prague, Trappe 1491 (OSC). Salatin, 622944 (PRM). Svojanov, 619147 (PRM). Vonsklasy, 619144, 619151 (all PRM). **DENMARK:** Arhus, ML 4462 (C). **FINLAND:** Soderholm 401 (OULU), Soderholm 755 (H). Mustiala, leg Karsten (HOLOTYPE of *Rhizopogon virens* Karsten and *Rhizopogon virescens* Karsten) (UPS). **FRANCE:** Grandis Rhone, leg Rouchet (MPU). Larrau, Trappe 9748 (OSC). Nice, leg Boudier (S). **GERMANY (EAST):** Elsterberg, leg John (HAL), leg Krien (W). Gotha, leg Rauschert (JE). Larrau, Trappe 9748 (OSC). **GERMANY (WEST):** herb Hesse, leg Hesse 1900 (all FH), leg Hesse (MB), Gross 66 (M, OSC), leg Killerman, Gross 60, Gross 142, Gross 276, Gross 287, Gross 314, Gross 353, Soehner 184, Soehner 264a, Soehner 264b, Soehner 399, Soehner 501, Soehner 570b, Soehner 614, Soehner 653, Soehner 726, Soehner 809, Soehner 834, Soehner 836, Soehner 855, Soehner 861, Soehner 862, Soehner 863, Soehner 900, Soehner 950, Soehner 971, Soehner 1071, Soehner 1095, Soehner 1105, Soehner 1107, Soehner 1148, Soehner 1163, Soehner 1168, Soehner 1260, Soehner 1409, Soehner 1425, Soehner 1432

(HOLOTYPE of *H. hessei* Soehner), Soehner 1433, Soehner 1434, Soehner 1435, Soehner 1439, Soehner 1444, Soehner 1520, Soehner 1524, Soehner 1635, Soehner 1660, Soehner 1697, Soehner 1701, Soehner 1723, Soehner 1759, Soehner 1831, Soehner 1839, Soehner 1891, Soehner 1898, Soehner 1899, Soehner 1901, Soehner 1908, Soehner 1942, Soehner 1951, Soehner 1958, Soehner 2075, Soehner 2010, Soehner 2020, Soehner 2030, Soehner 2112, Soehner 2116, Soehner 2122, Soehner 2137, Soehner 2139, Soehner 2144, Soehner 2170, Soehner 2218, Soehner 2233 (HOLOTYPE of *Hysterangium knappii* Soehner), Soehner 2240, Soehner 2235, Soehner 2238, Soehner 2265, Soehner 2293, Soehner 2362, Soehner 2365, Soehner 2367 (all M), leg Haas 1950, leg Haas 15-JUNE-1949, leg Haas 1935 (all STU), leg Huber (BP 22225, S, W). **HUNGARY:** Szekszard, 22228, 22229 (all BP). leg Szemere (BP 31939, S). **ITALY:** Tridentina (UPS), leg Bresadola AUG-1906, leg Bresadola AUG-1898 (all S). Torino (TO). **NORWAY:** Ostfold, leg Hoiland (OSLO). Oppland, leg Eckbald (OSLO). Akershus, leg Kvavik (OSLO, UPS). **POLAND:** Janinow, leg Nayinanowicz (LOD). **ROMANIA:** Transylvania, leg Hollós (FH), 22227 (BP). **RUSSIA:** Moskow, Bucholtz 216 (BP, BRA, HBG, K, L, LE, M, W), Bucholtz 283 (FH), leg Bucholtz (FH, NY). **SPAIN:** Cuenca, leg Calonge MA 7921 (MA). **SWEDEN:** Kers 4984 (MICH), leg Soot (S), leg R. Fries (S, UPS, FH), Hawker 141, Hawker 142, leg Buchwald (all K), leg Th.C.E. Fries, leg E.A. Fries (all FH), leg Lagerheim, leg Th.M. Fries (all UPS), H. Smith 2256 (C, S, UPS, W). **SWITZERLAND:** Bern, Fischer 19, Fischer 20, Fischer 21 (all UC). Valais, 31746 (G). Zurich, leg Thellung (MPU). **THE NETHERLANDS:** Baarn, De Vries 714, De Vries 716, De Vries 734a, De Vries 744 (all OSC). **ALASKA:** Anchorage, leg Culver (MICH). Fairbanks, Trappe 5864 (OSC). **ARIZONA:** Coconino Co., F 2912, F

2914 (all MICH), AHF 312 (FSLF). **CALIFORNIA:** El Dorado Co., HDT 32273 (SFU). Humboldt Co., HDT 47094 (SFU). Marin Co., Parks 2717 (UC). Lake Co., 1319117 (UC). Monterey Co., HS 2884 (SFU). Riverside Co., Trappe 7342 (OSC), Watling 17179, Watling 17239 (all E). San Bernardino Co., Trappe 6732 (OSC), HS 1860, HS 1861 (all SFU). Santa Cruz Co., HS 2387 (SFU). Sierra Co., HDT 30015, HS 1465, HS 1521, HS 1950, HS 1963, HS 2895, HS 2902, HS 2935 (all SFU), Trappe 9455, Trappe 9479, Trappe 9480, Trappe 9489, Trappe 9505, Trappe 9535, Trappe 9536, Trappe 9538 (all OSC). Siskiyou Co., HDT 44548 (SFU), Trappe 8133, Trappe 8137, W.B. Cooke 42662 (all OSC), leg Cooke (NY). Stanislaus Co., HDT 17179 (SFU). Tuolumne Co., HS 1541, HDT 32486 (all SFU). Yuba Co., HS 1480 (SFU).

COLORADO: Boulder Co., F 205, F 214, F 220, F 226, F 229, F 235, F 236, F 239, F 250, F 264e, F 281, F 302, F 313, F 388, F 474, F 656, F 980, F 1108, F 2941 (all MICH). Chaffee Co., leg Fogel (MICH). Clear Creek Co., F 481, F 667, F 685, F 687, F 693 (all MICH). Eagle Co., F 2385, F 2387 (all MICH). Gilpin Co., F 364, F 365, F 2357, F 2358 (all MICH). Gunnison Co., leg Fogel (MICH). Jackson Co., F 668 (MICH). Larimer Co., F 646, F 650, F 672, F 676, F 1053 (all MICH). Pitkin Co., A 7029, SM 85793, SM 86824, SM 86837, SM 86928a, SM 86928b, SM 86928c, SM 89066, SM 89086 (all MICH), JFA 8183 (WTU).

IDAHO: Adams Co., SM 65230, SM 65231, SM 65317, SM 65324, SM 65325, SM 65327, SM 65328, SM 65329, SM 65357, SM 65358, SM 65359, SM 65581, SM 65610, SM 65611, SM 65612, SM 65822, SM 68871, SM 68900, SM 68902, SM 68903 (all MICH), SM 65326, SM 65376 (all MICH, K). Bonner Co., SM 67907, SM 67926, SM 68008, SM 68012, SM 68036, SM 68039, SM 68049, SM 68306, SM 68349, SM 68453, SM 68457, SM 68536, SM 68538, SM 68603, SM 68659, SM 71342 (all MICH), leg Hawker (K), 109169 (DAOM).

Custer Co., SM 65490 (MICH). Idaho Co., SM 65375 (MICH). Kootenai Co., Trappe 2958 (OSC). Nez Perce Co., Tylutki 7042 (ID). Valley Co., NSW 3483, SM 69312, SM 64987, SM 65033, SM 65080, SM 65107, SM 65110, SM 65111, SM 65161, SM 66182, SM 66183, SM 66191, SM 66195, SM 66216, SM 66217, SM 68922 (all MICH), S. Miller 743 (OSC). **MAINE:** York Co., leg Thaxter 10—JULY—1897, leg Thaxter DEC—1901, leg Thaxter 6—JUNE—1886 (all FH). **MONTANA:** Missoula Co., Trappe 3652, Trappe 3655 (all OSC). **NEVADA:** F 2524, F 2538, F 2539, F 2540, F 2567, F 2569, F 2722, F 2725 (all MICH). **OREGON:** Benton Co., F 137, F 162, F 263, F 375, F 378, F 497, F 499, F 503, F 504, F 507, F 526, F 534, F 548, F 605, F 851, F 858, F 896 (all MICH), Stewart 295, Stewart 485, Stewart 526, Stewart 1061, Stewart 530, Trappe 910, Trappe 2892, Trappe 5049, Trappe 6496 (all OSC), Trappe 3983 (OSC, K). Clackamas Co., leg Gilkey (NY), Trappe 2169, Trappe 5333 (all OSC). Deschutes Co., F 1088, F 1175, F 1185 (MICH), Trappe 8275 (OSC). Douglas Co., leg Zeller (NY). Hood River Co., Trappe 623, Trappe 624 (all OSC), SM 71175 (MICH). Jackson Co., leg Houven (MICH), Trappe 6249, Trappe 6254, Trappe 6258 (all OSC). Josephine Co., Trappe 7896, Trappe 9413 (all OSC). Klamath Co., Trappe 578 (OSC), F 2107 (MICH). Lane Co., Stewart 22, Trappe 2855 (all OSC), F 622 (MICH). Linn Co., Trappe 618, Trappe 621, Trappe 628, Trappe 912, Trappe 917, Trappe 5723, Trappe 8015 (all OSC). Polk Co., Stewart 1028 (OSC). Wallowa Co., Trappe 1911, Trappe 2247, Trappe 5223 (all OSC), leg Rogers (FH, NY). Wasco Co., Oswald 6 (MICH). Yamhill Co., Trappe 1557 (OSC). **UTAH:** Grand Co., F 2630, F 2635 (all MICH). Iron Co., F 2541, F 2549 (all MICH). Kane Co., F 2589 (MICH). Uintah Co., F 2422 (MICH). Utah Co., HDT 25440, HDT 25445, HDT 25448, HDT 25461, HDT 25466, HDT 25620 (all SFU). Washington Co., leg Fogel

(MICH). **WASHINGTON:** Jefferson Co., DRH 179, DRH 187 (ELRG). Pend Oreille Co., SM 68128, SM 68129, SM 68130, SM 68131, SM 68133, SM 68134, SM 68135, SM 68136, SM 68137, SM 68138, SM 68139, SM 68210, SM 68241, SM 68393, SM 68423 (all MICH). Pierce Co., DRH 64, DRH 326 (ELRG), SM 30113 (MICH), Stewart 20, Stewart 41, Stewart 43, Stewart 44, Stewart 47, Stewart 48, Stewart 707 (all OSC). **WYOMING:** Crook Co., WHF 40 (FSLF). Fremont Co., WHF 82 (FSLF).

DISCUSSION: The most commonly encountered and widely distributed *Hysterangium* species, it has also been subjected to the most confusion by way of identity. This confusion dates from Hesse (1891) who proposed *H. coriaceum* while misinterpreting the original concept of *H. clathroides* Vitt. Reexamination of *H. coriaceum* specimens collected and identified by Hesse allowed a more accurate description of spore size, glebal color upon drying, and peridial characters than originally published. Hesse identified mature *H. coriaceum* collections as *H. clathroides*, while basing *H. coriaceum* on fairly immature specimens. I studied specimens of *H. clathroides* which were sent to Tulasne (in PC) from Vittadini, these agree entirely with Fischer's description (1938). *Hysterangium clathroides* Vitt. sensu Zeller and Dodge (1929) is actually a more complete description of *H. coriaceum* Hesse. Later Zeller (1941) published *H. separabile* and cited collections that he and Dodge (1928) had assigned to *H. clathroides*. Because of confusion resulting from the ambiguous descriptions, specimens identified as *H. separabile* by Calonge et al. (1977), Lange (1956), States (1984), Trappe and Guzmán (1971) and Zeller and Dodge (1929) are for the most part *H. coriaceum*.

Examination of type material of *H. fuscum* Hark., *H. graveolens* Vel., *H. hessei* Soehner, *H. knappii* Soehner, *Rhizopogon virens* Karsten, and *R.*

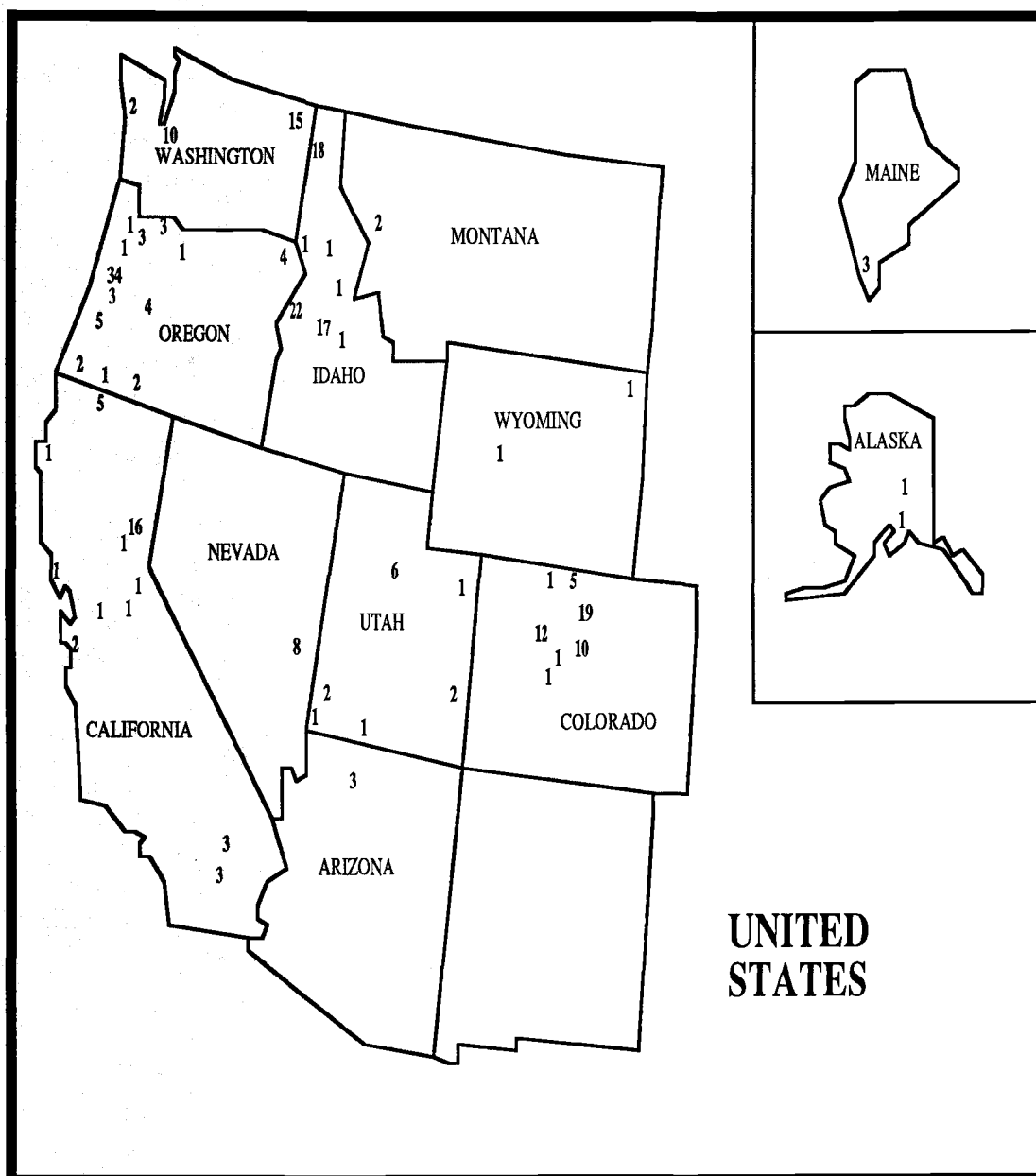
virescens Karsten, reveal them as synonyms of *H. coriaceum*.

Hysterangium coriaceum is macroscopically similar to *H. crassirhachis* but has large parenchyma-like cells in the peridium in contrast to the interwoven, albeit somewhat inflated, hyphal peridium of *H. crassirhachis*. *Hysterangium coriaceum* stains brown to pinkish-brown when bruised, whereas *H. crassirhachis* stains pink. *Hysterangium coriaceum* differs from *H. affine* of the Southern Hemisphere and *H. aureum* of the Northern Hemisphere by its subcutis of interwoven hyphae. *Hysterangium fragile* and *H. epiroticum* both have much larger spores than *H. coriaceum*. *H. separabile* has larger more fusiform spores, basidia which are half as long (up to 28 μm) and occurs only with *Quercus* spp., while *H. coriaceum* occurs with many different conifers.

Hunt and Trappe (1987) and Fogel (1976) found *H. coriaceum* produced up to 26% and 18.7 %, respectively, of the total number of hypogeous sporocarps (9.8% and 19.2%, respectively, of total dry weight) in a western Oregon Douglas-fir stand. In ten different Douglas-fir stands in western Oregon *Hysterangium coriaceum* produced nearly 100% of its sporocarps in the spring, primarily April (Luoma, unpublished data).

Castellano and Trappe (1985) unsuccessfully used *H. coriaceum* (as *H. separabile*) spores to inoculate Douglas-fir seedlings. Molina and Trappe (1982a) reported *H. coriaceum* (as *H. separabile*) formed mycorrhizae with *Larix occidentalis*, *Tsuga heterophylla*, *Pinus monticola* and *P. contorta* in pure culture. *H. coriaceum* (as *H. separabile*) also forms mycorrhizae with *Arbutus menziesii* and *Arctostaphylos uva-ursi* in pure culture (Molina and Trappe 1982b) .

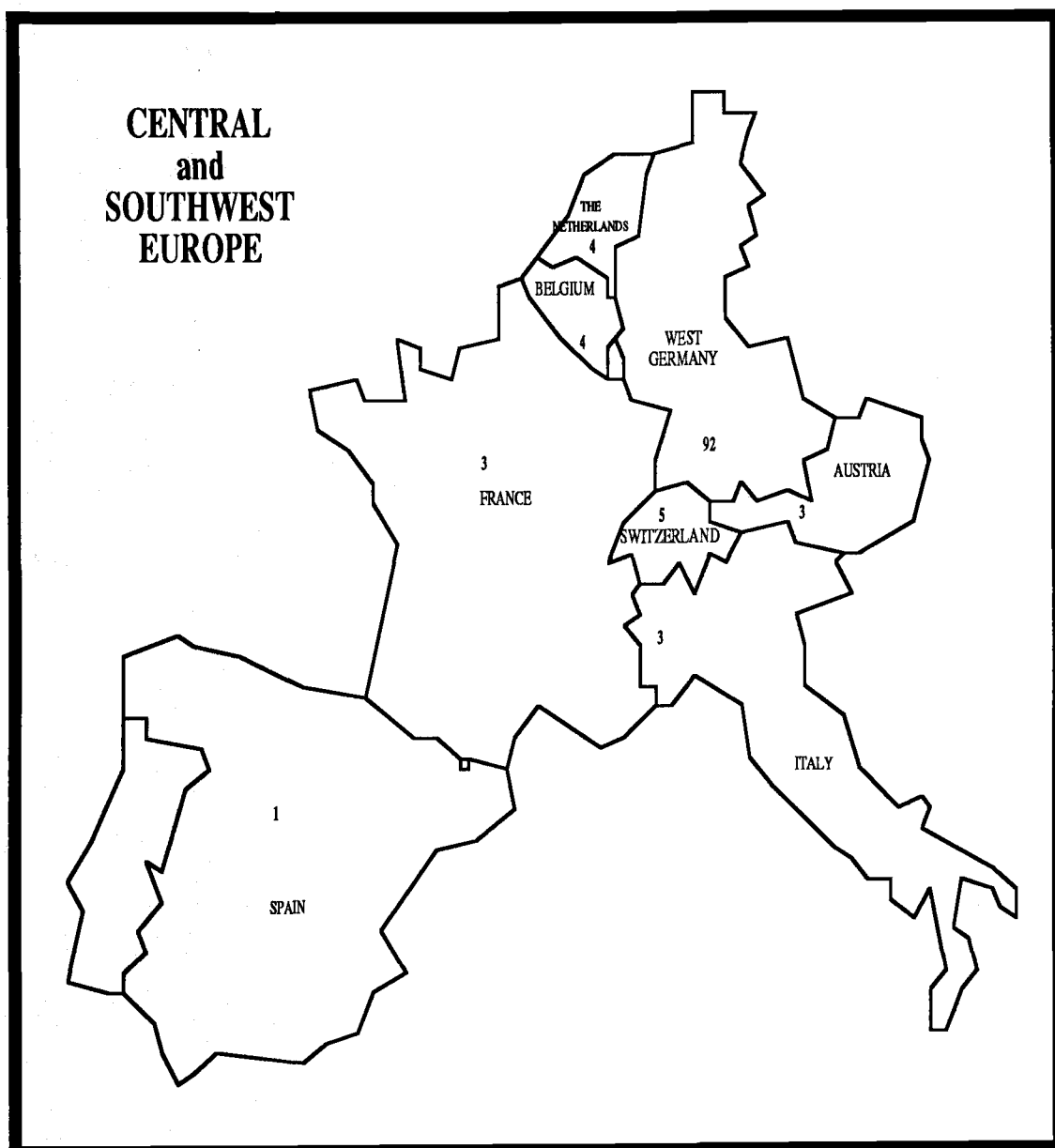
Rehsteiner (1892) describes the development of *H. coriaceum* (as *H. clathroides*) in detail.



Map 12. Distribution of *Hysterangium coriaceum* in North America. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.



Map 13. Distribution of *Hysterangium coriaceum* in northern and eastern Europe. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.



Map 14. Distribution of *Hysterangium coriaceum* in central and southwestern Europe. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium crassirhachis Zeller & Dodge, Ann. Mo. Bot. Gard. 16:101–102. pl. 1, fig 4, pl. 3, fig. 20. 1929.

Basidiomata 1–2.5 cm in diam, globose to depressed, often reniform, eggshell white, bruising pink to pinkish buff, snuff brown when dry, surface glabrous, FeSO₄ aqua blue–green, KOH nonreactive. **Gleba** tough and rubbery, pale green, grayish olive to dark grayish olive, FeSO₄ aqua blue–green, KOH nonreactive; locules elongate, mostly empty. **Rhizomorph** usually single, 1–2 mm in diam, attached to base, concolorous with peridium. **Columella** gelatinous to cartilaginous, distinct, thick, 1–2 mm broad at base, subpercurrent to dendroid, translucent to opaque when fresh, white as dried. **Odor** occasionally aromatic, faintly of iodine.

Peridium easily separable from gleba, 420–630 µm thick, two layered; epicutis 370–580 µm thick, of hyaline, thin-walled, compactly interwoven, swollen (rhomboidal), hyphae (subparenchyma-like), 10–15 x 20–30 µm in diam, somewhat smaller near surface where the hyphae are more periclinal, clamp connections absent; subcutis 20–50 µm thick, of hyaline, thin-walled, subpericlinal to interwoven hyphae, 2–4 (–8) µm in diam, clamp connections common to scattered.

Trama 100–300 µm thick, of hyaline, loosely interwoven hyphae (3–4 µm in diam) in a gelatinized matrix, clamp connections scattered. **Basidia** hyaline, clavate to elongate with a restricted base, 10 x 30 µm, 2 (4) spored.

Spores minutely verrucose, (11–) 13–15 x 4–5.5 μm , ellipsoid to subfusiform; apex acutely blunt, base slightly appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** distinct in age, wrinkled, mostly adhering to the spore wall, occasionally slightly loosened. **Spore color** in KOH hyaline singly, pale green to olive in mass. (Figs. 22 & 23).

ETYMOLOGY: "thick rachis" in reference to the prominent columella.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Abies magnifica*, *Pseudotsuga macrocarpa*, *P. menziesii*, *Pinus coulteri*, *P. murrayana* and possibly *Quercus garryana*; throughout the year but primarily spring through autumn.

COLLECTIONS EXAMINED: HOLOTYPE: **OREGON:** Benton Co., Corvallis, 6–MAY–1922, leg Boozer, Zeller 2319 (NY), ISOTYPES (OSC, L, MPU). **OTHER COLLECTIONS — ALASKA:** Trappe 8361 (OSC).

CALIFORNIA: Alpine Co., HDT 32794 (SFU). Del Norte Co., Trappe 8587 (OSC). Fresno Co., Trappe 4061 (OSC). Mendocino Co., HS 1797, HS 1798 (all SFU). Riverside Co., Watling 17212, Watling 17274 (all E), Trappe 7332 (OSC). Santa Clara Co., Parks 156 (M, L, NY, UC). Santa Cruz Co., HS 2635 (SFU). San Diego Co., Watling 17122 (E). Sierra Co., HS 978, HS 1450, HS 1919, HS 3093, HDT 32443, HDT 34834 (all SFU), Trappe 9492, Trappe 9517, Trappe 9518, Trappe 9521 (all OSC). Siskiyou Co., Trappe 7580 (OSC).

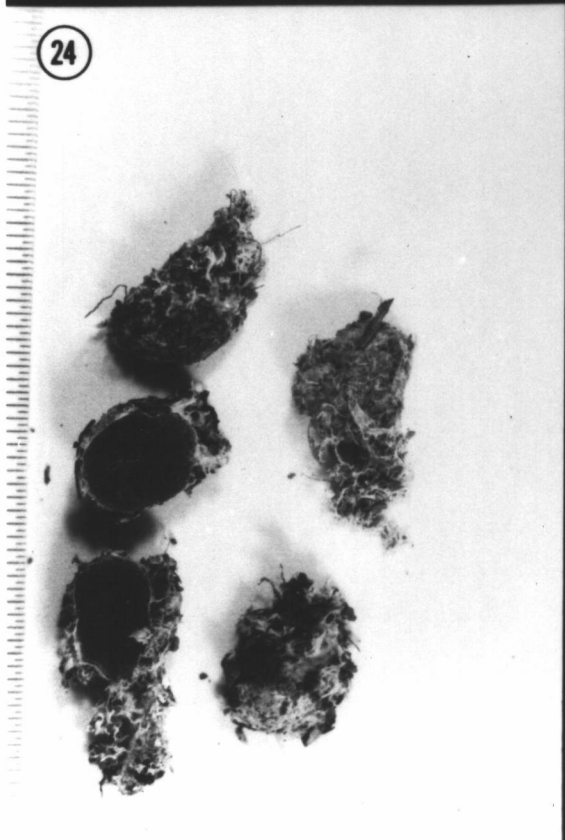
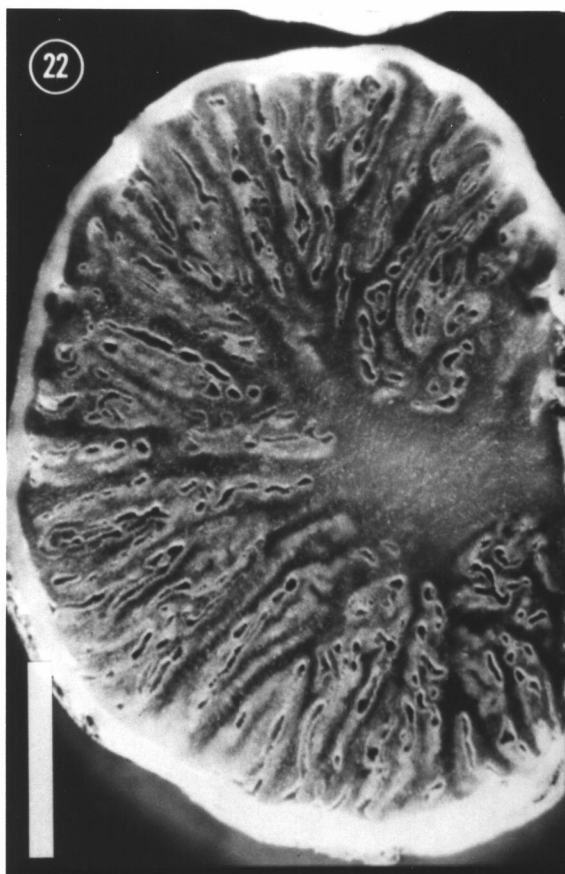
IDAHO: Bonner Co., Watling 3722 (E). **OREGON:** Benton Co., Trappe 679, Trappe 943, Trappe 3975, Trappe 5439, Trappe 5981, Trappe 6199, Trappe 6215, Trappe 6780, Trappe 7213, Trappe 8735, Stewart 78, Stewart 305, Stewart 1018 (all OSC), Brown 101 (MICH, NY), Zeller 2343, Zeller 2348 (all NY, OSC), Zeller 6813, Zeller 8228, Doty 856 (all NY), F 92, F 153, F 161, F

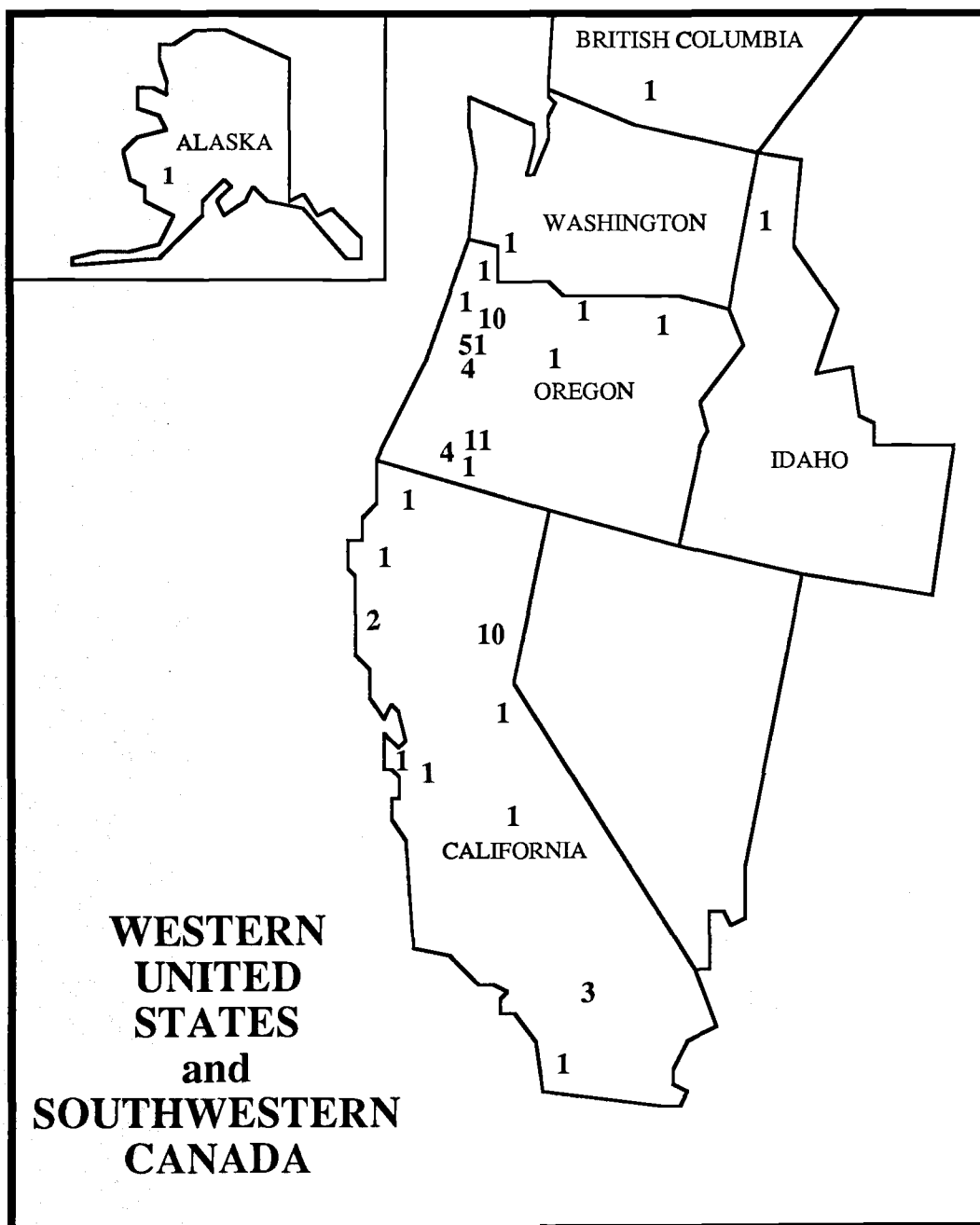
271, F 328, F 343, F 517, F 526, F 548, F 586, F 605, F 746, F 753, F 774, F 779, F 786, F 788, F 821, F 826, F 829, F 851, F 896, F 977 (all MICH). Columbia Co., leg Zeller 10-JUNE-1939 (NY). Crook Co., Trappe 8623 (OSC). Douglas Co., Trappe 7877 (OSC), Zeller 8329, Zeller 8359, Zeller 8391, Zeller 8463 (all NY). Jackson Co., Trappe 5781, Trappe 8590, Trappe 8595 (all OSC), Trappe 5774 (WTU, OSC, CUP, MICH). Josephine Co., Trappe 7891, Stewart 370, Stewart 372, Stewart 383, Stewart, 386, Stewart 456 (all OSC). Lane Co., Trappe 4522, Trappe 4530, Trappe 5613, Trappe 5865 (all OSC). Linn Co., Trappe 620, Trappe 633, Trappe 634, Trappe 5921, Trappe 5998, Trappe 6198, Trappe 8276 (all OSC), Zeller 8309, Zeller 8508 (all NY). Marion Co., Trappe 2745, Trappe 7958 (all OSC). Polk Co., Trappe 1611, Trappe 1615, Trappe 1621, Trappe 2646, Trappe 2652, Stewart 1031, Stewart 1035, Stewart 1037 (all OSC). Union Co., Trappe 4785 (OSC). Wasco Co., Trappe 7307 (OSC). **WASHINGTON:** Skamania Co., Trappe 5212 (OSC). **CANADA: BRITISH COLUMBIA** leg Savale (MICH).

