AN ABSTRACT OF THE DISSERTATION OF

Admir J. Giachini for the degree of Doctor of Philosophy in Forest Science presented on May 5, 2004.
Title: Systematics, Phylogeny, and Ecology of *Gomphus sensu lato*.

Abstract approved: Signature redacted for privacy.

James M. Trappe

The nomenclatural history of *Gomphus sensu lato* began with Persoon in 1797. Over 200 years species of *Gomphus sensu lato* have been variously classified also under *Cantharellus, Craterellus, Chloroneuron, Chlorophyllum, Gloeocantharellus, Nevrophyllum,* and *Turbinellus.*

Species of *Gomphus sensu lato* have been historically characterized as having aboveground fruiting, fleshy basidiomata with funnel- or fan-shaped pilei. They are mainly known from North America and Europe but also in parts of Asia, Australasia, Africa, and Central and South America.

Parsimony and maximum likelihood (MCMC) analyses of the nuclear large subunit ribosomal DNA (nuc-25S-rDNA), mitochondrial small subunit ribosomal DNA (mit-12S-rDNA), and mitochondrial *atp*6 DNA (mit-*atp*6-DNA) combined sequences revealed *Gomphus sensu lato* to be non-monophyletic. This resulted in the recombination of its species into 4 genera: *Gomphus sensu stricto, Gloeocantharellus, Phaeoclavulina,* and *Turbinellus.*

Gomphus sensu stricto currently contains only 3 species: *G. brunneus, G. clavatus*, and *G. crassipes*. *Gloeocantharellus* is composed of 10 agaricoid-gomphoid species. *Phaeoclavulina* has 41 species: 6 formerly in *Gomphus sensu lato* and 35 previously assigned to *Ramaria* subgenus *Echinoramaria*. *Turbinellus* has 5 species distributed mainly in the northern hemisphere.

Species of *Gomphus sensu lato* have long been recognized as close related to other members of the Gomphales and to the orders Gautieriales, Hysterangiales, and Phallales and the families Geastraceae and Sphaerobolaceae. Phylogenetic analyses of the three combined loci described above suggested the cantharelloid-gomphoid morphology, the lignicolous substrate affinity, and the presence of clamp connections as ancestral for the order Gomphales. These features were independently gained and lost several times during the evolution of these fungi.

Ecological studies of *G. clavatus* and *T. floccosus* indicate some ecosystem components are directly associated with their distribution in the forests of the Pacific northwestern USA. *Gomphus clavatus* is related to volume of coarse woody debris (CWD). In other words, the probability (odds) of its occurrence increases with the volume of CWD. *Turbinellus floccosus*, on the other hand, is related to both volume of well-decayed CWD and stand age. The older the stand and the higher the volume of CWD in late stages of decomposition, the higher the probability (odds) of finding it.

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Systematics, Phylogeny, and Ecology of *Gomphus sensu lato*

by

Admir J. Giachini

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...systematics fundamentally means any investigation of relations between natural things and natural processes insofar as they have the character of conformity to law.

W. Hennig 1966

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SYSTEMATICS, PHYLOGENY, AND ECOLOGY OF *GOMPHUS SENSU LATO*

CHAPTER 1

General Introduction

The epigeous basidiomycete genus *Gomphus sensu lato* is a member of the family Gomphaceae in the order Gomphales, which also includes *Beenakia, Clavariadelphus, Gautieria, Gloeocantharellus, Kavinia, Lentaria, Ramaria,* and *Ramaricium* (Donk 1964, Humpert *et al.* 2001, Pine *et al.* 1999, Villegas *et al.* 1999). It's species range considerably in shape, from pileate, to merismatoid (composed of several pilei), or ramarioid (multibranched like a coral). Pileate species may be single (mesopodal) or branched (pleuropodal), funnel-shaped (infundibuliform) or fan-shaped (flabelliform), and glabrous to scaly. It's hymenia is composed of folded decurrent hymenial gills. Their spores may be ellipsoid to obovoid or lacrimoid, echinulate to verrucose, subreticulate or reticulate, inamyloid and generally cyanophilic. The tissue contains gleoplerous hyphae and clamp connections. Some species have rhizomorphs with conspicuous, generally ampulliform hyphae. For the most part, this dissertation is based upon specimens in the 18th and 19th centuries in many different parts of the world and deposited in over 30 herbaria worldwide.

Certain species of *Gomphus sensu lato* have long been among the many taxa of fungi of concern to land managers (especially public) and mycologists in the Pacific northwestern USA (PNW). Publication of the Forest Management and Assessment Team (USDA and USDI 1994ab) report (Record of Decision – ROD) on the habitat requirements for the northern spotted owl led to expanded interest in many other organisms as well, the fungi included. The document was written to

manage habitat for scarce and endangered species of animals, plants, and fungi linked to mature and old growth forests of the Pacific northwestern USA. It included *Gomphus sensu lato* as a "genus of concern" due to its apparent scarcity. It further stated that general surveys ought to be done for the species of the genus before the approval of any forest management activity on federally- and state-owned properties.

The ROD document originally listed 4 of the 35 species described for *Gomphus sensu lato* (*G. bonarii, G. clavatus; G. floccosus* and *G. kauffmanii*). Several species of *Gomphus sensu lato* are hard to differentiate from each other on morphology alone. Petersen (1971a) and Corner (1950, 1966), who described most species in the genus, employed morphological, ecological, and geographic aspects to support their species descriptions. My studies were designed initially to (1) provide a more reliable classification of this group, (2) improve understanding of its evolutionary links to other members of the Gomphales, and (3) clarify the distribution and occurrence of the species throughout the PNW. This required: (1) review the taxonomic/systematics of described species of *Gomphus sensu lato*, (2) verification of the evolutionary relationships within *Gomphus sensu lato* and among other members of the order Gomphales, and (3) exploration of the relationship of ROD listed species to various habitat characteristics. These objectives were pursued by employing specialized literature and advanced molecular tools, such as DNA sequencing, for intra- and inter-specific variation and evolutionary relationships of members of the orders Gomphales, Phallales, and Hysterangiales. This inexorably led to taxonomic and phylogenetic studies of these fungi worldwide. Ecological related objectives were pursued by conducting several field trips to forested areas of Oregon, Washington, and northern California to collect data on the species distribution and habitat.

Many people contributed to this study directly or indirectly by providing specimens or information regarding the site of occurrence for species targeted in the ROD document. The new collections made during this study are deposited in the OSC herbarium in Corvallis, Oregon.

This dissertation consists of 9 chapters. Chapter 2 provides an overview of the taxonomic history of *Gomphus sensu lato*. The early mycological history of *Gomphus sensu lato* is discussed and linked with the first collections by naturalists from 1790 to 1900. These were described by mycologists such as C.H. Persoon, E.M. Fries, M.J. Berkeley, M.A. Curtis, N.T. Patouillard, and C.H. Peck. In the 20th century, influential mycologists such as R.H. Petersen and E.J.H. Corner became increasingly involved with the taxonomy and systematics of the group. Corner (1966, 1970) published, among others things, an article and a monograph on cantharelloid fungi, describing many new species. Petersen (1971a) compiled a comprehensive manuscript on the species of *Gomphus* and *Gloeocantharellus* of North America, addressing many described species and describing additional ones. Both Corner (1950, 1966) and Petersen (1967, 1971b) provided innumerable insightful discussions on the placement of *Gomphus sensu lato* within the family Gomphaceae, suggesting evolutionary relationships among members of the genera *Ramaria, Clavariadelphus, Gloeocantharellus,* and *Gomphus sensu lato*. Many others have contributed to build a long list of *Gomphus* related studies, which altogether provide a solid taxonomic base for this group. Also in chapter 2 I propose a new classification for the species of *Gomphus sensu lato*, restricting *Gomphus sensu stricto* to selected species and accommodate the rest into *Gloeocantharellus*, and the resurrected *Phaeoclavulina* and *Turbinellus*.

Full descriptions of *Gomphus sensu stricto* and its respective species are presented in chapter 3. Here lies the core history for the genus, long ago described and center of many past disputed. *Gomphus sensu stricto* is recognized to accommodate 3 species: *G. brunneus*, *G. clavatus* (a ROD species), and *G. crassipes*.

Chapter 4 presents the morphological and molecular aspects of the resurrected genus *Turbinellus*. The genus and its 5 species are described, with a dichotomous key to species. *Turbinellus* contains two species of concern for management of public lands under federal guidance in the PNW of the USA: *T. floccosus* (*G. bonarii* and *G. floccosus*) and *T. kauffmanii*. This genus has a

complicated taxonomic history, with several subspecies, forms and varieties that needed further nomenclature attention.

Chapter 5 is dedicated to the genus *Gloeocantharellus*. A few species previously belonging to *Gomphus sensu lato* have been transferred to this genus based on morphological and molecular data. The genus is poorly known and much work needs to be done in all its aspects in the near future. *Gloeocantharellus*, together with *Gomphus sensu stricto*, make up the ancestral lineage from where *Turbinellus*, *Gautieria*, and *Ramaria* subgenera *Laeticolora* and *Ramaria* originates. More details of this placement are given in chapter 7.

Chapter 6 portrays the genus *Phaeoclavulina*, one of the larger genera of the Gomphaceae. This chapter contains a description and general discussion of its morphology and habitat aspects. This chapter also provides descriptions and a dichotomous key for its 41 described species.

Chapter 7 discusses on the evolutionary relationships of genera within the Gomphales and its close relationship to the Geastrales, Phallales, and Hysterangiales as shown by Hibbett *et al.* 1997, Humpert *et al.* 2001, Maire 1902, 1914, Petersen 1967, 1971b, Pine *et al.* 1999. Until now, however, no work has been done which included a large number of representatives from a wide number of genera. The results suggest a ramarioid morphology as ancestral for the Gomphales, corroborating results obtained by others (Humpert *et al.* 2001). Among independently derived basidiomata shapes are club, gomphoid, odontoid, resupinate, and sequestrate. This chapter also presents the future directions of research to unveil additional knowledge on the evolution of these related fungi.

Chapter 8 gives an overview on the ecological aspects and the relationships of stand age and coarse woody debris to *Gomphus clavatus* and *Turbinellus floccosus* in the PNW of the USA. It gives insights on the distribution, relative rarity, and fruiting patterns for those species.

Chapter 9 synthesizes results from all chapters and concludes the overall study.

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CHAPTER 2

Systematics of the Gomphales: The Genus *Gomphus* Pers. *Sensu Lato*

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ABSTRACT

The taxonomy of *Gomphus sensu lato* (Gomphales) has proven difficult because of the few reliable characters available for classification. Species of *Gomphus sensu lato* have been classified under *Cantharellus*, *Craterellus, Chloroneuron, Chlorophyllum, Gloeocantharellus, Nevrophyllum,* and *Turbinellus.* Morphology and molecular data were used in this study to provide a natural classification for the species of *Gomphus sensu lato.* In addition to macro- and microscopic characters, three genetic regions were examined: nuclear large subunit ribosomal DNA (nuc-25S-rDNA), mitochondrial small subunit ribosomal DNA (mit-12S-rDNA), and mitochondrial *atp*6 DNA (mit-*atp*6-DNA). Parsimony and maximum likelihood (MC^3) analyses of the 3 combined loci indicated *Gomphus sensu lato* to be non-monophyletic, which led to the recombination of its species into 4 genera: *Gomphus sensu stricto, Gloeocantharellus, Phaeoclavulina,* and *Turbinellus. Gomphus sensu stricto* have basidiomata with funnel- to fan-shaped pilei, presence of clamp connections, and verrucose spores. *Gloeocantharellus* is characterized by agaricoid-gomphoid basidiomata, presence or absence of clamp connections, and echinulate or verrucose spores. The genus *Phaeoclavulina* encompasses species of *Gomphus sensu lato* plus species of *Ramaria* subgenus *Echinoramaria.* It includes species with ramarioid, or unipileate to merismatoid basidiomata. The non-ramarioid species of *Phaeoclavulina* have funnel- to fan-shaped pilei. All species of the genus possess clamp connections and echinulate, verrucose, subreticulate or reticulate spores. Scaly, funnel- to fan-shaped pilei, verrucose spores and lack of clamp connections characterize *Turbinellus.* In addition to an inter-generic classification for *Gomphus sensu lato*, this study also focused on resolving intra-generic species boundaries within this diverse group and identifying reliable characters for species identification.

INTRODUCTION

Taxonomy is the oldest, broadest, and most basic of sciences. Taxonomy is the science of hierarchically classifying organisms into species and logical groups of species. It may also be defined as the study and classification of variation among organisms, its causes, consequences, and patterns. Species are grouped into higher-level taxa based primarily on apparent resemblance (homology) or by the possession of shared traits (pomorphy). With the widespread acceptance of the theory of evolution, more attempts have been made to group species in accordance with their evolutionary history.

Nomenclature is the process of providing scientific names to taxonomic groups of organisms. The purpose of naming a taxonomic group is not to indicate its characters or history, but to supply a means of referring to it and to indicate its taxonomic rank (Greuter *et al.* 2000). To be validly published, a name must follow the requirements of a "Code", generally specific to a group of organisms that explicitly define the rules for correct usage of names.

Systematic biology, on the other hand, is the study of the historical relationships of groups of organisms (**http://www.biosci.ohio-state.edu/~jfreuden/system.htm**). In other words, it is the recognition and understanding of evolution and biodiversity. Systematics includes the processes of identifying (taxonomy) the basic systematic unit (the species), discovering the patterns of relationships of species at successively higher levels (phylogenetic analysis), building classifications based on these patterns, naming appropriate taxa (nomenclature), and the application of this pattern of knowledge to studying changes in organismal features through time. It also includes the building and maintenance of biodiversity collections, upon which all products of systematic studies are based.

Gomphus sensu lato

Gomphus sensu lato is a genus of aboveground fruiting basidiomycetes in the family Gomphaceae, order Gomphales, which produces fleshy basidiomata that can have funnel-shaped (also referred to as mesopodal or infundibuliform) or fan-shaped (also referred to as flabelliform or pleuropodal) pilei. The genus was originally described by Persoon (Persoon 1797a) and over the past 200 years has undergone several taxonomic and nomenclatural changes. Currently *Gomphus* has 35 described species (Table 2.1). It is close related to other members of the Gomphales and somewhat related to the Phallales, Hysterangiales, Gautieriales, and the families Geastraceae and Sphaerobolaceae (Giachini *et al.*, *in preparation*).

Gomphus sensu lato is known mainly from North America and Europe but also occurs in parts of Australasia, Africa, and Central and South America. The genus associates with a variety of forest types, from conifer and deciduous in North America and Europe to broad-leaf tropical and subtropical elsewhere.

Two species, *G. clavatus* (Pers.) Gray and *G. floccosus* (Schwein.) Singer have been reported as ectomycorrhizal with conifers throughout their range. Masui (1926, 1927) first verified the association of *Cantharellus floccosus* Schwein. (≡*Gomphus floccosus*) with the roots of *Abies firma* Siebold & Zucc. and *Pinus densiflora* Siebold & Zucc. *Gomphus floccosus* has also been proposed as mycorrhizal with *Abies alba* Mill. (Khokhryakov 1956), *Abies nephrolepsis* (Trautr.) Maxim. (Bulakh 1978), *Abies religiosa* (H.B.K.) Schltr. & Cham. (Valdés-Ramirez 1972), *Abies* spp. and *Pinus* spp. (Guzmán and Villarreal 1985), *Pseudotsuga menziesii* (Mirb.) Franco (Trappe 1960), and *Tsuga heterophylla* (Raf.) Sarg. (Kropp and Trappe 1982, Trappe 1960).

Pantidou (1980) and Agerer *et al.* (1998) described the mycorrhizae of *G. clavatus* with *Abies cephalonica* Loudon and *Picea abies* (L.) H. Karst., respectively. Presumably other species of *Gomphus sensu lato* may form ectomycorrhizae with other host species. In North America and Europe the genus mainly associates with species of *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga*. In

Table 2.1. Location, year of description, and distribution for the species of *Gomphus sensu lato*.