DISCUSSION: This species occurs from northern California to Alaska and east to Idaho. It is a common ectomycorrhizal associate of *Pseudotsuga menziesii* and possibly other Pinaceae. The association of this species with *Quercus* (Zeller & Dodge 1929) is suspect. *Quercus garryana* commonly occurs in mixed stands with *Pseudotsuga menziesii* in the Corvallis area but appears to have a different complement of ectomycorrhizal fungi.

Hysterangium crassirhachis is easily distinguished from all other *Hysterangium* species by its unusually thick, opaque columella, and thick, glabrous, easily separable peridium which bruises pink on handling and which has an epicutis of compact, uniformly inflated hyphae underlain by a layer of noninflated interwoven hyphae.

Figures 22-25. *Hysterangium*. 22. Cross-sectional view of a *H. crassirhachis* sporocarp (Trappe 7877), notice the thick columella (arrow), bar = 5 mm. 23. *H. crassirhachis* sporocarps (SLM 746), bar = 2 cm. 24. *H. crassum* sporocarps (Trappe 1088), scale in mm. 25. Light micrograph of *H. crassum* spores (Lectotype, Tulasne 44), bar = 10 μ m.





Map 15. Distribution of *Hysterangium crassirhachis*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium crassum (Tulasne & Tulasne) Fischer, Schweiz. Zeitschr. Pilzk. 16:104. 1938.

≡ *Hysterangium clathroides* var. *crassum* Tulasne & Tulasne, Fung. Hypog. pp. 81–82. 1851.

Dried **basidiomata** up to 2 cm in diam, subglobose, pale brown to brown when dried, surface floccose, with abundant soil particles adhering to peridium. **Gleba** green to olive; locules irregular to elongate, filled with spores at maturity. **Rhizomorphs** numerous, small, concolorous with peridium. **Columella** of unknown consistency, narrow, dendroid, dark brown when dried.

Peridium separable from gleba, 130–290 μm thick, two-layered; epicutis 30–40 μm thick, of hyaline, thin-walled, loosely interwoven hyphae, 3–8 μm in diam, clamp connections absent; subcutis 100–250 μm thick, of hyaline, thin-walled, polyhedral to spherical cells (parenchyma-like), 10–20 μm in diam, clamp connections absent.

Trama 100–150 μm thick, of hyaline, collapsed, loosely interwoven hyphae (1–3 μm in diam) in a gelatinized matrix, clamp connections absent.

Basidia not observed.

Spores distinctly verrucose, 15–17 (–18) $\times$ 6–7 μm , broadly fusiform; apex acuminate to subpapillate, base pedicellate. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, appressed to spore wall, wrinkled, up to 1 μm thick. **Spore color** in KOH pale olive singly, olive brown in mass. (Figs. 24 & 25).

ETYMOLOGY: in reference to the “thick” peridium.

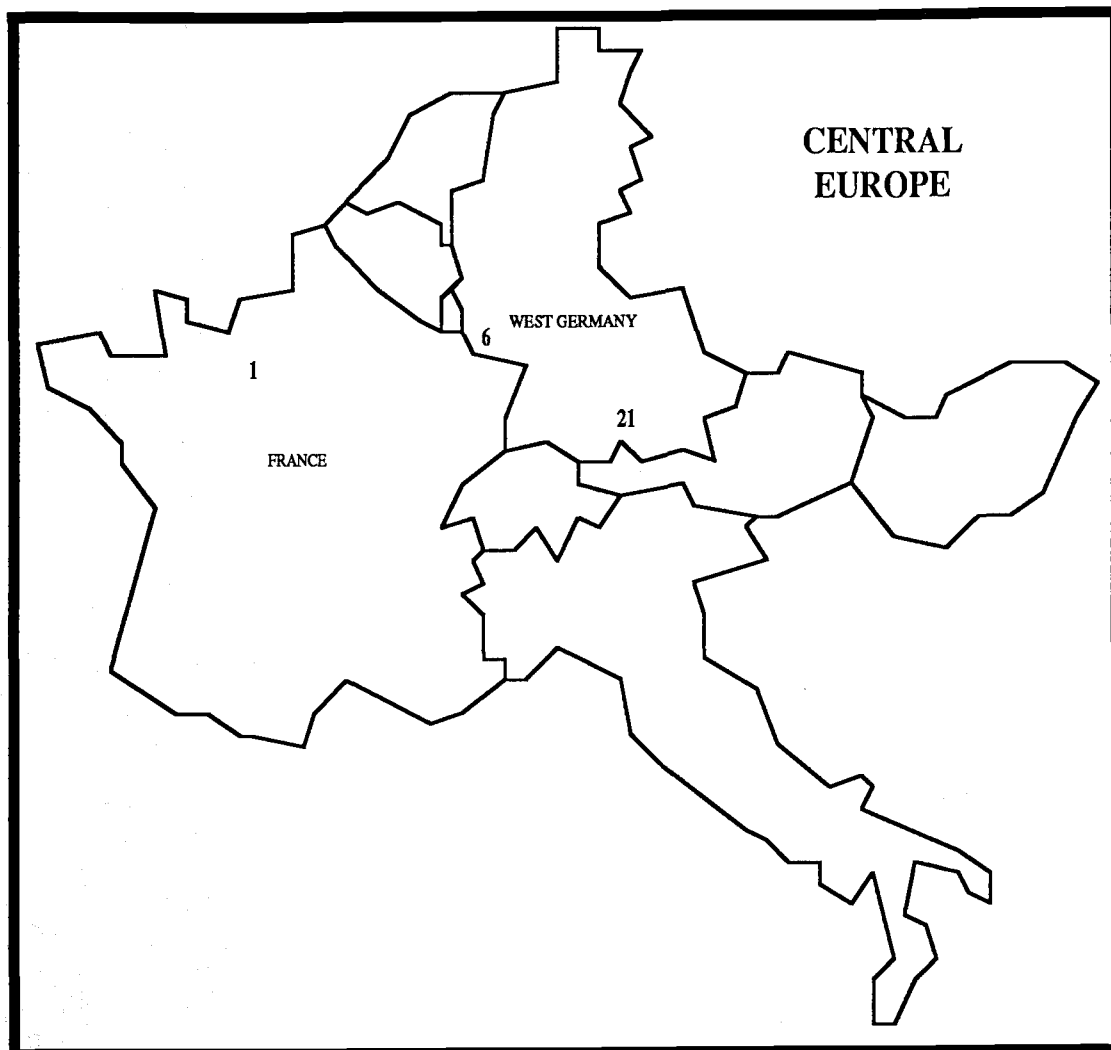
OTHER REFERENCES: De Vries (1971) p. 28, Gross (1980) p. 131.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Quercus*, *Fagus*, and *Carpinus*; May through September.

COLLECTIONS EXAMINED: LECTOTYPE: **FRANCE:** Maisons-Laffitte, près Paris, 1844, Tulasne 44 (PC), ISOTYPE (FH). **OTHER COLLECTIONS — GERMANY (WEST):** Munich, Soehner 112, Soehner 113 (all M). Volklingen, Gross 143, Gross 286 (all M). Sitterswald, Gross 65, Gross 80, Gross 131, Gross 214 (all M). locality unknown, Soehner 121, Soehner 122, Soehner 440, Soehner 502, Soehner 503, Soehner 746, Soehner 751, Soehner 801 Soehner 1403, Soehner 1405, Soehner 1406, Soehner 1407, Soehner 1408, Soehner 1409, Soehner 1410, Soehner 1413, Soehner 1440, Soehner 1442, Soehner 1443 (all M).

DISCUSSION: All collections cited by Zeller and Dodge (1929) and Zeller (1941) except the isotype (from FH) are not *H. crassum* and are mostly referable to *H. setchellii*. Subsequent workers have also had difficulty with this taxon (J. Trappe pers. comm.). *Hysterangium crassum* is restricted to (presumptive) mycorrhizal association with *Quercus*, *Fagus* or *Carpinus*.

Hysterangium crassum differs from all other *Hysterangium* species by its combination of double layered peridium with an epicutis of interwoven hyphae and a subcutis of parenchyma-like cells and verrucose, broadly fusiform spores which have a thick, wrinkled utricle.



Map 16. Distribution of *Hysterangium crassum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium epiroticum Pacioni, Nova Hedwigia 40:80–83. pl. 1, fig. 1.
1984.

Basidiomata up to 1.5 cm in diam, subglobose or pyriform, when fresh white with ochraceous tones, white to reddish brown when dry, surface felty.

Gleba green to dark green; locules elongate, empty. **Rhizomorphs** numerous, small, adherent, concolorous with peridium. **Columella** gelatinous, dendroid, narrow, arising from a sterile base, translucent.

Peridium easily separable from gleba, 400–600 μm thick, three-layered; epicutis 85–125 μm thick, of pale brown to brown, thin-walled, interwoven hyphae, 5–8 μm in diam; clamp connections absent; mesocutis 200–300 μm thick, of hyaline to pale brown, thin-walled, subglobose to broadly ellipsoid cells (parenchyma-like), 10–35 μm in diam; clamp connections absent; subcutis 20 μm thick, of pale brown, thin-walled, interwoven hyphae, 1–4 μm in diam, clamp connections absent

Trama $\pm$ 100 μm thick, of hyaline, collapsed, compactly interwoven hyphae (1–3 μm in diam) in a gelatinized matrix, clamp connections absent.

Basidia not rehydrating well, hyaline, 20–25 μm long, 2 or 4 spored.

Spores distinctly verrucose, 18–29 x 5–8 μm , fusiform; apex mostly acuminate in youth, papillate at maturity, base distinctly pedicellate, up to 3 μm long. **Spore wall** up to 1 μm thick. **Utricle** absent in youth, distinct, closely appressed at maturity. **Spore color** in KOH pale yellow singly, olive green in mass. (Figs. 26 & 27).

ETYMOLOGY: after “Epiro,” an ancient Albanian name.

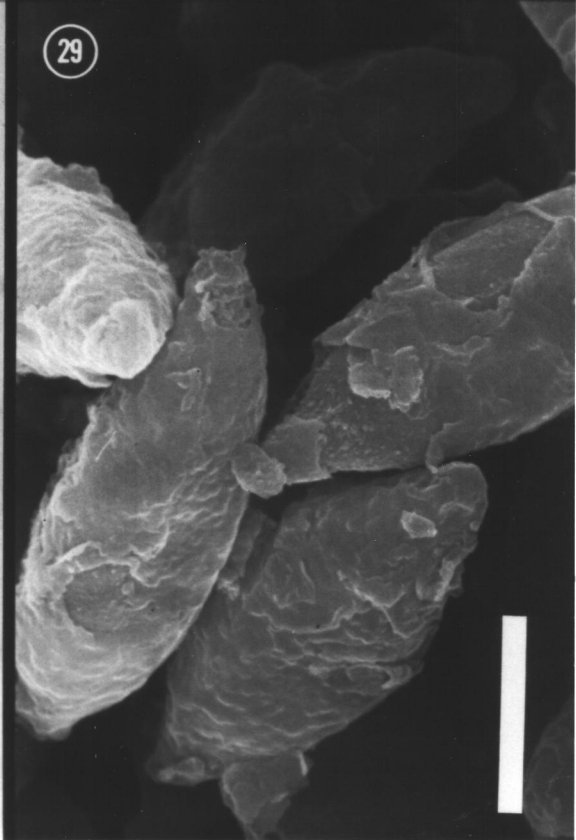
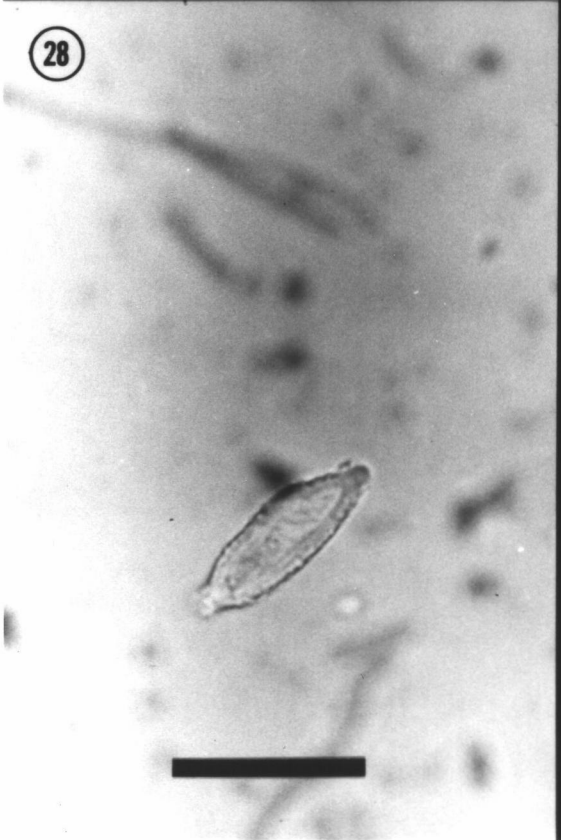
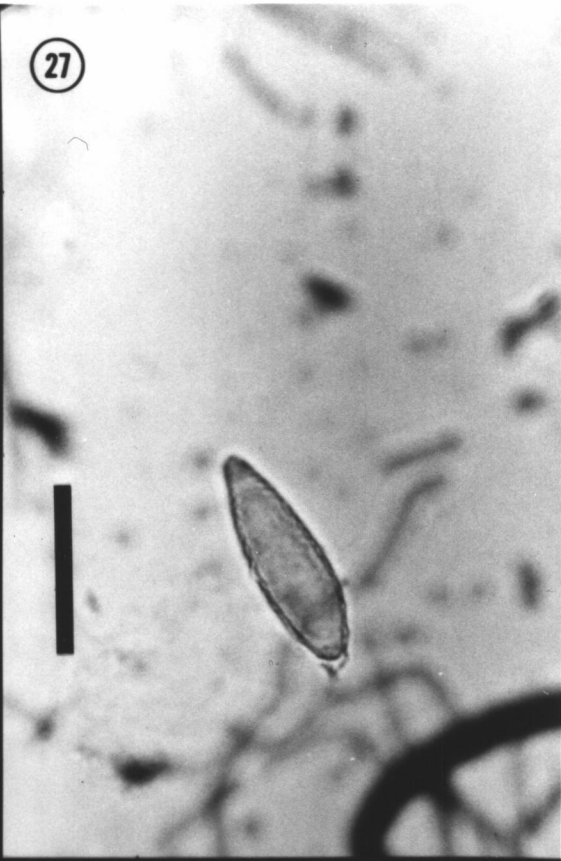
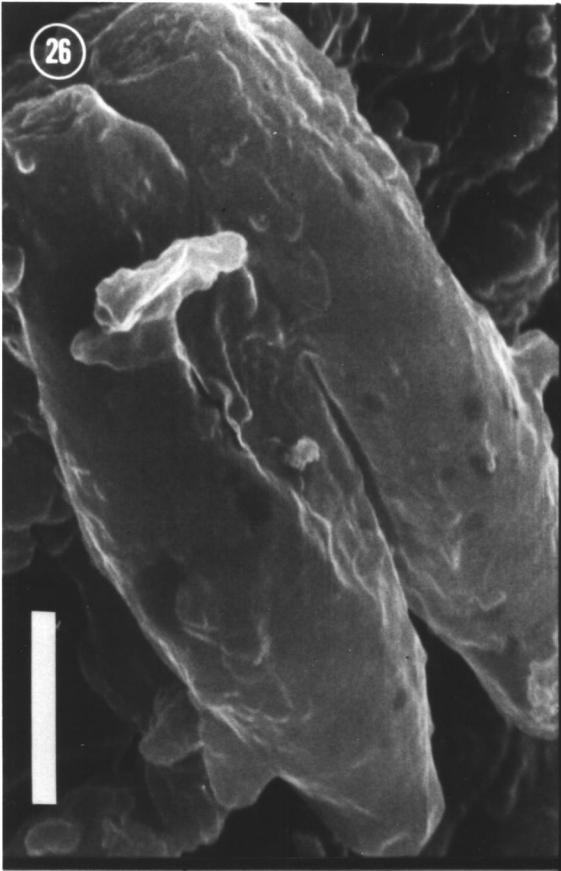
HABIT, HABITAT AND SEASON: Hypogeous in clay soil; probable mycorrhizal associates *Quercus trojana* and *Fagus*; March through October.

COLLECTIONS EXAMINED: HOLOTYPE: **ALBANIA:** Elbasan, 22-MAR-1982, leg Pacioni (AQUI). **OTHER COLLECTIONS — GERMANY (WEST):** Ettenberg, Soehner 1037, Soehner 1046 (all M). Holzkirchen, Soehner 183, Soehner 186 (all M). Munich, Soehner 727a, Soehner 1436, Soehner 1437 (all M). **HUNGARY:** Hárskút, 42104 (BP). Litke, 222235 (BP, S). Stubuya, leg Hollós (FH). Urkút, 31940 (BP). **ITALY:** Trento, leg Bresadola (PDD 8317).

DISCUSSION: *Hysterangium epiroticum* is similar to *H. fragile* but differs by its three-layered peridium and slightly longer and wider spores.

Restricted in its (presumptive) mycorrhizal association to *Quercus* and possibly *Fagus*.

Figures 26-29. *Hysterangium* spores. 26. SEM of *H. epiroticum* spores (Holotype, leg Pacioni), bar = 5 μm . 27. Light micrograph of *H. epiroticum* spores (Holotype, leg Pacioni), bar = 20 μm . 28. Light micrograph of *H. fragile* spores (Lectotype, leg Vittadini), bar = 20 μm . 29. SEM of *H. fragile* spores (Lectotype, leg Vittadini), bar = 6 μm .





Map 17. Distribution of *Hysterangium epiroticum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium fallax Castellano & Molina, nom. prov.

Basidiomata 8–17 mm in diam, subglobose to globose, white staining rose brown or rose, later brown overall, mottled reddish brown and white when dried, surface glabrous without adherent soil. **Gleba** green to olive when dried; locules subglobose to irregular, empty. **Rhizomorph** usually single attached to base, stout, ± 1 μm thick, concolorous with peridium. **Columella** gelatinous, dendroid, stout, ± 1 μm thick, opaque when dried.

Peridium not easily separable from gleba, 500–610 μm thick, two-layered; epicutis 500–600 μm thick, of hyaline to pale brown (outer and inner 100 μm), thin-walled, polyhedral cells, (20–) 30–50 (–70) μm in diam, clamp connections absent; subcutis 10–20 μm thick, of pale brown, thin-walled, slightly inflated cells, 4–8 μm in diam, clamp connections absent.

Trama 30–100 μm thick, of hyaline, interwoven hyphae (2–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, elongate to ovoid, 35–40 x 5–8 μm , 2–4 spored.

Spores minutely verrucose, 14–16 (–19) x 6–7 μm , ellipsoid to subfusoid; apex obtusely blunt, base appendiculate to 1.5 μm long. **Spore wall** up to 1 μm thick. **Utricle** distinct, closely appressed, up to 0.5 μm thick, wrinkled. **Spore color** in KOH pale green singly, greenish olive in mass.

ETYMOLOGY: in reference to its “similarity” to other *Hysterangium* species.

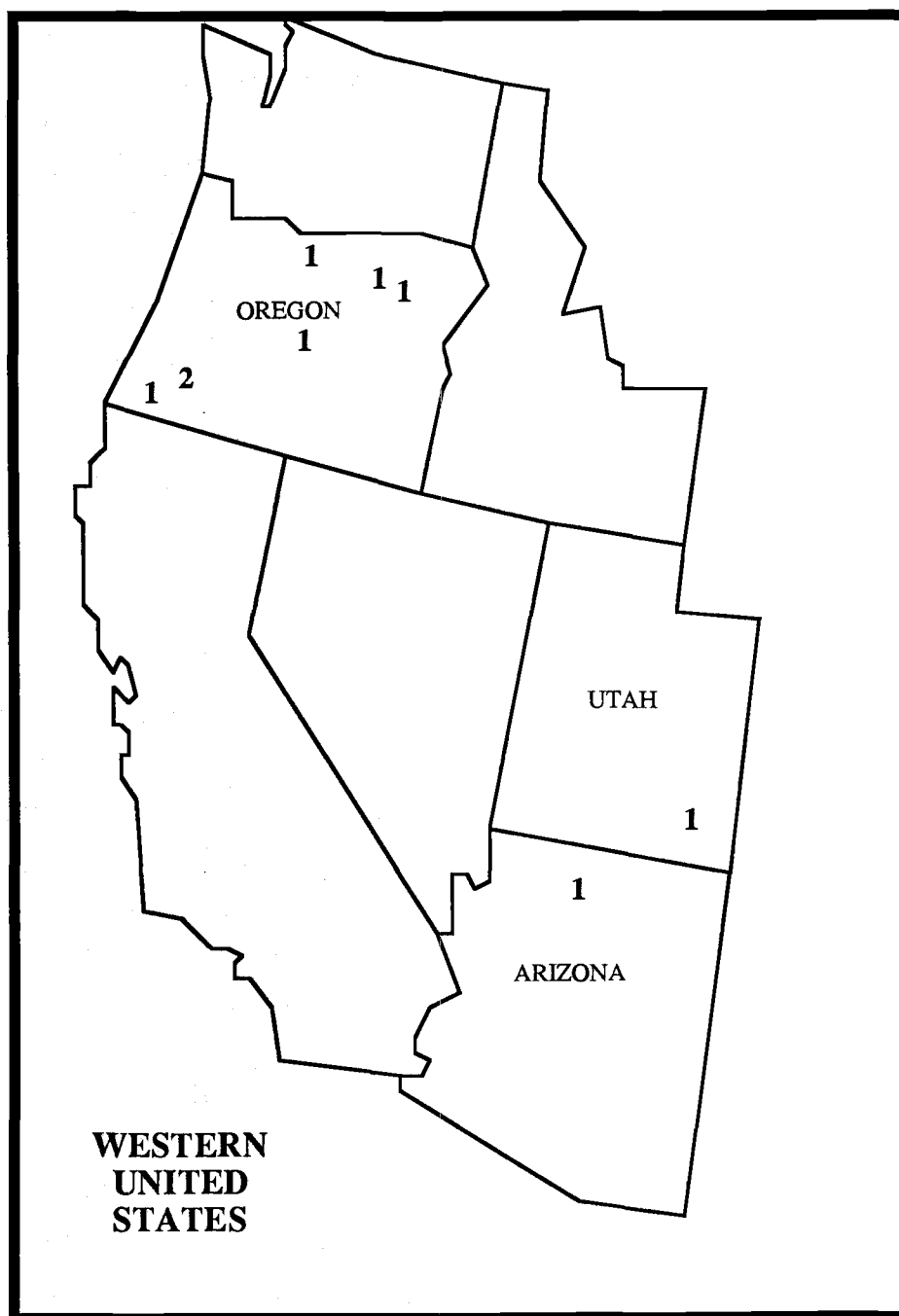
HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associate *Pinus ponderosa*; June through October.

COLLECTIONS EXAMINED: HOLOTYPE: **OREGON:** Crook Co., Ochoco Divide, 18-OCT-1976, leg Molina, Trappe 4794 (OSC). **OTHER COLLECTIONS — ARIZONA** Co., Coconino Co., AHF 78, AHF 110 (all FSLF). **OREGON:** Crook Co., Trappe 8608 (OSC). Lake Co., Trappe 7739 (OSC). Josephine Co., Trappe 7915, Trappe 8600, Trappe 8996 (all OSC). Umatilla Co., Trappe 5221 (OSC). **MONTANA:** Missoula Co., Ure 56 (OSC). **UTAH:** San Juan Co., UTHF 14 (FSLF).

DISCUSSION: *Hysterangium fallax* is similar to *H. separabile* but differs in having obtusely blunt, appendiculate, thick-walled spores in addition to the peridium which is not easily separable and a thinner subcutis of larger cells than in *H. separabile*.

States (1984) cites collections AHF 78 & AHF 100 as *H. separabile* Zeller.

Hysterangium fallax is (presumptive) mycorrhizal only with *Pinus ponderosa*, whereas *H. separabile* is mycorrhizal only with *Quercus*.



Map 18. Distribution of *Hysterangium fallax*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium fragile Vittadini, Monogr. Tuberac. p. 14. pl. 4, fig. 15. 1831.

= *Hysterangium stoloniferum* Tulasne, Ann. Sci. Nat. Bot. II. 19:376. pl. 11, fig. 8. 1843.

= *Hysterangium stoloniferum* var. *mutabile* Bucholtz, Soc. Imp. Nat. Moscou Bull. 4:467–470. 1908.

= *Hysterangium stoloniferum* var. *rubescens* (Quélet) Zeller & Dodge, Ann. Mo. Bot. Gard. 16: 112. 1929.

= *Hysterangium rubescens* Patouillard, Bull. Soc. Mycol. France 30:351–352. 1914. non Tulasne, Ann. Sci. Nat. II. 19:375. 1843.

Dried **basidiomata** up to 2 cm in diam, subglobose to globose, white to ochraceous when fresh, bruising red, brown to pale reddish brown when dry, surface glabrous. **Gleba** olive to pale brown; locules irregular, empty.

Rhizomorph single, stout, $\pm 1\ \mu\text{m}$ thick, concolorous with peridium.

Columella gelatinous to cartilaginous, dendroid to nearly percurrent, stout, translucent.

Peridium easily separable from gleba, 450–500 (–600) μm thick, two-layered; epicutis 350–400 μm thick, of hyaline, thin-walled, subglobose cells (parenchyma-like), 10–25 (–40) μm in diam, clamp connections absent; subcutis 80–110 μm thick, of hyaline, thin-walled, interwoven hyphae, 3–17 μm in diam, cells smaller near the gleba, clamp connections absent.

Trama variable in thickness, of hyaline, mostly collapsed, interwoven hyphae (3–4 μm in diam) in a gelatinized matrix, clamp connections scattered.

Basidia hyaline, cylindrical to subclavate, 25–35 x 7–12 μm , clamped at base, (1) 2 (3) spored.

Spores minutely verrucose, 20–24 x (5–) 6–7 μm , ellipsoid to fusoid; apex mostly acuminate to papillate, base distinctly pedicellate, up to 2 μm long. **Spore wall** up to 1 μm thick at maturity. **Utricle** absent when young, at maturity distinct, wrinkled, usually closely appressed. **Spore color** in KOH hyaline to pale green singly, pale green to pale olive in mass. (Figs. 28 & 29).

ETYMOLOGY: in reference to the “fragile” peridium, especially as dried.

OTHER REFERENCES: De Toni in Saccardo (1888) pp. 156–157, Hesse (1891) pp. 103–104, Hollós (1911) pp. 88–89, Lange (1956) p. 76 (as *H. stoloniferum*), Soehner (1924) p. 392, Tulasne & Tulasne (1851) p. 84, Winter in Rabenhorst (1883) p. 879, Zeller & Dodge (1929) pp. 118–119.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Betula*, *Carpinus*, *Corylus*, *Quercus* and *Fagus*; May through July.

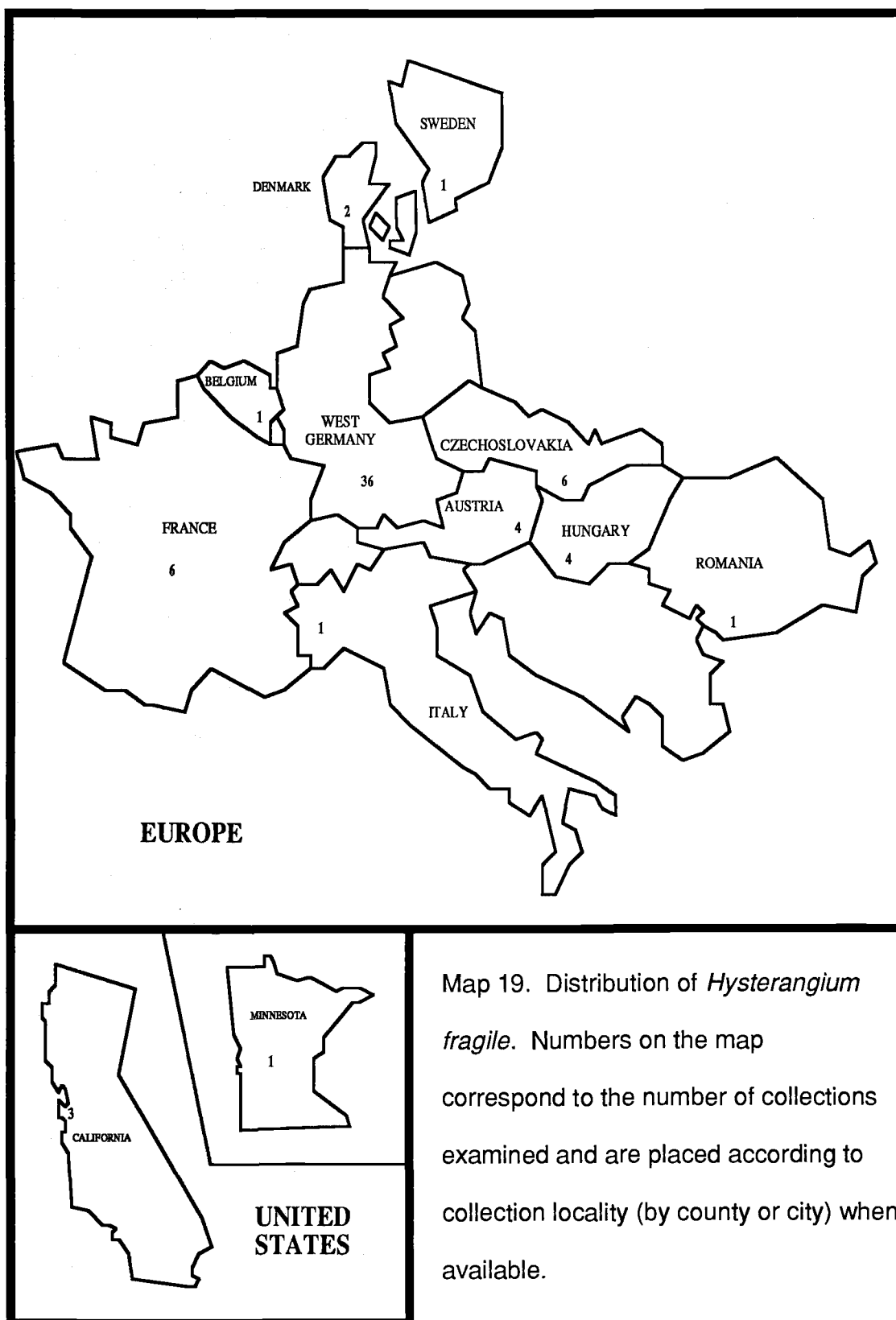
COLLECTIONS EXAMINED: LECTOTYPE: **ITALY:** leg Vittadini (PC).

OTHER COLLECTIONS — AUSTRIA: no locality, leg Ranel (W), Huber 434 (G, S, TRTC). leg Lawrynowicz (LOD). Neulengbach (FH). **BELGIUM:** De Vries 1084 (De Vries Herb). **CZECHOSLOVAKIA:** Cernosice, 619169 (PRM). Karlstejn, 616254, 619176, 619180 (all PRM). Larosice, 619170 (PRM). Trebotov, leg Vacek (PRM). **DENMARK:** Klinteskov (UPS, C), Stallerup (C). **FRANCE:** no locality, leg Quélet (K, UPS). Bonnes, (TYPE of *Hysterangium stoloniferum* Tulasne) leg Tulasne (FH). Gaillac (MPU). Jura, (TYPE of *Hysterangium rubescens* Patouillard) leg Patouillard (FH). Leponay, leg Patouillard 1908, 1909 (all FH). **GERMANY (WEST):** Babelsheim, Gross 71 (M). Ballweiler, Gross 64 (M). Coburg (JE). Gauting, Soehner 835 (M). Eimersdorf, Demoulin 4620 (LG), Gross 150, Gross 274 (all M). no locality, leg Fuckel (G, K, W), leg Keissler (W), Soehner 230, Soehner 286, Soehner 588,

Soehner 592, Soehner 622, Soehner 700, Soehner 1186, Soehner 1895, Soehner 2007 (all M). Munich, Soehner 111, Soehner 119, Soehner 147, Soehner 169, Soehner 431, Soehner 584, Soehner 1414, Soehner 1415, Soehner 1416, Soehner 1417, Soehner 1418, Soehner 1419, Soehner 1420, Soehner 1421, Soehner 1920 (all M). Saar, Gross 462, Gross 531 (all M), Gross 509 (LG). **HUNGARY:** Hárskút, leg Szemere (C), 47883, 48367 (all BP). Prencow (BPI, S). **ROMANIA:** Harghita (CLA). **SWEDEN:** Herrfallsang (UPS). **CALIFORNIA:** Santa Cruz Co., HS 2415, HS 2424, HS 2428 (all SFU). **MINNESOTA:** Weaver 1140 (MICH).

DISCUSSION: Material is unavailable from Vittadini's herbarium at Torino, Italy, so the above collection made by Vittadini and sent to Tulasne at Paris (PC) was selected as the type. Type material of *H. stoloniferum* var. *mutabile* could not be located but the detailed description leaves little doubt as to placement. This fungus is commonly found under hardwoods on limestone soils.

Hysterangium fragile resembles *H. epiroticum* but differs by its smaller spores and two-layered peridium.



Map 19. Distribution of *Hysterangium fragile*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium gardneri Fischer, Bot. Zeit. 66:164–166. pl. 6, fig. 19. 1908.

≡ *Hysterangium gardneri* Fischer, Ber. d. deut. bot. Ges. 25:276. 1907.

nom. nud.

= *Hysterangium fischeri* Zeller & Dodge, Ann. Mo. Bot. Gard. 16:109–110. pl. 1, fig. 2, pl. 3, fig. 8. 1929.

Basidiomata 0.4–1.6 cm in diam, subglobose to irregular, caespitose, white to pale brown, bruising pale pink when fresh, surface tomentose to felty, with numerous pieces of adherent organic matter and soil, KOH nonreactive. **Gleba** pale green, olive, dark gray green to nearly black; locules elongate, empty. **Rhizomorphs** few, small, appressed overall, concolorous with peridium. **Columella** gelatinous, dendroid, narrow, translucent when fresh, brown when dried.

Peridium not separable from gleba, a single layer 400–600 µm thick, of hyaline to pale brown, thin-walled, elongate to irregular, interwoven hyphae, 3–4 (–5) µm in diam near gleba, gradually inflated to 9–12 x 30–40 µm near outer edge, inner hyphae are hyaline, outer hyphae are gradually deeper brown with numerous adherent crystalline particles, clamp connections small, common. Occasionally hyphae of the peridium extend into the trama as veins which may or may not be contiguous with fertile locules.

Trama 80–120 µm thick, of hyaline, collapsed, interwoven hyphae (1–2 µm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindrical, 16–17 x ± 5 µm, 5 or 6 spored.

Spores smooth, (8-) 9-10 x 3.5-4 μm , ellipsoid; apex obtusely blunt, base truncate to slightly appendaged. **Spore wall** less than 0.5 μm thick, sometimes thickened near base. **Utricle** absent or when present irregular, broken, rarely inflated. **Spore color** in KOH hyaline to pale green singly, pale olive in mass. (Figs. 30 & 31).

ETYMOLOGY: named in honor of N.L. Gardner, the collector of the type.

OTHER REFERENCES: Fischer (1909) p. 194, Saccardo & Trotter in Saccardo (1912) p. 495, Zeller & Dodge (1929) p. 105.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Eucalyptus calophylla*, *E. globulus*, *E. resinifera* and *E. wandoo*; December through September.

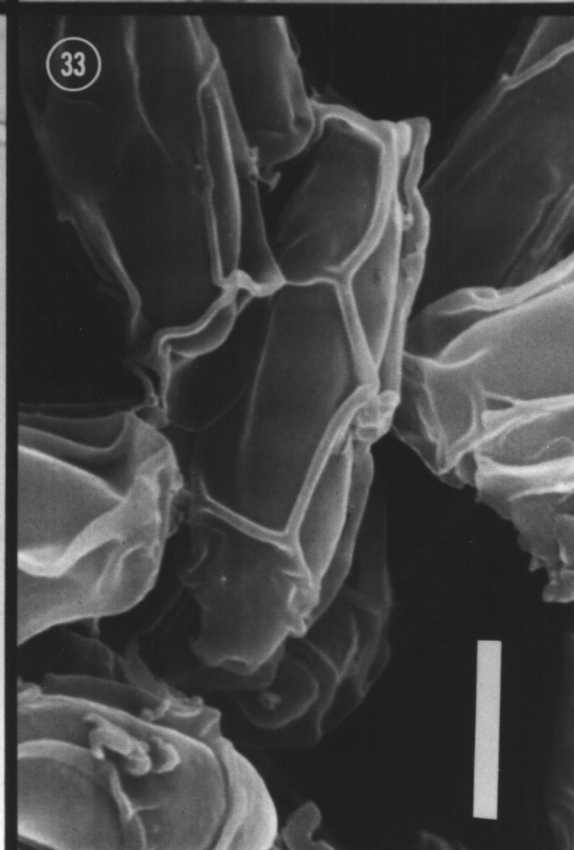
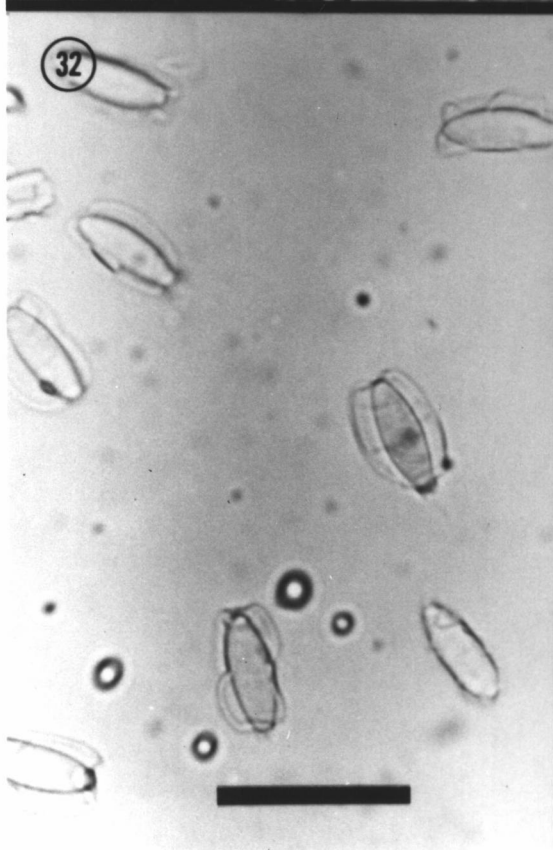
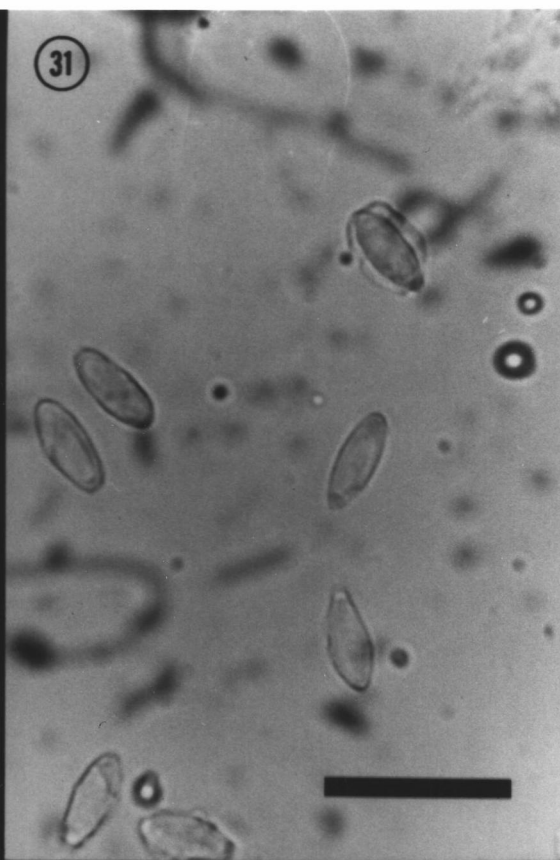
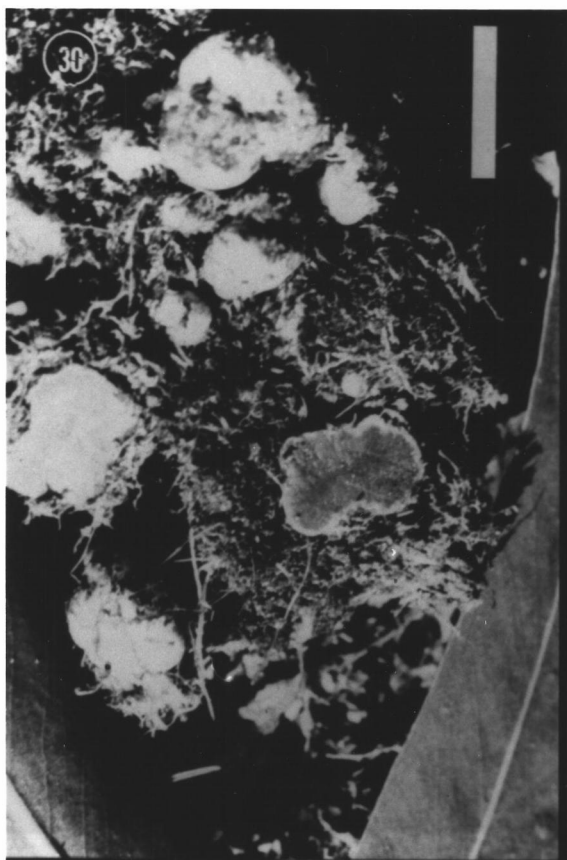
COLLECTIONS EXAMINED: HOLOTYPE: **CALIFORNIA:** Alameda Co., Campus of University of California at Berkeley, 19-NOV-1904, leg N. L. Gardner 214 (ZT), ISOTYPES (OSC, UC 126142). **OTHER COLLECTIONS — CALIFORNIA:** no locality, Gardner 70, Gardner 113, Gardner 114, Gardner 115, Gardner 122 (all UC). Alameda Co., Parks 1172 (NY). Berkeley, (HOLOTYPE of *H. fischeri* Zeller & Dodge) Gardner 258, Gardner 271 (FH, K, MICH, UC). Marin Co., Trappe 8497 (OSC). Mendocino Co., Trappe 5427 (OSC). San Francisco Co., leg Mitchell, HDT 40394 (all SFU). **ALGERIA:** (det. by Zeller and Dodge as the lectotype of *H. cistophilum*) Baali près Souma, leg Maire & Duvernoy (FH, MPU). **AUSTRALIA:** South Australia, Mt. Lofty (ADW 2503). Tasmania, Rodway 324 (HO). Victoria, leg Beaton (OSC). Western Australia, Lewana Park, Trappe 6958 (OSC). Glen Eagle State Forest, Trappe 6901 (OSC). Pinjarra, Trappe 6950 (OSC). Inglehope, Trappe 6952, Trappe 6953 (all OSC). **ITALY:** no locality, leg Pacioni (AQUI). Torre Fortore,

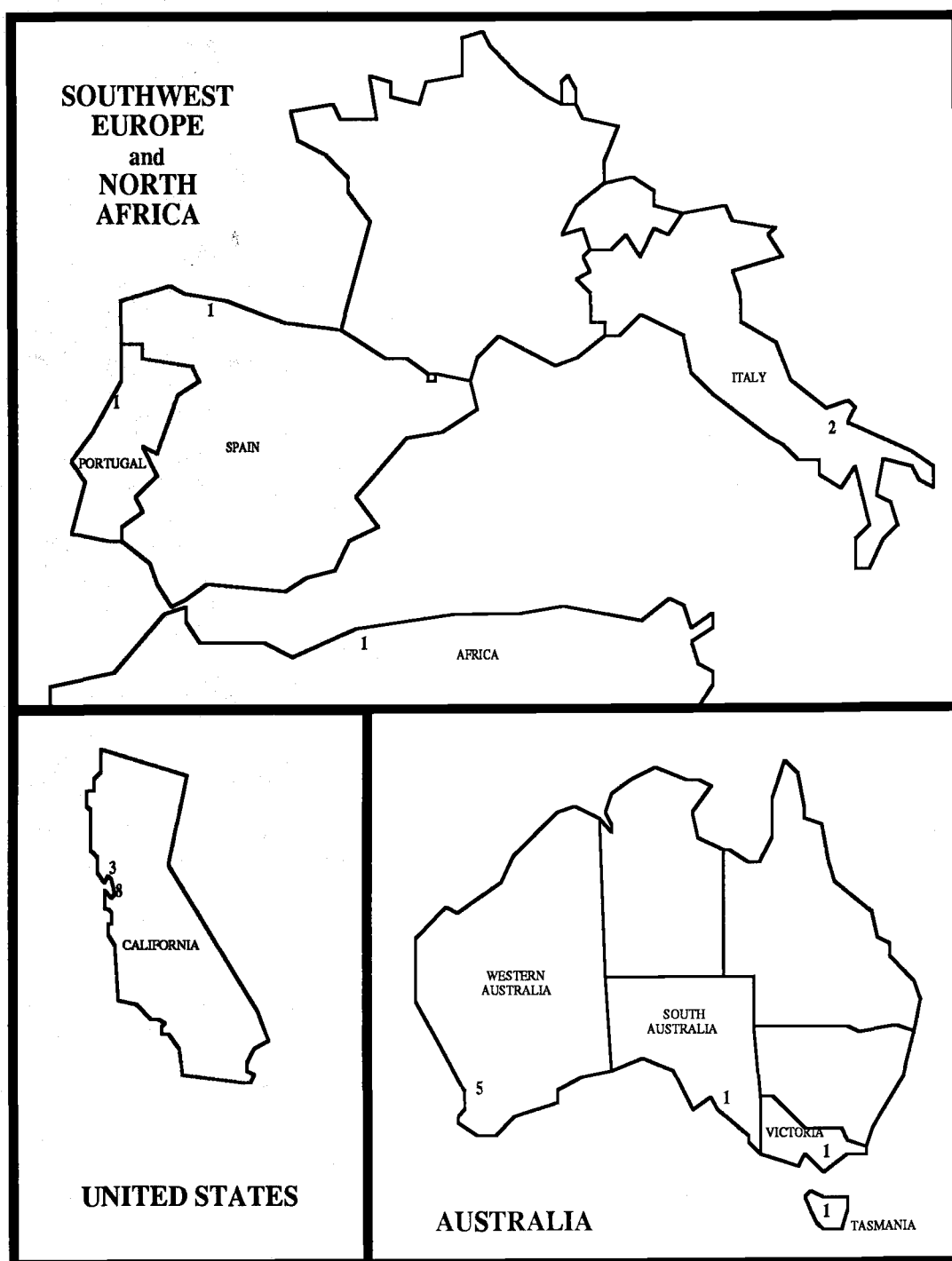
leg Pacioni (AQUI). **PORTUGAL:** Mousanto, leg Pinto Lopes (LG). **SPAIN:** Aleanedo, leg Trappe (OSC).

DISCUSSION: *Hysterangium gardneri*, although described first from a collection from California, was probably introduced from Australia with *Eucalyptus* seedlings. It is a common ectomycorrhizal fungus under *Eucalyptus globulus* on the California coast and in Australia and has apparently been introduced into Italy, Spain and Portugal. *Hysterangium gardneri* typically forms extensive mats of mycelium and rhizomorphs at the mineral soil–humus layer interface.

Hysterangium gardneri is similar to *H. inflatum* and *H. simulans* in peridial characters but lacks the distinct inflated utricle of either species. It also resembles *H. irregulare*, but *H. irregulare* has larger spores and a thinner peridium.

Figures 30-33. *Hysterangium*. 30. Sporocarps of *H. gardneri* (Trappe 8366), notice cross-sectional view (arrow), bar = 1.5 cm. 31. Light micrograph of *H. gardneri* spores (Trappe 8366), bar = 20 μm . 32. Light micrograph of *H. inflatum* spores (H 349), bar = 20 μm . 33. SEM of *H. inflatum* spores (H 381), bar = 5 μm .





Map 20. Distribution of *Hysterangium gardneri*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium gelatinosporum Cribb, Paps. Dept. Bot. Univ. Queensland, 3:156. fig. 6. 1958.

Basidiomata up to 1.5 cm in diam, subglobose to irregular, brown when fresh, dark reddish brown, surface rough and uneven when dry, numerous soil particles adhering to all sides. **Gleba** olive brown; locules irregular, empty to partially filled. **Rhizomorphs** single or numerous, stout, up to 0.5 mm in diam, dark reddish brown when dry. **Columella** gelatinous, small, finely branched, white when fresh, dark greenish brown when dry.

Peridium not separable from gleba, a single layer 140–300 μm thick, of thin-walled, somewhat agglutinated, subpericlinal to interwoven hyphae, 2–4 (–6) μm in diam, brown (near surface), hyaline (near gleba), crystalline particles abundant near surface, clamp connections absent.

Trama up to 130 μm thick, of hyaline, compactly interwoven hyphae (1–2 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** not observed, “2 spored” (Cribb 1958).

Spores minutely verrucose, 11 x 5.5 μm without utricle, 12–15 x 6–7.5 μm with utricle, broadly ellipsoid; apex obtusely blunt, base distinctly pedicellate, 2 μm wide x 1 μm long. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, saccate, inflated up to 2 μm , giving the spore a more or less square appearance, attached only at base. **Spore color** in KOH pale brownish green singly, pale brown in mass.

ETYMOLOGY: referring to the gelatinous-like covering of the spore.

HABIT AND SEASON: Hypogeous; June.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Queensland, Lamington Plateau, JUNE-1950, leg Herbert (DAR 21624), ISOTYPE (K, PDD 12325).

DISCUSSION: This species is known only from the type collection. Collection Beaton 9 cited by Beaton et al. (1985), is not *H. gelatinosporum* but an as yet undescribed genus.

The distinct inflated, saccate utricle makes this species easily distinguishable from all other *Hysterangium* species which possess a peridium consisting entirely of interwoven hyphae.



Map 21. Distribution of *Hysterangium gelatinosporum*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium inflatum Rodway, Paps. & Proc. Roy. Soc. Tasmania
1917:108. 1918.

= *Hysterangium eucalyptorum* Lloyd, Mycol. Notes 65:1031. 1921.

= *Hysterangium pterosporum* Donadini & RiOUSset, Trav. sci. Parc Nation.
Port-Cros 5:12. 1979.

Basidiomata 0.5 –2 cm in diam, subglobose, ellipsoid to irregularly lobed, white when fresh, readily handling pale brown to pale reddish brown, drying dark brown except in protected areas which are pale brown to almost white, surface smooth to felty when fresh, wrinkled slightly tomentose when dry, some soil particles adhering to surface when dry. **Gleba** bright greyish green to bright green when young, dark olive to almost black when mature; locules elongate, partially to completely filled with spores. **Rhizomorphs** numerous small, attached at base, concolorous with peridium. **Columella** gelatinous, dendroid, narrow, dark grey.

Peridium not easily separable from gleba, a single layer 140–150 (–250) μm thick, of brown (near surface), hyaline (near gleba), thin-walled, irregularly shaped, sometimes inflated hyphae, elongate to subglobose, only up to 5 μm in diam near gleba, usually up to 12 x 25 μm in mediostratum, numerous crystalline particles adhering to outer hyphae, clamp connections common.

Trama 40–100 μm thick, of hyaline, loosely to compactly interwoven hyphae (2.5–5 μm in diam) in a gelatinized matrix, hyphae mostly elongate, sometimes with nodose ends, clamp connections absent. **Basidia** rehydrating poorly, hyaline, (4) 6 spored.

Spores smooth, 9–12 x 4–5 μm without utricle, 9–12 x 8–9 with utricle, ellipsoid; apex obtuse, base sessile sometimes truncate. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, inflated up to 2.5 μm on a side, attached at base and apex, commonly forming a cylinder around the spore. **Spore color** in KOH hyaline singly, pale green in mass. (Figs. 32 & 33).

ETYMOLOGY: referring to the greatly “inflated” utricle which is attached at the base and to the apex of the spore.

OTHER REFERENCES: Beaton, Pegler & Young (1985) pp. 438–440, Lloyd (1922) pp. 1119–1120, Rodway (1924) p. 156, Trotter in Saccardo (1928) p. 1327, Zeller & Dodge (1929) pp. 98–99.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Eucalyptus calophylla*, *E. camaldulensis* x *trabutii*, *E. delegatensis*, *E. fastigata*, *E. globulus*, *E. nitens*, *E. regnans*, *E. resinifera* and other *Eucalyptus* spp.; February through July in Australia, Italy and France, April in New Zealand, September through December in California.

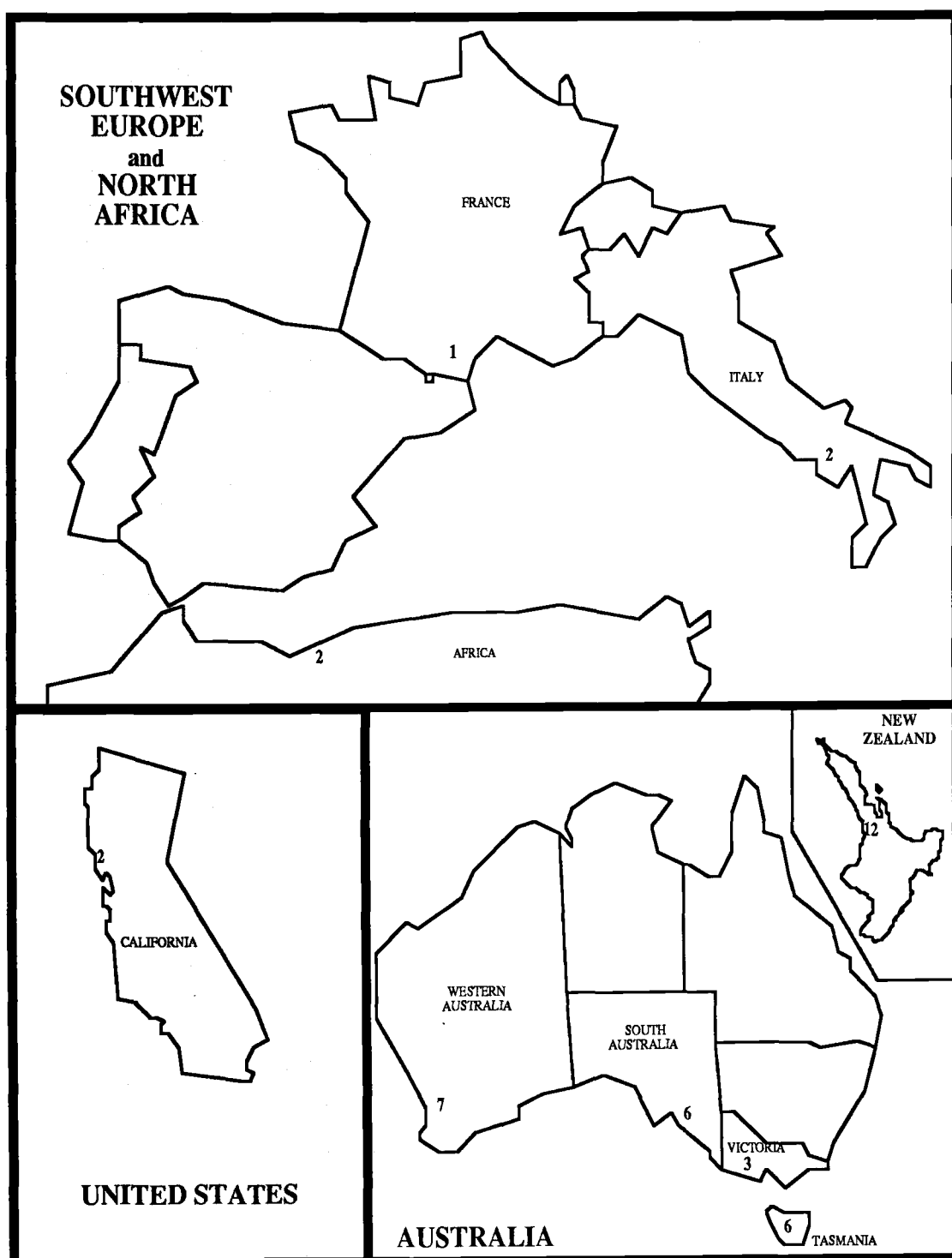
COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Mt. Wellington, FEB–1904, leg Rodway 1267 (HO 89531), ISOTYPES (OSC, NY, FH). **OTHER COLLECTIONS — ALGERIA:** Villa de Bois 10580 (MPU). Staoueli, 9902 (MPU). **AUSTRALIA:** South Australia, Watling 10433 (E), 2503, 6031, 6033, 6853 (all ADW). Tasmania 89520, 89527 (all HO), H 380, H 381 (DAR). Victoria, 6230 (MELU), Beaton 20, Beaton 29 (all K). Western Australia, Trappe 6931, Trappe 6961 (all OSC), H 56, H 92, H 122, H 151a, H 349 (all DAR). **ECUADOR:** Quito, (Type of *H. eucalyptorum* Lloyd) Mille 3 (NY, PDD 8309). **FRANCE:** Porquelles, (det. by RiOUSset as *H. pterosporum*) leg RiOUSset (OSC). **ITALY:** Campomarino, leg Pacioni (AQUI). Torre Fortore,

leg Pacioni (AQUI). **NEW ZEALAND:** Coromandel, Trappe 9895, Trappe 9897, Trappe 9898, Trappe 9899, Trappe 9900, Trappe 9901, Trappe 9902, Trappe 9903, Trappe 9904, Trappe 9905, Trappe 9906 (all OSC). Waiomu, Trappe 9887 (OSC). **CALIFORNIA:** Mendocino Co., HS 3331 (SFU, OSC), Trappe 5428 (OSC).

DISCUSSION: In contrast to Beaton, Pegler & Young (1985), I regard *Hysterangium tunicatum* Cunningham as a distinct, albeit invalidly published, species and have provisionally named it *Hysterangium neotunicatum*.

Hysterangium inflatum is easily distinguished from all other species by its unique, regularly inflated (balloon-like) utricle, which gives the spore a winged appearance. Non-type material of *Hysterangium pterosporum* from Rioussset proved to be conspecific with *Hysterangium inflatum*.

Hysterangium inflatum appears to be a common ectomycorrhizal associate of *Eucalyptus* spp. and has probably been introduced with *Eucalyptus* seedlings, especially *E. globulus*, in many parts of the world. Chu-Chou and Grace (1983) used *H. inflatum* spores to successfully inoculate *Eucalyptus saligna* seedlings in New Zealand. Chu-Chou and Grace (1982) found *H. inflatum* sporocarps in association *Eucalyptus nitens*, *E. delegatensis*, *E. fastigata* and *E. regnans* in New Zealand



Map 22. Distribution of *Hysterangium inflatum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium irregulare Castellano & Malajczuk, nom. prov.