Species	Year of description	Distribution
G. africanus R.H. Petersen	1976a	Uganda
G. bonarii (Morse) Singer f. *bonarii* *	1945	Canada (BC), Mexico, USA (CA, ID, OR, WA)
G. bonarii f. *novamexicanus* R.H. Petersen	1971a	Mexico and USA (AZ, CO, NM, UT)
G. bonarii f. *wilkinsae* (Morse) R.H. Petersen	1971a	USA (CA, OR, WA)
G. bonarii f. *wilsonii* R.H. Petersen	1971a	USA (CA, OR, WA)
G. brasiliensis Corner	1969	Brazil
G. brunneus (Heinem.) Corner	1966	Cameron, Democratic Republic of Congo, Uganda
G. canadensis (Berk.) Corner	1966	Canada, USA
G. cavipes Corner	1969	Trinidad and Tobago
G. clavatus (Pers.) Gray*	1821	Austria, Canada, China, Czech Republic, Europe, Japan, Lithuania, Mexico, Pakistan, Poland, Russia, Turkey, USA
G. crassipes (L.M. Dufour) Maire	1937	Algeria, Morocco, Spain
G. dingleyi Segedin	1984	New Zealand
G. flabellatus (Berk.) Corner	1966	Japan
G. floccosus (Schwein.) Singer f. *floccosus* *	1945	Canada, China, India, Japan, Mexico, Nepal, Korea, Pakistan, Tibet, USA
G. floccosus f. *coccineo-basalis* R.H. Petersen	1971a	USA (CA, OR, WA)
G. floccosus f. *cystidiophorus* R.H. Petersen	1971a	USA (CA, OR, WA), rarely in Eastern USA
G. floccosus f. *excavatus* (A.H. Sm. & Morse) Corner	1966	Canada (BC), Nepal, Pakistan, USA
G. floccosus f. *olivaceous* R.H. Petersen	1971a	USA (CA, OR, WA)
G. floccosus subsp. *rainieriensis* (A. H. Sm.) Corner	1966	Canada, Mexico, USA (CA, ID, OR, WA)
G. glutinosus (Pat.) R.H. Petersen	1971a	Vietnam
G. grandis Corner	1969	Borneo
G. guadelupensis (Pat.) D.A. Reid	1962	Guadeloupe
G. kauffmanii (A. H. Sm.) Corner*	1966	Canada, USA (CA, ID, MT, NV, OR, WA)
G. lateritius (Petch.) R.H. Petersen	1968	Sri Lanka
G. mamorensis Singer	1983	Bolivia
G. megasporus Corner	1969	Pakistan
G. novae-zelandiae Segedin	1984	New Zealand
G. okapaensis Corner	1966	Papua New Guinea, Solomon Islands
G. pallidus (Yasuda) Corner	1966	Guam, Hawaii, Japan, Russia
G. retisporus Corner	1966	Malaysia, Solomon Islands
G. stereoides Corner	1966	Africa, Malaysia, Turkey
G. subclavaeformis Corner	1969	Brazil
G. szechwanensis R.H. Petersen	1971a	North America
G. thiersii R.H. Petersen	1971a	USA (CA)
G. viridis (Pat.) Singer	1945	Australia, and tropical America

* Species listed as endangered in the "Record of Decision" (ROD) document (U.S.D.A & U.S.D.I. 1994).

Africa, Australasia, Indochina, Central and South America species of *Gomphus sensu lato* have been detected fruiting in Caesalpinaceae, Dipterocarpaceae, and Myrtaceae dominated habitats, suggesting they may be associated with plants of these families.

A large number of species is known for the northern hemisphere, especially the USA, which Corner (1966) and Petersen (1971a) considered to be the center of highest diversity for the genus. However, that may only be an artifact of the intensity of collecting compared to more remote places. Additionally, much of the diversity of *Gomphus sensu lato* in the USA resides in special 'forms' and 'subspecies'. If we accept the premise that many of these may only be phenotypes of particular species, the number of actual species is reduced considerably. The highest diversity of species may occur elsewhere, perhaps in tropical Africa, Indochina, or Central and South America. The number of species described from these places relative to the number of collecting visits is high. Corner (1966, 1970) often mentions at least one new species found for every trip he made to these places. This suggests that additional attention should be paid to these regions to unravel the complete diversity of these fungi.

Besides the mycorrhizal status of some species, little is known about their role in forest ecosystems. A few are considered rare and endangered, especially in the Pacific northwestern (PNW) USA. *G. bonarii, G. clavatus, G. floccosus*, and *G. kauffmanii* are listed as threatened in the Northwest Forest Plan of 1994 (U.S.D.A. and U.S.D.I. 1994a) because of their apparent close association with old-growth forests.

Gomphus sensu lato fruits during autumn in Europe, western USA, and southwestern Canada, and in spring and autumn in eastern USA and Canada. Near the tropics it generally fruits throughout the year, likely because of the higher temperatures and humidity characteristic of those places.

NOMENCLATURAL HISTORY OF *GOMPHUS SENSU LATO*

The nomenclatural history of *Gomphus* began in the 18th century, when Vaillant (1727) described *Fungus cibarius* from macroscopic characters of shape, color, stature, odor, and taste of the basidiomata. A few years later, Adanson (1763) described *Chanterel* (*Cantharellus*), in which he accepts the species name previously proposed by Vaillant but recombined it as *Cantharellus cibarius*. At that moment the concept of the cantharelloid shape for fungi was born. Cantharelloid in this sense refers to basidiomata being more or less agaricoid but with blunt, decurrent, usually anastomosing or forking hymenial folds.

The concept of *Gomphus sensu lato* was born when Persoon (1796) first mentioned the genus name *Merulius*, describing *M. clavatus* (=*Elvela purpurascens* Schaeff.) among 3 other species. Later Persoon (1797b) proposed 4 new combinations, including *M. violasceus* (=*M. clavatus* Pers). The original concept of *Merulius sensu* Donk (1958) did not include the resupinate forms now recognized but only the stalked basidiomata with irregularly folded or wrinkled hymenia.

In that same year Persoon (1797a) first introduced the name *Gomphus* as a genus, stating under its description "incrassatus, truncatus, teres, *latere* plicato-venosus, *pileus* oblitteratus", which roughly translates to "thickened, truncate, terete, laterally plicate-venose, the pileus weakly developed." However, he assigned no species to his newly created genus. Persoon (1801) then transferred *Gomphus* to *Merulius* section *Gomphus* with 3 described species [*M. clavatus, M. violasceus*, and *M. spadiceus* (=*Clavaria truncata* Schimdel)], and still later restored the genus rank to *Gomphus* (Persoon 1825) with 5 species including *G. truncatus* (=*M. clavatus* Pers.). Gray (1821) noted Persoon's terminology and accepted *Gomphus* as a monotypic genus with the species *G. clavatus*.

Fries (1821), in his *Systema Mycologicum I*, apparently combined Persoon and Adanson's concepts and described *Cantharellus* "tribus" (approximately equal to present-day subgenera or "tribes") *Gomphus* to accommodate the single species *C. clavatus*. In this same work, Fries described the subgenus *Gomphus* (under

Agaricus), referring to *A. glutinosus* and *A. rutilis*, which we currently regard as *Gomphidius glutinosus* and *G. rutilis*, respectively. Later Fries (1825) referred to *Gomphus* as "velum universale, glutinosum. Lamellae decurrentes. (*S. M. I. p. 314*)." He referred to the *Systema Mycologicum I*, which, again, would correspond to what we know now as the genus *Gomphidius*. However, in that same work Fries introduced the genus *Gomphora* and under its description stated: "Receptaculum turbinatum subvenosum, demum apice dehiscens. (*S. M. I. p. 314* Canth. Gomphus; nomen secundum Linn. Phil. Bot. paululum mutandum)." Here again he referred back to the *Systema Mycologicum I* and asserted that what was described by Persoon and adopted by others as *Gomphus* should actually be called *Gomphora*. No species were mentioned under this newly created genus name.

Subsequently new species currently accepted under the genus *Gomphus sensu lato* were published as members of the genus *Cantharellus*. Schweinitz (1831) described *C. floccosus*, and Berkeley (1839) and Berkeley and Curtis (1859) described *C. canadensis* and *C. princeps*, respectively. Fries (1838) transferred *Merulius clavatus* to the genus *Craterellus*.

Doassans and Patouillard (1886) combined the information available from previous taxonomic work and described *Nevrophyllum* to accommodate *Cantharellus* (*Craterellus*) *clavatus*, which they asserted had orange spores unlike other species of *Cantharellus*. In 1887, Peck, probably unaware of the work of Patouillard, adopted the name *Cantharellus* to accommodate a few species of *Gomphus sensu lato* into section *Eucantharellus*, consequently discarding the genus name *Nevrophyllum*. Later, however, Patouillard (1888) divided *Nevrophyllum* into two parts: one represented by *N. clavatum* (smooth spores), and the other by *N. viride* (rough spores). He also described *Stereum guadelupense* (Fr.) Pat. (Patouillard 1899), another species later transferred to *Gomphus sensu lato* (Reid 1962).

Yet another name referred to the genus was *Gomphos* (Kuntze 1891), an alternative rejected because supposedly it only represented an orthographic variant of the original name *Gomphus* (Donk 1941). However, the name *Gomphos sensu*

Kuntze was intended for species of the genus *Gomphidius* and not *Gomphus* as assumed by Donk (1941) and Petersen (1971a). Earle (1909), using notes of Schweinitz (1831) on *Cantharellus floccosus*, described *Turbinellus* to accommodate some species formerly assigned to *Cantharellus*. Meanwhile, and in an attempt to better separate the species described by Patouillard, Murrill (1910) described the genus *Chlorophyllum*; upon finding that name already taken for another group (Massee 1898), changed it to *Chloroneuron* (Murrill 1911).

The pace of these nomenclatural changes abated until the mid 20th century. During all this time the genus was commonly referred to as *Cantharellus*. Then Singer (1945), using Hesler's *Cantharellus purpurascens* as type (Smith and Hesler 1943), described *Gloeocantharellus*, with the key diagnostic character of gleocystidia separating it from *Cantharellus*, but also, and more importantly here, recognized *Gomphus* as a genus name and recombined *Cantharellus bonarii* Morse as *G. bonarii* (Morse) Singer. Morse had described *C. bonarii* in 1930, suggesting it to closely resemble "*C. floccosus* Schwein." (Morse 1930).

Meanwhile, Smith and Morse (1947) continued to employ the name *Cantharellus* for cantharelloid (hymenium decurrent, gilled) and gomphoid (hymenium decurrent, with gill-folds) species alike and divided the genus into 5 sections: *Eu-Cantharellus, Excavatus, Gomphus, Polyozellus,* and *Tubaeformis*. Species assigned to the then current genus *Gomphus sensu lato* were placed either in section *Gomphus* or *Excavatus*. Section *Gomphus* included *C. clavatus* (designated as type species), *C. pseudoclavatus,* and *C. brevipes*, the later described by Peck (1887) but later accepted as a synonym of *G. clavatus* by Harper (1913, 1914). They mentioned "it is interesting to note in this group that clamp-connections are abundant on the type species, *C. clavatus*, which is circumpolar in distribution, but absent on the other two which appear to be relatively local segregates of it" (Smith and Morse 1947). They also stated that this section was previously recognized as two distinct genera: "*Nevrophyllum* Patouillard and *Gomphus* S. F. Gray, both based on *C. clavatus*," and this, in their estimation, was not acceptable, because it was difficult to find characters other than general aspect

which would separate these species from those in section *Eu-Cantharellus* (Smith and Morse 1947).

In Smith and Morse's new classification, section *Excavatus* included species with an innately fibrillose scaly to floccose pileus and lacking clamp connections. This section included *C. bonarii, C. floccosus* (referred as the type for the section), *C. kauffmanii,* and *C. wilkinsae.*

The natural classification of this group of fungi was somewhat clarified by Corner (1950, 1966, 1969), Petersen (1967, 1968, 1969, 1971ab), and acceptance of the classifications proposed by Donk (1933, 1941, 1949). After 1950, Donk continued to expand knowledge and the literature on this group of fungi, culminating with the creation of the new family Gomphaceae (Donk 1961). Donk's (1964) familial classification included Gomphaceae to accommodate *Gomphus sensu lato* and related genera, and a conspectus of the families of fungi belonging to the Aphyllophorales. The family Gomphaceae was considered a member of the Aphyllophorales until Jülich (1981) proposed the order Gomphales to include the families Beenakiaceae (*Beenakia* and *Ramaricium*), Gomphaceae (*Gloeocantharellus, Gomphus*), Lentariaceae (*Lentaria*), and Ramariaceae (*Ramaria*).

Corner and Petersen worked extensively on the genus *Gomphus sensu lato*, resurrecting species from *Cantharellus*, proposing new combinations, and describing many new species, forms and varieties. From 1966 to 1969 Corner described 9 new species and proposed 10 new combinations (Corner 1966, 1969). Corner (1966) also divided the genus into subgenus *Chloroneuron*, subgenus *Gomphorellus*, and subgenus *Gomphus* with sections *Gomphus* and *Excavatus*. He listed 20 species under this new classification, many as new combinations.

Petersen (1971a), on the other hand, proposed two subgenera: *Excavatus* and *Gomphus*, including a total of 16 species. He described 10 new species and proposed 5 new combinations for *Gomphus sensu lato* (Petersen 1968, 1971a, 1976a).

After 1984, when two more species were described from New Zealand (Segedin 1984), studies on these fungi were quiescent until Villegas *et al.* (1999) published their work on phylogenetics of the Gomphaceae *sensu lato*. Nevertheless, they proposed no major taxonomic changes.

Since 1821 the name *Gomphus* (Pers.) Gray has generally been accepted over other alternatives. Donk (1941), before considering Gray's "Natural Arrangement" (Gray 1821) as post-Friesian, proposed conservation of the name *Gomphus* Pers.:Pers. (Persoon 1825), the first re-publication of the name after 1821, against *Gomphora* Fr. (Fries 1825). After recognizing Gray's book as post-Friesian, Donk (1949a) withdrew the proposal as superfluous. Donk (1949b) then reconsidered and suggested conserving *Gomphus* over *Gomphora*. However, Fries (1821) applied the name *Gomphus* as a subgenus of *Agaricus*, referring to species of the presently known genus *Gomphidius*, or a subgenus under *Cantharellus*. According to the International Code of Botanical Nomenclature (Greuter *et al.* 2000) a name has no priority outside its rank (article 11.2). Therefore, the nomenclatural starting point for this genus is not Fries 1821. Accordingly, we must reexamine the works of Persoon from 1796 to 1825 for clues to the correct resolution of this nomenclatural dilemma. Persoon (1797a) introduced *Gomphus* as a segregate genus from *Clavaria*, *Geoglossum*, *Mitrula,* and *Spathularia*, and briefly described his new genus. Therefore, '***Gomphus* Pers. (1797a), Tentamen dispositionis methodicae fungorum in classes, ordines, genera et familias.'** is the correct author citation for the genus *Gomphus*. Fries' *Gomphora*, published in the *Systema Orbis Vegetabilis* (Fries 1825) might seem to have priority, but this publication is not considered a part of the starting-point *Systema Mycologicum* (Greuter *et al.* 2000). Thus both *Gomphora* Fr. and *Gomphus* (Pers.) Gray are to be considered as superfluous names.

SYSTEMATICS, TAXONOMY, AND EVOLUTIONARY BIOLOGY

Recurring nomenclatural changes, new combinations, and new taxa have created a formidable puzzle involving 35 species, subspecies, forms, and varieties described under the name *Gomphus* (Table 2.1). Smith and Morse (1947) described a few (5 species) of these 35 taxa, initially under the genus *Cantharellus* and later recombined under *Gomphus* by Corner (1966, 1969) and Petersen (1971a, 1976a). All authors suggest subdividing *Gomphus* into subgenera, sections, or subsections. These proposed subdivisions are based on a few characters. Species with floccose pilei are in a separate subgenus from those with glabrous pilei, species with echinulate spores are separated from those with verrucose spores, etc. A particular problem in these classifications is the erection of many new forms, varieties, and subspecies based mostly on one or a few morphological characters, mostly involving the size and ornamentation of the spores. Some are based on specific colors of the basidiomata or "scaliness" of the pileus. A good example is *Gomphus floccosus* f. *olivaceous,* considered distinct due to the 'ecru olive' pileus (Petersen 1971a); aside from that, all other characters perfectly fit the description of *G. floccosus* f. *floccosus*. Still other taxa are based on the locality where found, such as *G. bonarii* f. *novamexicanus*, restricted to the southwestern states of the USA, with features similar if not the same to those observed in *G. bonarii* f. *bonarii.* Some species have been described from a single collection. Some of these have never been found again, even by collecting in the type locality, suggesting they may represent phenotypes of one particular genotype.

Most difficulties in identifying taxa of *Gomphus sensu lato* arise because of the many subspecies assigned to individual species. Some authors have referred to groups of these species by the affix 'complex' to avoid the frustration of trying to identify species that may fit several descriptions. For example *G. bonarii* and *G. floccosus* have been called the '*bonarii-floccosus* complex (Petersen 1971a).' This "complex" alone contains 14 forms and/or subspecies.

Distinctive clusters of species can be consistently separated by morphology. Most are united by a few consistent features, such as fan-shaped and lilaceous vs. funnel-shaped and orangish brown pilei, scaly vs. inconspicuously fibrous pileus surface, presence vs. absence of clamp connections, echinulate vs. verrucose spores, tropical vs. temperate habitat, etc.

Given the difficulty in identifying species of *Gomphus sensu lato* by morphological characters this study was designed to combine morphological and molecular data to answer these questions: (a) is *Gomphus sensu lato* monophyletic? (b) If not, how many genera does it encompass? (c) How many species properly reside in the genus *Gomphus sensu stricto*? And (d) finally, are morphological features reliable to identify species or interspecific taxa?