Basidiomata 6–8 mm in diam, subglobose to slightly flattened, white, bruising rose, surface scabrous, with adherent soil particles. **Gleba** grayish green fresh and as dried; locules elongate, partially filled. **Rhizomorphs** numerous, small, attached to base, concolorous with peridium. **Columella** dendroid, narrow, translucent.

Peridium not easily separable from gleba, a single layer 100–200 μm thick, of pale brown, thin-walled, irregularly inflated hyphae (pseudoparenchyma-like), usually 4–5 μm in diam, up to 15 μm in diam, clamp connections scattered on uninflated hyphae near gleba.

Trama 50–100 μm thick, of hyaline, loosely interwoven hyphae (3–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, clavate, 33–36 x 5–8 μm , 2 & 4 spored.

Spores smooth, 10–11 x 5 μm , broadly ellipsoid; apex acuminate, base sessile to slightly appendaged. **Spore wall** up to 0.5 μm thick. **Utricle** inconspicuous, tightly adherent, making the spore appear to be slightly roughened. **Spore color** in KOH hyaline to pale green singly, pale green in mass. (Fig. 34).

ETYMOLOGY: in reference to the “irregular” structure of the peridium.

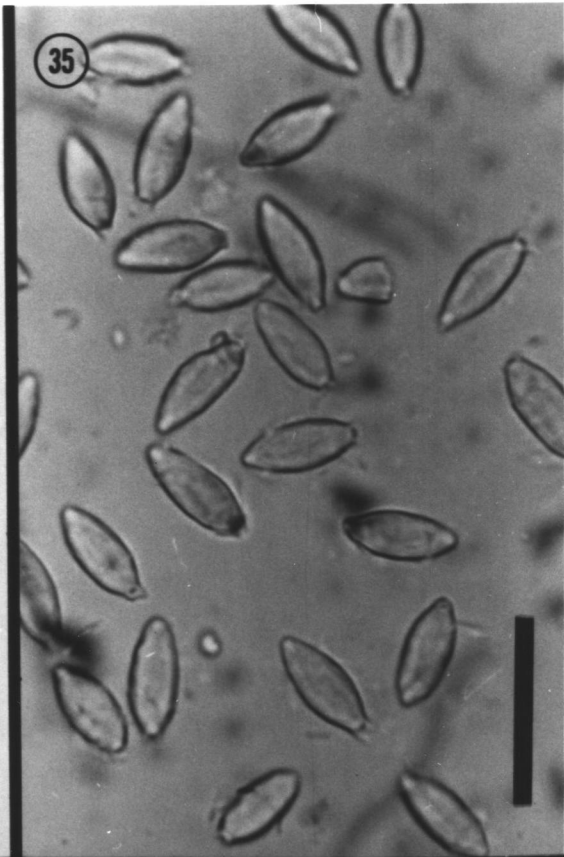
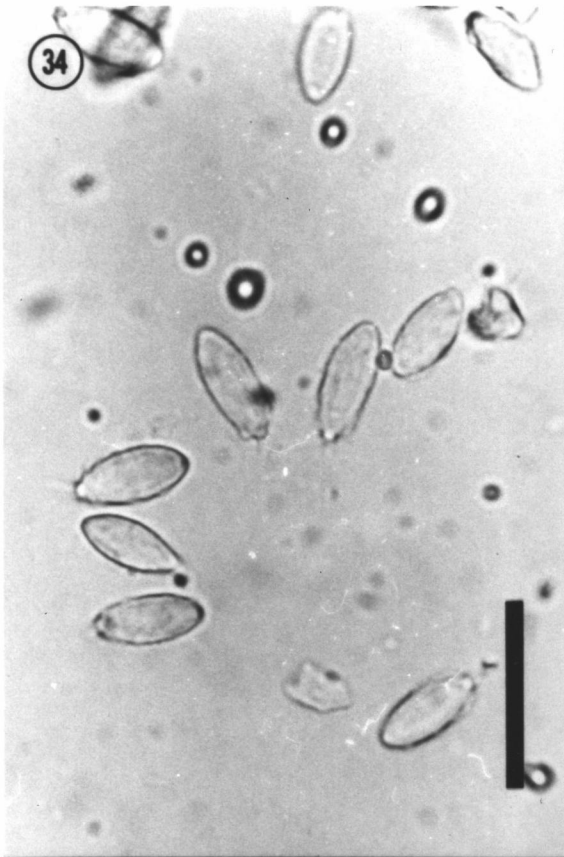
HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Eucalyptus calophylla* and *E. wandoo*; September.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Western Australia, 3 km west of Bindoon Hotel, 21-SEPT-1982, Trappe 6965 (OSC).

OTHER COLLECTIONS — AUSTRALIA: Western Australia, Glen Eagle State Forest, H 2019 (DAR, OSC).

DISCUSSION: The scabrous peridium which is white at first, soon becoming rose, in conjunction with the smooth, small (10–11 x 5 μ m), broadly ellipsoid spores separate this from all other *Hysterangium* species.

Figures 34-37. *Hysterangium* spores. 34. Light micrograph of *H. irregulare* spores (Holotype, Trappe 6965), bar = 20 μm . 35. Light micrograph of *H. malaiense* spores (Holotype, Corner 739), bar = 20 μm . 36. Light micrograph of *H. membranaceum* spores (Lectotype, leg Vittadini), bar = 10 μm . 37. SEM of *H. membranaceum* spores (Harkness 84), bar = 5 μm .





Map 23. Distribution of *Hysterangium irregulare*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium malaiense (Corner & Hawker) Castellano nom. prov.

≡ *Hysterangium purpureum* var. *malaiense* Corner & Hawker, Trans. Brit. Mycol. Soc. 36:135–136. fig. 2 e. 1953.

Basidiomata 1–3.5 cm in diam, globose, depressed, sometimes lobed or irregular, white with olivaceous tones, bruising dull “raspberry” red (Corner & Hawker 1953), surface glabrous with scattered finely tomentose areas, some soil particles adhering to base. **Gleba** olive to dark brownish olive; locules irregular to elongate, filled or partially filled. **Rhizomorphs** few, 0.5–1 mm wide, attached to indented base, white. **Columella** gelatinous, distinct, dendroid, arising from a thick basal pad, translucent to gray, dark reddish black when dried. **Odor** faint, sweet as over-ripe blackberries.

Peridium easily separable from gleba, a single layer 500–1000 μm thick, of brown, thin-walled, inflated, compactly interwoven hyphae, 5–20 μm in diam, crystalline particles absent, clamp connections absent.

Trama 50–100 μm thick, of hyaline, compact, more or less parallel hyphae (2–4 (–5) μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, clavate, $\pm 25 \times \pm 7 \mu\text{m}$, 4 spored.

Spores smooth, 8–12 $\times$ 4–5 μm , fusiform; apex acuminate, base appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** absent. **Spore color** in KOH pale green singly, brownish green in mass. (Fig. 35).

ETYMOLOGY: in reference to the country where found, Malaysia.

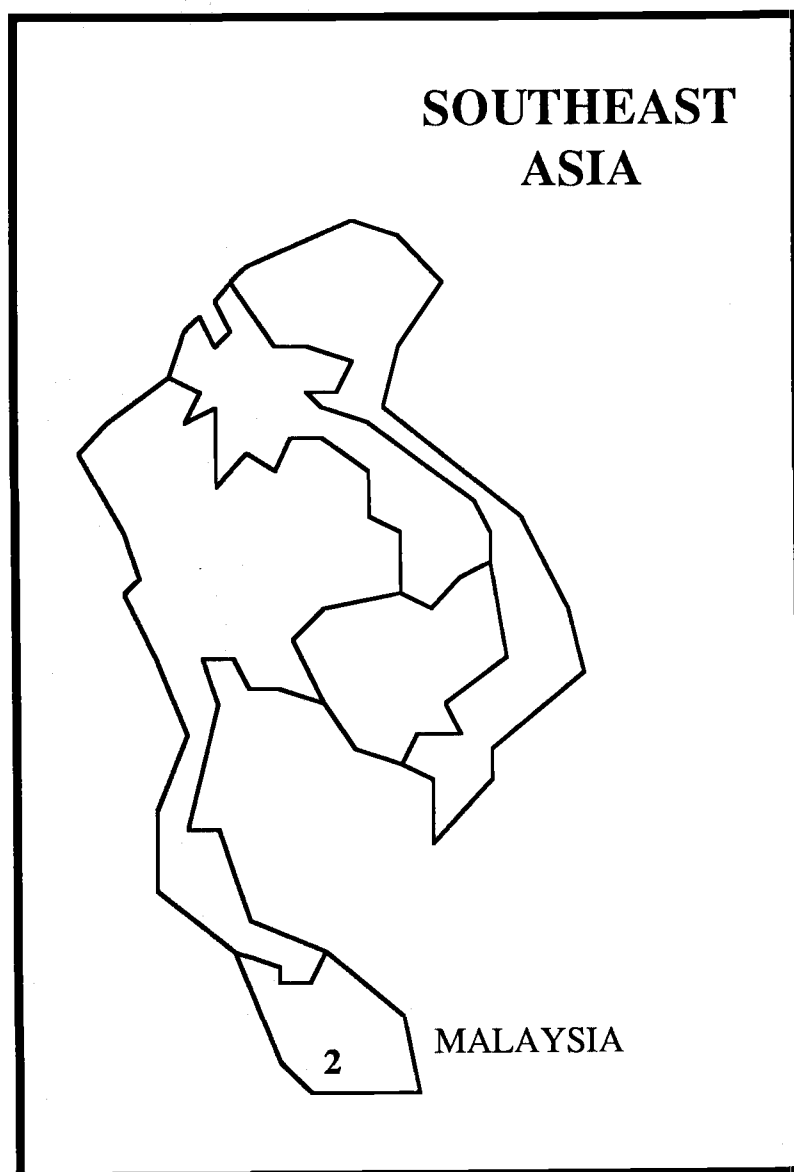
HABIT, HABITAT AND SEASON: On surface of ground under humus in jungle; January and February.

COLLECTIONS EXAMINED: HOLOTYPE: **MALAYSIA:** Singapore, Bukit Timah, 23-FEB-1931, Corner 739 (K), ISOTYPES (L, PC). **OTHER COLLECTIONS — MALAYSIA:** Singapore, Bukit Timah, Jalan Kutu, 17-JAN-1941, Corner 741 (K).

DISCUSSION: Comparison of type material of *H. purpureum* Zeller & Dodge and *H. purpureum* var. *malaiense* Corner & Hawker reveal enough differences in spore and peridial characters to provisionally raise *H. malaiense* to the species rank.

The extremely thick peridium of brown, inflated, compactly interwoven hyphae in conjunction with the rather small, smooth, fusiform spores which lack a utricle allow this species to be easily differentiated from all other *Hysterangium* spp.

Collection 740 as cited by Corner & Hawker (1953) could not be located.



Map 24. Distribution of *Hysterangium malaiense*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium membranaceum Vittadini, Monogr. Tuberac. p. 14. pl. 4, fig. 15. 1831.

= *Splanchnomyces membranaceus* (Vittadini) Corda, Icones Fung. 6:41. pl. 8, fig. 78. 1854.

= *Hysterangium harknessii* Zeller & Dodge, Ann. Mo. Bot. Gard. 16: 102–103. pl. 3, fig. 24. 1929.

Basidiomata up to 2 cm in diam, globose, subglobose or flattened, pale brown to reddish brown with white mottles, much wrinkled when dry, glabrous above. **Gleba** pale olive gray to olive gray when dried; locules irregular, empty. **Rhizomorphs** numerous, up to 1 mm in diam, attached at base and sides, mostly white when dry, occasionally concolorous with peridium.

Columella of unknown consistency, narrow, translucent when dry.

Peridium separable from gleba, a single layer 100–200 (–350) μm thick, of pale brown, thin-walled, irregularly shaped, interwoven hyphae, 2–5 (–6) μm in diam, with scattered groups of inflated cells (parenchyma-like), (10–) 15–30 (–50) μm in diam, clamp connections absent.

Trama 50–100 μm thick, of hyaline, compactly interwoven to subparallel hyphae ($\pm 3 \mu\text{m}$ in diam) in a gelatinized matrix, clamp connections absent.

Basidia not observed.

Spores distinctly verrucose, 15–18 (–20) $\times$ 6–7 (–8) μm , fusiform to broadly fusiform; apex acuminate to papillate, base pedicellate. **Spore wall** 1–1.5 μm thick. **Utricle** distinct, roughened or wrinkled, up to 1 μm thick.

Spore color in KOH hyaline singly, pale olive brown in mass. (Figs. 36 & 37).

ETYMOLOGY: possibly in reference to the "membranous," easily separable peridium.

OTHER REFERENCES: De Toni in Saccardo (1888) p. 156, Rodway (1912) p. 26, (1924) p. 157, Tulasne & Tulasne (1851) p. 83, Winter in Rabenhorst (1883) p. 879, Zeller & Dodge (1929) pp. 104–105.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Quercus dumosa*, *Q. garrayana*, and *Fagus*; throughout the year, primarily May and June.

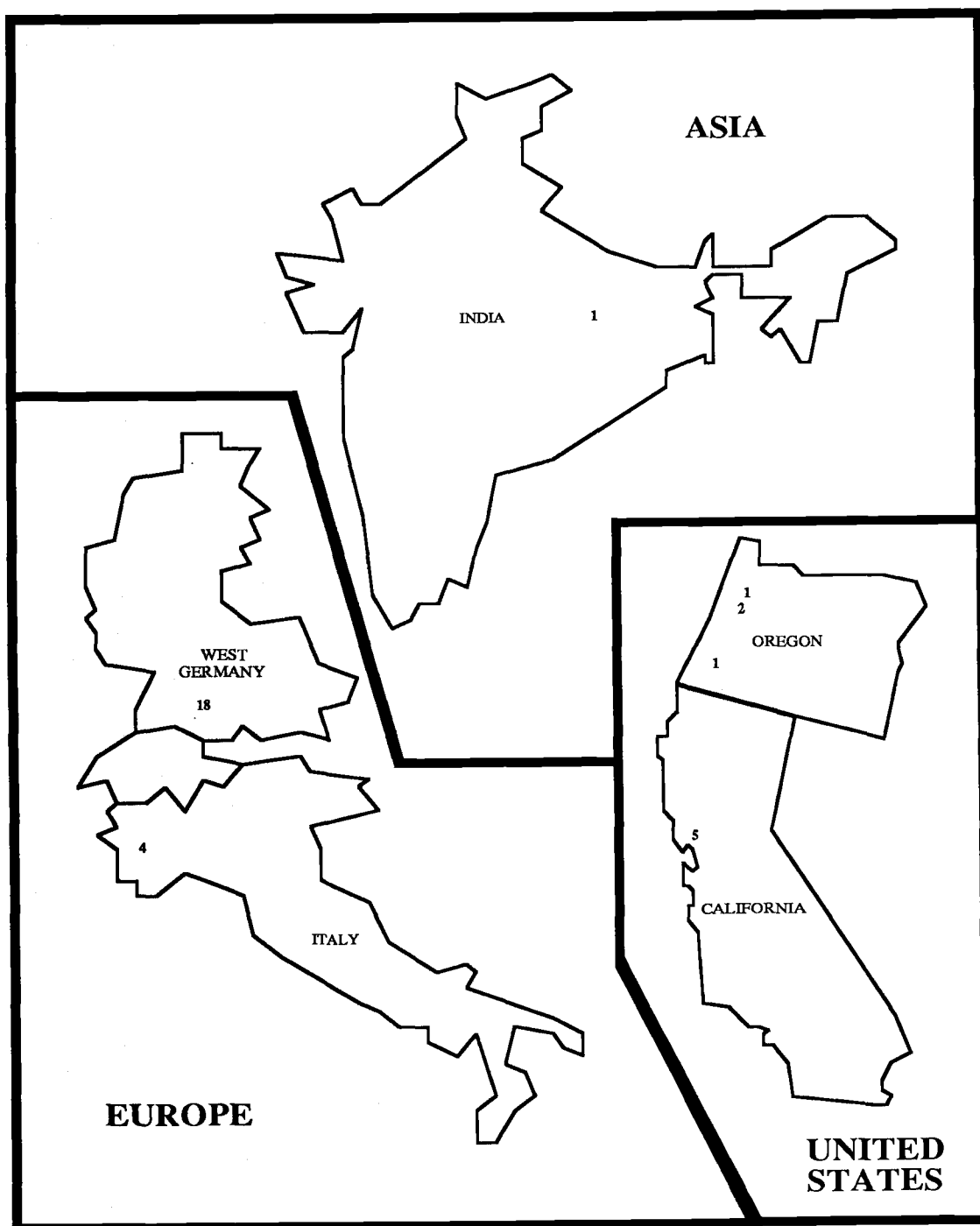
COLLECTIONS EXAMINED: LECTOTYPE: **ITALY:** leg Vittadini (PC).

OTHER COLLECTIONS — GERMANY (WEST): Esienberg, Soehner 1038 (M). Munich, Soehner 33, Soehner 149, Soehner 814, Soehner 1441 (all M). Salzburg, Soehner 1045 (NY). Untersburg, Soehner 1068 (M). no locality, Soehner 271, Soehner 504, Soehner 1031, Soehner 1064, Soehner 1069, Soehner 1070, Soehner 1529, Soehner 1530, Soehner 1927, Soehner 1940, Soehner 2019 (all M). **INDIA:** Nundali (K). **ITALY:** Milan, leg Vittadini (FH). locality unknown, leg Vittadini (FH). Locality unknown, ex Hollós Herb (PREM, OSC). **CALIFORNIA:** Marin Co., (HOLOTYPE of *Hysterangium harknessii* Zeller & Dodge) Harkness 84 (BPI). San Mateo Co., Parks 2228 (UC). Mendocino Co., Trappe 3101 (OSC). Santa Clara Co. Parks 149 (NY), Parks 385 (OSC, UC, NY). **OREGON:** Benton Co., Zeller 7056, Zeller 7058 (all OSC). Douglas Co., Zeller 8354 (NY). Polk Co., Stewart 1029 (OSC).

DISCUSSION: The species concept of *Hysterangium membranaceum* has been confused since the time of the Tulasne brothers. The difficulty is probably attributable to the lack of type material for study by the Tulasne brothers and subsequent workers. The material sent to the Tulasne brothers by Vittadini (apparently after publication of *Fungi Hypogaei*) was selected as the type by me. Additional material may be at Torino (TO) but could not be obtained for study.

Hysterangium membranaceum resembles *H. crassum* and *H. setchellii* but differs by its slightly larger spores and the peridium of interwoven hyphae which contain isolated areas of parenchyma-like cells.

Specimens identified as *H. membranaceum* by Rodway (1924) belong to an as yet undescribed genus. Specimens identified as *Hysterangium membranaceum* by Calonge et al (1977) is actually *Trappea darkeri* (Zeller) Castellano.



Map 25. Distribution of *Hysterangium membranaceum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium neotunicatum Castellano nom. prov.

≡ *Hysterangium tunicatum* Cunningham, Trans. Roy. Soc. New Zeal.
67:409. 1938. nom. illeg.

Basidiomata up to 2 cm in diam, subglobose, irregular to reniform, when fresh yellowish brown to ferrugineous, surface somewhat glabrous.

Gleba olive to dark olive; locules elongate, empty or partially filled.

Rhizomorph single, small, attached to base, concolorous with peridium.

Columella gelatinous, distinct, dendroid, arising from a sterile base.

Peridium not easily separable from gleba, 600–900 µm thick, two-layered; epicutis 500–700 µm thick, of hyaline, thin-walled, irregularly inflated cells (parenchyma-like), 20–65 µm in diam, clamp connections absent; subcutis 100–200 µm thick, of hyaline, thin-walled, interwoven hyphae, 3–8 µm in diam, clamp connections absent.

Trama 50–70 (–200) µm thick, of hyaline, compactly interwoven hyphae (2–3 µm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** rehydrating poorly, hyaline, 6 spored.

Spores smooth, 11–14 x (4–) 5–6.5 µm, fusiform to broadly fusiform; apex acuminate, base shortly pedicellate. **Spore wall** less than 0.5 µm thick. **Utricle** distinct, irregularly loose or baggy. **Spore color** in KOH pale green singly, green in mass. (Figs. 38 & 39).

ETYMOLOGY: the new "*tunicatum*" in reference to the invalidly published earlier name.

OTHER REFERENCES: Cunningham (1942) p. 70 (as *Hysterangium tunicatum* Cunningham).

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Kunzea ericoides* and *Eucalyptus* spp.; February through November.

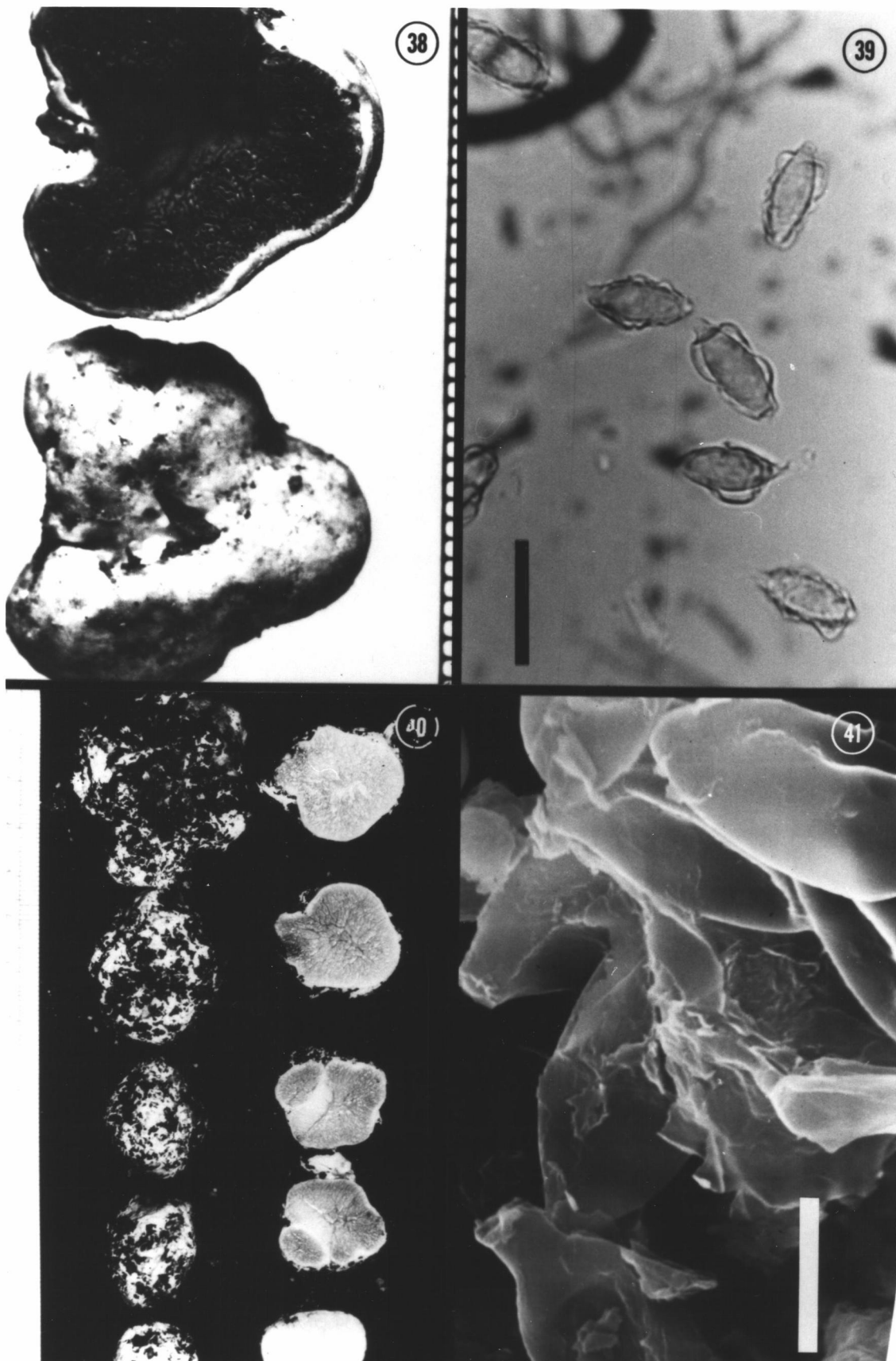
COLLECTIONS EXAMINED: HOLOTYPE: **NEW ZEALAND:** Nelson, Fringe Hill, NOV-1923, leg Cunningham, (PDD 8321), ISOTYPE (DAOM 116180). **OTHER COLLECTIONS — AUSTRALIA:** New South Wales (DAR 28830). Tasmania, Hobart (HO 89520). Victoria, Beaton 81 (K). Western Australia, Boyicup, Trappe 5454 (OSC). **ARGENTINA:** Neuquen, 23997 (BAFC). Rio Negro, 30371 (BAFC). **NEW ZEALAND:** Auckland 8318, 8320, 12226, 24551, 24592, 28379, 28579, 29232, 30171 (all PDD), 4605 (K). Coromandel 51796 (PDD). Otago 8322 (PDD). Wellington 10842 (PDD). Whangarei 32186, 32293 (all PDD).

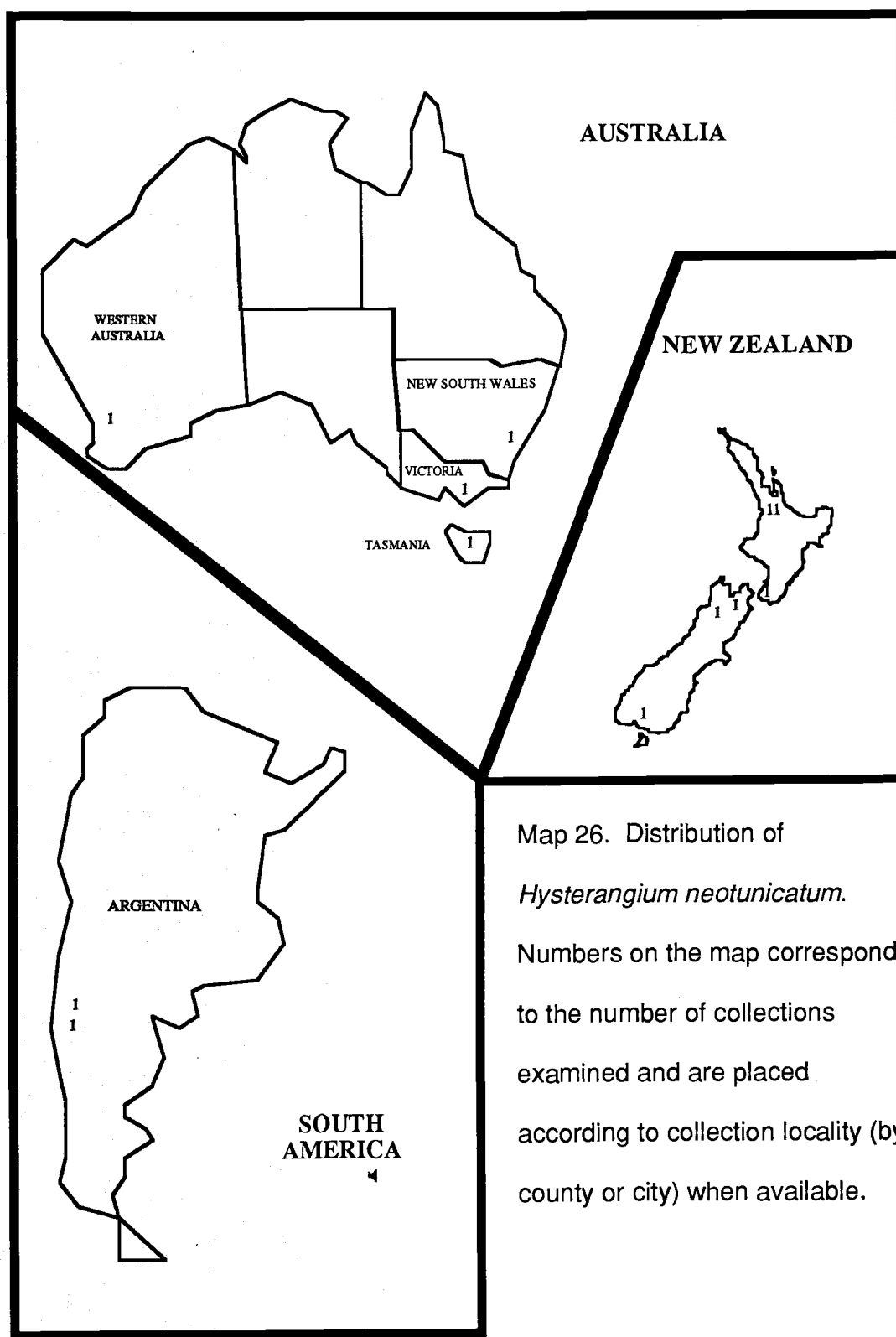
DISCUSSION: *Hysterangium tunicatum* Cunningham was published after 1935 without a Latin diagnosis, so is declared illegal in accordance with the Botanical Code, Article 36.1.

The epithet *neotunicatum* is proposed to accommodate this species, which has spores similar to those of *H. inflatum* but with an irregularly inflated utricle; the two species differ vastly in peridial characters. *Hysterangium neotunicatum* differs from *H. rugisporum*, which also occurs under *Kunzea*, by its smooth spores, whereas *H. rugisporum* has ornamented (verrucose) spores. *Hysterangium neotunicatum* has much larger spores than *H. parvisporum*.

Apparently restricted to a (presumptive) mycorrhizal association with *Kunzea ericoides* and possibly *Eucalyptus* spp.

Figures 38-41. *Hysterangium*. 38. Sporocarps of *H. neotunicatum* (PDD 48321), upper half in cross-section, scale in mm. 39. Light micrograph of *H. neotunicatum* spores (PDD 48321), bar = 20 μ m. 40. Sporocarps of *H. occidentale* (Trappe 8480), cross-sectional view on right side, scale in mm. 41. SEM of *H. occidentale* spores (HS 2630), bar = 5 μ m.





Hysterangium nephriticum Berkeley, Ann. & Mag. Nat. Hist. 13:350. 1844.

≡ *Splanchnomyces nephriticum* (Berkeley) Corda, Icones Fung. 6:79.

1854.

Basidiomata 2–2.5 cm in diam, subglobose to reniform, white at first or with a pale reddish pink cast when fresh, pale ochraceous when dry, surface downy tomentose with variously attached rhizomorphs, numerous soil particles adhering to entire surface. **Gleba** pale blue or gray with a green or pinkish cast, pale greenish brown when dry; locules irregular, nearly filled with spores and hyphal strands at maturity. **Rhizomorphs** few, tomentose, less than 1 mm in diam, pale yellow, ochraceous or white when dry. **Columella** gelatinous, dendroid, arising from a sterile base, translucent to pale bluish gray or pale pink when fresh, pale brown when dry. **Odor** not offensive.

Peridium easily separable from gleba (especially upon drying), 140–350 μm thick, two-layered; epicutis 100–250 μm thick, of hyaline, thick-walled ($\pm 1 \mu\text{m}$), loosely interwoven to periclinal hyphae 3–4 μm in diam, with abundant crystalline particles adhering to the outer hyphae, clamp connections absent; subcutis 40–100 μm thick, of hyaline, thin-walled, irregular to subglobose hyphal cells (subparenchyma-like), 5–8 μm in diam, clamp connections absent.

Trama 20–30 μm thick, of hyaline, interwoven hyphae (1–2 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindrical, 9–10 x $\pm 30 \mu\text{m}$, 2 spored.

Spores smooth at first, minutely verrucose in age, $13\text{--}18 \times 4\text{--}6 \mu\text{m}$, ellipsoid, adhering to each other; apex blunt, base appendaged. **Spore wall** less than $0.5 \mu\text{m}$ thick. **Utricle** wrinkled, up to $1 \mu\text{m}$ in age. **Spore color** in KOH hyaline to pale brown singly, pale brown in mass.

ETYMOLOGY: referring to the "kidney-shaped" sporocarps.

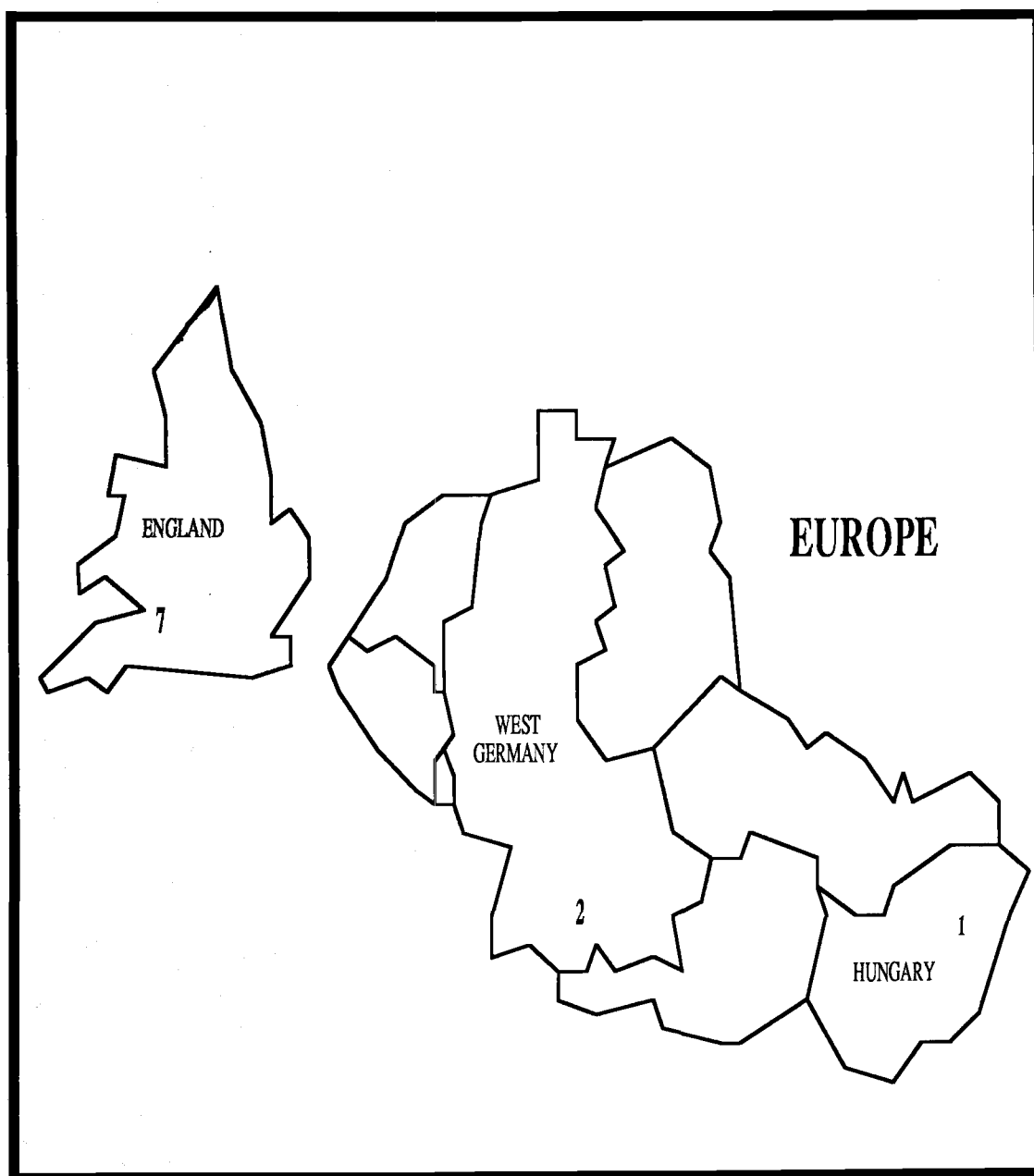
OTHER REFERENCES: Berkeley (1860) p. 294, Cooke (1871) p. 358, De Toni in Saccardo (1888) p. 156, Gross (1980) p. 132, Hawker (1954) pp. 509–510, Hesse (1891) pp. 104–105, Massee (1889) pp. 37–38, Rea (1922) p. 25, Soehner (1952) pp. 260–261, Tulasne & Tulasne (1851) p. 82.

HABIT, HABITAT AND SEASON: Hypogeous in calcareous soil; probable mycorrhizal associates *Fagus*, *Quercus cerris*, and possibly *Pinus*; August through February.

COLLECTIONS EXAMINED: HOLOTYPE: **ENGLAND:** Bristol, near Clifton, FEB–1844, leg Broome (K), ISOTYPE (FH). **OTHER COLLECTIONS — ENGLAND:** Bristol (NY, M). Kings Cliff (K). Leigh Wood (E, G, K). no locality, Hawker 754 (DAOM 107785), leg Berkeley (LE), leg Berkeley 1844/12 (RO). **HUNGARY:** no locality, leg Szemere (BP). **GERMANY (WEST):** no locality, Soehner 1440, Knapp 1223 (all M).

DISCUSSION: *Hysterangium nephriticum* is uncommon but forms extensive mycelial mats in calcareous soils (Hawker 1954) in (presumptive) mycorrhizal association with *Quercus* and *Fagus*.

Hysterangium nephriticum resembles *H. asperulatum* and *H. thwaitesii* but differs from *H. asperulatum* by its narrower and slightly longer spores and the thicker subcutis and differs from *H. thwaitesii* by its nongelatinized epicutis, larger subcuticular cells, and spores which at maturity are finely verrucose and slightly smaller and thinner than those of *H. thwaitesii*.



Map 27. Distribution of *Hysterangium nephriticum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium occidentale Harkness, Cal. Acad. Sci. Proc. III. 1:255. 1899.

Basidiomata up to 6 cm in diam, subglobose to somewhat depressed or irregularly lobed, white to pale brown, bruising brown, surface covered with mycelium and rhizomorphs, numerous soil particles adhering to surface, FeSO₄ bluish green. **Gleba** fleshy, not cartilaginous except for columella, white or pale pink when young, deep pink, pale red or pale brownish red when mature; locules elongate, empty. **Rhizomorphs** numerous, less than 1 mm thick, adhering everywhere on sporocarp, especially near base, pale pinkish brown at maturity. **Columella** gelatinous, distinct, dendroid, up to 3 mm wide at base, white when fresh, brown when dry. **ODOR** absent or pleasant.

Peridium easily separable from gleba, 380–770 µm thick, two layered; epicutis 180–220 µm thick, of hyaline, loosely interwoven to mostly periclinal hyphae, 2–4 (–5) µm in diam, crystalline particles absent, clamp connections common; subcutis 200–450 µm thick, of hyaline, compactly interwoven hyphae which are elongate and swollen (pseudoparenchyma-like), 10–15 x 18–35 µm, much smaller and more loosely arranged near gleba, clamp connections absent.

Trama 40–200 µm thick, of hyaline, compactly interwoven hyphae (2–3 µm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindric, 20–25 x 6–8 µm, 2 (4) spored.

Spores smooth, 12–16 (–19) x 5–7 (–8) µm, ellipsoidal, fusiform to mostly citriform; apex blunt, base pedicellate. **Spore wall** less than 0.5 µm thick. **Utricle** apparently absent, but some spores stuck together in pairs. **Spore color** in KOH hyaline singly, pale pink to ochraceous in mass. (Figs. 40 & 41).

ETYMOLOGY: the "western" *Hysterangium*.

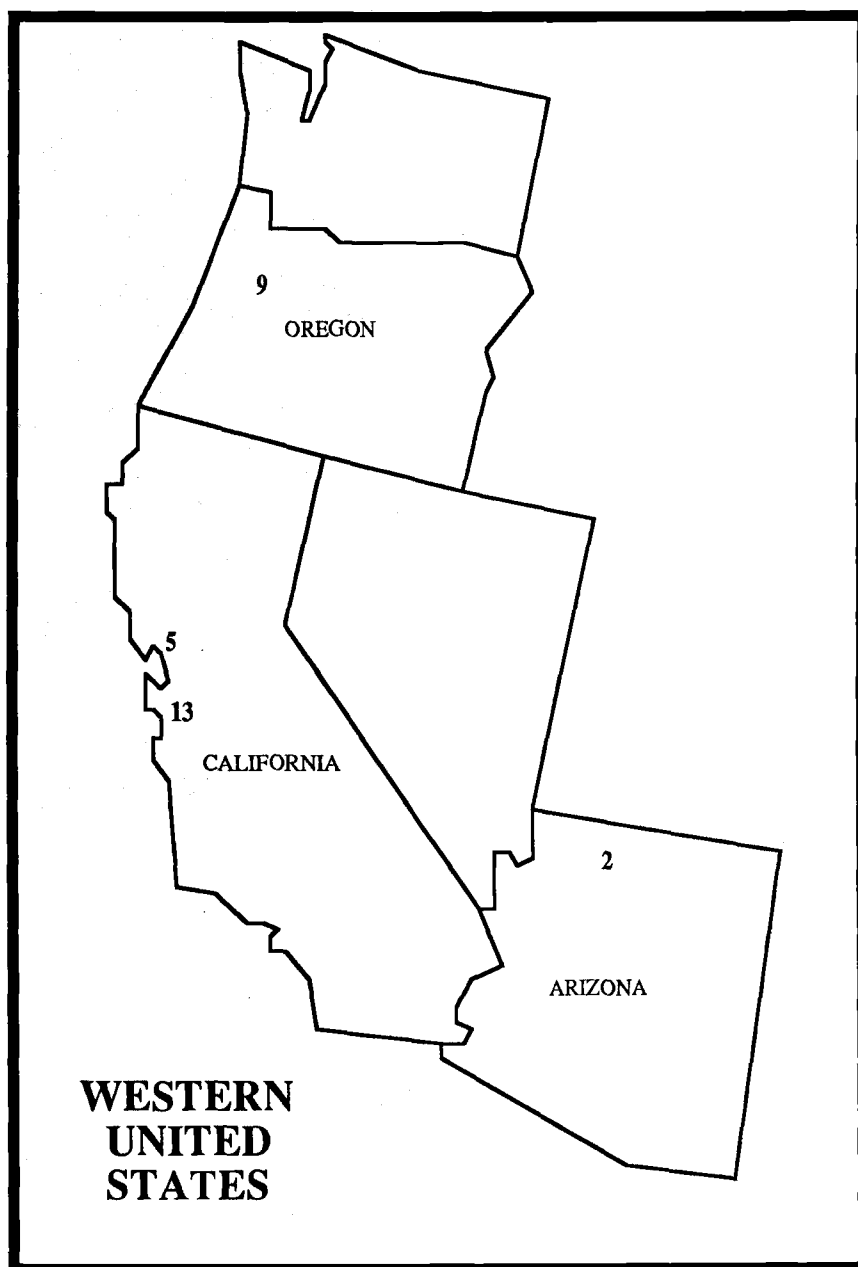
OTHER REFERENCES: Saccardo & Sydow in Saccardo (1902) p. 245, Zeller & Dodge (1929) p. 89.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Pseudotsuga menziesii*, *Pinus ponderosa*, *Quercus garrayana* and other *Quercus* spp.; April through October, mostly April and May.

COLLECTIONS EXAMINED: HOLOTYPE: **CALIFORNIA:** Marin Co., Mt. Tamalpais, MAY, Harkness 242 (BPI). **OTHER COLLECTIONS — ARIZONA:** Coconino Co., AHF 355, AHF 518 (all FSLF). **CALIFORNIA:** Marin Co., leg Evans (BPI), Parks 2109, Parks 2135 (all UC). Santa Clara Co., Parks 126, Parks 157, Parks 386, Parks 413, Parks 468 (all NY, UC), Parks 141, Parks 816 (UC), Parks 86 (NY). Santa Cruz Co., Trappe 8480 (OSC), HS 2629, HS 2630, HS 2631 (all SFU), Parks 959 (MPU, NY). Sonoma Co., Heblack 113 (OSC). **OREGON:** Benton Co., Zeller 7063 (NY, OSC), F 904, F 787 (all MICH), Trappe 760, Trappe 7476, Trappe 7492 (all OSC), Zeller 7193 (NY). Linn Co., Trappe 7935, Trappe 7937 (all OSC).

DISCUSSION: *Hysterangium occidentale* commonly fruits within a dense mat of mycelium and rhizomorphs at and immediately below the mineral soil-humus interface.

The pink gleba of the fresh sporocarp distinguishes this species from all others except possibly *H. pompholyx* and *H. ochraceogleba*. *Hysterangium occidentale* has smooth, citriform spores which lack a utricle while *H. pompholyx* has spores which are smooth when young, verrucose with age and a thick utricle and *H. ochraceogleba* has smooth spores which are broadly ellipsoid.



Map 28. Distribution of *Hysterangium occidentale*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium ochraceogleba Castellano & States, nom. prov.

Basidiomata up to 1.8 cm in diam, subglobose, white with pale ochraceous patches mottled white and brown when dried, surface tomentose with much adherent soil particles. **Gleba** bright ochraceous when fresh, cinnamon brown when dried; locules irregular, filled at maturity, FeSO₄ deep blue green, KOH slightly sorid. **Rhizomorphs** few, small, attached to base, concolorous with peridium. **Columella** gelatinous, dendroid, arising from a sterile base, narrow, greenish gray to translucent when fresh, reddish brown when dried.

Peridium easily separable from gleba, a single layer 300–400 µm thick, of hyaline to pale brown, thin-walled, agglutinated, irregularly shaped, compactly interwoven hyphae, 5–8 µm in diam, numerous crystalline particles scattered across cells, clamp connections absent.

Trama 20–40 µm thick, of hyaline, interwoven hyphae (1–3 µm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, elongate, thin-walled, clamped at base, $\pm 30 \times \pm 5$, 2 spored.

Spores smooth, 12–15 (–19) $\times$ 5.5–7 µm, broadly ellipsoid to irregularly shaped; apex obtusely blunt to slightly papillate, base appendiculate. **Spore wall** up to 1 µm thick, thicker at apex. **Utricle** absent or inconspicuous, spores adherent to each other by way of what appears as a mucilaginous substance on the spore wall. **Spore color** in KOH pale green singly, pale brown or buff in mass. (Figs. 42 & 43).

ETYMOLOGY: in reference to the “ochraceous” color of the fresh gleba.

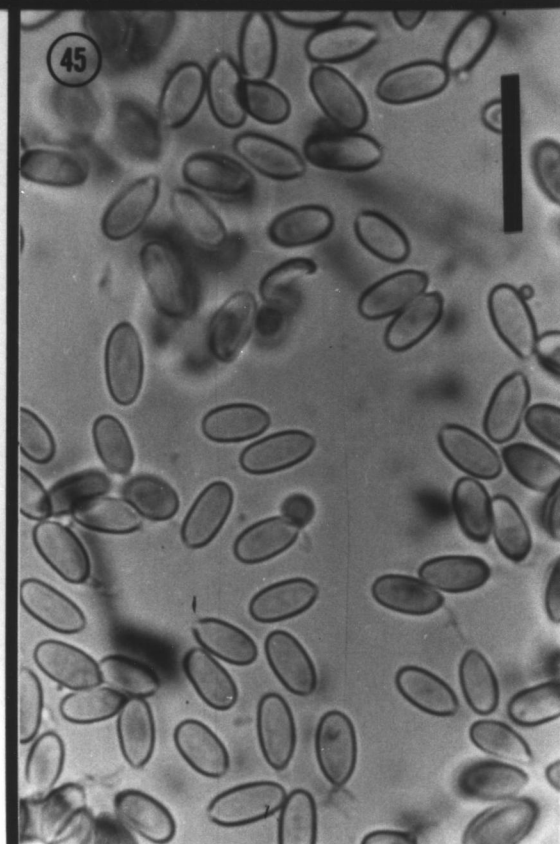
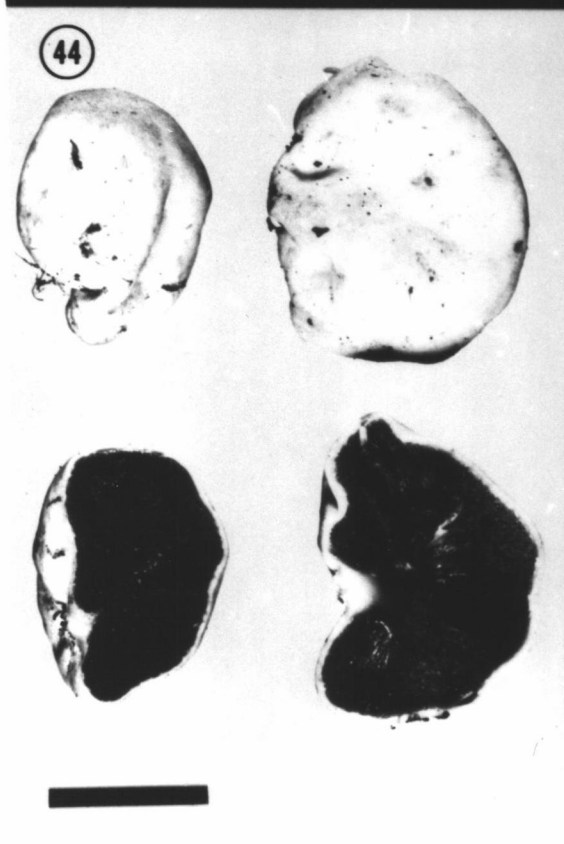
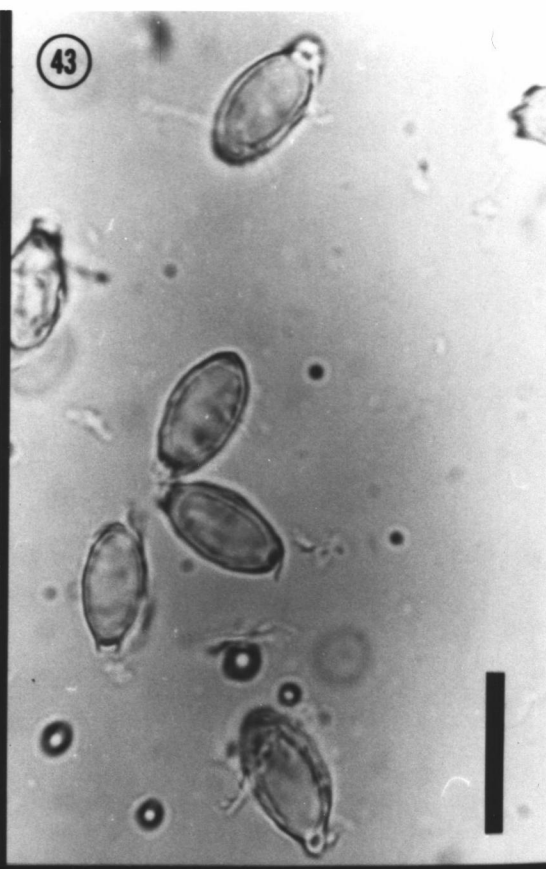
HABIT, HABITAT, AND SEASON: Hypogeous; probable mycorrhizal associate, *Pinus ponderosa*; April and September.

COLLECTIONS EXAMINED: HOLOTYPE: **ARIZONA:** Cochise Co., Coronado National Forest, south of Cave Creek, 27–April–1986, leg States AHF 490 (FSLF), ISOTYPE (OSC). **OTHER COLLECTIONS:** **ARIZONA:** Coconino Co., Coconino National Forest, oak creek canyon, 18–September–1988, leg States (Trappe 9944) (OSC, FSLF).

DISCUSSION: *Hysterangium ochraceogleba* is similar to *H. occidentale* but differs by its ellipsoid, thick-walled spores, and the peridium which in *H. ochraceogleba* is of agglutinated, irregularly shaped hyphae but in *H. occidentale* is of two layers with a subcutis of inflated hyphal cells.

Hysterangium ochraceogleba forms a dense white mycelial mat in the lower duff layer under *Pinus ponderosa*.

Figures 42-45. *Hysterangium*. 42. Sporocarps of *H. ochraceogleba* (Trappe 9944), cross-sectional view on bottom, bar = 4 cm. 43. Light micrograph of *H. ochraceogleba* spores (Holotype, AHF 490), bar = 20 μ m. 44. Sporocarps of *H. parvisporum* (PDD 48798), cross-sectional view on bottom, bar = 1 cm. 45. Light micrograph of *H. parvisporum* spores (PDD 48798), bar = 15 μ m.





Map 29. Distribution of *Hysterangium ochraceogleba*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium olivaceonigrum Castellano & Malajczuk, nom. prov.

Basidiomata 5–20 mm in diam, subglobose, irregular to flattened, white when fresh, unchanging when bruised, surface tomentose with much adherent soil. **Gleba** dark gray green to greenish black; locules irregular to elongate, filled. **Rhizomorphs** numerous, small, adherent to sporocarp, concolorous with peridium. **Columella** narrow, dendroid in youth, inconspicuous in age.

Peridium not easily separable from gleba, a single layer 100–200 μm thick, of hyaline (near surface), pale brown (near gleba), thin-walled, loosely interwoven hyphae, 4–5 (–7) μm in diam within, 2–3 μm in diam without, crystalline particles absent, clamp connections common.

Trama 40–80 μm thick, of hyaline, collapsed, compactly interwoven hyphae (1–2 μm in diam) in a gelatinized matrix, clamp connections absent.

Basidia not observed.

Spores smooth, 10–12 (–13) $\times$ $\pm$ 4 μm without utricle, elliptic; apex acuminate, base truncate. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, loosely inflated, irregular to baggy, usually not extending past spore apex. **Spore color** in KOH pale green singly, pale olive in mass.

ETYMOLOGY: in reference to the dark olive to almost black color of the gleba.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Eucalyptus globulus* and *E. wandoo*; September.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Western Australia, Jarrahdale, 13-SEPT-1982, leg J. Trappe, M. Trappe & L. Sanfelieu, Trappe 6923 (H 288) (OSC), ISOTYPE (DAR). **OTHER**

COLLECTIONS — AUSTRALIA: Western Australia, Jarrahdale, Trappe 6925 (H 290), Trappe 6924 (all OSC). Glen Eagle State Forest, Trappe 6900 (H 312) (OSC, DAR).

DISCUSSION: The white peridium which is unchanging upon bruising or drying in conjunction with the dark gray green to nearly black gleba separate this species from all other *Hysterangium*.



Map 30. Distribution of *Hysterangium olivaceonigrum*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium parvisporum Castellano nom. prov.

Dried **basidiomata** up to 2 cm in diam, irregularly lobed, white bruising pinkish brown when fresh, surface glabrous. **Gleba** dark olive to olive brown; locules irregular, partially empty. **Rhizomorphs** numerous, small, attached at base, concolorous with peridium. **Columella** of unknown consistency, distinct, dendroid, arising from a sterile base, nearly black when dried.

Peridium not separable from gleba, 575–750 μm thick, two-layered; epicutis 500–600 μm thick, of hyaline, thin-walled, spherical cells (parenchyma-like), 25–50 μm in diam, clamp connections absent; subcutis 75–150 μm thick, of pale brown, thin-walled, gelatinized, interwoven to subpericlinal hyphae, 1–3 μm in diam, clamp connections absent.

Trama 150–225 μm thick, of hyaline, collapsed, loosely interwoven hyphae (1–4 μm in diam) in a gelatinized matrix, clamp connections absent.

Basidia rehydrating poorly, hyaline, 6 (7) spored.

Spores smooth, (6–) 7–9 x 3–4 μm , oblong; apex obtusely blunt, base distinctly pedicellate, 1 x 1 μm . **Spore wall** less than 0.5 μm thick. **Utricle** absent. **Spore color** in KOH pale green singly, pale olive brown in mass. (Figs. 44 & 45).

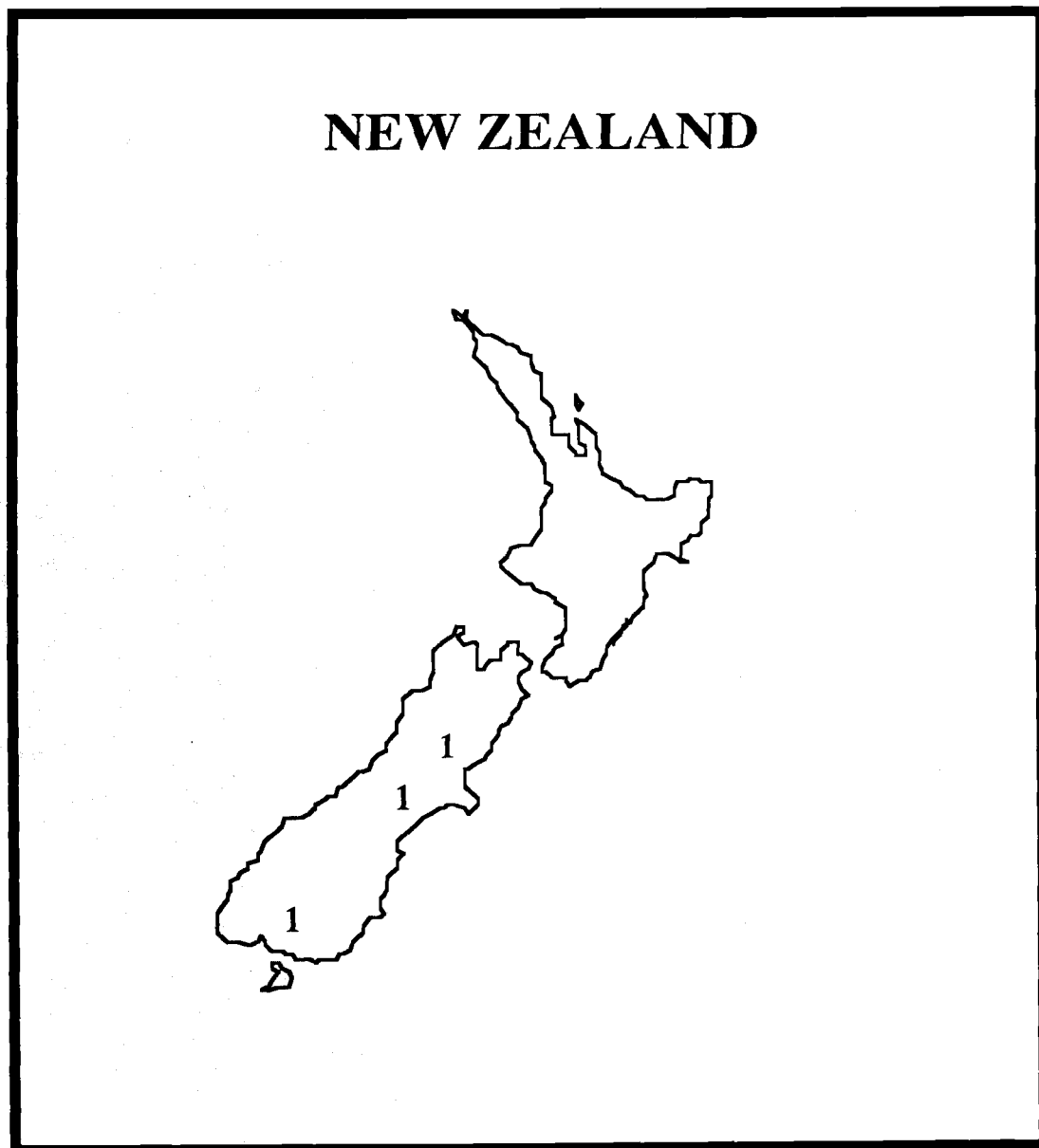
ETYMOLOGY: “small spored.”

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Nothofagus cliffortioides*, *N. fusca*, and *N. solandii*; May and June.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW ZEALAND:** Whakapupanui stream, 30–APR–1967, leg McNabb (PDD 45878), ISOTYPE (OSC). **OTHER COLLECTIONS — NEW ZEALAND:** Buller, 48792, 48794,

48795, 48796 (all PDD). Canterbury, 31458 (PDD). Otago, 21165 (PDD).
Taupo, 48798 (PDD).

DISCUSSION: *Hysterangium parvisporum* possesses the smallest spores of any *Hysterangium* species. On the basis of spores and glebal characters *H. parvisporum* seems to be closely related to the genus *Claustula*, which also occurs with *Nothofagus* in New Zealand.



Map 31. Distribution of *Hysterangium parvisporum*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium pompholyx Tulasne & Tulasne, Ann. Sci. Nat. Bot. II. 19:375. pl. 17, figs. 17–19. 1843.

= *Hysterangium rubricatum* Hesse, Jahrb. f. wiss. Bot. 15:631. pl. 32. 1884.

Basidiomata 1–1.5 (–4) cm in diam, reniform, globose to depressed, reddish brown to dark brown when fresh, surface floccose. **Gleba** at first white, then pale reddish brown, brown or olive brown when dried; locules elongate, partially filled. **Rhizomorphs** numerous, less than 1 mm thick, adherent to all areas of the peridium, concolorous with peridium. **Columella** gelatinous, distinct, dendroid, translucent.

Peridium not separable from gleba, a single layer 200–250 μm thick, of dark reddish brown, thin-walled, polyhedral cells (subparenchyma-like) up to 50–70 μm in diam, abundant crystalline particles scattered throughout, clamp connections common.

Trama 25–100 μm thick, of hyaline, compactly interwoven hyphae (2–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** not rehydrating well, hyaline, more or less cylindrical, 35–40 x 7–8 μm , 2 (3) spored.

Spores at first smooth, verrucose at maturity, ornamentation almost striate, 12–16 x 5–7 μm , broadly fusiform; apex blunt, base distinctly appendaged. **Spore wall** usually less than 0.5 μm thick, sometimes thickened at apex. **Utricle** distinct, roughened or wrinkled, 1 μm thick, spores often stuck together in pairs from mid-spore to base. **Spore color** in KOH pale brown singly, pale brown in mass. (Fig. 46).

ETYMOLOGY: Greek, "blister" or "bubble," of unknown relevance.

OTHER REFERENCES: De Toni in Saccardo (1888) p. 157. Gross (1980) p. 132, Tulasne & Tulasne (1851) pp. 83–84.