MATERIAL AND METHODS

Collections examined

Several specimens of all species of *Gomphus sensu lato* available for loan were studied. Species for which specimens were not available for loan were characterized from the original descriptions. More than 400 collections of Gomphales species were analyzed for distinct macro- and micro-morphological features. About 200 of those were selected for molecular characterization. Twenty-nine of the 35 known species of *Gomphus sensu lato* were sampled. The other 6 were either not located or not granted for loan, generally because of the age and fragility of the specimens. All holotype plus other collections were examined and sampled when available. Specimens were obtained from the following herbaria: BPI, BR, CANB, CUP, DAOM, DAR, F, FH, GH, H, K, L, LPS, M, MICH, NCU, NY, NYS, OULU, OSA, OSC, PC, PDD, PERTH, PH, S, SFSU, SUC, TENN, TNS, UC, UPS, WTU, and ZT (http://www.nybg.org/bsci/ih/ih.html). A few

samples from Europe were provided by Dr. Andy Taylor, Swedish University of Agricultural Sciences, Uppsala. Names of authorities are according to Brummit and Powell (1992).

Fresh specimens obtained from field trips made to northern California, Idaho, Oregon, and Washington were also examined. These were collected mostly in late September to mid December, which in general coincided with the rainy and hence the fruiting season.

Selected collections were photographed and macroscopic features recorded. All were then dried within 24 hours of collection with a forced-air food dehydrator set at 38-40 C and deposited at OSC.

Macroscopic characters

Macroscopic features are based on the original descriptions and notes accompanying herbarium collections supplemented by my own data on fresh or dried specimens. Features of the cap, hymenium, stipe, flesh, odor and taste were recorded whenever possible. Size of basidiomata may vary depending on conditions of the fruiting season, so the ranges of minimum and maximum sizes were annotated.

Microscopic characters

Features observed with a compound microscope were described from free-hand sections mounted in Melzer's reagent, 5% KOH, cotton blue, or water. Structures were measured with an optical micrometer at × 1000 magnification, mostly in 5% KOH, water, or Melzer's reagent. The ranges for hypha measurements are as follows: thin walls $\leq$0.5 μm wide, thick walls >0.5 μm wide. The pileipellis and stipitipellis were examined in surface view. When material was

available, dimensions of structures were recorded from at least 3 specimens from each of at least 5 collections; both mature and immature specimens were examined for developmental changes. Maturity was judged by the relative abundance of fully ornamented spores.

Spore shape was determined as the length-width ratio of 20-30 randomly selected spores. Dimensions are given as: minlength-maxlength × minwidth-maxwidth, excluding ornamentation and apiculus. Immature or oversized spores were not included in the measurements, though variation was noted.

Molecular characterization

A hundred and sixty-six high quality sequences of *Gomphus sensu lato* representing 69 taxa were sampled for molecular characterization and phylogenetic analysis. Three combined genetic loci were investigated: nuclear large subunit ribosomal DNA (nuc-25S-rDNA), mitochondrial small subunit DNA (mit-12S-rDNA), and mitochondrial *atp*6 DNA (mit-*atp*6-DNA). The analysis also included 123 sequences from members of other closely related genera in the order Gautieriales (*Gautieria*), Gomphales (*Beenakia, Clavariadelphus, Gloeocantharellus, Kavinia, Lentaria*, and *Ramaria*), Hysterangiales (*Gallacea, Hysterangium*), and Phallales (*Clathrus, Mutinus, Phallus, Protubera, Pseudocolus,*), and the families Geastraceae (*Geastrum*) and Sphaerobolaceae (*Sphaerobolus*), plus 3 outgroup taxa (*Bondarzewia* sp., *Cortinarius iodes,* and *Russula* sp.) (Table 2.2).

Table 2.2. Taxa included in the molecular characterization of the Gomphales.

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp*6-rDNA
Beenakia fricta Maas Geest.	2083	K	AY574693	AY574766	AY574833
Clathrus cibarius (Tul.) E. Fisch.	107652	OSC	AY574641	AY574715	AY574783
Clavariadelphus lovejoyae V.L. Wells & Kempton	61068	OSC	AY577827	AY577854	AY577865
C. ligula (Schaeff.) Donk	67068	OSC	AY574650	AY574723	AY574793
C. occidentalis Methven	37018	OSC	AY574648	AY574721	AY574791
C. truncatus Donk	67280	OSC	AY574649	AY574722	AY574792
Gallacea Scleroderma (Cooke) Lloyd	59621	OSC	AY574645	AY574719	AY574787
Gautieria monticola Harkn.	65121	OSC	AY574651	AY574724	AY574794
G. parksiana Zeller & C.W. Dodge	58907	OSC	AY574652	AY574725	AY574795
Geastrum saccatum Fr.	23765	Trappe	AY574646	AY574720	AY574788
Gloeocantharellus dingleyae (Segedin) Giachini	30179*	PDD	AY574668	AY574741	–
G. novae-zelandiae (Segedin) Giachini	44960*	PDD	AY574666	AY574739	AY574809
G. pallidus (Yasuda) Giachini	54917*	BPI	AY574673	AY574746	AY574815
G. papuanus Giachini, Bougher, Castellano & Trappe	06707114*	PERTH	AY574667	AY574740	AY574810
G. purpurascens (Hesler) Singer	12793	TENN	AY574683	AY574756	AY574823
G. purpurascens (Hesler) Singer	14265*	TENN	AY574684	AY574757	AY574824
Gomphus brunneus (Heinem.) Corner	034190-46	BR	AY574680	AY574753	AY574821
G. clavatus (Pers.) Gray	97588	OSC	AY577836	AY577863	AY577874
G. clavatus (Pers.) Gray	97616	OSC	AY574664	AY574737	AY574807
G. clavatus (Pers.) Gray	s.n.	UPS	AY574665	AY574738	AY574808
Hysterangium coriaceum R. Hesse	64939	OSC	AY574686	AY574759	AY574826
H. crassum (Tul. & C. Tul.) E. Fisch.	110447	OSC	AY574687	AY574760	AY574827
H. occidentalis Harkn.	47048	OSC	AY574685	AY574758	AY574825
Kavinia alboviridis (Morgan) Gilb. & Budington	102140	O	AY574692	AY574765	AY574832
K. himantia (Schwein.) J. Erikss.	102156	O	AY574691	AY574764	AY574831
Lentaria pinicola (Burt) R.H. Petersen	M89**	SUC	AY574688	AY574761	AY574828
Lentaria pinicola (Burt) R.H. Petersen	M46	SUC	AY574689	AY574762	AY574829
Lentaria pinicola (Burt) R.H. Petersen	M560	SUC	AY574690	AY574763	AY574830
Mutinus elegans (Mont.) E. Fisch.	107657	OSC	AY574643	AY574717	AY574785
Phaeoclavulina africana (R.H. Petersen) Giachini	39621*	TENN	AY574653	AY574726	AY574796

Table 2.2. Taxa included in the molecular characterization of the Gomphales (*cont.*).

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp*6-rDNA
P. angustata (Lév.) Giachini	s.n.*	BPI	AY577847	–	–
P. apiahyna (Speg.) Giachini	13259*	LPS	AY577840	–	–
P. argentea (R.H. Petersen) Giachini	41370*	TENN	AY577839	–	–
P. campestris (K. Yokoy. & Sagara) Giachini	1502*	TNS	AY577851	–	–
P. campoi (Speg.) Giachini	39622*	LPS	AY577842	–	–
P. capucina (Pat.) Giachini	288*	GH	AY577845	–	–
P. cokeri (R.H. Petersen) Giachini	36030*	TENN	AY574701	AY574774	AY574843
P. curta (Fr.) Giachini	8711	OSC	AY574713	–	AY574858
P. curta (Fr.) Giachini	s.n.	NYS	AY577848	–	–
P. cyanocephala (Lév.) Giachini	37827	TENN	AY574710	AY574779	AY574854
P. decolor (Berk. & M.A. Curtis) Giachini	s.n.*	FH	AY577843	–	–
P. eumorpha (P. Karst.) Giachini	36218	TENN	AY574712	AY574781	AY574856
P. eumorpha (P. Karst.) Giachini	37842	TENN	–	AY574782	AY574857
P. flaccida (Fr.) Giachini	s.n.*	FH	AY577846	–	–
P. gigantea (Pat.) Giachini	109*	FH	AY574703	AY574776	AY574845
P. grandis (Corner) Giachini	073158-06*	BR	AY574678	AY574751	AY574820
P. guadelupensis (Pat.) Giachini	120*	FH	AY574682	AY574755	–
P. guyanensis (Pat.) Giachini	84*	FH	AY574706	–	AY574848
P. insignis (Pat.) Giachini	104*	FH	AY574704	–	AY574846
P. longicaulis (Pat.) Giachini	33826	TENN	AY574700	AY574773	AY574842
P. mutabilis (Schild & R.H. Petersen) Giachini	39893*	TENN	AY577839	–	–
P. ochracea (Bres.) Giachini	s.n.*	S	AY577850	–	–
P. ochraceo-virens (Jungh.) Giachini	23475	OSC	AY574714	–	AY574859
P. ochraceo-virens (Jungh.) Giachini	M322	SUC	AY577852	–	–
P. ochraceo-virens (Jungh.) Giachini	M506	SUC	AY577853	–	–
P. pancaribbea (R.H. Petersen) Giachini	31836*	TENN	AY574707	–	AY574849
P. subclaviformis (Berk.) Giachini	073159-07*	BR	AY574679	AY574752	–
P. tropicalis (R.H. Petersen) Giachini	551*	NY	AY577841	–	–
P. viridis (Pat.) Giachini	97708	OSC	AY574675	AY574748	AY574817
P. viridis (Pat.) Giachini	1853	FH	AY574676	AY574749	AY574818

Table 2.2. Taxa included in the molecular characterization of the Gomphales (*cont.*).

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp*6-rDNA
P. viridis (Pat.) Giachini	4302	PERTH	AY574677	AY574750	AY574819
P. zealandica (R.H. Petersen) Giachini	43383*	PDD	AY577849	–	–
P. zippelii (Lév.) Giachini	s.n.*	FH	AY577844	–	–
Phallus impudicus L.	107655	OSC	AY574642	AY574716	AY574784
Protubera nothofagi Castellano & Beever	59699	OSC	AY574644	AY574718	AY574786
Pseudocolus fusiformis (E. Fisch.) Lloyd	96-033	DSH	AF518641	AF026666	–
Ramaria apiculata (Fr.) Donk	23549	OSC	AY574695	AY574768	AY574836
R. apiculata var. *brunnea* R.H. Petersen	53935	TENN	AY574696	AY574769	AY574837
R. araiospora var. *araiospora* Marr & D.E. Stuntz	M739*	SUC	AF213068	AF213141	AY574838
R. araiospora var. *araiospora* Marr & D.E. Stuntz	M556	SUC	AY574697	AY574770	AY574839
R. botrytis var. *botrytis* (Pers.) Ricken	M457	SUC	AY574698	AY574771	AY574840
R. botrytis var. *botrytis* (Pers.) Ricken	M740	SUC	AY574699	AY574772	AY574841
R. circinans (Peck) Marr & D.E. Stuntz	s.n.	NYS	AY574702	AY574775	AY574844
R. circinans var. *anceps* Marr & D.E. Stuntz	M615*	SUC	AY574711	AY574780	AY574855
R. gelatiniaurantia var. *violeitingens* Marr & D.E. Stuntz	M830	SUC	AY574708	AY574777	AY574851
R. rainieriensis Marr & D.E. Stuntz	M231	SUC	AF213115	AF213135	AY574834
R. rainieriensis Marr & D.E. Stuntz	M431	SUC	AY574694	AY574767	AY574835
R. rubribrunnescens Marr & D.E. Stuntz	M844*	SUC	AF213098	AF213142	AY574852
R. stuntzii Marr	M214	SUC	AF213102	AF213134	AY574850
R. suecica (Fr.) Donk	s.n.	BPI	AY574705	–	AY574847
R. vinosimaculans Marr & D.E. Stuntz	23287	OSC	AY574709	AY574778	AY574853
Sphaerobolus stellatus Tode	96-015	DSH	AF393077	AF026662	AY574789
S. stellatus Tode	SS28	–	AY574647	AY488024	AY574790
Turbinellus flabellatus (Berk.) Giachini	191[†]	FH	AY574674	AY574747	AY574816
T. flabellatus (Berk.) Giachini	1770*	K	AY574681	AY574754	AY574822
T. floccosus (Schwein.) Earle	MY-1839	OSA	AY574654	AY574727	AY574797
T. floccosus (Schwein.) Earle	MY-1840	OSA	AY574655	AY574728	AY574798
T. floccosus (Schwein.) Earle	69167	OSC	AY574656	AY574729	AY574799
T. floccosus (Schwein.) Earle	33233	TENN	AY574657	AY574730	AY574800
T. floccosus (Schwein.) Earle	21238[†]	SFSU	AY574658	AY574731	AY574801

Table 2.2. Taxa included in the molecular characterization of the Gomphales (*cont.*).

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp*6-rDNA
T. floccosus (Schwein.) Earle	33295†	TENN	AY574659	AY574732	AY574802
T. floccosus (Schwein.) Earle	5588†	MICH	AY574660	AY574733	AY574803
T. floccosus (Schwein.) Earle	10721†	MICH	AY574661	AY574734	AY574804
T. floccosus (Schwein.) Earle	759902†	UC	AY574662	AY574735	AY574805
T. floccosus (Schwein.) Earle	924302†	UC	AY574663	AY574736	AY574806
T. floccosus (Schwein.) Earle	9166	DAOM	AY577828	AY577855	AY577866
T. floccosus (Schwein.) Earle	030	G	AY577829	AY577856	AY577867
T. floccosus (Schwein.) Earle	97652	OSC	AY577833	AY577860	AY577871
T. floccosus (Schwein.) Earle	33170†	TENN	AY577831	AY577858	AY577869
T. floccosus (Schwein.) Earle	32175	TENN	AY577832	AY577859	AY577870
T. floccosus (Schwein.) Earle	34502	TENN	AY577835	AY577862	AY577873
T. floccosus (Schwein.) Earle	32285	TENN	AY577830	AY577857	AY577868
T. floccosus (Schwein.) Earle	1203147	UC	AY577834	AY577861	AY577872
T. fujisanensis (S. Imai) Giachini	MY-1841	OSA	AY574670	AY574743	AY574812
T. fujisanensis (S. Imai) Giachini	MY-1842*	OSA	AY574669	AY574742	AY574811
T. kauffmanii (A.H. Sm.) Giachini	10069*	MICH	AY574671	AY574744	AY574813
T. kauffmanii (A.H. Sm.) Giachini	97561	OSC	AY577837	AY577864	AY577875
T. kauffmanii (A.H. Sm.) Giachini	97590	OSC	AY574672	AY574745	AY574814
Outgroup					
Bondarzewia berkeleyi (Fr.) Bondartsev & Singer	93-190	DSH	SARn	U27026	–
Cortinarius iodes Berk. & M.A. Curtis	JM96/23	–	AF042613	AF026675	AF388826
Russula sp.	s.n.	–	U11926	U27074	AF002148

[a] Epithets according to Giachini (2004a), Humpert *et al.* (2001), Marr and Stuntz (1973), and Petersen (1981, 1988).

[b] * Indicates holotype specimens; ** indicates paratype specimens; s.n. indicates no number; † indicates type for older name (see Giachini 2004a for details).

[c] Herbarium for source of collections: BPI = U.S. National Fungal Collections – Beltsville; BR = Herbarium of the National Botanical Garden of Belgium – Meise; DAOM = National Mycological Herbarium – Ottawa; DSH = Personal collection of Dr. David S. Hibbett, Biology Department, Clark University – Worcester; FH = Farlow Herbarium of Cryptogamic Botany –

Cambridge; G = Personal collection of Admir J. Giachini, Department of Forest Science, Oregon State University – Corvallis; GH = Gray Herbarium at Harvard University – Cambridge; K = Royal Botanic Gardens Herbarium – Kew; LPS = Herbarium of the Instituto de Botánica Carlos Spegazzini – Buenos Aires; MICH = University of Michigan Fungus Collection – Ann Arbor; NY = New York Botanical Garden – Bronx; NYS = Herbarium of the New York State Museum – Albany; O = Herbarium of the Botanical Museum of Oslo – Oslo; OSA = Osaka Museum of Natural History – Osaka; OSC = Oregon State University Herbarium – Corvallis; PDD = New Zealand Plant Diseases Division Herbarium – Auckland; PERTH = CSIRO Forestry and Forest Products Herbarium – Perth; S = Herbarium of the Swedish Museum of Natural History – Stockholm; SFSU = Harry D. Thiers Herbarium at San Francisco State University – San Francisco; SUC = State University of New York Herbarium – Oneonta; TENN = University of Tennessee Herbarium – Knoxville; Trappe = Personal collection of Dr. James M. Trappe, Department of Forest Science, Oregon State University – Corvallis; UC = University of California Herbarium – Berkeley; UPS = Herbarium of the Uppsala Botanical Museum of Uppsala University – Uppsala.

DNA extraction

DNA was extracted by a modified CTAB extraction protocol (Gardes and Bruns 1993) and purified with a Glassmilk kit (BIO 101, Carlsbad, CA, USA).

DNA amplification

The large subunit of the nuclear ribosomal DNA (nuc-25S-rDNA) was amplified with different combinations of primer-pairs. Initially LROR (5'-ACC CGC TGA ACT TAA GC-3') and LR3 (5'-CCG TGT TTC AAG ACG GG-3') were employed (Vilgalys and Hester 1990, White *et al.* 1990). When this failed (mainly because of aged basidiomata which tend to have degraded DNA), an extra pair of primers, RAM 1 (5'-CGY GAC TGA CTT CAA RCG-3') and RAM 3 (5'-GCG AAC AAG TAC CGT GAG-3'), was also used (Humpert *et al.* 2001). LROR was coupled with RAM3, and LR3 with RAM1. This approach reduced the size of the template DNA to be amplified and increased the yield of DNA amplification. For the mit-12S-rDNA, several primer sets had to be employed. A few extra primers were designed to allow for DNA amplification. Primers employed in the amplification of the mit-12S-rDNA template included Gom1[1] (5'-AYG ARA TMT CCC AAG TAG AG-3'), Gom2 (5'-TAC TYA CAA GGC GGA ATG G-3'), MS1 (5'-CAG CAG TCA AGA ATA TTA GTC AAT G-3') (White *et al.* 1990), MS2 (5'-GCG GAT TAT CGA ATT AAA TAA C-3') (White *et al.* 1990), Phal1 (5'-CCA KAA GAC TCG GTA AKG-3'), Phal2 (5'-TTA CCG AGT CTT CTG GCA C-3'), Phal3 (5'-AGA CTC GGT AAK GCC ARA G-3'), and U1 (5'- TAA TTT TGG TGC CGA TTG AAC G-3'), the latter designed at T.D. Bruns mycology laboratory, Berkeley, CA (http://plantbio.berkeley.edu/~bruns/primers.html). These were paired accordingly to generate the highest amplification yields. For the *atp6*

[1] Primers Gom 1, 2, and Phal 1, 2, 3 were designed by Kentaro Hosaka, Oregon State University, Corvallis, OR, USA.

region, the primer set primarily used was *atp*6-2 (5'-TAA TTC TAN WGC ATC TTT AAT RTA-3') and *atp*6-3 (5'-TCT CCT TTA GAA CAA TTT GA-3') (Kretzer and Bruns 1999). The primers *atp*6-5 (5'-ATY GCT TTA GAA AGT TYM TTT GC-3') and *atp*6-6 (5'-GGD ATR AAR WAW GAR AAR AAR TG-3') were designed and intended to amplify those samples that did not amplify when using primer pair *atp*6-2 and *atp*6-3.

DNA sequencing

Amplified DNA was detected via gel electrophoresis (1-2%) and visualized with ethidium bromide under a transiluminator. Positive PCR products were then purified with one of the following kits: Glassmilk kit (BIO 101, Carlsbad, CA, USA), Geneclean kit (BIO 101, Carlsbad, CA, USA), or Exosap-IT kit (Amersham Biosciences UK Limited, Little Chalfont Buckinghamshire, England), and yield determined in agarose gels (1-2%). Nucleotide sequences were determined by the cyclic reaction termination method with fluorescence-labeled dideoxyribonucleotide triphosphates. Sequencing reactions and processing of reaction products were performed according to instructions for the ABI PRISM™ (PE Applied Biosystems, Foster City, CA, USA) and Amersham™ Dye Terminator Cycle Sequencing Core Kit (Amersham Biosciences UK Limited, Little Chalfont Buckinghamshire, England). Electrophoresis and data collection were performed on an ABI Model 373A DNA Sequencer (Perkin-Elmer Corporation, Wellesley, MA, USA). Sequencing Analysis (version 2.1.2) and Sequence Navigator (version 1.0.3) were used to process raw data.

Sequence alignment and phylogenetic analyses

Sequences were manually aligned in PAUP* version 4.0b10 editor and a color font (Swofford 2002). Sequences immediately adjacent to priming sites of sequencing primers and some hypervariable regions were of low quality in some of the sequences and therefore excluded from the analyses. Within the areas included in the active data set, most single-basepair alignment gaps were parsimony informative and treated as missing data. Ambiguous insertions/deletions (indels) were treated as missing data. Phylogenetic analyses were performed in PAUP* 4.0b10 (Swofford 2002) on the combined dataset of the three genetic loci mentioned above. Combinability of the data was tested via the Shimodaira and Hasegawa (1999) test ($p \leq 0.05$) built in PAUP. Uninformative characters plus non-alignable areas of the dataset were removed to reduce noise and increase reliability of the results. Most parsimonious trees were recovered by the heuristic search option (TBR and MULPARS on) with 10000 replicates of random sequence addition. Support for individual branches was tested with bootstrap analysis with full sequence addition (TBR and MULPARS on) with 500 replicates. Additionally, a second analysis was run with Mr. Bayes (Metropolis-Coupled Markov Chain Monte Carlo or MC^3) v. 3.0 (Huelsenbeck and Ronquist 2002) under the posterior probability theorem with 3000000 chains.

ACCEPTED NAMES, NEW COMBINATIONS, AND SYNONYMS IN *GOMPHUS SENSU LATO*

Persoon (1796, 1797ab, 1801, 1825) and Fries (1821, 1838) created the foundation for the taxonomy of one portion of this genus, concentrating on *G. clavatus*. For many years following these early workers, the taxonomic premise for classifying agaricoid or cantharelloid basidiomycetes was the configuration of the hymenial surface, specifically for the cantharelloid species a hymenial surface of

variously undulating or semi differentiated, decurrent hymenial folds. This feature forced species of *Gomphus sensu lato* into the genus *Cantharellus* for many years. Reexamination of the generic types by morphological and molecular approaches revealed the inadequacy of some characters used by early workers to differentiate species within *Gomphus sensu lato*. Additionally, the genetic data strongly suggest that *Gomphus sensu lato* is not monophyletic (Figures 2.1 and 2.2). Rather, it originated several times within the order Gomphales (a complete discussion on evolutionary aspects of the Gomphales is presented in chapter 7). Because basidioma morphology and overall microscopic characteristics differentiate among species in many clades within *Gomphus sensu lato*, segregation of species into the genera *Gomphus sensu stricto*, *Gloeocantharellus*, *Phaeoclavulina* (some species of *Gomphus sensu lato* and all species of *Ramaria* subgenus *Echinoramaria*), and *Turbinellus* is proposed. The only species fitting the original concept of *Gomphus* Pers. are *G. brunneus*, *G. clavatus*, and *G. crassipes*, which have rosaceous, sordid yellow, orange-brown to violet, fan-shaped (generally compound) to somewhat funnel-shaped basidiomata, clamp connections, and verrucose spores.

A detailed description of all species listed here, with respective collections examined is presented in each genus-individualized chapter following this chapter.

KEY TO GENERA SEGREGATED OUT OF *GOMPHUS SENSU LATO*

1. Basidiomata unipileate or merismatoid (composed of several pilei); pileus mostly funnel-shaped, surface almost glabrous to fibrillose, appressed-floccose, squamose scaly or with heavy recurved scales; clamp connections sometimes present but mostly absent; spores verrucose..... 2

1. Basidiomata ramarioid, unipileate or merismatoid; pileus, when present, fan- to funnel-shaped, surface glabrous; clamp connections always present; spores echinulate, verrucose, subreticulate or reticulate..... 3

    2. Pileus minutely to strongly scaly, orange-yellow to orange-scarlet, blood red, pale orange, orange, or brown, often changing color on drying; scales generally darker than pileus surface; hymenium wrinkled..... *Turbinellus*

    2. Pileus glabrous to tomentose, off-white, pale yellow, pale yellow-brown, yellow-pink, pale to livid orange, orange-pink, pink, pale brown, dark yellow-orange, dark rusty brown, pale red; hymenium decurrent, supported by either true lamellae, bifurcating broad hymenial folds, or wrinkled folds..... *Gloeocantharellus*

3(1). Basidiomata unipileate or merismatoid, terrestrial; pileus fan-shaped to slightly funnel-shaped, bright violet, pale olivaceous or brown; hymenium wrinkled to almost poroid, violet, vinaceous brown to milky-coffee colored; spores verrucose..... *Gomphus*

3. Basidiomata ramarioid, unipileate or merismatoid, sometimes lignicolous; pileus, when present, funnel-shaped or fan-shaped, pileus and branch surfaces white, brownish green, pale to sordid olivaceous, violet, brownish yellow or reddish cinnamon, gray, brick red, or pale to dark orange-yellow; hymenium smooth in some species, sublamellate or irregularly wrinkled with decurrent folds in others, in general yellow to orange-red or brown, pale to sordid olivaceous, violet; spores echinulate (mostly with acute spines), verrucose, subreticulate or reticulate..... *Phaeoclavulina*

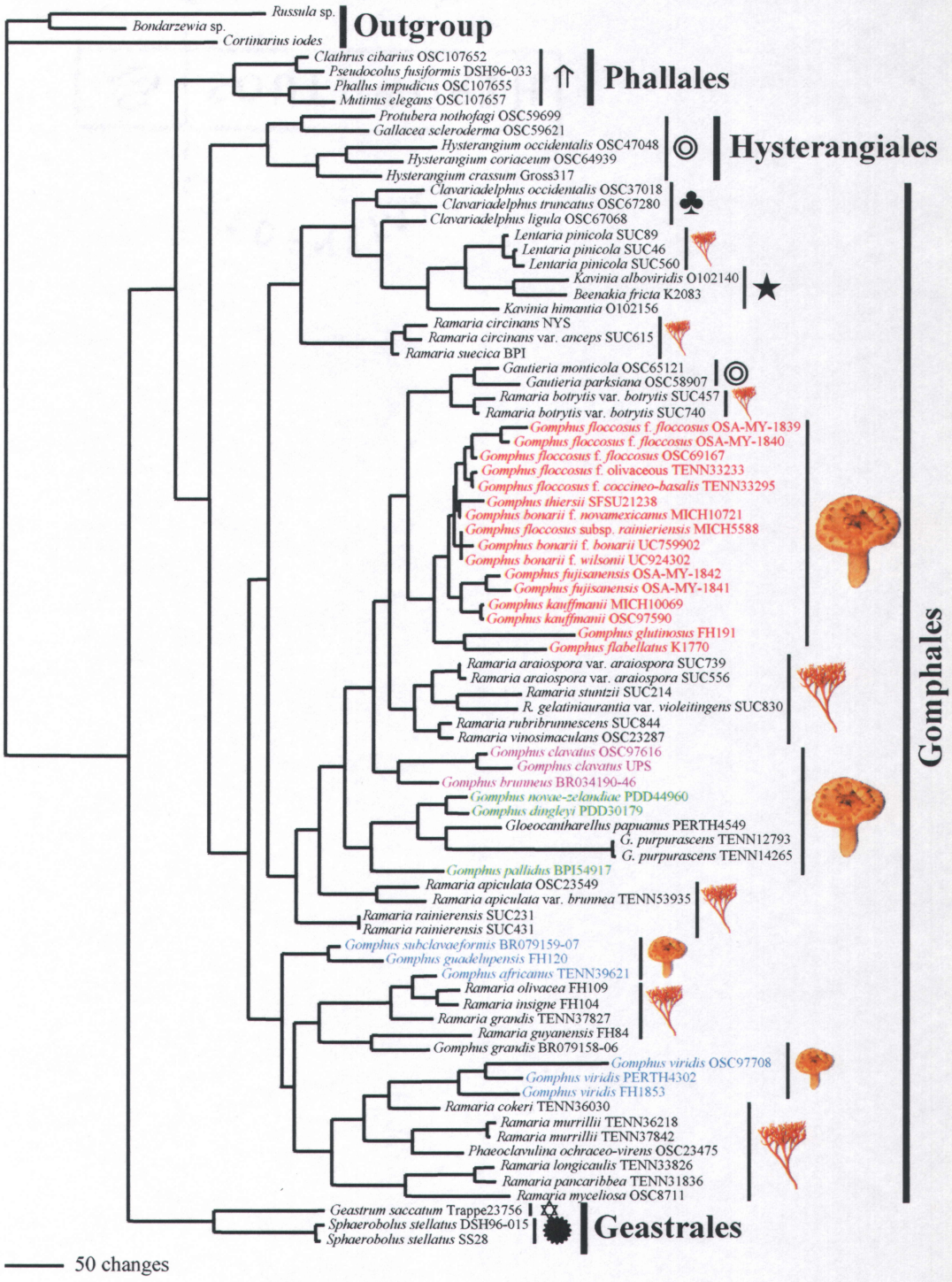

Figure 2.1. Phylogram of 1 of 3 most parsimonious (MP) trees recovered from phylogenetic analyses of the nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA combined sequences. Tree length = 4967; CI=0.287, RI=0.566, RC=0.163. Basidiomata morphology: = ramarioid; ♣ = club; = cantharelloid-gomphoid; ⇑ = stink horn; ◎ = sequestrate; ✡ = earth-star; ● = cannon ball; ★ = odontoid/resupinate.

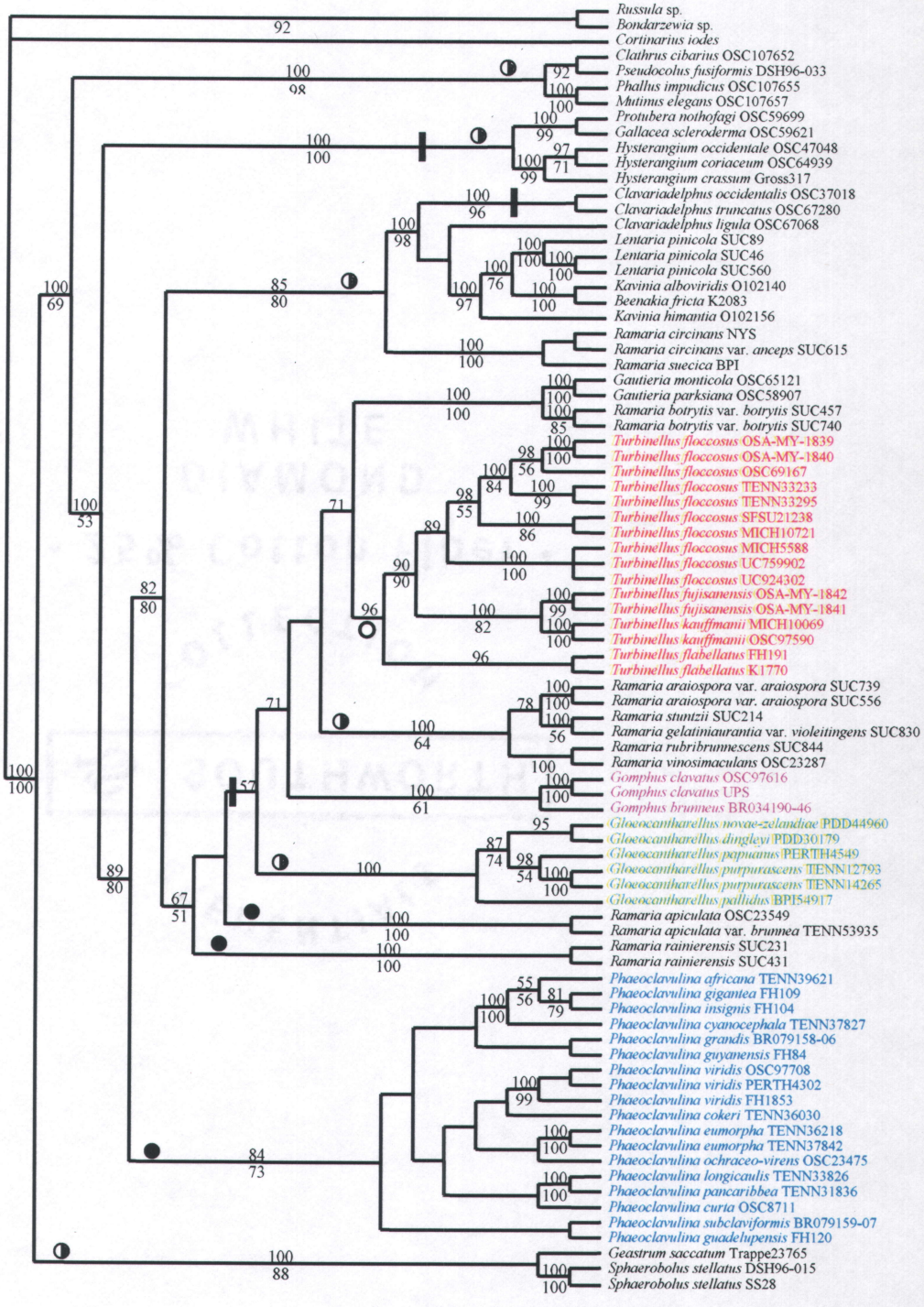

Figure 2.2. Strict consensus cladogram of 3 equally parsimonious (MP) trees of 4967 steps based on nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA combined sequences. MCMC and Bootstrap values above 50% are indicated above and below respective internode, respectively. CI=0.287, RI=0.566, RC=0.163. Transition to a terricolous substrate affinity is indicated by the symbol ▌. Clamp connections are indicated with the following symbols: ○ = clamp connection present; ● = clamp connections absent; ◑ = clamp connections present in some species while absent in others.