HABIT, HABITAT AND SEASON Hypogeous; probable mycorrhizal associates *Carpinus*, *Crataegus*, *Fagus*, *Corylus* and *Quercus*; March through November.

COLLECTIONS EXAMINED: LECTOTYPE: **FRANCE:** Bois de Meudon, APR–1843, leg Tulasne (PC), ISOTYPE (FH). **OTHER COLLECTIONS** —

FRANCE: Clamart (PC). Foret de Marley (PC, NY, FH).

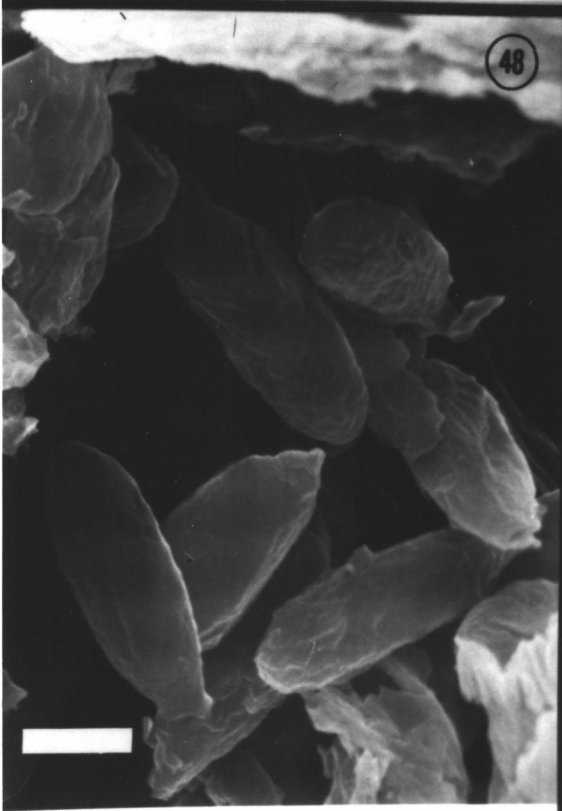
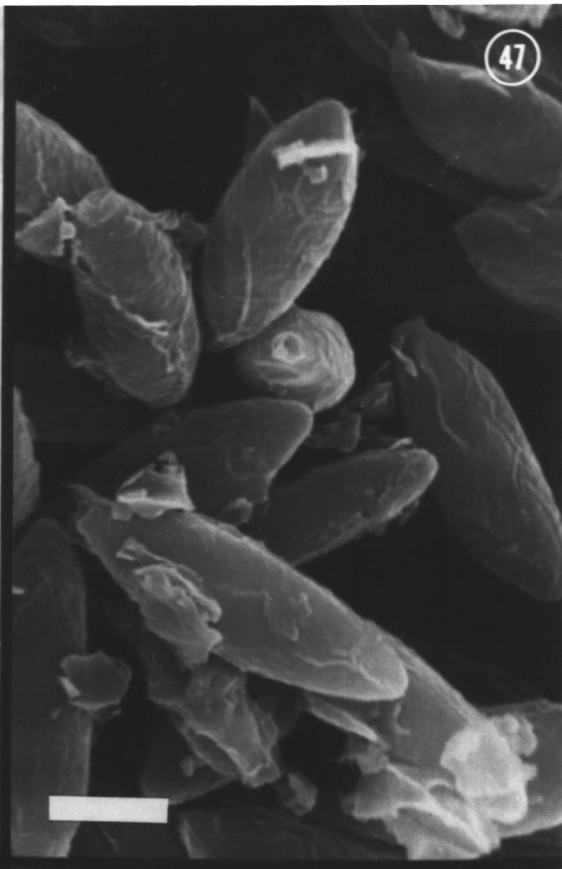
CZECHOSLOVAKIA: Cernosice (PRM 619167). **GERMANY (WEST):**

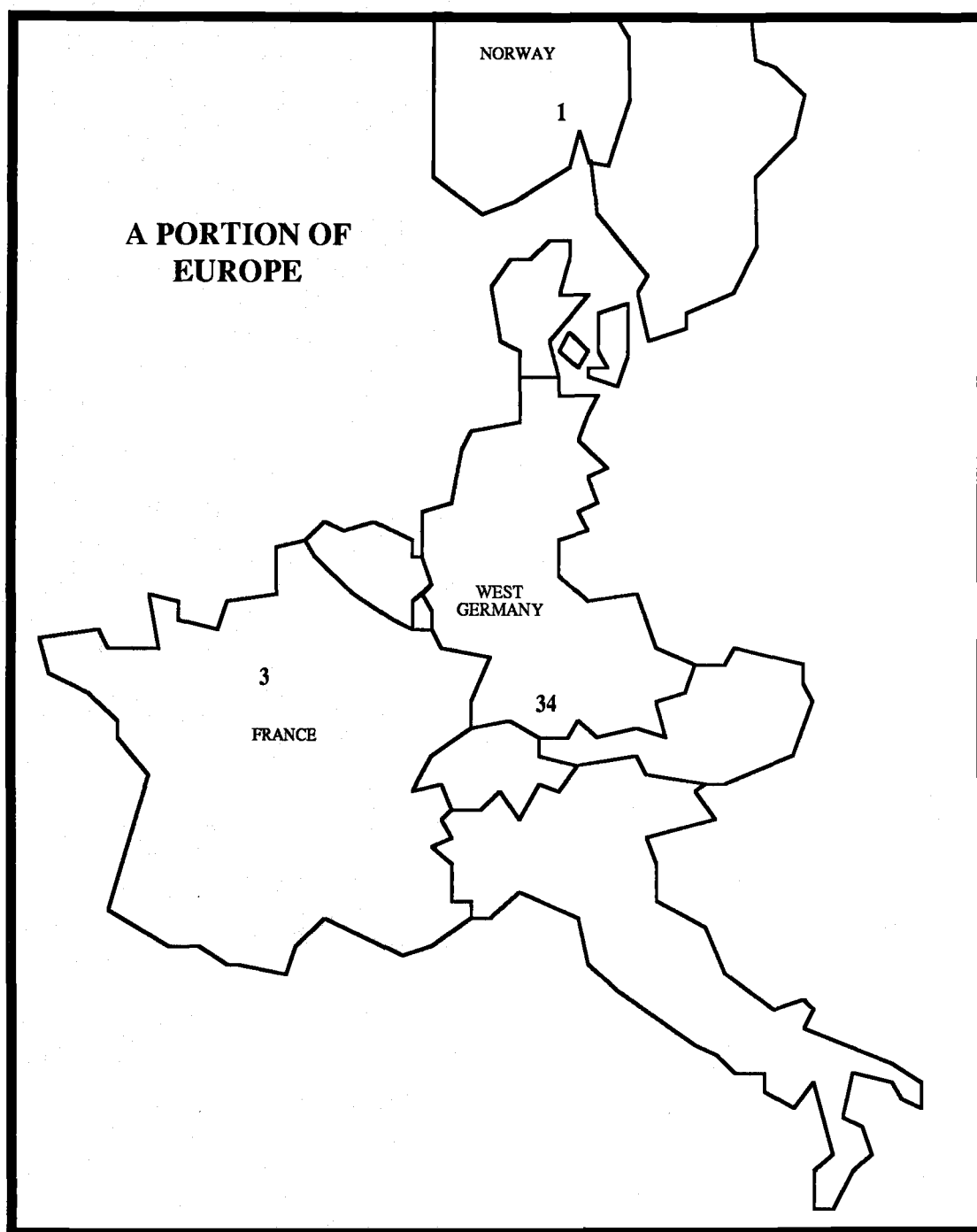
Buntsandstein (ZT). Gauting, Soehner 422, Soehner 443, Soehner 464, Soehner 486, Soehner 839 (all M). Mindelheim, Soehner 199, Soehner 209, Soehner 245, Soehner 254, Soehner, 255, Soehner 259, Soehner 260, Soehner 329, Soehner 337, Soehner 772, Soehner 1048, Soehner 1438, Soehner 1926, Soehner 1928, Soehner 1939, Soehner 1956, Soehner 2177 (all M). Munich, Soehner 138, Soehner 139, Soehner 1486, Soehner 2294 (all M). Regensburg, Killerman 3, leg Killerman (all M). no locality, herb. Hesse, Bucholtz 279 (all FH), Gross 14, Gross 19, Gross 23, Gross 42, Gross 270, Gross 281 (all M). **NORWAY:** Oslo (UPS).

DISCUSSION: Hesse (1884) established *H. rubricatum* without studying material of *H. pompholyx*. For the most part all collections identified as *H. rubricatum* by Gross (1980), Hesse (1884, 1891), Soehner (1952), and Zeller and Dodge (1929) are *H. pompholyx*.

Of the *Hysterangium* which lack a green color to the gleba, *H. pompholyx* is unique in its coarsely verrucose (almost striate) ornamentation of the broadly fusiform spores. The spores are often stuck together in pairs from mid-spore to the base.

Figures 46-49. *Hysterangium*. 46. Light micrograph of *H. pompholyx* spores (Herb. Hesse), bar = 10 μ m. 47. SEM of *H. rhodocarpum* spores (Holotype, Trappe 6889), bar = 5 μ m. 48. SEM of *H. rugisporum* spores (Holotype, PDD 4605), bar = 5 μ m. 49. Sporocarps of *H. rugisporum* (PDD 51927), bar = 1 cm.





Map 32. Distribution of *Hysterangium pompholyx*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium rhodocarpum Castellano & Malajczuk nom. prov.

Basidiomata 6–12 mm in diam, globose to subglobose, white, staining deep rose, surface glabrous. **Gleba** dark grayish green when fresh; locules irregular to elongate, empty to partially filled. **Rhizomorph** single, small, less than 0.5 mm in diam, attached at base, concolorous with peridium.

Columella gelatinous, dendroid, narrow, translucent.

Peridium not easily separable from gleba, 440–540 μm thick, two-layered; epicutis 430–500 μm thick, of hyaline (except near surface which are golden brown), thin-walled, polyhedral to spherical, inflated cells (parenchyma-like), 20–30 x 30–59 (–75) μm in diam, crystalline particles adherent to outer golden brown cells, clamp connections absent; subcutis 10–40 μm thick, of hyaline to pale yellow, thin-walled, irregular, compactly interwoven hyphae, 3–5 μm in diam, clamp connections absent.

Trama 50–80 μm thick, of hyaline, mostly collapsed, loosely interwoven hyphae (1–2 μm in diam) in gelatinized matrix, clamp connections absent.

Basidia not observed.

Spores smooth, 12–13 x 4.5–5 μm , ellipsoid to subfusiform; apex acuminate, base truncate to slightly appendaged. **Spore wall** less than 0.5 μm thick when young, 1 μm thick in age. **Utricle** absent or when present inconspicuous, irregular to slightly inflated, up to 1 μm , occasionally calyptrate, attached at apex and base of spore. **Spore color** in KOH pale green singly, pale olive in mass. (Fig. 47).

ETYMOLOGY: referring to the “deep rose” staining of the sporocarp.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Eucalyptus calophylla*, *E. diversicolor*, *E. jacksoniina* and *E. marginata*; July through September.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Western Australia, Beedelup National Park, 9-SEPT-1982, leg N. Malajczuk & J. Trappe, Trappe 6889 (OSC). **OTHER COLLECTIONS — AUSTRALIA:** Western Australia, Boyicup, Trappe 5465 (OSC). Inglehope, Trappe 6947 (OSC). Jarrahdale, Trappe 6936, Trappe 6941 (all OSC). Quininip, HDT 43203 (SFU). Walpole National Park, Trappe 6910 (OSC).

DISCUSSION: The clamp connections of the subcuticular hyphae and the thick-walled spores separate *H. rhodocarpum* from *H. coriaceum*.

Hysterangium rhodocarpum is found in (presumptive) mycorrhizal association only with *Eucalyptus* in the southern hemisphere while *H. coriaceum* is mycorrhizal only with members of the Pinaceae.



Map 33. Distribution of *Hysterangium rhodocarpum*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium rugisporum Castellano nom. prov.

Basidiomata 1–1.75 cm in diam, subglobose to irregularly lobed with an indented base, white when fresh handling pale pink, pink overall in time, mottled buff, white and reddish brown when dry, surface finely pubescent which is easily rubbed off in handling, soil particles adhering everywhere.

Gleba green to pale olive; locules irregular to elongate, empty.

Rhizomorphs single, becoming branched several mm from point of attachment, up to 0.5 mm in diam, attached at base, concolorous with peridium.

Columella gelatinous, dendroid, $\pm$ 1 mm thick, arising from a sterile base, translucent when fresh, greenish brown to olive or nearly black when dry.

Peridium not easily separable from gleba, up to 800 μ m thick, three-layered; epicutis 80–300 μ m thick, of hyaline, thin-walled, compact, bead-like hyphae, which are elongate to subglobose, 2–5 (–8) μ m in diam, encrusted with crystalline particles, clamp connections absent; mesocutis 200–400 μ m thick, of hyaline, thin-walled, compact, irregularly inflated, subglobose to polyhedral hyphae (subparenchyma-like), up to 20 μ m in diam, crystalline particles absent, clamp connections absent; subcutis 60–80 (–100) μ m thick, appears as collapsed parenchyma-like cells which are golden brown and appear as more or less periclinal hyphae, clamp connections absent.

Trama 100–300 μ m thick, of hyaline, compactly interwoven hyphae (1–2 μ m in diam) in a gelatinized matrix, clamp connections absent. **Basidia** rehydrating poorly, hyaline, $\pm$ 10 μ m long, 4 spored.

Spores minutely verrucose, 12–16 x 5–6 μm , broadly ellipsoid; apex blunt, base appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, 1 μm thick, wrinkled, usually adhering to the spore wall. **Spore color** in KOH pale green singly, greenish brown in mass. (Figs. 48 & 49).

ETYMOLOGY: in reference to the "*rugose*" utricle surrounding the spores.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Leptospermum scoparium* & *Kunzea ericoides*; April through October.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW ZEALAND:** Auckland, Little Barrier Island, Oct–1945, leg Dingley (PDD 4605), ISOTYPE (DAOM 116179, OSC). **OTHER COLLECTIONS — NEW ZEALAND:** Auckland, Coromandel, Trappe 9890 (OSC), 51927 (PDD). Waiomu, Trappe 9883, Trappe 9885, Trappe 9886 (all OSC). Waitemata, 29233, 35052 (all PDD). Titirangi, Atkinson Park 24704 (PDD).

DISCUSSION: *Hysterangium rugisporum* is (presumptive) mycorrhizal with *Leptospermum* and *Kunzea* spp.

Hysterangium rugisporum has ornamented (minutely verrucose) spores as opposed to the smooth spores of *H. neotunicatum* or *H. parvisporum*.

Hysterangium salmonaceum Beaton, Pegler & Young, Kew Bull. 40: 440–442. figs. 23 a–c, 24 l–m. 1985.

Basidiomata 7–13 mm in diam, globose to subglobose, depressed at base, salmon pink with reddish gray mottling, brown when dry, surface glabrous. **Gleba** olive green; locules elongate, partially or completely filled. **Rhizomorphs** numerous, attached at base, concolorous with peridium. **Columella** gelatinous, dendroid to almost percurrent, $\pm$ 1 mm thick, translucent when fresh, nearly black when dried.

Peridium not easily separable from gleba, a single layer up to 600 μ m thick, of pale reddish brown, thin-walled, much inflated, agglutinated hyphae, 5–43 μ m in diam, crystalline particles absent; clamp connections scattered to inconspicuous.

Trama up to 400 μ m thick, of hyaline, interwoven to subparallel hyphae (2–10 μ m in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindric to clavate, 35–55 x 4–6 μ m, 4 spored.

Spores smooth, 15–20 x 4.5–6 μ m, elliptic-fusoid or cylindric; apex acuminate, base appendaged. **Spore wall** less than 0.5 μ m thick. **Utricle** distinct, loosely wrinkled, slightly thickened to slightly inflated, attached at base. **Spore color** in KOH pale green singly, pale brownish green in mass. (Fig. 50).

ETYMOLOGY: in reference to the “salmon” color of the peridium.

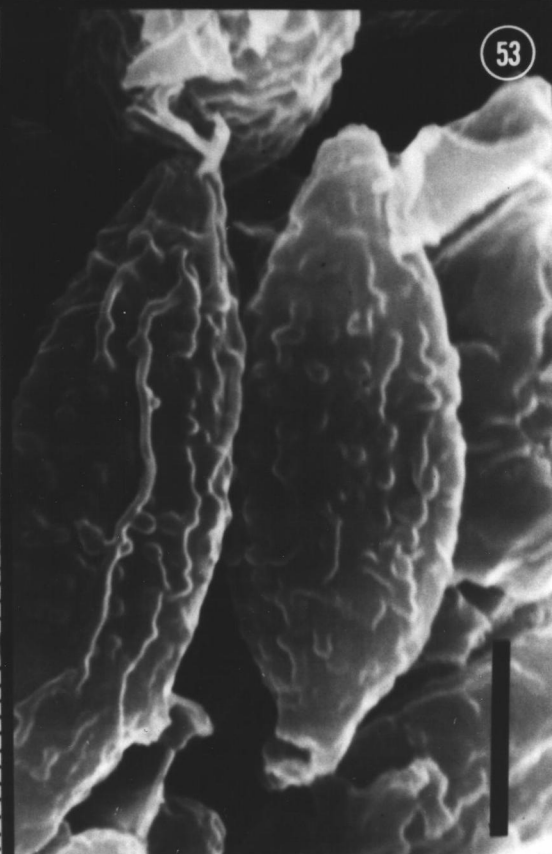
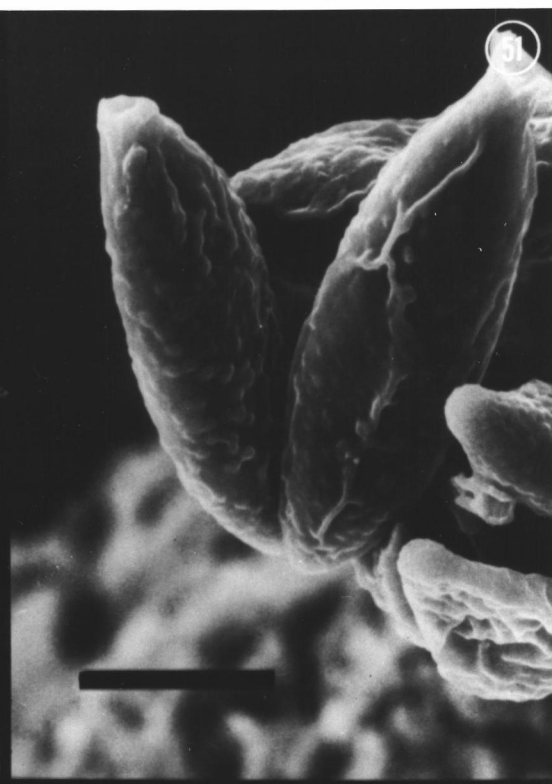
HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associate *Eucalyptus regnans*; July.

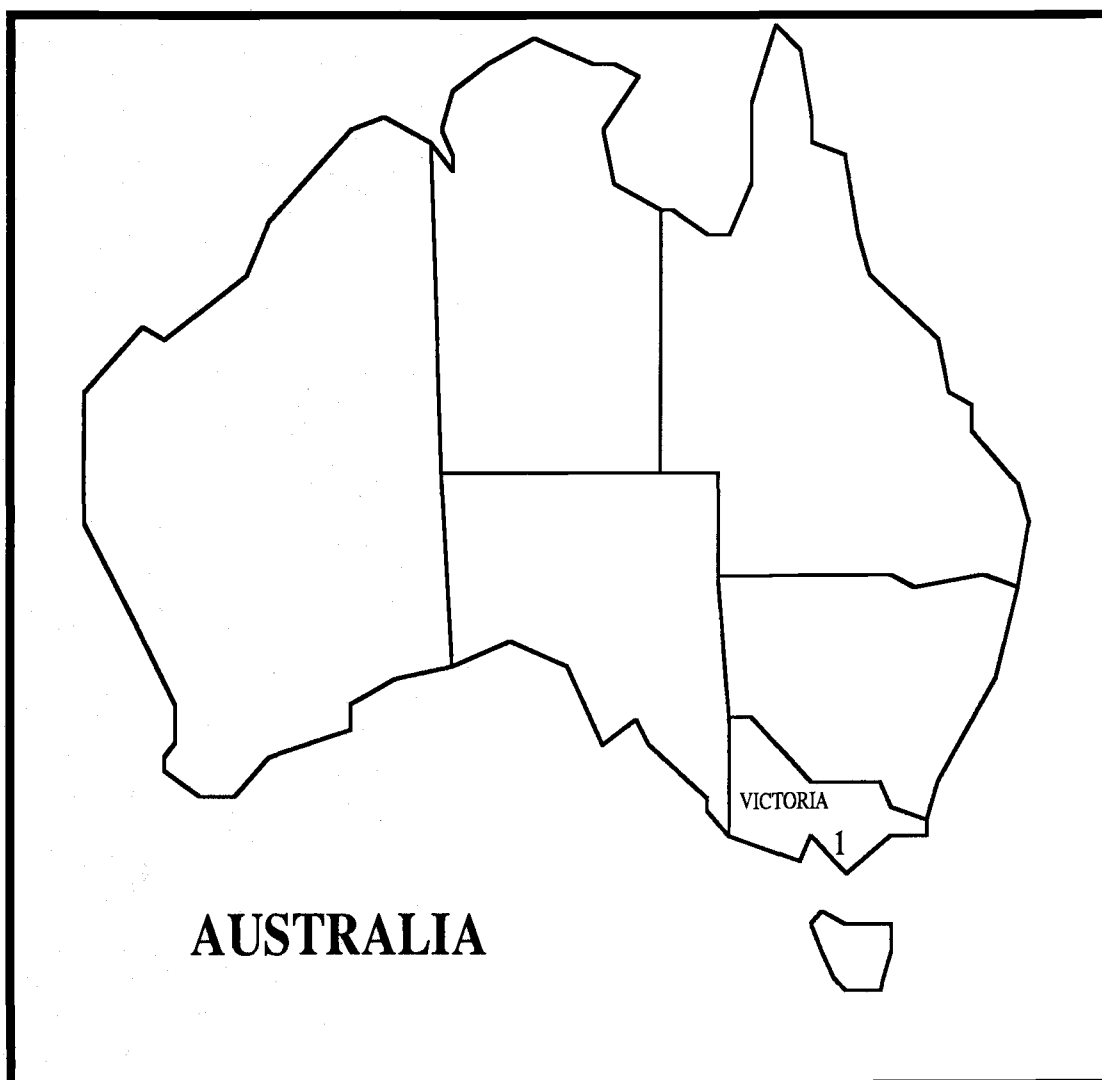
COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Victoria, Otway Range, Grey River Res., 18-JULY-1982, leg Weste, K. & G. Beaton 33 (K).

DISCUSSION: Spores of *H. salmonaceum* closely resemble those of *H. neocaledonicum* Pat. but the type collection of *H. neocaledonicum* is poorly preserved and does not allow critical comparison of sterile tissues. Further investigation and familiarity with these species may reveal that they are conspecific.

Hysterangium salmonaceum differs from *H. calcareum* by the longer and wider spores and the hyphae in the peridium of *H. salmonaceum* is much more inflated than in *H. calcareum*.

Figures 50-53. *Hysterangium*. 50. SEM of *H. salmonaceum* spores (Holotype, Beaton 33), bar = 5 μ m. 51. SEM of *H. separabile* spores (Gilkey 1061), bar = 6 μ m. 52. Sporocarps of *H. separabile* (Trappe 1599), upper two sporocarps and bottom left are cross-sectional view, bar = 1 cm. 53. SEM of *H. separabile* spores (UC 292005), bar = 5 μ m.





Map 35. Distribution of *Hysterangium salmonaceum*. Number on the map corresponds to the only collection examined and is placed according to collection locality (by county or city).

Hysterangium separabile Zeller, Mycologia 33:203–204. 1941.

≡ *Hysterangium clathroides* Vittadini sensu Zeller & Dodge pro parte,
Ann. Mo. Bot. Gard. 16:95–96. 1929.

Basidiomata 1–3 cm in diam, irregularly lobed to subglobose with basal depression, white when fresh, bruising brown to yellowish brown or pinkish brown, surface glabrous to slightly pubescent when fresh, later polished, usually nested in dense white mycelium; KOH yellow on white areas, dark brown on brown areas, FeSO₄ dark green, ETOH nonreactive. **Gleba** bright olive green, gray olivaceous to dark gray green, KOH nonreactive, FeSO₄ green, ETOH nonreactive; locules elongate, empty. **Rhizomorphs** prominent, single or double attached to base, 1–1.5 mm in diam, concolorous with peridium. **Columella** gelatinous, dendroid, 1–3 mm in diam at base, pale grey to pale grey blue when fresh, gray to reddish brown or pink. **Odor** of iodine. **Taste** of peridium extremely bitter.

Peridium easily separable from gleba, 390–450 (–850) µm thick, two-layered; epicutis 350–400 µm thick, of hyaline, thin-walled, polyhedral to spherical cells (parenchyma-like), 20–75 µm in diam, clamp connections absent; subcutis 40–60 µm thick, of pale brown, thin-walled, interwoven to subpericlinal hyphae, 2–4 µm in diam, clamp connections common.

Trama 100–150 µm thick, of hyaline, compact, interwoven to parallel hyphae (2–3 µm in diam) in a gelatinized matrix, clamp connections common.

Basidia hyaline, elongate, 26–28 x 7–9 µm, 4 or 6 spored.

Spores distinctly verrucose, 12–17 (–20) x 5–6.5 μm , ellipsoid to fusiform; apex acuminate, base appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, wrinkled, usually adhering to spore wall. **Spore color** in KOH hyaline to pale olive singly, olive in mass. (Figs. 51-53).

ETYMOLOGY: in reference to the easily “separable” peridium.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Quercus agrifolia*, *Q. garrayana*, *Q. kelloggii*, and other *Quercus* spp. and possibly *Arbutus menziesii*; September through May.

COLLECTIONS EXAMINED: HOLOTYPE: **OREGON:** Linn Co., Trout Cr. Forest Camp Recreational Area, 21–MAY–1938, Zeller 8479 (NY), ISOTYPE (OSC). **OTHER COLLECTIONS — ARIZONA:** Coconino Co., AHF 529 (FSLF), Trappe 6727 (OSC). **CALIFORNIA:** Contra Costa Co., Trappe 9791 (OSC). Marin Co., Gardner 261, Gardner 271, Parks 2043, Parks 2069, Parks 2504, Parks 2621, Parks 2630, Parks 2633, Parks 3037, Parks 3038, Setchell 34, Setchell 35 (all UC). Riverside Co., HS 1817 (SFU), Watling 17132 (E, OSC), Trappe 7344, Trappe 7352 (all OSC). San Bernardino Co., O.K. Miller 20945 (OSC), Trappe 7972, Trappe 8225 (all OSC). Santa Clara Co., Parks 38, Parks 60, Parks 78, Parks 96, Parks 292, Parks 326, Parks 347, Parks 363, Parks 382, Parks 383, Parks 406, Parks 452, Parks 869, Parks 912, Parks 949, Parks 1012, Parks 1029 (all UC), Gilkey 1061 (OSC). Santa Cruz Co., HS 2229, HS 2252, HS 2420, HS 2430 (all SFU), Parks 2163 (UC). San Mateo Co., HS 2274, HDT 24687 (all SFU). **OREGON:** Benton Co., Trappe 1599, Trappe 7197, Zeller 2074, Zeller 2582, Zeller 7197 (all OSC). Deschutes Co., Trappe 7965 (OSC). Douglas Co., Trappe 7884 (OSC). Lane Co., Trappe 6082 (OSC). Linn Co., Trappe 7260 (OSC). Polk Co., Stewart 198 (OSC),

Trappe 1605 (NY, OSC, FH, BPI, MICH).

DISCUSSION: The large type collection (wet and dry material) contains *H. crassirhachis* and *H. coriaceum* as well as *H. separabile*. These three species have some characters in common and have been confused one for another. In addition, the type collection contains sporocarps of *Rhizopogon* and *H. setchellii*, two species not easily mistaken for *H. separabile*. Apparently Zeller did not completely sort out the taxa from a portion of a collecting trip. Collections cited by Zeller and Dodge (1929) and Zeller (1941) are sometimes *H. separabile*, sometimes *H. coriaceum*, and sometimes neither. It is difficult to sort out the true concept of *H. separabile* as Zeller conceptualized, so I chose that element that produces the least nomenclatural uproar and change. Specimens from the type collections that have large, fusoid spores, parenchyma-like cells in the epicutis, and a moderately thick subcutis of interwoven hyphae are referred to *H. separabile*. *Hysterangium separabile* appears to be restricted to a mycorrhizal association with *Quercus* spp. and possibly *Arbutus* spp. in the western United States.

Hysterangium separabile is macroscopically similar to *H. crassirhachis* but has large parenchyma-like cells in the peridium in contrast to the interwoven, albeit somewhat inflated, hyphae of the peridium *H. crassirhachis*. *Hysterangium separabile* stains brown to pinkish-brown when bruised, whereas *H. crassirhachis* stains pink. *Hysterangium separabile* differs from *H. affine* of the Southern Hemisphere by its larger, more fusiform spores. *Hysterangium fragile* and *H. epiroticum* both have much larger spores than *H. separabile*. *Hysterangium aureum* has small more ellipsoid spores without a utricle and a peridium without a subcutis. *H. coriaceum* has smaller more narrow spores, basidia which are twice as long (up to 50 μm) and occurs with

conifers, while *H. separabile* occurs only with *Quercus*.

Because of the confusion resulting from the mixed type collection and resulting ambiguous descriptions, specimens identified as *H. separabile* by Calonge et al. (1977), Lange (1956), States (1984), Trappe and Guzmán (1971) and Zeller and Dodge (1929) are for the most part *H. coriaceum* or other taxa.



Map 36. Distribution of *Hysterangium separabile*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium setchellii Fischer, Ber. Schweiz. Bot. Ges. 48:33. fig. 1.
1938.

≡ *Hysterangium clathroides* var. *crassum* Tulasne & Tulasne sensu Zeller
& Dodge, non sensu Tulasne, Ann. Mo. Bot. Gard. 16:96–97. 1929.

Basidiomata 0.75–1.5 cm in diam, globose to subglobose, white at first quickly bruising yellowish brown, surface covered with much adherent mycelium, FeSO₄ on unbruised surface nonreactive, FeSO₄ on bruised surface instantly blue, KOH nonreactive except when applied to the blue FeSO₄ reaction then instantly red. **Gleba** green, olive to dark olive green, locules elongate, empty or occasionally partially filled. **Rhizomorphs** numerous, less than 0.5 mm in diam, adherent to all sides of the sporocarp, at first white then quickly yellowish brown to pale brown. **Columella** gelatinous, distinct in youth, thick, opaque, a few branches reach the peridium, soon becoming indistinct and translucent. **Odor** faint, pleasant.