ACCEPTED NAMES AND NEW COMBINATIONS

Gomphus Pers. Tentamen Dispositionis Methodicae Fungorum, p. 74. 1797a [*non Gomphus* (Fr.) Weinm., Hymeno- et Gastero-mycetes Hucusque in Imperio Rossico Observatos, p. 38. 1826; *Gomphus* (Fr.) P. Kumm., Der Führer in die Pilzkunde, pages 21, 23, and 93. 1871].

≡*Merulius* Pers., Observationes Mycologicae 1:21. 1796.

≡*Merulius* sect. *Gomphus* Pers., Synopsis Methodica Fungorum, p. 498. 1801.

≡*Cantharellus* trib. *Gomphus* (Pers.) Fr., Systema Mycologicum 1:322. 1821.

≡*Gomphus* Gray, A Natural Arrangement of British Plants 1:638. 1821.

≡*Gomphora* Fr., Systema Orbis Vegetabilis, p. 88. 1825.

≡*Nevrophyllum* Pat., *in* Doassans and Patouillard, Revue Mycologique 8:26. 1886 (*non Neurophyllum* Torrey & Gray, A Flora of North America. 1840; *Neurophyllum* Haenke & Presl, Reliquiae Haenkeanae seu Descriptiones et Icones Plantarum, quas in America Meridionali et Boreali, in Insulis Philippinis et Marianis 1, p. 356. 1830).

≡*Neurophyllum* subg. *Eu-neurophyllum* Heim., *p. p.*, Revue Mycologique 19:51. 1954.

≡*Cantharellus* sect. *Gomphus* A.H. Sm. & Morse, Mycologia 39:499. 1947.

≡*Gomphus* subg. *Gomphus* sect. *Gomphus* (Pers.) Corner, *p. p.*, Annals of Botany Memoir 2:113. 1966.

≡*Gomphus* subg. *Gomphus* (Pers.) R.H. Petersen, *p. p.*, Nova Hedwigia 21:18. 1971a.

Type species: *Gomphus clavatus* (Pers.) Gray, A Natural Arrangement of British Plants 1:638. 1821 [≡*Cantharellus clavatus* (Pers.) Fr., Systema Mycologicum 1:322. 1821.].

Gomphus brunneus (Heinem.) Corner, Annals of Botany Memoir 2:116. 1966.

≡*Neurophyllum brunneum* Heinem., Bulletin du Jardin Botanique de L'etat, Bruxelles 28:435. 1958.

=*Gomphus clavatus* var. *parvisporus* Corner, Annals of Botany Memoir 2:118. 1966.

Gomphus clavatus (Pers.) Gray, A Natural Arrangement of British Plants 1:638. 1821.

≡*Merulius clavatus* Pers., Observationes Mycologicae 1:21. 1796.

≡*Cantharellus clavatus* (Pers.) Fr., Systema Mycologicum 1:322. 1821.

≡*Craterellus clavatus* (Pers.) Fr., Epicrisis Systema Mycologicum, p. 533. 1838.

≡*Nevrophyllum clavatum* (Fr.) Pat. & Doass., *in* Doassans and Patouillard, Revue Mycologique 8:26. 1886.

≡*Cantharellus clavatus* (Pers.) Lloyd, Mycological Notes 53:762. 1918.

≡*Neurophyllum clavatum* (Pers.) Pat., *in* Petersen, Nova Hedwigia 21:16. 1971a (orthographic variant).

=*Merulius violaceus* Pers., Commentario de Fungis Clavaeformibus, p. 28. 1797b.

=*Gomphus truncatus* Pers., Mycologia Europeae 2:9. 1825.

=*Cantharellus brevipes* Peck, Annual Report of the New York State Museum of Natural History 33:21. 1880.

=*Cantharellus nucleatus* Schröd., Centralblatt für das Gesamte Forstwesen 34:398. 1908.

=*Craterellus carneus* Sacc., Flora Italica Cryptogama, fasc. 14-15:1135. 1916.

Gomphus crassipes (L.M. Dufour) Maire, *in* Maire and Werner, Mémoires de la Société des Sciences Naturelles du Maroc 45:81. 1937.

≡*Cantharellus crassipes* L.M. Dufour, Revue Générale de Botanique 1:358. 1889.

≡*Nevrophyllum crassipes* (L.M. Dufour) Maire, Bulletin de la Société Mycologique de France 30:214. 1914.

Gloeocantharellus Singer, Lloydia 8:140. 1945.

=*Linderomyces* Singer, Farlowia 3:156. 1947.

Type species: *Cantharellus purpurascens* Hesler, *in* Smith and Hesler, Lloydia 6:248. 1943.

Gloeocantharellus corneri (Singer) Corner, Nova Hedwigia 18:799. 1969.

≡*Linderomyces corneri* Singer, Vellozia 1:14. 1961 (not located, *fide* Corner, Nova Hedwigia 18: 799. 1969).

Gloeocantharellus dingleyae* (Segedin) Giachini, *comb. prov.

≡*Gomphus dingleyi*[2] Segedin, New Zealand Journal of Botany 22:536. 1984.

Gloeocantharellus echinosporus Corner, Nova Hedwigia 18:801. 1969.

Gloeocantharellus lateritius (Petch) Corner, Nova Hedwigia 18:803. 1969.

≡*Paxillus lateritius* Petch, Annals of the Royal Botanic Gardens, Peradeniya 6:202. 1917.

≡*Linderomyces lateritius* (Petch) Singer, Farlowia 3:157. 1947.

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[2] The termination 'i' is an orthographic error (International Code of Botanical Nomenclature, article 23.5) to be replaced with an 'ae' because it represents a feminine possessive form (Greuter *et al.* 2000).

≡*Gomphus lateritius* (Petch) R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:380. 1968.

Gloeocantharellus mamorensis* (Singer) Giachini, *comb. prov.

≡*Gomphus mamorensis* Singer, *in* Singer *et al.*, Beihefte zur Nova Hedwigia 77:17. 1983.

Gloeocantharellus novae-zelandiae* (Segedin) Giachini, *comb. prov.

≡*Gomphus novae-zelandiae* Segedin, New Zealand Journal of Botany 22:533. 1984.

Gloeocantharellus okapaensis (Corner) Corner, Nova Hedwigia 18:803. 1969.

≡*Gomphus okapaensis* Corner, Annals of Botany Memoir 2:123. 1966.

Gloeocantharellus pallidus* (Lloyd) Giachini, *comb. prov.

≡*Cantharellus pallidus* Lloyd, Mycological Notes 47:661. 1917.

≡*Gomphus pallidus* (Lloyd) Corner, Annals of Botany Memoir 2:123. 1966.

Gloeocantharellus papuanus* Giachini, Bougher, Castellano et Trappe, *nom. ined.

Gloeocantharellus purpurascens (Hesler) Singer, Lloydia 8:140. 1945.

≡*Cantharellus purpurascens* Hesler, *in* Smith and Hesler, Lloydia 6:248. 1943.

≡*Gomphus purpurascens* (Hesler) R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:380. 1968.

Phaeoclavulina Brinkmann, Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst 25:197. 1897.

≡*Clavaria* sect. *Phaeoclavulina* (Brinkmann) Killerm., *in* Engler and Prantl, Die Natürlichen Pflanzenfamilien 6:155. 1928 (not located, *fide* Petersen, Bibliotheca Mycologica 79:44. 1981).

=*Lachnocladium* sect. *Dendrocladium* Pat., Journal de Botanique 3:26. 1889.

≡*Dendrocladium* (Pat.) Lloyd, Mycological Notes 60:870. 1919.

≡*Ramaria* subg. *Echinoramaria* sect. *Dendrocladium* (Pat.) R.H. Petersen, Bibliotheca Mycologica 79:44. 1981.

=*Chloroneuron* Murrill, Mycologia 3:25. 1911.

≡*Chlorophyllum* (Pat.) Murrill, *nom. illeg.*, North American Flora 9:172. 1910.

=*Clavaria* sect. *Clavariella* subsect. *Terrestres* Killerm., *in* Engler and Prantl, Die Natürlichen Pflanzenfamilien 6:154. 1928 (not located, *fide* Petersen, Bibliotheca Mycologica 79:100. 1981).

=*Neurophyllum* subg. *Chloroneuron* Heim., Revue Mycologique 19:51. 1954.

=*Ramaria* subg. *Echinoramaria* Corner, Beihefte zur Nova Hedwigia 33:238. 1970.

≡*Ramaria* subg. *Echinoramaria* ser. *Grandisporae* Corner, Beihefte zur Nova Hedwigia 33:239. 1970.

=*Ramaria* subg. *Echinoramaria* ser. *Flaccidae* Corner, Beihefte zur Nova Hedwigia 33:239. 1970.

≡*Ramaria* subg. *Echinoramaria* sect. *Flaccidae* (Corner) R.H. Petersen, Bibliotheca Mycologica 79:100. 1981.

=*Ramaria* subg. *Echinoramaria* ser. *Virescentes* Corner, Beihefte zur Nova Hedwigia 33:239. 1970.

=*Gomphus* subg. *Phaeoclavulinoides* R.H. Petersen, Mycologia 68:432. 1976a.

Type species: *Phaeoclavulina macrospora* Brinkmann, Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst 25:198. 1897.

Phaeoclavulina africana* (R.H. Petersen) Giachini, *comb. prov.

≡*Gomphus africanus* R.H. Petersen, Mycologia 68:429. 1976a.

Phaeoclavulina angustata* (Lév.) Giachini, *comb. prov.

≡*Merisma angustatum* Lév., Annales des Sciences Naturelles Botanique 3(5):158. 1846.

≡*Thelephora angustata* Fr., Nova Acta Regiae Societatis Scientiarum Upsaliensis 3:116. 1854.

≡*Ramaria angustata* (Fr.) Corner, Beihefte zur Nova Hedwigia 33:242. 1970.

Phaeoclavulina apiahyna* (Speg.) Giachini, *comb. prov.

≡*Clavaria apiahyna* Speg., Boletin de la Academia Nacional de Ciencias de Córdoba 23:435. 1918.

≡*Ramaria apiahyana* (Speg.) Corner, Annals of Botany Memoir 1:555. 1950.

Phaeoclavulina argentea* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria argentea* R.H. Petersen, Bibliotheca Mycologica 79:111. 1981.

=*Ramaria incognita* R.H. Petersen, Bibliotheca Mycologica 79:145. 1981.

=*Ramaria incongrua* R.H. Petersen, Bibliotheca Mycologica 79:147. 1981.

Phaeoclavulina articulotela* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria articulotela* R.H. Petersen, Bibliotheca Mycologica 79:115. 1981.

Phaeoclavulina camellia* (Corner) Giachini, *comb. prov.

≡*Ramaria camellia* Corner, Darwiniana 11:200. 1957.

Phaeoclavulina campestris* (K. Yokoy. & Sagara) Giachini, *comb. prov.

≡*Ramaria zippelii* var. *campestris* K. Yokoy. & Sagara, Transactions of the Mycological Society of Japan 14:302. 1973.

≡*Ramaria campestris* (K. Yokoy. & Sagara) R.H. Petersen, Bibliotheca Mycologica 79:57. 1981.

Phaeoclavulina campoi* (Speg.) Giachini, *comb. prov.

≡*Clavaria campoi* Speg., Boletin de la Academia Nacional de Ciencias de Córdoba 25:28. 1921.

Phaeoclavulina capucina* (Pat.) Giachini, *comb. prov.

≡*Clavaria capucina* Pat., Bulletin de la Société Mycologique de France 33:50. 1917.

≡*Ramaria capucina* (Pat.) Corner, Annals of Botany Memoir 1:565. 1950.

Phaeoclavulina cervicornis* (A.L. Sm.) Giachini, *comb. prov.

≡*Clavaria cervicornis* A.L. Sm., Journal of the Linnean Society of London. Botany 35:10. 1901.

≡*Ramaria cervicornis* (A.L. Sm.) Corner, Annals of Botany Memoir 1:565. 1950.

Phaeoclavulina clavarioides* (Schild) Giachini, *comb. prov.

≡*Ramaria clavarioides* Schild, Zeitschrift für Mykologie 64:60. 1998.

Phaeoclavulina cokeri* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria cokeri* R.H. Petersen, The Distributional History of the Biota of the Southern Appalachians, p. 291. 1976b.

=*Clavaria echinospora* Berk. & Broome, Journal of the Linnean Society of London. Botany 14:75. 1875.

=*Clavaria echinospora* Henn., *nom. illeg.*, Monsunia 1:141. 1899.

=*Clavaria fragillima* Sacc. & P. Syd., Sylloge Fungorum Omnium Hucusque Cognitorum 16:206. 1902.

≡*Clavariella fragillima* (Sacc. & Syd.) Overeem, *in* Overeem and Weese, Icones Fungorum Malayensium I-IV. 1923.

≡*Ramaria fragillima* (Sacc. & Syd.) Corner, Annals of Botany Memoir 1:588. 1950.

Phaeoclavulina curta* (Fr.) Giachini, *comb. prov.

≡*Clavaria curta* Fr., Monographia Hymenomycetum Sueciae 2(69):281. 1863.

≡*Ramariopsis curta* (Fr.) Corner, Annals of Botany Memoir 1:639. 1950.

=*Clavaria pusilla* Peck, Bulletin of the Buffalo Society of Natural Science 1:62. 1873 (*non C. pusilla* (Pers.:Fr.) Pers., Mycologia Europeae 1:187. 1822).

≡*Ramaria pusilla* (Peck) Corner var. *pusilla*, Annals of Botany Memoir 1:617. 1950.

=*Clavaria myceliosa* Peck, Bulletin of the Torrey Botanical Club 31(4):182. 1904.

≡*Ramaria myceliosa* (Peck) Corner var. *myceliosa*, Annals of Botany Memoir 1:607. 1950.

≡*Ramaria myceliosa* var. *microspora* R.H. Petersen, Bibliotheca Mycologica 79:157. 1981.

=*Clavaria decurrens* var. *australis* Coker, The Clavarias of the United States and Canada, p. 177. 1923.

≡*Ramaria pusilla* var. *australis* (Coker) Corner, Annals of Botany Memoir 1:618. 1950.

≡*Ramaria decurrens* var. *australis* (Coker) R.H. Petersen, Bibliotheca Mycologica 79:127. 1981.

=*Ramaria subdecurrens* var. *burnhami* R.H. Petersen, Bibliotheca Mycologica 79:171. 1981.

Phaeoclavulina cyanocephala* (Berk. & M.A. Curtis) Giachini, *comb. prov.

≡*Clavaria cyanocephala* Berk. & M.A. Curtis, The Journal of the Linnean Society of London. Botany 10:338. 1869.

≡*Ramaria cyanocephala* (Berk. & M.A. Curtis) Corner, Annals of Botany Memoir 1:568. 1950.

≡*Ramaria grandis* f. *cyanocephala* (Berk. & M.A. Curtis) R.H. Petersen, Bibliotheca Mycologica 79:71. 1981.

=*Clavaria grandis* Peck, Bulletin of the Torrey Botanical Club 29(2):73. 1902.

≡*Ramaria grandis* (Peck) Corner f. *grandis*, Annals of Botany Memoir 1:595. 1950.

=*Clavaria spiculospora* G.F. Atk., Annales Mycologici 7:368. 1909.

≡*Clavaria spiculisperma* (G.F. Atk.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 21:426. 1912 (*lapsus calamitus*).

=*Ramaria zippelii* f. *aeruginosa* R.H. Petersen, Bibliotheca Mycologica 79:96. 1981.

Phaeoclavulina decolor* (Berk. & M.A. Curtis) Giachini, *comb. prov.

≡*Clavaria decolor* Berk. & M.A. Curtis, Proceedings of the American Academy of Arts and Sciences 4:124. 1858.

≡*Ramaria decolor* (Berk. & M.A. Curtis) R.H. Petersen, Persoonia 12(3):231. 1984.

=*Ramaria zippelii* var. *cristatospora* Corner, Proceedings of the Linnean Society of London 178:103. 1967.

≡*Ramaria cristatospora* (Corner) R.H. Petersen, Bibliotheca Mycologica 79:64. 1981.

Phaeoclavulina echinovirens* (Corner, K.S. Thind & Dev) Giachini, *comb. prov.

≡*Ramaria echinovirens* Corner, K.S. Thind & Dev, Transactions of the British Mycological Society 40:473. 1957.

Phaeoclavulina eumorpha* (P. Karst.) Giachini, *comb. prov.

≡*Clavariella spinulosa* subsp. *eumorpha* P. Karst., Bidrag till Kännedom af Finlands Natur och Folk 37:185. 1882.

≡*Clavaria eumorpha* (P. Karst.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:701. 1888.

≡*Clavaria spinulosa* subsp. *eumorpha* (P. Karst.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:701. 1888.

≡*Clavariella eumorpha* (P. Karst.) P. Karst., Bidrag till Kännedom af Finlands Natur och Folk 48:388. 1889.

≡*Ramaria eumorpha* (P. Karst.) Corner, Annals of Botany Memoir 1:575. 1950.

=*Clavaria patagonica* Speg., Flora Patagonica 11:19. 1887.

≡*Clavulinopsis patagonica* (Speg.) Corner, Annals of Botany Memoir 1:383. 1950.

≡*Ramaria patagonica* (Speg.) Corner, Darwiniana 11:203. 1957.

=*Clavaria invalii* Cotton & Wakef., Transactions of the British Mycological Society 6:176. 1919.

≡*Ramaria invalii* (Cotton & Wakef.) Donk, Bibliotheca Mycologica 29:113. 1933.

≡*Clavaria flaccida* subsp. *invalii* (Cotton & Wakef.) Konrad & Maubl., Icones Selectae Fungorum, p. 7. 1935.

≡*Clavaria flaccida* var. *invalii* (Cotton & Wakef.) J. Favre, Matériaux pour la Flore Cryptogamique Suisse 10(3):32. 1948.

=*Clavaria murrillii* Coker, The Clavarias of the United Sates and Canada, p. 190. 1923.

≡*Ramaria murrillii* (Coker) Corner, Annals of Botany Memoir 1:607. 1950.

Phaeoclavulina flaccida* (Fr.) Giachini, *comb. prov.

≡*Clavaria flaccida* Fr., Systema Mycologicum 1:471. 1821.

≡*Clavariella flaccida* (Fr.) P. Karst. var. *flaccida*, Revue Mycologique 3:21. 1880.

≡*Ramaria flaccida* (Fr.) Bourdot var. *flaccida*, Revue Scientifique du Bourbonnais et du Centre de la France 11:235. 1898.

=*Clavaria abietina* Fr. f. *abietina*, Systema Mycologicum 1:469. 1821 (*non Clavaria abietina* Pers., Mycologia Europeae 1:164. 1822).

=*Clavaria crispula* Fr., Systema Mycologicum 1:470. 1821.

≡*Clavariella crispula* (Fr.) P. Karst., Revue Mycologique 3:21. 1880.

≡*Ramaria crispula* (Fr.) Quél., Flore Mycologique de la France, p. 464. 1888.

=*Clavaria decurrens* Pers. Mycologia Europeae 1:164. 1822.

≡*Ramaria decurrens* (Pers.) R.H. Petersen var. *decurrens*, Bibliotheca Mycologica 79:124. 1981.

=*Clavaria corrugata* P. Karst., Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar 9:371. 1868.

≡*Clavariella corrugata* P. Karst., Revue Mycologique 3:21. 1880.

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≡*Ramaria subdecurrens* (Coker) Corner var. *subdecurrens*, Annals of Botany Memoir 1:626. 1950.

=*Ramaria ligustri* Velen., Novitates Mycologicae, p. 162. 1939.

=*Ramaria fuscobrunnea* Corner, *in* Balfour-Browne, Bulletin of the British Museum of Natural History 1:200. 1955.

=*Ramaria flaccida* var. *longiramosa* Corner, Beihefte zur Nova Hedwigia 33:250. 1970.

=*Ramaria perfluo-punicea* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:100. 1988.

Phaeoclavulina gigantea* (Pat.) Giachini, *comb. prov.

≡*Lachnocladium giganteum* Pat., Journal de Botanique 3:34. 1889.

≡*Ramaria gigantea* (Pat.) R.H. Petersen f. *gigantea*, Bibliotheca Mycologica 79:66. 1981.

=*Lachnocladium olivaceum* Henn., Hedwigia 36:196. 1897b.

=*Lachnocladium echinosporum* Bres., Annales Mycologici 9:551. 1911.

=*Ramaria zippelii* var. *gracilis* Corner, Annals of Botany Memoir 1:635. 1950.

=*Ramaria gigantea* f. *tenuispora* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:97. 1988.

Phaeoclavulina glauco-aromatica* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria glauco-aromatica* R.H. Petersen, Bibliotheca Mycologica 79:141. 1981.

Phaeoclavulina grandis* (Corner) Giachini, *comb. prov.

≡*Gomphus grandis* Corner, Nova Hedwigia 18:812. 1969.

Phaeoclavulina griseobrunnea* (Singer) Giachini, *comb. prov.

≡*Ramaria griseobrunnea* Singer, *in* Singer *et al.*, Beihefte zur Nova Hedwigia 77:19. 1983.

Phaeoclavulina guadelupensis* (Pat.) Giachini, *comb. prov.

≡*Stereum guadelupense* Pat., Bulletin de la Société Mycologique de France 15:201. 1899.

≡*Gomphus guadelupensis* (Pat.) D.A. Reid, Persoonia 2:134. 1962.

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≡*Cantharellus ochraceus* (Pat.) Sacc. & D. Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 17:36. 1905.

≡*Gomphus ochraceus* (Pat.) Singer, Lloydia 8:140. 1945.

Phaeoclavulina guyanensis* (Pat.) Giachini, *comb. prov.

≡*Lachnocladium guyanense* Pat., Journal de Botanique 3:35. 1889.

≡*Ramaria guyanensis* (Pat.) Corner, Annals of Botany Memoir 1:596. 1950.

=*Lachnocladium leucoceras* Pat., Journal de Botanique 3:33. 1889.

≡*Ramaria leucoceras* (Pat.) Corner, Annals of Botany Memoir 1:600. 1950.

Phaeoclavulina insignis* (Pat.) Giachini, *comb. prov.

≡*Lachnocladium insigne* Pat., Journal de Botanique 3:34. 1889.

≡*Ramaria insigne* (Pat.) R.H. Petersen, Bibliotheca Mycologica 79:77. 1981.

Phaeoclavulina longicaulis* (Peck) Giachini, *comb. prov.

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≡*Ramaria longicaulis* (Peck) Corner, Annals of Botany Memoir 1:600. 1950.

***Phaeoclavulina macrospora* Brinkmann,** Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst 25:198. 1897.

≡*Ramaria macrospora* (Brinkmann) Corner, Annals of Botany Memoir 1:603. 1950 (*non Ramaria macrospora* Velen., Opera Botanica Čechica 4:90. 1947).

=*Clavaria broomei* Cotton & Wakef., Transactions of the British Mycological Society 6:170. 1919.

≡*Phaeoclavulina broomei* (Cotton & Wakef.) Overeem, Bulletin du Jardin Botanique de Buitenzorg 3(5):277. 1923.

≡*Ramaria broomei* (Cotton & Wakef.) R.H. Petersen, Bibliotheca Mycologica 79:53. 1981.

=*Ramaria nigrescens* (Brinkmann) Donk var. *nigrescens*, Bibliotheca Mycologica 21:104. 1933 [*nom. illeg.*, *sensu* Coker, The Clavarias of the United States and Canada, p. 187, *in. obs.* 1923].

=*Ramaria nigrescens* var. *americana* Corner, Annals of Botany Memoir 1:608. 1950.

≡*Ramaria americana* (Corner) R.H. Petersen, Bibliotheca Mycologica 79:48. 1981.

Phaeoclavulina mutabilis* (Schild & R.H. Petersen) Giachini, *comb. prov.

=*Ramaria mutabilis* Schild & R.H. Petersen, *in* Petersen, Bibliotheca Mycologica 79:149. 1981.

Phaeoclavulina ochracea* (Bres.) Giachini, *comb. prov.

≡*Lachnocladium ochraceum* Bres., *in* Bresadola and Saccardo, Bulletin de la Société Royale de Botanique de Belgique 38:157. 1899.

≡*Ramaria ochracea* (Bres.) Corner var. *ochracea*, Annals of Botany Memoir 1:610. 1950.

=*Clavaria intricatissima* Speg., Anales del Museo Nacional de Buenos Aires 19:279. 1909.

≡*Ramaria intricatissima* (Speg.) Corner, Annals of Botany Memoir 1:598. 1950.

=*Ramaria luteo-flaccida* Corner, Annals of Botany Memoir 1:601. 1950.

=*Ramaria flaccida* var. *chilensis* Lazo, Mycologia 64:73. 1972.

=*Ramaria ochracea* var. *sicco-olivacea* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:98. 1988.

Phaeoclavulina ochraceo-virens* (Jungh.) Giachini, *comb. prov.

≡*Clavaria ochraceo-virens* Jungh., Linnaea 5:407. 1830.

≡*Ramaria ochraceovirens* (Jungh.) Donk var. *ochraceovirens*, Bibliotheca Mycologica 21:112. 1933.

=*Clavaria abietina* Pers. f. *abietina*, *nom. illeg.*, Mycologia Europeae 1:164. 1822 (*non Clavaria abietina* Fr., Systema Mycologicum 1:469. 1821).

≡*Merisma abietina* (Pers.) Spreng., Systema Vegetabilium 4:495. 1827.

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≡*Ramaria abietina* (Pers.) Quél., Flore Mycologique de la France, p. 467. 1888.

=*Clavaria abietina* var. *virens* Gillet, Tableaux Analytiques des Hyménomycètes de France, p. 183. 1884.

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≡*Ramaria virescens* Gramberg, *in* Michael, Führer für Pilzfreunde 3:320. 1927.

=*Clavaria cyanescens* S. Lundell, *in* Krok and Almquist, *Svensk Flora för Skolor*, 5 ed., 2:286. 1932 (not located, *fide* Corner, Annals of Botany Memoir 1: 611. 1950).

=*Ramaria ochrochlora* Furrer-Ziogas & Schild, *in* Schild, Fungorum Rariorum Icones Coloratae 5:17. 1971.

=*Ramaria ochraceovirens* var. *parvispora* K.S. Thind, Khurana & S.C. Kaushal, Kavaka 11:33. 1982.

Phaeoclavulina pancaribbea* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria pancaribbea* R.H. Petersen f. *pancaribbea*, Bibliotheca Mycologica 79:88. 1981.

=*Ramaria pancaribbea* f. *caerulea* R.H. Petersen, Bibliotheca Mycologica 79:90. 1981.

Phaeoclavulina quercus-ilicis* (Schild) Giachini, *comb. prov.

≡*Ramaria quercus-ilicis* Schild, Zeitschrift für Mykologie 64:53. 1998.

Phaeoclavulina retispora* (Corner) Giachini, *comb. prov.

≡*Gomphus retisporus* Corner, Annals of Botany Memoir 2:124. 1966.

Phaeoclavulina roellinii* (Schild) Giachini, *comb. prov.

≡*Ramaria roellinii* Schild, Schweizerische Zeitschrift für Pilzkunde 56:97. 1978.

Phaeoclavulina sikkimia* (S.S. Rattan & Khurana) Giachini, *comb. prov.

≡*Ramaria sikkimia* S.S. Rattan & Khurana, Bibliotheca Mycologica 66:18. 1978.

Phaeoclavulina subclaviformis* (Berk.) Giachini, *comb. prov.

≡*Thelephora subclavaeformis*[3] Berk., Bulletin of Miscellaneous Information 8:238. 1856.

≡*Gomphus subclavaeformis* (Berk.) Corner, Nova Hedwigia 18:815. 1969.

=*Gomphus cavipes* Corner, Nova Hedwigia 18:808. 1969.

Phaeoclavulina tropicalis* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria tropicalis* R.H. Petersen, Bibliotheca Mycologica 79:173. 1981.

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[3] The 'ae' connective is an orthographic error (International Code of Botanical Nomenclature, article 60G.1) to be replaced with an 'i' (Greuter *et al.* 2000).

Phaeoclavulina vinaceipes* (Schild) Giachini, *comb. prov.

≡*Ramaria vinaceipes* Schild, Zeitschrift für Mykologie 56(1):131. 1990.

Phaeoclavulina viridis* (Pat.) Giachini, *comb. prov.

≡*Nevrophyllum viride* Pat., Journal de Botanique 2:406. 1888.

≡*Chlorophyllum viride* (Pat.) Murrill, *nom. illeg.*, North American Flora 9:172. 1910.

≡*Gomphus viridis* (Pat.) Singer, Lloydia 8:140. 1945.

=*Cantharellus patouillardii* Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 9:65. 1891.

Phaeoclavulina zealandica* (R.H. Petersen) Giachini, *comb. prov.

≡*Ramaria pancaribbea* var. *zealandica* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:1988.

Phaeoclavulina zippelii* (Lév.) Giachini, *comb. prov.

≡*Clavaria zippelii* Lév., Annales des Sciences Naturelles Botanique 3(2):215. 1844.

≡*Phaeoclavulina zippelii* (Lév.) Overeem, Bulletin du Jardin Botanique de Buitenzorg 3(5):276. 1923.

≡*Ramaria zippelii* (Lév.) Corner f. *zippelii*, Annals of Botany Memoir 1:632. 1950.

=*Merisma guadelupense* Lév., Annales des Sciences Naturelles Botanique 3(5):157. 1846.

≡*Pterula guadelupensis* (Lév.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:742. 1888.

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=*Clavaria nigrescens* Fr., Nova Acta Regiae Societatis Scientiarum Upsaliensis 3:116. 1854.

=*Clavaria thwaitesii* Berk. & Broome, Journal of the Linnean Society of London. Botany 14:75. 1875.

=*Lachnocladium hookeri* Berk., *in* Berkeley and Broome, Journal of the Linnean Society of London. Botany 14:75. 1875.

=*Lachnocladium englerianum* Henn., Die Natürlichen Pflanzenfamilien, 1 ed., p. 138. 1897a.

=*Clavaria aeruginosa* Pat., Bulletin de la Société Mycologique de France 14:189. 1898.

≡*Ramaria zippellii* var. *aeruginosa* (Pat.) R.H. Petersen, Bibliotheca Mycologica 79:96. 1981.

=*Lachnocladium albidum* Pat., Bulletin de la Société Mycologique de France 14:188. 1898.

≡*Ramaria albida* (Pat.) Corner, Annals of Botany Memoir 1:554. 1950.

=*Clavaria phaeocladia* Pat., Bulletin de la Société Mycologique de France 14:189. 1898.

=*Lachnocladium neglectum* Massee, ?, (not located, *fide* Corner, Annals of Botany Memoir 1:633. 1950).

Turbinellus Earle, Bulletin of the New York Botanical Garden 5:407. 1909.

≡*Chanterel* (Adans.) Murrill, North American Flora 9:168. 1910.

≡*Cantharellus* sect. *Excavatus* A.H. Sm. & Morse, Mycologia 39:500. 1947.

≡*Gomphus* subg. *Gomphus* sect. *Excavatus* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:113. 1966.

≡*Gomphus* subg. *Excavatus* (A.H. Sm. & Morse) R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:381. 1968.

=*Gomphus* subg. *Gomphorellus* Corner, *p. p.*, Annals of Botany Memoir 2:113. 1966.

Type species: *Cantharellus floccosus* Schwein., Transactions of the American Philosophical Society 4:153. 1831.

Turbinellus flabellatus* (Berk.) Giachini, *comb. prov.

≡*Cantharellus flabellatus* Berk., Challenger Report 3:50. 1873.

≡*Gomphus flabellatus* (Berk.) Corner, Annals of Botany Memoir 2:119. 1966.

=*Cantharellus glutinosus* Pat., Bulletin de la Société Mycologique de France 25:7. 1909.

≡*Gomphus glutinosus* (Pat.) R.H. Petersen, Nova Hedwigia 21:91. 1971a.

Turbinellus floccosus (Schwein.) Earle, Bulletin of the New York Botanical Garden 5:407. 1909.

≡*Cantharellus floccosus* Schwein. f. *floccosus*, Transactions of the American Philosophical Society 4:153. 1831.

≡*Craterellus floccosus* Boud., Bulletin de la Societé Botanique de France 24:308. 1877.

≡*Chanterel floccosus* (Schwein.) Murrill, North American Flora 9:168. 1910.

≡*Gomphus floccosus* (Schwein.) Singer f. *floccosus*, Lloydia 8:140. 1945.

≡*Cantharellus floccosus* f. *typicus* A.H. Sm. & Morse, Mycologia 39:521. 1947.