Peridium separable from gleba, 200–450 µm thick, usually ca. 250 µm thick, at times appearing two-layered sometimes appearing one-layered; epicutis 100–200 µm thick, of hyaline to pale brown, thin-walled, loosely interwoven hyphae, 3–5 µm in diam, erect hyphal elements projecting from the cutis, clamp connections common; subcutis 75–150 (–250) µm thick, of hyaline, thin-walled, compactly interwoven hyphae, 2–3 µm in diam, occasionally inflated (subglobose cells) up to 10 µm in diam, clamp connections absent.

Trama extremely thick in youth, 200–300 μm thick at maturity, of hyaline, interwoven hyphae (3–10 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline to occasionally pale brown, clavate, 4–8 x 20–22 μm , 4 spored.

Spores minutely verrucose in age, 14–19 x 5–6 μm , fusiform; apex subpapillate to papillate, base subpedicellate. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, less than 1 μm thick, wrinkled and closely adhering to spore wall. **Spore color** in KOH pale brown to pale green singly, brown in mass. (Figs. 54 & 55).

ETYMOLOGY: named for Dr. W. A. Setchell, mycologist at the University of California at Berkeley in the early 1900's.

OTHER REFERENCES: Zeller (1941) pp. 204–206 (as *H. crassum* (Tulasne) Fischer).

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Pseudotsuga menziesii*, *Tsuga heterophylla* and possibly *Quercus*; throughout the year but mainly April through June.

COLLECTIONS EXAMINED: HOLOTYPE: **CALIFORNIA:** Santa Clara Co., Sunset Park, 17–MAY–1903, Gardner 146 (ZT), ISOTYPES (UC, NY).

OTHER COLLECTIONS — CALIFORNIA: Butte Co., Trappe 5805 (OSC). Marin Co., Gardner 260, Parks 2461, Parks 3050 (all UC). Santa Clara Co., Parks 38, Parks 491 (all UC), Parks 148 (NY). San Mateo Co., Parks 2223, Parks 2346, Parks 2347, 1062884 (all UC). Sierra Co., HS 1448 (SFU). Yuba Co., HS 1403, HS 3356 (all SFU). **OREGON:** Benton Co., F 96, F 138, F 162, F 174, F 274, F 502, F 505, F 525, F 537, F 547, F 551, F 556, F 562, F 607, F 610, F 726, F 743, F 750, F 775, F 785, F 841, F 846, F 849, F 850, F 857, F

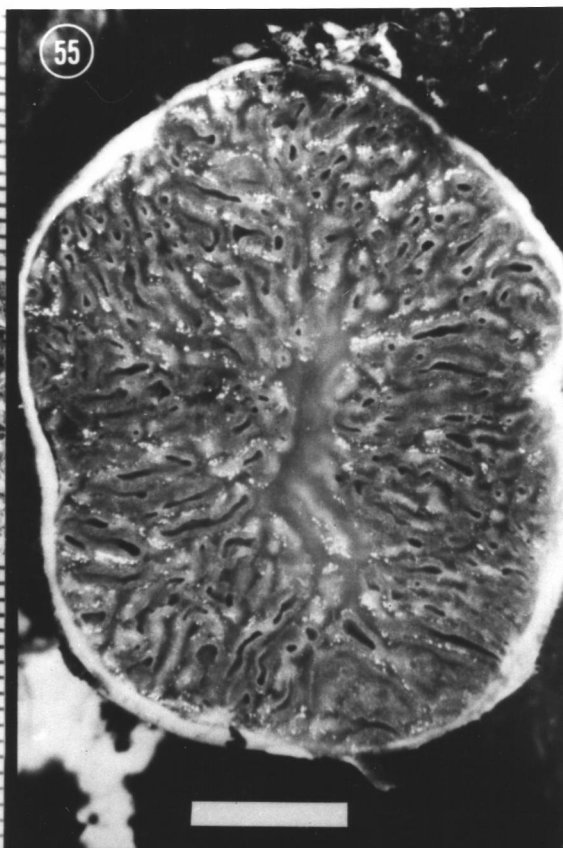
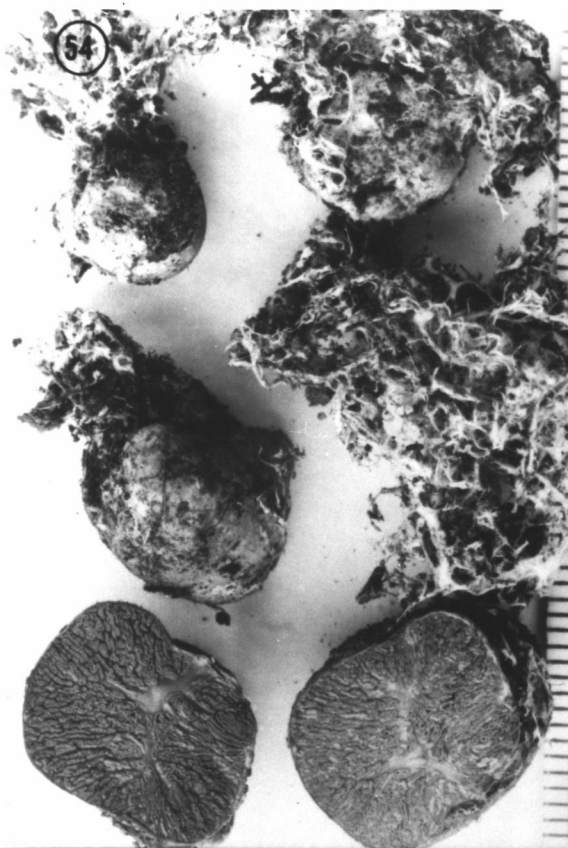
897, F 903, F 934, F 966, F 968, F 978, F 1006 (all MICH), Trappe 1576, Trappe 2653, Trappe 6482, Trappe 6487, Trappe 8865, Stewart 301, Stewart 354, Stewart 503, Stewart 1036, Stewart 1066, Stewart 1074 (all OSC). Clackamas Co., Trappe 9378, Zeller 8259 (all OSC), F 1003 (MICH). Douglas Co., leg Zeller, Zeller 8352 (all NY). Josephine Co., F 1040 (MICH). Lincoln Co., Stewart 323 (OSC). Linn Co., Trappe 8360 (OSC). Polk Co., Trappe 1616 (OSC).

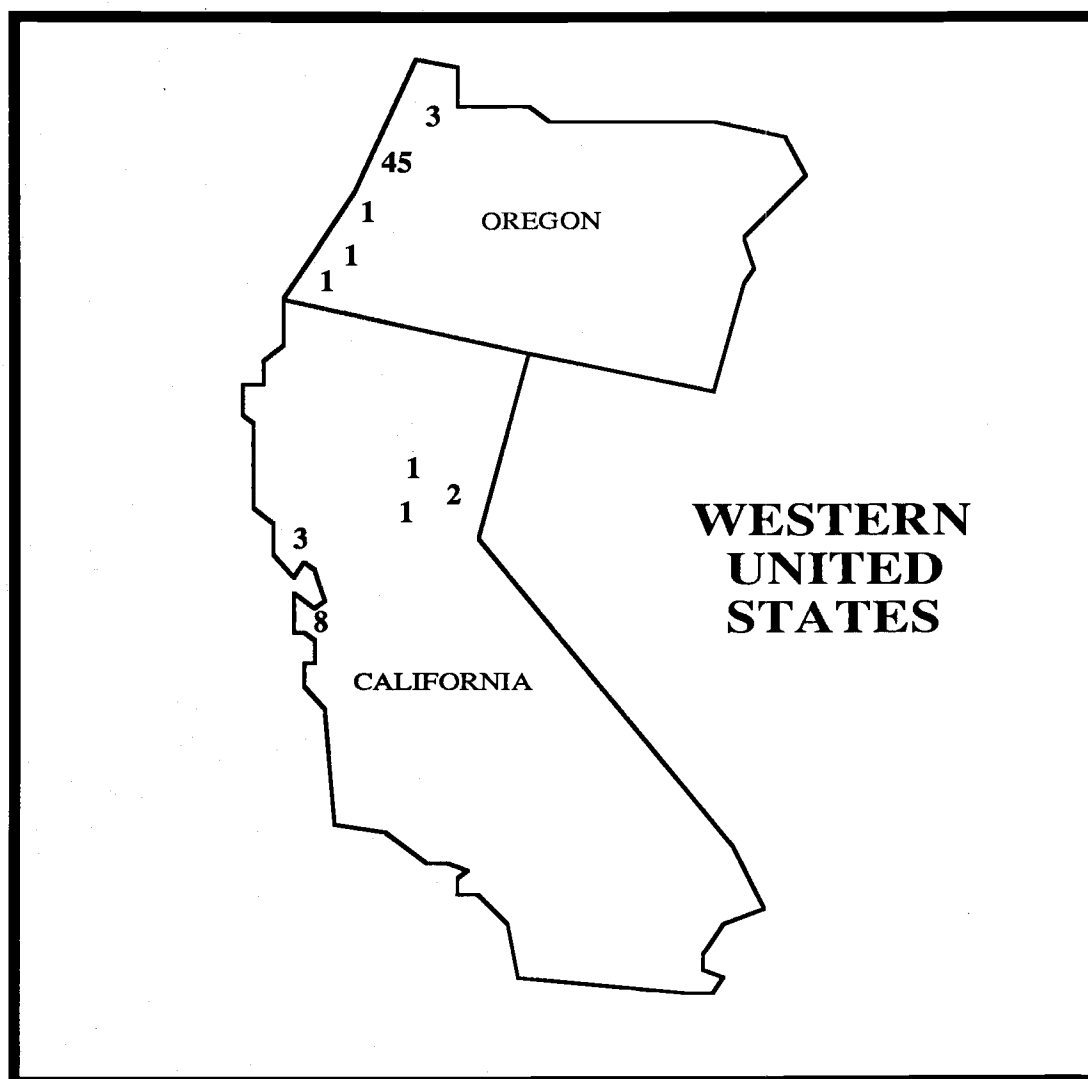
DISCUSSION: *Hysterangium setchellii* abounds in the *Pseudotsuga menziesii* and *Tsuga heterophylla* forests of Oregon and California. Often clustered, it always occurs embedded in a mass of white mycelium and mycelial strands at or below the mineral soil–humus interface. Fogel (1976) and Hunt and Trappe (1987) found *H. setchellii* (listed as *H. crassum* Fischer) fruiting every month of the year, where it produced from 25 to 50% of all hypogeous sporocarps/year and up to 53% of the hypogeous sporocarp biomass/year. Cromack et al. (1979) found that fungal mats of *H. setchellii* (as *H. crassum*) occupied a mean of 9.6% of the upper 10 cm of soil in a 40–65 yr old *Pseudotsuga menziesii* stand. They also report that *H. setchellii* exudes large amounts of oxalic acid which in turn precipitates with Ca to form CaC_2O_4 (oxalate) and suggest that the oxalate can accelerate weathering of primary minerals and clays and function in Fe and Al transport.

Hysterangium setchellii is similar to *H. clathroides*, from which it differs by the thin-walled, loosely interwoven hyphae of the epicutis and thinner, finely verrucose spores, while *H. clathroides* has a peridium of thick-walled, compact hyphae and broadly fusiform, distinctly verrucose spores.

For the most part collections cited by Zeller and Dodge (1929) as *H. crassum* are *H. setchellii*. Zeller and Dodge may have been confused in their species concept of *H. crassum* and *H. setchellii* because of the relative immaturity of the holotype of *H. setchellii*.

Figures 54-57. *Hysterangium*. 54. Sporocarps of *H. setchellii* (Trappe 1576), bottom two sporocarps are cross-sectional view, scale in mm. 55. Close-up of a cross-sectional view of a *H. setchellii* sporocarp (Trappe 9357), notice central columella, bar = 0.5 cm. 56. Light micrograph of *H. strobilus* spores (Couch 7416), bar = 10 μ m. 57. Light micrograph (Nomarski optics) of *H. strobilus* spores (Couch 7435), bar = 10 μ m.





Map 37. Distribution of *Hysterangium setchellii*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium simulans Castellano & Malajczuk, nom. prov.

Basidiomata 0.75–1.5 cm in diam, subglobose to irregularly lobed, mottled white, pale brown and pale orange brown when dried, surface glabrous. **Gleba** bright green to green; locules elongate, empty.

Rhizomorphs numerous, small, attached to base, concolorous with peridium.

Columella inconspicuous, opaque when dried.

Peridium easily separable from gleba except when dried, a single layer 100–150 μm thick, of pale golden brown, thin-walled, more or less uniform, compactly interwoven hyphae, 4–7 (–10) μm in diam, with much adherent crystalline particles, clamp connections inconspicuous and scattered.

Trama 50–150 μm thick, of hyaline, mostly collapsed, interwoven hyphae (1–2 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, elongate to cylindrical, $\pm 30 \times 7\text{--}8 \mu\text{m}$, 6 spored.

Spores smooth, 10–12 (–13) $\times$ 4–4.5, ellipsoid to fusoid; apex acuminate, base truncate. **Spore wall** less than 0.5 μm thick. **Utricle** absent in youth, distinct in age, irregularly inflated up to 2 μm thick. **Spore color** in KOH hyaline to pale green singly, pale green in mass.

ETYMOLOGY: in reference to its “similarity” to *Hysterangium inflatum* Rodway.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Eucalyptus wandoo*.; June through October.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Western Australia, Inglehope, 20 km east of Dwellingup, 25-JUNE-1981, leg N. Malajczuk, H 148 (DAR), ISOTYPE (OSC). **OTHER COLLECTIONS** --

AUSTRALIA: Western Australia, Amphion, H 279 (DAR). Jarrahdale, H 321 (DAR). Manjimup, H 172, H 369 (pro parte), no locality, H 1169, H 2024 (all DAR).

DISCUSSION: *Hysterangium simulans* resembles *H. inflatum* but lacks the distinct uniformly, inflated utricle of *H. inflatum*. *Hysterangium simulans* also resembles *H. olivaceonigrum* but differs in the bruising reaction of its peridium, uniform size of the cells in the peridium, and its paler glebal color.



Map 38. Distribution of *Hysterangium simulans*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Hysterangium strobilus Zeller & Dodge, Ann. Mo. Bot. Gard. 16:90. pl. 1, fig. 6, pl. 3, fig. 11. 1929.

≡ *Hysterangium clathroides* Vittadini sensu Coker & Couch, non Vittadini, Gast. Eastern United States, pp. 17–19. figs. 16 & 105 1928.

Basidiomata 1–1.5 cm in diam when fresh, 1 cm when dry, globose to subglobose, white to flesh, buff or clay colored when dried, brown in alcohol, surface glabrous above, occasionally finely tomentose below with some adhering soil particles. **Gleba** “chocolate brown” (Zeller and Dodge 1929) when fresh, pale olive to dark olive brown when dry; locules irregular to elongate, partially filled. **Rhizomorphs** few to numerous, less than 1 mm in diam, attached at base, concolorous with peridium. **Columella** gelatinous to cartilaginous, distinct, dendroid to subpercurrent, translucent. **Odor** of “strong cheese” (Gardner field notes).

Peridium easily separable from gleba, a single layer 100–200 μm thick, of hyaline to golden brown, thin-walled, compactly interwoven, elongate or irregularly shaped to slightly inflated, swollen tipped hyphae, 2–3 μm in diam near peridial surface and gleba, 6–8 μm in diam in the middle, with some crystalline particles adhering to outer hyphae, clamp connections common.

Trama 50–150 μm thick, of hyaline, mostly collapsed, compactly interwoven hyphae (1–3 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindrical, 30–42 x 5–9 μm , 2 (4) spored.

Spores coarsely verrucose, 12–17 (–18) x 5–6 μm , broadly fusiform; apex acuminate to subpapillate at first, papillate at maturity, base slightly appendaged. **Spore wall** less than 0.5 μm thick. **Utricle** distinct, saccate, up to 2 μm thick, enveloping the entire spore except where attached at base, wrinkled and rough. **Spore color** in KOH hyaline, pale green to pale brown singly, pale brown to golden brown in mass. (Figs. 56 & 57).

ETYMOLOGY: in reference to the columella which resembles cross-sections of cones of *Pinus strobus* when seen in section.

OTHER REFERENCES: Eckblad and Ellingsen (1984) pp. 39-40.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Fagus* and *Quercus* (black); July and August.

COLLECTIONS EXAMINED: HOLOTYPE: **TENNESSEE:** Burbank, leg Thaxter B4H (FH), ISOTYPE (NY). **OTHER COLLECTIONS — IOWA:** Boone Co., Trappe 5285 (OSC). **MISSOURI:** Oregon Co., Gardner 197 (UC & OSC). **NORTH CAROLINA:** Bookers Cr., Couch 7496, Couch 7501 (all NCU & OSC). Bowlings Cr., Couch 7416 (NCU, OSC, PDD 8310). Chapel Hill, Couch 7435 (NCU, FH, OSC).

DISCUSSION: This species occurs only east of the Rockies and is a probable ectomycorrhizal associate of *Fagus*. Specimens from China cited by Eckblad and Ellingsen (1984) could not be located. Coker & Couch (1928) mistakenly interpreted this species as *Hysterangium clathroides* Vitt. Placement in *Hysterangium* is tentative pending examination of fresh specimens.

Hysterangium strobilus is distinguished by its pale brown, broadly fusiform, coarsely verrucose, papillate spores that are enclosed in a thick, wrinkled, saccate utricle which is attached only at the base of the spore.



Map 39. Distribution of *Hysterangium strobilus*. Numbers on the map correspond to the number of collections examined and are placed according to collection locality (by county or city) when available.

Hysterangium thwaitesii Berkeley & Broome, Ann. & Mag. Nat. Hist. II.
2:267. 1848.

≡ *Splanchnomyces thwaitesii* (Berkeley & Broome) Corda, Icones Fung.
p. 42. 1854.

= *Hysterangium rickenii* Soehner, Pilz- und Kräuterfreund 4:190–192.
1921.

= *Hysterangium rickenii* var. *pinetorum* Soehner, Pilz- und Kräuterfreund
4:191. 1921.

Basidiomata up to 2 cm in diam, subglobose to irregularly lobed, white when fresh, sometimes bruising pale red, surface floccose. **Gleba** brownish olive when dried; locules irregular to elongate, filled with spores at maturity. **Rhizomorphs** numerous, less than 0.5 mm in diam, adherent to all sides of sporocarp, concolorous with peridium. **Columella** gelatinous, dendroid, narrow, translucent.

Peridium separable from gleba, especially upon drying, 140–300 μm thick, two-layered; epicutis 70–150 μm thick, of brown, thick-walled, compactly interwoven, gelatinized hyphae 2–3 μm in diam, numerous crystalline particles present, clamp connections absent; subcutis 70–150 μm thick, of hyaline, thin-walled, interwoven hyphae, 5 μm in diam, crystalline particles absent, clamp connections absent.

Trama 20–40 (–90) μm thick, of hyaline, interwoven hyphae (3–4 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** not observed.

Spores smooth, 16–19 x 5–7 μm , fusiform; apex acuminate to subpapillate, base sessile to subpedicellate. **Spore wall** $\pm 0.5 \mu\text{m}$ thick. **Utricle** mostly absent, when present more or less appressed to spore wall, usually not wrinkled. **Spore color** in KOH pale olive singly, yellow brown in mass.

ETYMOLOGY: in honor of Mr. Thwaites, a British collector of fungi.

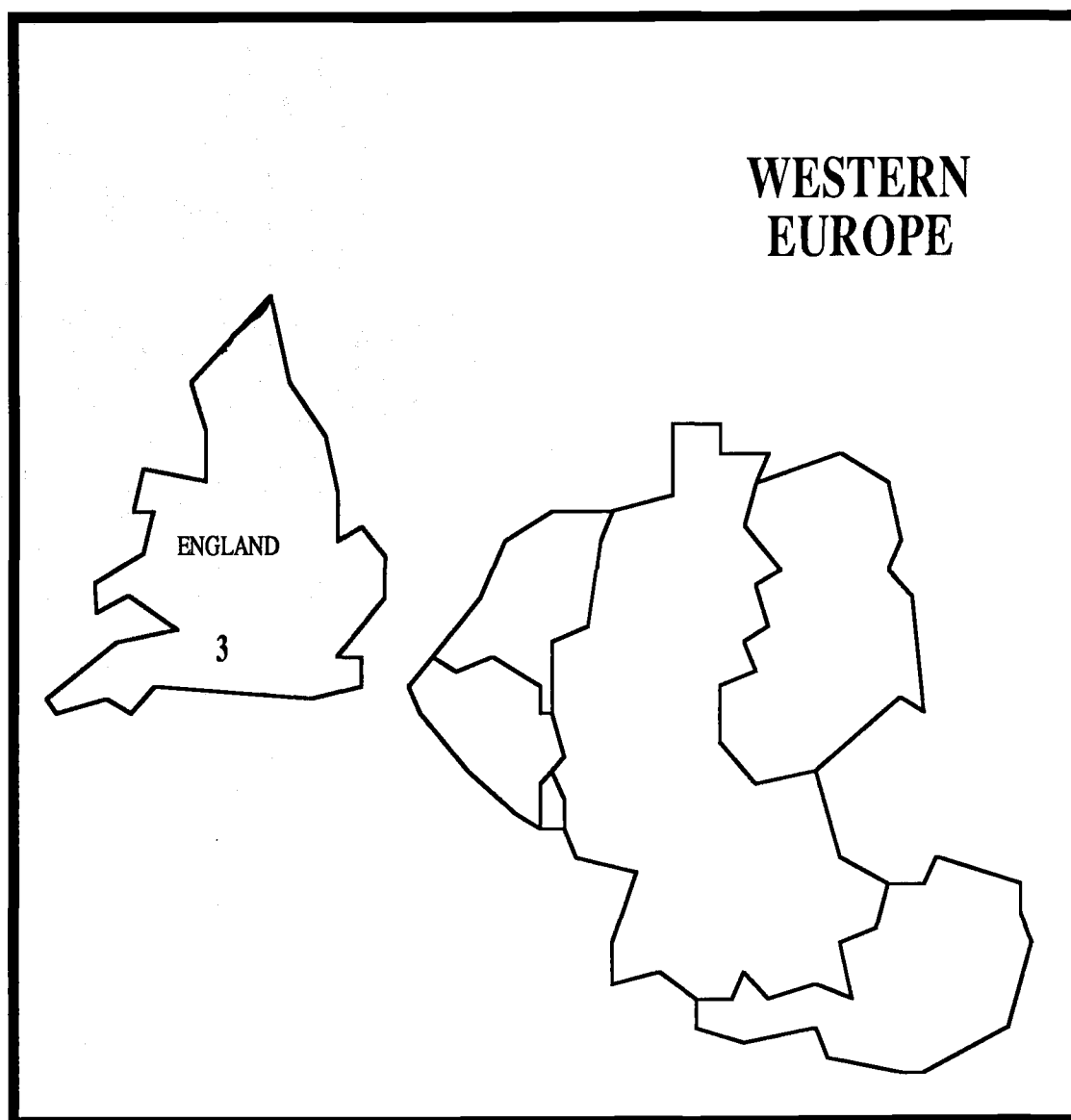
OTHER REFERENCES: Berkeley (1860) p. 294, Cooke (1871) p. 358, Gross et al. (1980) p. 133, Hawker (1954) p. 511, Hesse (1891) p. 105, Masee (1889) p. 38, Rea (1922) p. 25, Soehner (1952) pp 251–256, Tulasne & Tulasne (1851) pp. 82–83, Zeller & Dodge (1929) pp. 116–117.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Fagus*, *Quercus* and *Corylus*; April through November.

COLLECTIONS EXAMINED: HOLOTYPE: **ENGLAND:** Leigh Wood, 2–AUG–1848 (K), ISOTYPE (FH). **OTHER COLLECTIONS — ENGLAND:** Leigh Wood, OCT–1859 (E, K). Somersetshire (H). **GERMANY (WEST):** Munich, Soehner 1429 (Holotype of *Hysterangium rickenii* Soehner), Wolfratshausen Soehner 725 (Holotype of *Hysterangium rickenii* f. *pinetorum* Soehner)

DISCUSSION: *Hysterangium thwaitesii* is similar to *H. nephriticum* but differs on the basis of its thinner epicutis of gelatinized hyphae and its smooth spores which are slightly longer and wider.

Usually found surrounded by abundant white mycelium (Hawker 1954), relatively uncommon.



Map 40. Distribution of *Hysterangium thwaitesii*. Number on the map corresponds to the number of collections examined and is placed according to collection locality (by county or city) when available.

Excluded Taxa

Taxa are arranged alphabetically by species epithet.

Hymenogaster atratus (Rodway) Zeller & Dodge in Dodge & Zeller, Ann. Mo. Bot. Gard. 21:656–657. pl. 18. fig. 4. 1934.

≡ *Hysterangium atratum* Rodway, Proc. & Paps. Roy. Soc. Tasmania 1919:112. 1920.

OTHER REFERENCES: Cunningham (1942) pp. 212–213.

The dark brown, minutely alveolate spores exclude this taxa from *Hysterangium* and place it correctly in the genus *Hymenogaster*.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Mt. Nelson Range, SEPT–1919, leg Rodway 1265 (HO 89538), ISOTYPE (NY).

Hymenogaster australis (Spegazzini) Spegazzini, Rev. Chilena Hist. Natur. 21:171. 1917.

≡ *Hymenogaster australis* (Spegazzini) Horak, Sydowia 17:202–203. figs. 4a, 4b. 1963. comb. illeg.

≡ *Hysterangium australe* Spegazzini, Fungi Argentini 4:237. 1884.

The olive–brown, apiculate, ornamented spores exclude this taxa from *Hysterangium* and correctly place it in *Hymenogaster*. Horak (1963) mistakenly duplicated the combination of this species into *Hymenogaster* that was already published by Spegazzini (1917).

COLLECTIONS EXAMINED: HOLOTYPE: **ARGENTINA:** Buenos Aires, Boca del Riachuelo, 22–MAY–1881, leg Spegazzini (LPS 13340), ISOTYPE (NY).

Protubera burburiana (Rodway) Castellano comb. prov.

≡ *Hysterangium burburianum* Rodway, Proc. & Paps. Roy. Soc.

Tasmania, 1917:109. 1918.

OTHER REFERENCES: Cunningham (1942) p. 213.

This species is characterized by small spores (4–5 x 2 µm), and a thick “tramal” peridium which is divided into sections by radial sutures. The radial sutures are contiguous with, and of similar structure to, the inner subcutis surrounding the gleba and the outer epicutis surrounding the “tramal” peridium. These characters place it in the genus *Protubera*.

Cunningham (1942) mistakenly interpreted this fungus to be a phalloid egg, suggesting that it was close to *Aseroe rubra*.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Launceston, MAY–1916, leg F. E. Burbury, Rodway 1269 (HO 89532), ISOTYPE (FH).

Truncocolumella carneorosea (Horak) Castellano comb. prov.

≡ *Hysterangium carneoroseum* Horak, Sydowia, 17:200–201. figs 2a, 2b. 1963.

Basidiomata 5–22 mm in diam, globose to pear-shaped, frequently depressed at the base, white when young, red, reddish vinaceous or pale purple on bruising at maturity, surface glabrous, KOH yellow, NH₃ red, HCL negative. **Gleba** gray to grayish olive; locules elongate, empty.

Rhizomorphs absent but “rarely with a short stipe–columella up to 3 mm long” (Horak 1963). **Columella** narrow, dendroid, translucent.

Peridium 80–150 μm thick, two-layered; epicutis 50–100 μm , of hyaline, thick-walled, interwoven hyphae, 2–4 μm in diam, interspersed are subspherical to irregularly inflated cells (parenchyma-like), 7–15 μm in diam, subcutis 30–50 μm , of hyaline, gelatinized, parallel hyphae, 3–4 μm in diam, clamp connections absent.

Trama of hyaline, compactly interwoven hyphae (2–3 μm in diam) in a gelatinized matrix, appearing very coarse. **Basidia** hyaline, cylindrical, 15–25 x 5–7 μm , 4 spored.

Spores smooth, 18–20 (–21) x 5–6 μm , ellipsoid to elongate; apex blunt, base sessile to slightly pedicellate. **Spore wall** less than 0.5 μm thick.

Utricle absent or when present wrinkled, loosely adhering to spore. **Spore color** in KOH hyaline to pale green singly, pale green in mass.

ETYMOLOGY: referring to fresh sporocarps which bruise “flesh to pink” when handled.

OTHER REFERENCES: Horak (1980) pp. 16–17.

HABITAT AND SEASON: Hypogeous or epigeous; probable mycorrhizal associates *Nothofagus pumilio*, *N. antarctica*, *N. betuloides* and *N. dombeyi*; March.

COLLECTIONS EXAMINED: HOLOTYPE: **ARGENTINA:** Tierra del Fuego, Valle del Glacier Martial, leg Horak #64/23 (ZT), ISOTYPE (LPS 38204).

DISCUSSION: The boletoid spores and stipe–columella exclude this species from *Hysterangium*. This is the first report of the genus *Truncocolumella* from the southern Hemisphere.

Protubera cerebrina (Lloyd) Castellano comb. prov.

≡ *Rhizopogon cerebrinum* Lloyd, Mycol. Notes, pp. 889–890. fig 1545.

1919.

≡ *Hysterangium cerebrinum* (Lloyd) Lloyd, 1922

This species is characterized by a thick “tramal” peridium divided into sections by radial sutures and by its small spores (3.5 x 2 µm).

This taxa is correctly placed in the genus *Protubera*.

COLLECTIONS EXAMINED: HOLOTYPE: JAPAN: Mikawa Province, 13–OCT–1914, leg Yasuda 262 (BPI), ISOTYPE (NY, FH).

Hysterangium cinereum Harkness, Cal. Acad. Sci. Proc. III. 1:254. pl. 42, fig. 2. 1899.

OTHER REFERENCES: Zeller & Dodge (1929), Saccardo & Sydow in Saccardo (1902).

No TYPE material of this taxa could be located in the Harkness collections at National Fungus Collections (BPI).

Hysterangium darkeri Zeller. Mycologia 31:17–18. Figs. 32, 33. 1939.

This species is excluded from *Hysterangium* based on the presence of layer of persistent sterile locules at sporocarp maturity and the small smooth spores. The generic name *Trappea* was proposed for this and a related species (*Hysterangium phillipsii* Harkness).

Trappea Castellano, gen. prov.

TYPUS: *Hysterangium darkeri* Zeller, Darker 5957 (NY).

Basidiomata hypogeous to epigeous, globose to irregularly lobed, white when fresh and quickly staining pink or brown when exposed. **Peridium** sometimes evanescent, variable in thickness, of interwoven (sometimes inflated) hyphae. **Gleba** green to olive, with scattered to abundant sterile locules contained in a gelatinized layer located just within the true peridium; locules empty. **Columella** distinct, dendroid to sub-percurrent. **Spores** smooth, small, hyaline to pale green, ellipsoid to oblong.

ETYMOLOGY: In honor of Dr. James M. Trappe, mentor and friend, for his studies of hypogeous Basidiomycotina and Ascomycotina.

DISCUSSION: The genus *Trappea* is segregated from *Hysterangium* by its formation of a persistent layer of sterile locules located just within the true peridium and its smooth, bacilloid spores. *Trappea* appears phylogenetically intermediate between the Clathraceae and *Hysterangium*.

Trappea darkeri (Zeller) Castellano, comb. prov.

≡ *Hysterangium darkeri* Zeller. Mycologia 31:17–18, Figs. 32, 33; 1939.

Basidiomata 1–6 cm diam, globose, subglobose, to irregularly lobed; white at first, becoming buff, pale orange, brown to yellowish brown with handling, drying buff to orange brown; surface glabrous to finely pubescent, later polished. **Gleba** gelatinous, olive to olive brown to bright olive green; KOH olive gray to dark brown; locules empty, globose to irregular, 20–60 x

100–300 (–600) μm . **Sterile locules** persistent, numerous, contained in a gelatinized layer (up to 1–2 mm thick) adjacent to the true peridium, lined with large pyriform to subclavate cells, 15–26 x 7–10 μm , clamps present near base, stuffed with hyaline, clamped, thin-walled hyphae. **Rhizomorphs** emergent from base of columella, white, single or clustered and branching, 2 cm (or more) x 1 mm at point of attachment. **Columella** distinct, to 8 mm thick near base, typically dendroid and reaching to 2/3 of the sporocarp, occasionally subpercurrent, grey to translucent blue-gray. **Odor** unpleasant, suggesting stinkhorns or gasoline.

Peridium 35–100 (–200) μm thick, mostly of interwoven to subpericlinal, relatively compact, hyaline to yellow brown, clamped hyphae, 2–4 μm in diam, with scattered crystalline particles and occasional areas with inflated cells 10–15 (–25) μm in diam; FeSO_4 negative, ETOH pale yellow, Melzer's reagent pale brown with a pale yellow margin, KOH pale yellow to golden.

Trama variable in thickness, of clamped, hyaline, closely interwoven capitate hyphae in a gelatinized matrix, 2–6 μm in diam, sometimes inflated up to 17 μm in diam, contiguous with the layer of sterile locules. **Subhymenium** of closely interwoven hyphae 3–4 μm in diam, sometimes inflated up to 15 μm in diam. Crystalline particles scattered within the tramal and subhymenial tissues. **Cystidia** absent. **Basidia** hyaline, irregularly cylindrical to clavate, (11–) 17–28 (–30) x 3–7 μm , clamp connections present near base; (4–) 6 (–8) spored. **Sterigmata** $\pm$ 0.5 μm in length or inconspicuous.

Spores smooth, 4–5 (–5.5) x 2–3 (–3.5) μm , ellipsoid to oblong; apex blunt, base sessile or occasionally with a short pedicel, or with a slightly tapered to truncate point of attachment. **Spore wall** less than 0.5 μm thick. **Utricle**

absent. **Spore color** in KOH hyaline to pale green singly, olive green in mass, in Melzer's reagent hyaline singly, pale olive in mass.

ETYMOLOGY: named for collector of the type, G. D. Darker.

HABIT, HABITAT, AND SEASON: Epigeous, partially exposed to hypogeous; Spain, India and western North America; epigeous or hypogeous, solitary to scattered; India under *Deodar* in November, Spain in June, in western North America, May through November, presumptively mycorrhizal with *Pseudotsuga menziesii*, *Picea engelmannii*, *Pinus contorta*, *P. ponderosa*, *Abies concolor*, *A. grandis*, *A. magnifica*, *A. procera*, or *Tsuga heterophylla*.

COLLECTIONS EXAMINED: HOLOTYPE: **UTAH:** Salt Lake Co., Canyon east of Brighton (Silver Lake), elev. 9600 ft., 3-AUG-1936, leg G. D. Darker 5957 (NY), ISOTYPES (DAOM, FH, NY, OSC). **OTHER COLLECTIONS —**
ALASKA: Chitina, Wells 6 (MICH). **ARIZONA:** Coconino Co., AHF313, AHF402 (all FSLF). Pima Co., F2180 (MICH, OSC). **CALIFORNIA:** Los Angeles Co., leg Benjamin (OSC); Placer Co., Trappe 3900 (OSC). Humboldt Co., Trappe 4024, 4564 (all OSC). Sierra Co., Thiers 44447, leg Teague, leg Saylor & Thiers, leg Fuller, HS 2095, 2931 (all SFU), Trappe 8077, 8078, 9459, 9525 (all OSC), HS 1494, HS 1956, HS 3204, Trappe 8320 (all OSC, SFU). Shasta Co., Cooke 34138, 34185, (all MICH). Tulare Co., Trappe 7418 (OSC). **COLORADO:** Chaffee Co., F182 (MICH). Clear Creek Co., F194 (MICH). Fraser Co., Kerrigan 1256 (SFU). Garfield Co., F 2393 (MICH, OSC). San Miguel Co., F 2162 (MICH, OSC). **IDAHO:** Adams Co., O.K. Miller 24 (MICH, OSC). Bonner Co., Smith 68341, 68706, 74217 (all MICH). Boulder Co., Smith 59083 (MICH). Valley Co., Smith 65178 (MICH, OSC). **MONTANA:** Missoula Co., Trappe 3649 (OSC). **OREGON:** Benton Co., Trappe 622, 3712, 3747 (all

OSC), Zeller 1849, leg Rogers (all NY). Umatilla Co., leg Rogers (NY). Deschutes Co., Trappe 9931 (OSC). Coos Co., Trappe 2694 (OSC). Malheur Co., Trappe 4899 (OSC). Linn Co., Trappe 7415 (OSC). Josephine Co., Trappe 7916 (OSC). Jackson Co., F 1580 (MICH). **SOUTH DAKOTA:** Pennington Co., F 2500, F 2501 (all MICH, OSC). **WASHINGTON:** Pend Oreille Co., Smith 68140, 68209, 68237 (all MICH), Watling 3224 (E). **SPAIN:** Guadalajara, leg Calonge (MA 2745). **INDIA:** Dehra Dun, leg Bakshi (K). **CANADA:** Alberta, Danielson 2167 (OSC).

DISCUSSION: Morphologically *T. darkeri* appears to be closer to *Phallogaster* than *Hysterangium*. The small, smooth spores and the well-developed columella with attached rhizomorphs indicate placement near *Phallogaster saccatus* Morgan. It is usually found at high elevation (3000–9600 ft) in montane forests and is commonly found fruiting above or at the surface of the ground. Calonge (1982) misidentified a collection of *T. darkeri* from Spain as *Hysterangium membranaceum* Vitt. The specimen from Spain also has spores on the large end of the scale and the pyriform cells of the sterile locules are larger than normal (20–40 μm long $\times$ ± 13 μm wide). The specimen from India is parasitized which make peridial characters impossible to distinguish.

Rhizopogon luteolus Fries & Nordholm in Fries, Syst. Mycol. 2:294. 1823.

≡ *Hysterangium duriaeanum* Tulasne in Chantelát, Actes Soc. Linn. de Bordelaise 13:263. 1844.

This species lacks a columella, this character in conjunction with the texture of the gleba and size and character of the spores exclude it from *Hysterangium*. The placement of this taxa in *Rhizopogon* is correct based on this collection.

COLLECTION EXAMINED: HOLOTYPE: of *H. duriaeanum* (PC).

Hysterangium fusisporum Masee & Rodway, Kew Bull. Misc. Info. 1898:127. 1898.

≡ *Hymenogaster fusisporus* ;(Masee & Rodway) Cunningham, Proc. Linn. Soc. New S. Wales 59:168. Sept. 1934.

≡ *Hymenogaster fusisporus* (Masee & Rodway) Zeller & Dodge in Dodge & Zeller, Ann. Mo. Bot. Gard. 21:673. pl. 18, fig. 11. Dec. 1934. comb. illeg.

≡ *Hysterogaster fusisporum* (Masee & Rodway) Zeller & Dodge in Gaumann and Dodge, Comp. Morph. Fungi, pp. 488 & 684. 1928. comb. illeg.

OTHER REFERENCES: Cunningham (1942) p. 50, Zeller & Dodge (1929) p. 121, Beaton, Pegler & Young (1985) pp. 588–590, Saccardo & Sydow in Saccardo (1902) p. 247, Rodway (1912) p. 26, (1924) p. 155.

This species has a yellow brown gleba and smooth, yellow brown, fusiform spores which are distinctly dextrinoid. These characters exclude it from both *Hysterangium* and *Hymenogaster*. The generic name *Hysterogaster* was invalidly published so cannot be accepted here. The unique spore characters of this taxon require establishment of a new genus.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Hobart, Waterworks, 6-JUNE-1896, leg Rodway 276 (HO 89558), ISOTYPES (K, NY, PDD 8265). **OTHER COLLECTIONS — AUSTRALIA:** Tasmania, 89555, 89522, 89554, 89521 (all HO).

Circulocolumella hashashimensis (Ito & Imai) Ito & Imai, Sci. Rep. Yokohama Nat. Univ. Sec. II, 6:4. pl. 1, figs. 1-8. 1957.

≡ *Hysterangium hashashimense* Ito & Imai, Sapporo Nat. Hist. Soc. Trans. 15:10-11. fig. 2. 1937.

≡ *Gelopellis hashashimensis* (Ito & Imai) Zeller, Mycologia 39:284-285. 1947.

≡ *Stalactocolumella hashashimensis* (Ito & Imai) Imai, Bot. Mag. Tokyo, 63:28. 1950. nom. nud.

This species is characterized by small spores ($4 \times 1.5 \mu\text{m}$), a thick uninterrupted "tramal" peridium and a thick percurrent columella. This unusual percurrent columella excludes it from *Gelopellis* from which it is closely related and places it into the closely related, monotypic genus *Circulocolumella*.

COLLECTION EXAMINED: ISOTYPE: **JAPAN:** Bonin Island, Hashasima, 20-NOV-1936, leg Imai (OSC).

Hysterangium hautu Cunningham, Trans. Roy. Soc. New Zeal. 67:409. 1938. nom. nud.

OTHER REFERENCES: Cunningham (1942) pp. 66-67.

This species is characterized by a thick "tramal" peridium which is divided into sections by radial sutures and by its small, smooth spores, $4-5.5 \times 1.5-2 \mu\text{m}$.

This taxon has not been validly published but should be placed in the genus *Protubera*. Specimens cited by Cribb (1958) are not this species and are best placed in a as yet undescribed genus.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW ZEALAND:** Auckland, Waimarino, FEB-1930, Cunningham 8311 (PDD), ISOTYPES (DAOM, K, OSC). **OTHER COLLECTIONS — NEW ZEALAND:** Auckland, 13629, 13628, 6229 (all PDD). Wellington, 45877 (PDD). Glen Esk Valley, 5581 (PDD).

Chondrogaster pachysporus Maire, Bull. Soc. Mycol. France 40:293–316. 1924.

≡ *Hysterangium incarceratum* Malençon, Rev. Mycol. 34:283–286. fig. 2. 1975.

The spores, which are smooth when immature but soon ornamented with irregular to amorphous globules (which measure up to 7–9 μm thick on a side) at maturity, exclude this species from *Hysterangium*.

This species is a synonym of ***Chondrogaster pachysporus*** Maire (1924) which is only found under *Eucalyptus* spp. I was unable to locate the type of *Hysterangium incarceratum* Malençon, but the excellent description and figures of the fungus described by Malençon leaves no doubt as to placement.

COLLECTIONS EXAMINED: (HOLOTYPE of *Chondrogaster pachysporus* Maire): **ALGERIA:** Staouili, under *Cistus*, October and November, Maire 6026 (MPU).

Phallobata alba Cunningham, Trans. Roy. Soc. New Zeal. 56:73. 1926.

≡ *Hysterangium lobatum* Cunningham, Trans. Roy. Soc. New Zeal.
67:408. pl. 7, figs. 1, 2. 1938.

OTHER REFERENCES: Cunningham (1942) p. 66.

The small spores (2–3.5 x 1–1.5 μ m), and prominent sterile lobes of the peridium exclude this species from *Hysterangium*. This taxa belongs in a genus onto itself, and I prefer Cunninghams original placement in *Phallobata*.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW ZEALAND:** Wellington, Whakatikei Forest Reserve, JUNE–1923, leg Meyers & Neill (PDD 1187), ISOTYPES (FH, K, NY, DAOM 116182).

Rhizopogon marchii (Bresadola) Zeller & Dodge, Ann. Mo. Bot. Gard.
16:121–122. 1929.

≡ *Hysterangium marchii* Bresadola, Fung. Trident. 2:99. pl. 211, fig. 2.
1900.

OTHER REFERENCES: Saccardo & Sydow in Saccardo (1902) p. 246,
Bataille (1923) p. 166.

The gleba is ochraceous and lacks a columella. The pale brown spores are 8–11 x 4–5 μ m with a truncate base. This fungus is best placed in *Rhizopogon*.

COLLECTIONS EXAMINED: HOLOTYPE: **ITALY:** Trieste, Verla, SEPT–
1897, leg Bresadola (S), ISOTYPE (M, FH). **OTHER COLLECTIONS —**
GREECE: Maire 921 (MPU). **GERMANY (WEST):** leg Haas (STU).

Hysterangium moselei (Berkeley & Broome) Zeller & Dodge in Dodge & Zeller, Ann. Mo. Bot. Gard. 21:682. 1934.

≡ *Hymenangium moselei* Berkeley & Broome, J. Linnean Soc. 16:40. 1840.

≡ *Hymenogaster moselei* (Berkeley & Broome) De Toni in Saccardo, Syll. Fung. 7:172. 1888.

OTHER REFERENCES: Cunningham (1942) pp. 68–69.

The gleba is friable, ochraceous when fresh, drying pale to moderate brown, the spores are smooth, pale yellow and fusiform. I am uncertain of the best generic placement for it, but it does not belong in *Hysterangium* because of the color and texture of the gleba and unusual characters of the spores.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** New South Wales, Pennant Hills (K), ISOTYPE (FH). **OTHER COLLECTIONS —**
AUSTRALIA: Tasmania 89551, 89525, 89540, 89539, 89549, 89523, 89541 (all HO), Rodway 1270 (NY).

Hysterangium neglectum Masee & Rodway in Masee, Kew Bull. Misc. Info. 1899:181. 1899.

OTHER REFERENCES: Cunningham (1942) p.68, Rodway (1912) p. 27, (1924) p. 156, Saccardo & Sydow in Saccardo (1902) p. 247, Zeller & Dodge (1929) p. 88.

The dark brown gleba and somewhat ovate, smooth, pedicellate, pale brown spores exclude this species from *Hysterangium*. Correct placement of this taxon is uncertain.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Cascades, Old Huon Rd., 5-NOV-1897, leg Rodway 614 (HO 89556), ISOTYPES (K, NY). **OTHER COLLECTIONS — AUSTRALIA:** Tasmania, leg Rodway 644 (HO 89557, NY), leg Rodway (HO 89560).

Hysterangium neocaledonicum Patouillard, Soc. Mycol. France Bull. 31:34. 1915.

OTHER REFERENCES: Trotter in Saccardo (1925) p. 598, Zeller & Dodge (1929) p. 113.

The TYPE material is poorly preserved so it is difficult to determine the generic position of this taxon. Further investigation may reveal it to be conspecific with *Hysterangium salmonaceum* Beaton, Pegler & Young.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW CALEDONIA:** summer-1910, leg LeRat (FH), ISOTYPE (NY).

Rhizopogon niger (Lloyd) Zeller & Dodge, Ann. Mo. Bot. Gard. 16:122. 1929.

≡ *Hysterangium niger* Lloyd, Mycol. Notes 68:1173. fig. 2325. 1923.

OTHER REFERENCES: Verwoerd (1925) p. 163.

The color and texture of the gleba and the characters of the spores correctly place this taxa in the genus *Rhizopogon*.

COLLECTION EXAMINED: ISOTYPE: **SOUTH AFRICA:** Knysna, leg Duthie (NY).

Hysterangium obtusum: see *Hysterangium sclerodermum*.

Hysterangium petri Mattiolo, Malpighia 14:262–263. 1900.

OTHER REFERENCES: Saccardo & Sydow in Saccardo (1902) p. 247, Zeller & Dodge (1929) pp. 119–120.

I was unable to study TYPE material which is undoubtedly located in Mattiolo's herbarium at Torino, Italy (TO).

Hysterangium phillipsii Harkness, Cal. Acad. Sci. Proc. III. 1:255. pl.42, fig. 1. 1899.

The distinct persistent layer of sterile locules at sporocarp maturity and small smooth spores excludes this species from *Hysterangium* and place it in the genus *Trappea* alongside *Trappea darkeri*. Specimens cited by Zeller & Dodge (1929) from Ohio proved to be *Phallogaster saccatus* Morgan (Zeller 1939).

Trappea phillipsii (Harkness) Castellano, comb. prov.

≡ *Hysterangium phillipsii* Harkness, Cal. Acad. Sci. Proc. III. 1:255, pl. 42, fig. 1. 1899.

Basidiomata 1–4 cm diam, subglobose to irregular, white at first but quickly staining livid pink to pale pinkish brown, brown in alcohol; base indented. **Gleba** soft–gelatinous, dark green to bright jade green; locules minute, empty. **Sterile locules** contained in a gelatinized layer (up to 500 µm thick) adjacent to the true peridium, persistent, few to abundant, sometimes contiguous with the peridium, lined with large subclavate cells, 15–26 x 7–10 µm, clamps present near base, stuffed with hyaline, clamped, thin-walled hyphae. **Rhizomorphs** white, when fresh, staining pink when handled,

numerous, branched, attached at base, $\pm$ 1 mm thick. **Columella** distinct, translucent, dendroid branching at middle of sporocarp. **Odor** unpleasant, of gasoline.

Peridium 100–350 μ m thick, of hyaline, clamped, interwoven hyphae, 3–5 μ m in diam, near the surface the hyphae inflated up to 25 μ m in diam, FeSO₄ greenish blue grey.

Trama 30–50 μ m thick, of hyaline, interwoven hyphae in a gelatinized matrix, 1–3 μ m in diam. **Subhymenium** of interwoven hyphae, 2–4 μ m in diam, with some cells inflated up to 6 x 9 μ m. **Cystidia** absent. **Basidia** cylindric, 10–20 x 2–5 μ m; 6 (–8) spored. **Sterigmata** absent.

Spores subsessile, smooth, 3–6 x 1–2 (–2.5) μ m, oblong; in KOH hyaline singly, pale green in mass, in Melzer's reagent hyaline singly, pale olive in mass.

ETYMOLOGY: Latin, *phillipsii*, in honor of the collector of the type, C. L. Phillips.

HABIT, HABITAT, AND SEASON: usually solitary on or in rotten wood, presumptively mycorrhizal with *Pseudotsuga menziesii*, *Pinus ponderosa*, *Abies concolor*, *Abies magnifica* var. *shastensis* and possibly *Quercus* spp.; January to September.

COLLECTIONS EXAMINED: HOLOTYPE: **CALIFORNIA:** Placer Co., Wire Bridge, JAN–1899, leg C. L. Phillips, Harkness 234 (BPI). **OTHER COLLECTIONS —CALIFORNIA:** El Dorado Co., Trappe 8427 (OSC). Humboldt Co., Parks 4124 (UC). Los Angeles Co., CAHF 35 (OSC, FSLF). Marin Co., Parks 3046, 3051 (all UC). San Bernardino Co., Trappe 6734 (OSC), CAHF 22 (OSC, FSLF). Santa Clara Co., Gilkey 1064 (OSC). Shasta Co.,

Cooke 13263, 15679 (all NY). Yuba Co., Thiers 28931 (OSC, SFU). **NEVADA:** Clark Co., F 2767 (OSC, MICH). **OREGON:** Deschutes Co., Stewart 60 (OSC).

DISCUSSION: Specimens cited by Zeller & Dodge (1929) from Ohio proved to be *Phalloascus saccatus* Morgan (Zeller 1939). This species is not as frequently encountered as *T. darkeri* and is easily distinguished from it in the field by the distinct pink staining reaction of the peridium when bruised, the peridium of *T. darkeri* stains brown when bruised. *Trappea phillipsii* is found at 2000–8000 ft in elevation.

Hysterangium pseudoacaciae (Fries) De Toni in Saccardo, Syll. Fung. 7:159. 1888.

≡ *Mylitta pseudoacaciae* Fries, Syst. Orb. Veg. 1:154. 1825.

The collection cited below are legume root nodules. Type material could not be located, but Fries description fits the concept of legume nodules.

COLLECTIONS EXAMINED: ITALY: Piemonte, leg Cesati (FH, RO, MEISE).

Hysterangium pseudostoloniferum Svrcek in Pilát, Flora CSR, Rada B, Svazek I, pp. 100 & 720.

A thorough search of the herbarium at Prague could not locate any collections identified as this taxon.

Hysterangium pumilum Rodway, Paps. & Proc. Roy. Soc. Tasmania 1917:109. 1919.

≡ *Hysterangium pumilum* Rodway in Zeller & Dodge, Ann. Mo. Bot. Gard. 16: 115–116. pl. 1, fig. 3, pl. 3, fig. 25. 1929.

OTHER REFERENCES: Rodway (1924) p. 155, Rodway in Trotter in Saccardo (1928) p. 1324.

The trama which is composed of loosely interwoven, nongelatinized hyphae exclude this species from *Hysterangium*. Generic placement is uncertain, but based on spore characters this fungus is possibly allied to the Boletales.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Tasman's Peninsula, JUNE–1916, Rodway 785 (HO 89533), ISOTYPES (HO 89559, K, OSC, NY).

Truncocolumella purpurea (Zeller & Dodge) Castellano comb. prov.

≡ *Hysterangium purpureum* Zeller & Dodge, Ann. Mo. Bot. Gard. 16:110–111. pl. 1, fig. 5, pl. 3, fig. 21. 1929.

Basidiomata up to 2 cm in diam, globose, subglobose to irregular, when fresh bright, dark lavender to purplish red at maturity, becoming dark dull red on bruising, grayish olive to pale olive when dry except in crevasses which are dull lavender, surface smooth except in protected areas which are finely pubescent. **Gleba** purplish brown to almost black at maturity (Halling 1981); locules elongate, partially filled. **Rhizomorphs** numerous, small, attached to reduced stipe. **Columella** gelatinous, distinct, dendroid, translucent continuous with a reduced stipe which is up to 4 mm long.

Peridium not easily separable from gleba, 500–900 μm thick, two layered; epicutis 300–400 μm thick (70–80 μm when collapsed), of hyaline, thin-walled, spherical cells (parenchyma-like), 10–15 μm in diam, clamp connections absent, subcutis 500 μm thick, of hyaline, thin-walled, agglutinated, compactly interwoven hyphae, 6–8 μm in diam, occasionally 15–20 μm in diam, rarely 60–70 μm in diam, the larger cells are near the epicutis, clamp connections absent.

Trama 50–110 μm thick, of hyaline, interwoven hyphae (2–3 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** hyaline, cylindrical, 35–40 x 6–7 μm , 4 (5) spored.

Spores smooth, 15–18 (–19) x 5–6 μm , fusiform, elliptic to irregular, commonly asymmetrical; apex acuminate, base sessile to appendiculate. **Spore wall** less than 0.5 μm thick. **Utricle** absent. **Spore color** in KOH hyaline to pale green or brown singly, pale yellowish brown in mass.

ETYMOLOGY: referring to the bright lavender color of the fresh peridium.

OTHER REFERENCES: Halling (1981) p. 866, Horak (1980) pp. 14–16.

HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Nothofagus* and *Cryptocarya alba*; February and April.

COLLECTIONS EXAMINED: LECTOTYPE: **CHILE:** Puntas Arenas, 24–FEB–1906, Thaxter 4716 dried material (NY), ISOTYPE (wet material FH, NY, dried material FH). **OTHER COLLECTIONS — CHILE:** Concepcion, Garrido 418–A (OSC).

DISCUSSION: The asymmetrical boletoid spores and short stipe-columella place this species in *Truncocolumella*. This is the second of three *Truncocolumella* species from South America which were previously assigned to the genus *Hysterangium*. Horak (1980) synonymized *Truncocolumella violacea* (as *Hysterangium violaceum*) with *T. purpurea* (as *Hysterangium purpureum*) without studying the type of the later. I regard them as distinct species in that *T. purpurea* has thicker dimensions of both the peridial layers and subcuticular tissues, and wider, non-pedicellate spores.

It fruits "by the dozen growing in groups 2–3 to 20" (Thaxter's field notes cited in Halling 1981).

Rhizopogon rubescens (Tulasne & Tulasne) Tulasne & Tulasne, Giorn. Bot. Ital. 2:58. 1844.

≡ *Hysterangium rubescens* Tulasne & Tulasne, Ann. Sci. Nat. II. 19:375. 1843.

The color and texture of the gleba and the characters of the spores indicate placement of this taxon in the genus *Rhizopogon*.

COLLECTIONS EXAMINED: LECTOTYPE: **FRANCE:** La Teste de Buch, OCT–1843, leg Tulasne (K).

Hysterangium sclerodermum (Cooke) Cunningham, Proc. Linnean Soc. New S. Wales 59:165. 1934.

≡ *Mesophellia scleroderma* Cooke, Grevillea 14:11. 1885.

= *Rhizopogon violaceus* Cooke & Massee in Cooke, Grevillea 21:1. 1892.

≡ *Gallacea scleroderma* (Cooke) Lloyd, Lycoper. Austral. p. 38. 1905.

= *Hysterangium obtusum* Rodway, Proc. Roy. Soc. Tasmania 1919:112. 1920.

= *Gallacea violacea* (Cooke & Massee in Cooke) Lloyd, Mycol. Notes p. 1201. 1923.

= *Hymenogaster pachydermis* Zeller & Dodge in Dodge & Zeller, Ann. Mo. Bot. Gard. 21:637. 1934.

This taxon has the glebal and spore characters of *Claustula*. I am uncertain as its proper placement at this time.

COLLECTIONS EXAMINED: HOLOTYPE: **NEW ZEALAND:** leg Reader 50 (K). **OTHER COLLECTIONS — NEW ZEALAND:** (HOLOTYPE of *Rhizopogon violaceus*) leg Kirk 382 (K). (ISOTYPE of *Hymenogaster pachydermis* Zeller & Dodge) South Island, Nelson, Dun Mtn. Leg J. C. Neill (NY). **AUSTRALIA:** (HOLOTYPE of *Hysterangium obtusum*) Tasmania, Mt. Nelson, Rodway 1264 (HO 89530), ISOTYPE (NY).

Hysterangium subglobosum Cribb, Paps. Dept. Bot. Univ. Queensland 3:157. fig. 8. 1958.

The dark brown gleba and spores which are small (4–4.5 x 3–4 µm), subglobose to obovate and narrowly pedicellate exclude this taxa from *Hysterangium*. The meager amount of material in the type collection does not allow generic placement.

COLLECTION EXAMINED: HOLOTYPE: AUSTRALIA: Queensland, Mudgeeraba, 7-APR-1955, leg Cribb (DAR 21624).

Gelopellis thaxteri (Zeller & Dodge) Zeller, Mycologia 31:22. 1939.

≡ *Hysterangium thaxteri* Zeller & Dodge, Ann. Mo. Bot. Gard. 16:114-115. pl. 2, fig. 5, pl. 3, fig. 28. 1929.

The small spores (3-4 x 1.5-2 μ m) and thick (> 1.5 μ m), uninterrupted highly gelatinized peridium exclude this species from *Hysterangium*. Study of a portion of the type confirms its correct placement in the genus *Gelopellis*.

COLLECTIONS EXAMINED: ISOTYPE: ARGENTINA: Buenos Aires, leg Thaxter (NY).

Truncocolumella violacea (Horak) Castellano comb. prov.

≡ *Hysterangium violaceum* Horak, Sydowia 17:198-200. fig 1. 1963.

Basidiomata 0.8-1.5 (-2) cm in diam, globose to ovoid or depressed, indented at base, violet at maturity, bruising lilac purple to lavender, reddish brown or pale brown with dark violet areas when dried, surface tomentose, no adherent soil particles. **Gleba** olive when young, dark olive to dark olive brown when dried; locules irregular to elongate, empty. **Rhizomorphs** not seen. **Columella** distinct, dendroid, arising from a sterile base, white to brown when dried. **Odor** sour to indistinct.

Peridium not separable from gleba, 500–800 μm thick, two-layered; epicutis 300–500 μm thick, of pale red, thin-walled, compact, spherical to polyhedral, inflated cells, 15–40 (–60) μm in diam; clamp connections absent, subcutis 200–300 μm thick, of hyaline, thin-walled, densely compact, interwoven, bead-like hyphae, 2–4 μm in diam, clamp connections absent.

Trama 30–125 μm thick, of hyaline, occasionally collapsed, elongate, interwoven to subparallel hyphae (2–3 μm in diam) in a gelatinized matrix, clamp connections absent. **Basidia** not observed.

Spores smooth, commonly asymmetrical, (12–) 16–18 (–20) $\times$ 4–5 (–6) μm , mostly elongate, occasionally ellipsoid or irregular; apex acuminate, base pedicellate. **Spore wall** less than 0.5 μm thick. **Utricle** absent. **Spore color** in KOH pale green singly, green in mass.

ETYMOLOGY: Latin, in reference to the “violet” color of the fresh peridium.

OTHER REFERENCES: Horak (1980) pp. 14–16.

HABIT, HABITAT AND SEASON: Hypogeous; probable mycorrhizal associates *Nothofagus pumilio*, *N. betuloides*, *N. dombeyi* and *Fuchsia magellanica*; May.

COLLECTIONS EXAMINED: HOLOTYPE: **ARGENTINA:** Patagonia, Province Rio Negro, 12–MAY–1962, leg Horak 64/24–483 (ZT), ISOTYPE (LPS 38203).

DISCUSSION: The asymmetrical, smooth spores and distinct columella place this species in *Truncocolumella*. This is the third of three species of *Truncocolumella* from South America originally described as *Hysterangium* species.

Hymenogaster viscidus (Massee & Rodway) Dodge & Zeller, Ann. Mo. Bot. Gard. 21:642. pl. 18, fig. 38. 1934.

≡ *Hysterangium viscidum* Massee & Rodway in Massee, Kew Bull. Misc. Info. 1898:127. 1898.

OTHER REFERENCES: Cunningham (1942) pp. 50–51, Rodway (1912) pp. 27–28, (1924) p. 155, Saccardo & Sydow in Saccardo (1902) p. 246, Zeller & Dodge (1929) p. 120.

This species is excluded from *Hysterangium* on the basis of its dark brown gleba and subglobose, areolate spores. It is correctly placed in *Hymenogaster*.

COLLECTIONS EXAMINED: HOLOTYPE: **AUSTRALIA:** Tasmania, Rodway 270 (HO 89552), ISOTYPE (K). **OTHER COLLECTIONS — AUSTRALIA:** South Australia, 89546 (HO).

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