≡*Nevrophyllum floccosum* (Schwein.) R. Heim, Revue Mycologique 19:51. 1954.

=*Cantharellus canadensis* (Klotzsch) Berk., The Annals and Magazine of Natural History 1(3):380. 1839.

≡*Craterellus canadensis* (Klotzsch) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:519. 1888.

≡*Gomphus canadensis* (Klotzsch) Corner, Annals of Botany Memoir 2:116. 1966.

=*Cantharellus princeps* Berk. & M.A. Curtis, The Annals and Magazine of Natural History 3(4):293. 1859.

=*Cantharellus bonarii* Morse, Mycologia 22:219. 1930.

≡*Gomphus bonarii* (Morse) Singer f. *bonarii*, Lloydia 8:140. 1945.

=*Cantharellus floccosus* f. *excavatus* A.H. Sm. & Morse, Mycologia 39:525. 1947.

≡*Gomphus floccosus* f. *excavatus* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:121. 1966.

=*Cantharellus floccosus* f. *rainieriensis* A.H. Sm. & Morse, Mycologia 39:521. 1947.

≡*Gomphus floccosus* f. *rainieriensis* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:121. 1966.

≡*Gomphus floccosus* subsp. *rainieriensis* (A.H. Sm. & Morse) R.H. Petersen, Nova Hedwigia 21:48. 1971a.

=*Cantharellus floccosus* f. *wilsonii* A.H. Sm. & Morse, Mycologia 39:523. 1947.

≡*Gomphus floccosus* f. *wilsonii* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:121. 1966.

≡*Gomphus bonarii* (Morse) Singer f. *wilsonii* (A.H. Sm. & Morse) R.H. Petersen, Nova Hedwigia 21:37. 1971a.

=*Cantharellus wilkinsae* Morse, *in* A.H. Sm. and Morse, Mycologia 39:528. 1947.

≡*Gomphus wilkinsae* (Morse) Corner, Annals of Botany Memoir 2:128. 1966.

≡*Gomphus bonarii* f. *wilkinsae* (Morse) R.H. Petersen, Nova Hedwigia 21:35. 1971a.

=*Gomphus floccosus* f. *cystidiophorus* R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:376. 1968.

=*Gomphus megasporus* Corner, Nova Hedwigia 18:813. 1969.

=*Gomphus bonarii* f. *novamexicanus* R.H. Petersen, Nova Hedwigia 21:44. 1971a.

=*Gomphus floccosus* f. *coccineo-basalis* R.H. Petersen, Nova Hedwigia 21:52. 1971a.

=*Gomphus floccosus* f. *olivaceous* R.H. Petersen, Nova Hedwigia 21:54. 1971a.

=*Gomphus szechwanensis* R.H. Petersen, Nova Hedwigia 21:102. 1971a.

=*Gomphus thiersii* R.H. Petersen, Evolution in the Higher Basidiomycetes, p. 363. 1971b.

Turbinellus fujisanensis* (S. Imai) Giachini, *comb. prov.

≡*Cantharellus fujisanensis* S. Imai, The Botanical Magazine 55:519. 1941.

≡*Neurophyllum fujisanensis* (S. Imai) S. Ito, Mycological Flora of Japan 2:103. 1955.

Turbinellus kauffmanii* (A.H. Sm.) Giachini, *comb. prov.

≡*Cantharellus kauffmanii* A.H. Sm., *in* Smith and Morse, Mycologia 39:516. 1947.

≡*Gomphus kauffmanii* (A.H. Sm.) Corner, Annals of Botany Memoir 2:122. 1966.

Turbinellus stereoides* (Corner) Giachini, *comb. prov.

≡*Gomphus stereoides* Corner, Annals of Botany Memoir 2:124. 1966.

=*Gomphus brasiliensis* Corner, Nova Hedwigia 18:807. 1969.

DISCUSSION

Gomphus, as discussed earlier, was originally proposed to accommodate the single species *G. clavatus*. Many other were later added, expanding not only the diversity but also the known distribution of the genus. The similarities in spore morphology and the configuration of the hymenium were the main features used to accommodate species in *Gomphus sensu lato*; many of these species now prove to belong to genetically distinct genera.

Most previous studies on gomphoid fungi have discussed the close evolutionary relationships of members within the Gomphales. Petersen (1968,

1971ab), following Heim (1954) and Maire (1902), eloquently elaborated on the evolution of basidioma shape within the family Gomphaceae. The characters discussed earlier, in one state or another, are seen in almost all the genera that compose the family Gomphaceae, and are considered the morphological 'signature' uniting the members of this family. In addition, other features typify the representatives of the Gomphaceae (this topic will be discussed in chapter 7).

Hibbett *et al.* (1997), Pine *et al.* (1999), and later Humpert *et al.* (2001) have shown the genus *Ramaria,* long recognized as having morphological features similar to *Gomphus sensu lato*, to be evolutionarily close related to the species of that genus. Aside from the overall evolutionary relationships of *Gomphus sensu lato* and *Ramaria*, the data from this study reveal a closer relationship of some species of *Gomphus sensu lato* with species of *Ramaria* subgenus *Echinoramaria* (see figures 2.1 and 2.2). Although unforeseen at first because of the quite distinct shape of the basidiomata – funnel-shaped or fan-shaped pilei for the former versus ramarioid for the latter, they share similar macroscopic and especially microscopic features. Perhaps the most striking similarities are the presence of clamp connections, observed in all species, and their mostly tropical to subtropical distribution. Species of *Ramaria* subgenus *Echinoramaria* are also morphologically distinct from other species of *Ramaria*: they possess clamp connection and have echinulate or verrucose spores, and can be either terrestrial or lignicolous. As observed in figures 2.1 and 2.2, species of *Ramaria* subgenus *Echinoramaria* cladded in a separate group from other *Ramaria* species, corroborating the non-monophyletic status of the genus *Ramaria* (Humpert *et al.* 2001). Even though not all species of *Ramaria* subgenus *Echinoramaria* were genetically sampled, overall similarities suggest the species of *Ramaria* subgenus *Echinoramaria* and those of *Gomphus sensu lato* forming a monophyletic group to be combined under a single generic name. The oldest name employed for a member of that clade is *Phaeoclavulina* (Brinkmann 1897). Therefore, for reasons of priority, in accordance to the International Code of Botanical Nomenclature (Greuter *et al.* 2000), species of *Ramaria* subgenus *Echinoramaria* and *G. africanus, G. grandis,*

G. guadelupensis, G. subclavaeformis, and *G. viridis* are here transferred to the resurrected genus *Phaeoclavulina* (Figures 2.2 and 2.3). This transfer is justified by both morphology and genetics. Because *Phaeoclavulina* composes the most basal node on the topological arrangement obtained, its placement is of crucial importance to understand the evolution and systematic biology of species within the order Gomphales.

Of the genera treated here, *Gomphus* and *Phaeoclavulina* share the most macro- and microscopic features. Although *Phaeoclavulina* is mostly ramarioid, it also includes a few pileate species previously in *Gomphus sensu lato*. Therefore, both *Gomphus* and *Phaeoclavulina* have unipileate or merismatoid species that present fan- to somewhat funnel-shaped pilei. Nearly all species have decurrent hymenia with wrinkled hymenial folds, and all species, with no exception, possess clamp connections. The main difference between *Gomphus* and *Phaeoclavulina* resides in spore ornamentation, which can be echinulate, verrucose, subreticulate or reticulate for the latter while strictly verrucose for the former. These similarities are by no means coincidence, as *Phaeoclavulina* represents the ancestral lineage of the Gomphales.

Turbinellus, another genus name resurrected here, was originally proposed by Earle (1909) to accommodate *Cantharellus floccosus* Schwein. (Schweinitz 1831). Earle (1909) assigned 3 species to this genus, all from North America and according to him having more in common with the club-shaped species of *Craterellus* than with species of *Cantharellus*. *Turbinellus* species were later transferred to *Gomphus* (Singer 1945), then *Cantharellus* (Smith and Morse 1947), *Nevrophyllum* (Heim 1954 - only *T. floccosus*), and finally back to *Gomphus* (Corner 1966).

Most species previously described under *Gomphus sensu lato* are now placed in *Turbinellus*. The taxonomy of these species has been challenging over the years, especially because reliable morphological features for species-level identification were lacking, resulting in many synonyms. Accordingly, I sampled all species, forms, and subspecies and genetically determined the species

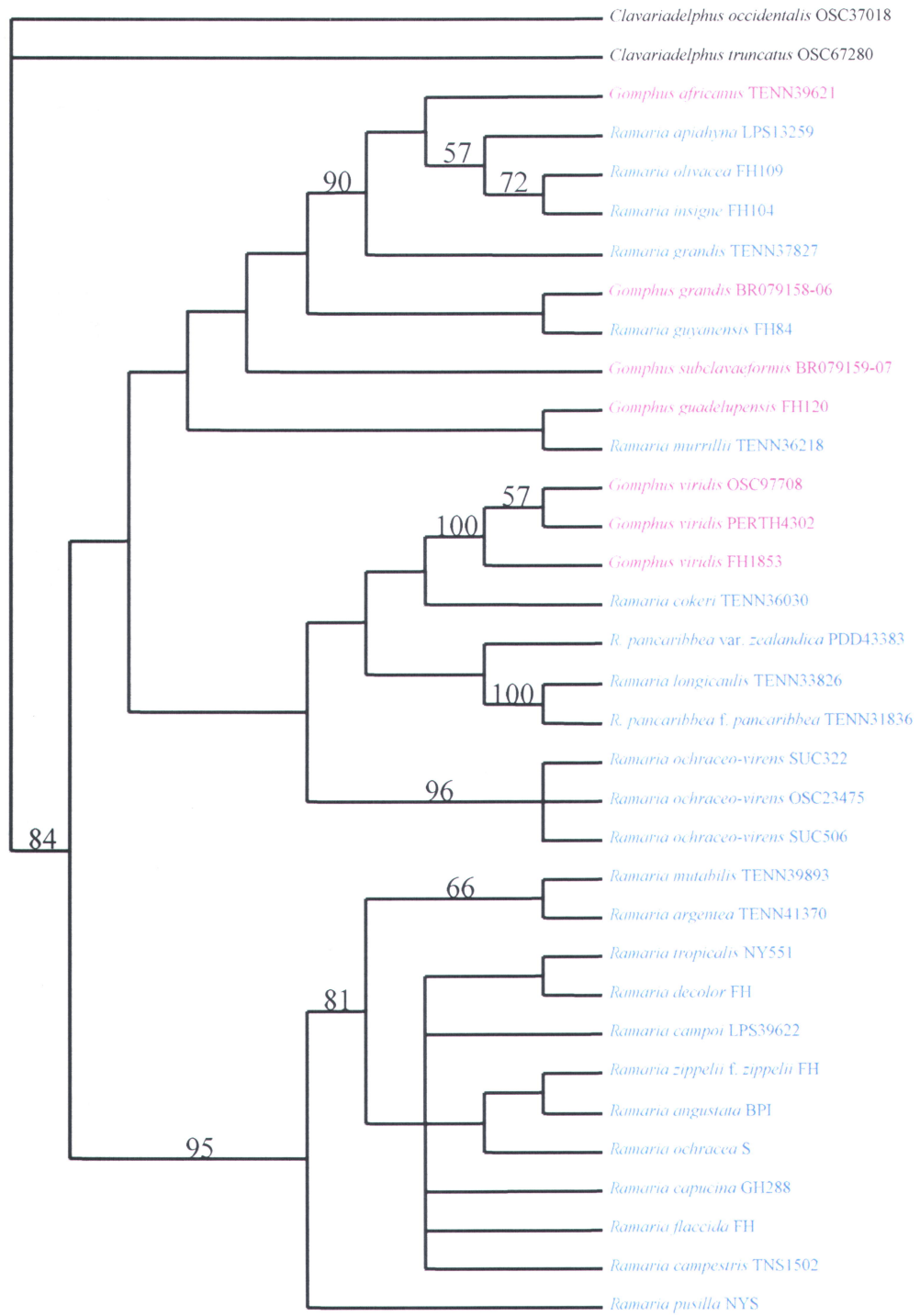

Figure 2.3. Strict consensus cladogram of 45 equally parsimonious (MP) trees of 483 steps based on nuc-25S-rDNA sequences. Bootstrap values above 50% are indicated at each respective internode. CI=0.416, RI=0.631, RC=0.263.

boundaries. Many species delimited on morphological grounds proved to be phenotypic variants of a few well-supported genetic species. According to the genetic data, *G. bonarii* and *G. floccosus* and all their forms and subspecies are phenotypes of only one genotype (Figures 2.2 and 2.4). Hence, the previously known species *G. bonarii* and *G. floccosus*, and their variants are here synonymized, with priority for the name *Turbinellus floccosus*. *Turbinellus* also contains the newly recombined species *T. flabellatus, T. fujisanensis, T. kauffmanii,* and *T. stereoides*.

Gomphus sensu stricto and *Gloeocantharellus* are fairly easily differentiate based on shape of the spores, presence of gleoplerous hyphae, and ubiquity of clamp connections in *Gomphus sensu stricto* vs. the irregular presence of these structures in *Gloeocantharellus*. *Gomphus sensu stricto* has rosaceous, sordid yellow, orange-brown to violet basidiomata with wrinkled to poroid hymenium, in contrast to *Gloeocantharellus*, which has brown-yellow, pink-orange to red basidiomata that can have true lamellate hymenia. Singer (1945) used Hesler's *Cantharellus purpurascens* as type (Smith and Hesler 1943) for *Gloeocantharellus* because it possessed gleocystidia, which *Cantharellus* lacks. However, only some species of *Gloeocantharellus* possesses gleocystidia. *Gloeocantharellus* is also characterized by massive numbers of gleoplerous hyphae dispersed among all hyphal tissues, separating it from other genera in the Gomphaceae. Only one species, *G. purpurascens* is known from North America. Most others are from Indochina or Central and South America. Because of the small number of species known for the genus, only superficial attention has been devoted to its biology and evolution in past discussions (Petersen 1971a). A thorough description of the species and a complete discussion regarding the placement of this genus among other members of the Gomphales is discussed in chapter 7.

For several decades now *Cantharellus pseudoclavatus* A.H. Sm. (Smith and Morse 1947) has been classified under *Gomphus sensu lato* (Corner 1966). After analyzing the type collection (MICH 6916), however, I concluded that it better fit the description of *Cantharellus*. The main morphological character justifying its

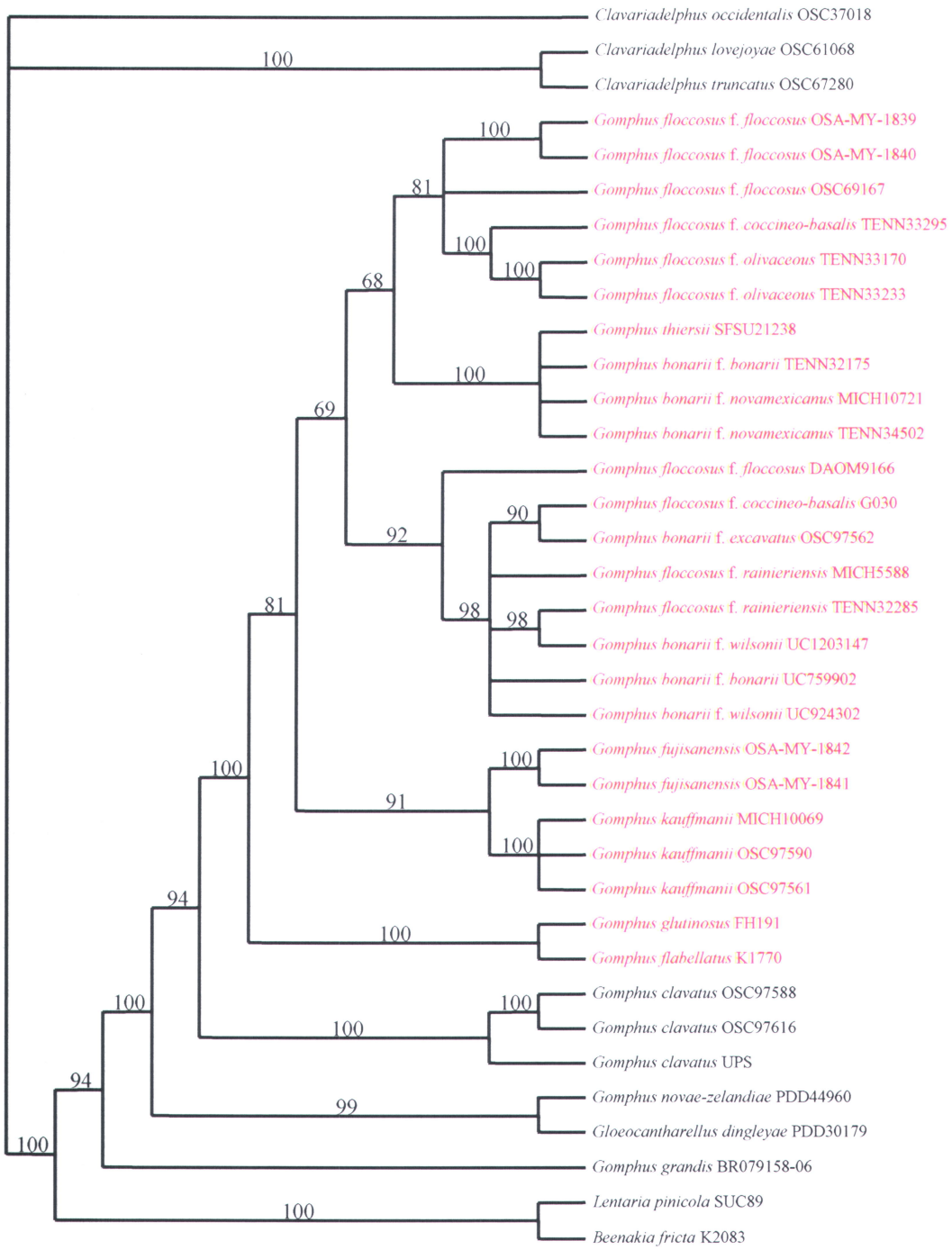

Figure 2.4. Strict consensus cladogram of 6 equally parsimonious (MP) trees of 881 steps based on nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA combined sequences. Bootstrap values above 50% are indicated at each respective internode. CI=0.537, RI=0.716, RC=0.381.

removal from *Gomphus sensu lato* is the 8-spored basidia, a feature otherwise never observed in *Gomphus* but occurring in *Cantharellus*. Petersen (1971a) transferred the species to *Pseudocraterellus*, although species in this genus also lack 8-spored sterigmata.

This genetic groundwork on the taxonomy and systematics of *Gomphus sensu lato* is fundamental for future studies on the evolutionary biology of the order Gomphales. Understanding the placement of ancestral genera and characterizing their morphological features is important to delineate a natural classification for the genera and species within the family Gomphaceae.

In the chapters to follow I will discuss specific aspects of nomenclature, taxonomy, systematics, and phylogenetics of *Gomphus, Gloeocantharellus*, *Phaeoclavulina,* and *Turbinellus*. These chapters will be followed by another focusing on the evolutionary biology of the Gomphales and relationships of this order to the Hysterangiales and Phallales. In a final chapter I will discuss aspects of habitat requirements, distribution and abundance of some species of *Gomphus sensu lato* in the Pacific northwestern USA.

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CHAPTER 3

Systematics of the Gomphales: The Genus *Gomphus* Pers. *Sensu Stricto*

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ABSTRACT

Gomphus sensu lato (Gomphales) was described to include species of cantharelloid-gomphoid fungi that had 'merulioid' (wrinkled) hymenia and verrucose spores. The overall morphology of the basidiomata resembles that of true species of *Cantharellus*, although the configuration of the hymenium and the spores differ considerably. *Gomphus sensu stricto* is currently characterized by unipileate to merismatoid basidiomata, depressed, funnel- to fan-shaped pilei, presence of clamp connections, and verrucose spores, and has three described species: *G. brunneus*, *G. clavatus*, and *G. crassipes*. *Gomphus brunneus* is restricted to Cameroon, the Democratic Republic of Congo, and Uganda. Its basidiomata unipileate, the pileus is depressed, funnel-shaped, and the hymenium is wrinkled. The northern hemisphere species *Gomphus clavatus*, also known as the 'pig's ears fungus', is characterized by unipileate to merismatoid basidiomata, fan-shaped, orangish brown, dark violet to creamy violet pilei, and strongly wrinkled hymenia. This is also the only species of the genus known to form ectomycorrhizae. *G. clavatus* is listed as rare in the Pacific northwestern USA by the Northwest Forest Plan. *G. crassipes* is only known from Algeria, Morocco, and Spain and is characterized by large, unipileate or occasionally merismatoid basidiomata, funnel- to fan-shaped, sordid yellow to orange pilei, violet, wrinkled hymenia, and finely verrucose spores. Basidiomata and spore features are reliable identifiers of *Gomphus sensu stricto* and easily separate its species from other genera in the Gomphales.

INTRODUCTION

The genus *Gomphus* Pers. was originally proposed as a segregate from the genera *Clavaria*, *Geoglossum*, *Mitrula*, and *Spathularia* and described as 'thickened, truncate, smooth, laterally plicate-venose, the pileus weakly developed' (Persoon 1797). No species were assigned to the genus when described. The first mention of a species for *Gomphus* came in 1821, when Gray (1821) described *G. clavatus* (Pers.) Gray based on *Merulius clavatus* Pers., a species known to have merismatoid (composed of several pilei) basidiomata, orangish brown to violet pilei, violet hymenia, and verrucose, non anastomosed ornamented spores.

From that moment, the systematics and nomenclature of *Gomphus* has had a checkered history. Before Giachini (chapter 2), who analyzed 320-plus collections of *Gomphus sensu lato* and related genera in the Gomphales and reviewed the systematics and nomenclatural history for this group of fungi, species of *Gomphus* were assigned to several different genera: *Cantharellus* (Fries 1821), *Craterellus* (Fries 1838), and *Nevrophyllum* (Doassans and Patouillard 1886).

The reduced number of distinctive morphological features, but most importantly, the lack of molecular data to clarify the systematics of this group, contributed to its confused classification. Nevertheless, the significant contributions made by many taxonomists have been crucial to a better understanding of the evolution and systematics of this group.

Giachini (chapter 2) emphasized that *Gomphus sensu stricto* is the only genus in the Gomphaceae with strictly violet, lavender-brown or milky-coffee rather than orange, brown or green-olive colored hymenia, characteristic of *Gloeocantharellus*, *Phaeoclavulina,* and *Turbinellus*. All *Gomphus* species have verrucose spores and clamp connections. The combination of its morphological characteristics is unique in the Gomphaceae and therefore separates *Gomphus* from other genera within the Gomphales.

Gomphus sensu stricto currently has only three described species: *G. brunneus,* which has basidiomata with somewhat funnel-shaped pilei, and *G.*

clavatus and *G. crassipes*, both having basidiomata with fan- to funnel-shaped pilei.

Gomphus clavatus is confined to but widely distributed in the northern hemisphere and suggested to form ectomycorrhizae with species of *Abies* (Pantidou 1980) and *Picea* (Agerer *et al.* 1998). It is the most easily identified of the three species, due primarily to the size and color of its basidiomata. Since the creation and implementation of the Northwest Forest Plan (U.S.D.A. and U.S.D.I. 1994ab, 2000, 2001), *G. clavatus* has been considered rare and potentially restricted to old-growth forests of the Pacific northwest (PNW), requiring all federal and state land to be surveyed for its presence before approved for any management activity.

Gomphus brunneus and *G. crassipes* are both known only from a few collections from Africa. *Gomphus brunneus* is known from Cameroon, the Democratic Republic of Congo, and Uganda, whereas *G. crassipes* is known only from Algeria, Morocco, and Spain. No species have been collected South of the equator.

The objective of this study is to review the important characters used to identify species of *Gomphus*, with a dichotomous key and complete descriptions of the three described species. For a discussion on the nomenclatural history of *Gomphus* see Giachini (chapter 2).

MATERIAL AND METHODS

Collections examined

Collections of *Gomphus* analyzed in this study were obtained from the following herbaria: BR, DAOM, FH, K, MICH, NYS, OSC, S, SFSU, TENN, and WTU (http://www.nybg.org/bsci/ih/ih.html). No collections were located for *G.*

crassipes, so it's description and further notes were taken from the relevant literature.

In addition to dried herbarium specimens, fresh specimens of *G. clavatus* from northern California, Oregon, and Washington were examined. These were collected mostly in late September to mid December, the usual fruiting season.

Selected collections were photographed and macroscopic features recorded. All were then dried within 24 hours of collection with a forced-air food dehydrator set at 38-40 C and deposited at OSC.

Habitat and fruiting patterns are based on information from the original descriptions or field observations. Names of authorities are according to Brummit and Powell (1992).

Macroscopic characters

Macroscopic features are based on the original descriptions and notes accompanying herbarium collections supplemented by our own data on fresh or dried specimens. Features of the cap, hymenium, stipe, flesh, odor and taste were recorded whenever possible. Size of basidiomata may vary depending on conditions of the fruiting season, so the ranges of minimum and maximum sizes are presented as the range for 5-10 collections. Several specimens were cut longitudinally through the vertical axis to examine the context and hyphal arrangement. Application of the various chemicals often used and referred to in the literature in describing species of *Gomphus sensu lato* provided little data of value and therefore are not reported in this study.

Microscopic characters

Features observed with a compound microscope were described from free-hand sections mounted in Melzer's reagent, 5% KOH, cotton blue, or water. Structures were measured with an optical micrometer at × 1000 magnification, mostly in 5% KOH, water, or Melzer's reagent. The ranges for hypha measurements are as follows: thin walls ≤0.5 μm wide, thick walls >0.5 μm wide. The pileipellis and stipitipellis were examined in surface view. When material was available, dimensions of structures were recorded from at least 3 specimens from each of at least 5 collections. Both mature and immature specimens were examined for developmental changes. Maturity was judged by the relative abundance of fully ornamented spores.

Spore shape was determined as the length-width ratio of 20-30 randomly selected spores. Dimensions are given as: minlength-maxlength × minwidth-maxwidth, excluding ornamentation and apiculus. Immature or oversized spores were not included in the measurements, though variation was noted.

SYSTEMATICS OF *GOMPHUS*

Key to species of Gomphus

1. Basidiomata unipileate and then merismatoid with up to 15 subpilei; pileus fan-shaped, orangish brown, creamy violet to dark violet; hymenium wrinkled, violet, vinaceous brown, lavender-brown; Asia, Europe, and North America..... *G. clavatus*

1. Basidiomata unipileate to merismatoid; pileus depressed, funnel-shaped, occasionally fan-shaped, brown to rosaceous, sordid yellow to orangish brown; hymenium wrinkled, reticulate to almost poroid, violet to milky-coffee colored; Africa and Spain..... 2

2. Basidiomata unipileate; pileus brown or occasionally rosaceous; hymenium slightly wrinkled, reticulate to almost poroid, pale violet to milky-coffee colored; spores 7.5-10 × 3.5-5 μm, verrucose; Cameroon, the Democratic Republic of Congo, and Uganda..... *G. brunneus*

2. Basidiomata occasionally merismatoid; pileus sordid yellow to orangish brown; hymenium wrinkled, violet; spores (11-) 13-15 (-17) × 5.5-6 (-7) μm, finely verrucose; Algeria, Morocco, and Spain.....*G. crassipes*

Descriptions

Species are described in alphabetical order. Descriptions include citation of all material examined and the herbarium where the type and other collections are deposited. Descriptions are based on notes available with collections, the observations made in this study, and literature reports.

Gomphus* Pers. Tentamen Dispositionis Methodicae Fungorum, p. 74. 1797a [*non Gomphus* (Fr.) Weinm.**, Hymeno- et Gastro-mycetes Hucusque in Imperio Rossico Observatos, p. 38. **1826.**; ***Gomphus* (Fr.) P. Kumm., Der Führer in die Pilzkunde, pages 21, 23, and 93. 1871], *emend.* Giachini & Trappe, *emend. prov.

≡*Merulius* Pers., Observationes Mycologicae 1:21. 1796.

≡*Merulius* sect. *Gomphus* Pers., Synopsis Methodica Fungorum, p. 498. 1801.

≡*Cantharellus* trib. *Gomphus* (Pers.) Fr., Systema Mycologicum 1:322. 1821.

≡*Gomphus* Gray, A Natural Arrangement of British Plants 1:638. 1821.

≡*Gomphora* Fr., Systema Orbis Vegetabilis, p. 88. 1825.

≡*Nevrophyllum* Pat., *in* Doassans and Patouillard, Revue Mycologique 8:26. 1886 (*non Neurophyllum* Torrey & Gray, A Flora of North America. 1840; *Neurophyllum* Haenke & Presl, Reliquiae Haenkeanae seu Descriptiones et Icones Plantarum, quas in America Meridionali et Boreali, in Insulis Philippinis et Marianis 1, p. 356. 1830).

≡*Neurophyllum* subg. *Eu-neurophyllum* Heim., *p. p.*, Revue Mycologique 19:51. 1954.

≡*Cantharellus* sect. *Gomphus* A.H. Sm. & Morse, Mycologia 39:499. 1947.

≡*Gomphus* subg. *Gomphus* sect. *Gomphus* (Pers.) Corner, *p. p.*, Annals of Botany Memoir 2:113. 1966.

≡*Gomphus* subg. *Gomphus* (Pers.) R.H. Petersen, *p. p.*, Nova Hedwigia 21:18. 1971a.

Type species: *Gomphus clavatus* (Pers.) Gray, A Natural Arrangement of British Plants 1:638. 1821 [≡*Cantharellus clavatus* (Pers.) Fr., Systema Mycologicum 1:322. 1821].

Macroscopic characters: **Basidiomata** up to 18 cm tall, erect, unipileate to merismatoid, when merismatoid with two to several pilei arising from a single stipe. **Pileus** 4-18 cm wide, plane to depressed, fan- to funnel-shaped, flexuous, fleshy, dry, glabrous (*G. brunneus*) to subpruinose, covered with brown hyphae that form minute separate and distinct patches toward the margin but merge into a continuous felty tomentum over the disc (*G. clavatus*), rosaceous, sordid yellow to orange-brown, creamy violet, violet, brown; margin lacerate to crenate. **Hymenium** decurrent, wrinkled, generally longitudinally orientated, dichotomous, anastomosing or occasionally so, reticulate to almost poroid (*G. brunneus*), especially near the stipe apex, more lamellate toward the margin of the pileus, violet, vinaceous brown to milky-coffee colored. **Stipe** up to 80 mm long, solid, cylindrical to tapering downward, generally dilating into the pileus, pale violet to brown, nearly black in *G. crassipes*, often pale red-brown where handled. **Context** firm, pliable, often with anastomosing cavities, especially in *G. clavatus*, white, off-white, violet, pale rose, brownish pink on exposure. **Odor** faint to sweet. **Taste** mild to bitter. **Spore print** brown for *G. brunneus* and *G. clavatus*, not recorded for *G. crassipes*.

Microscopic characters: **Pileipellis** of scattered to fasciculate, simple or branched, rarely slightly inflated hyphae, in *G. clavatus* with pileocystidia; clamp connections present. **Stipitipellis** of parallel hyphae at surface, interwoven beneath, hyaline, up to 2 µm wide; clamp connections present. **Pileus** and **stipe context** of interwoven, hyaline hyphae 2.5-6 µm wide, generally uninflated, except adjacent to the clamp connections. **Hymenial trama** of thin- to thick-walled hyphae; clamp connections present. **Subhymenial trama** of interwoven, hyaline hyphae up to 8 µm wide; clamp connections present. **Basidia** up to 100 µm long, 12 µm wide, clavate, in general with (2-) 4 slightly divergent, slightly incurved sterigmata; clamp connections present. Hymenial **cystidia** absent. **Spores** 7.5-17 × 3.5-7.5 µm, orange, yellow-brown to dark olive in mass, ellipsoid to obovoid; ornamentation verrucose, cyanophilic; apiculus eccentric (not recorded for *G. crassipes*).

Habit, habitat and distribution: Epigeous, solitary to gregarious or caespitose, in leaf litter or terrestrial. When gregarious, basidiomata are often separated by a few centimeters. Africa, parts of Asia, Europe, and North America.

Discussion: Defining boundaries for species within *Gomphus sensu lato* has been a constant challenge because of the lack of consistent morphological features. Only recently have morphology and molecular techniques been combined to provide a natural classification for the Gomphaceae. Giachini (chapter 2) verified that species of *Gomphus sensu stricto* (*G. brunneus, G. clavatus,* and *G. crassipes*) were separated from all other species of the previous *Gomphus sensu lato* based on molecular and morphological data. Currently *Gomphus sensu stricto* is reduced to three vs. the 35 species formerly assigned to *Gomphus sensu lato*. Main features to identify species of *Gomphus* are the smooth to subpruinose pileus, the wrinkled or poroid-like hymenium, and the presence of clamp connections. *Gomphus sensu stricto* species seem to be restricted to the northern hemisphere, including North Africa.

Gomphus brunneus **(Heinem.) Corner, Annals of Botany Memoir 2:116. 1966.**

Fig. 3.1

≡*Neurophyllum brunneum* Heinem., Bulletin du Jardin Botanique de L'etat, Bruxelles 28:435. 1958.

=*Gomphus clavatus* var. *parvisporus* Corner, Annals of Botany Memoir 2:118. 1966.

Macroscopic characters: **Basidiomata** up to 9 × 4 cm, unipileate, erect, clavate, truncate at apex (Figure 3.1). **Pileus** up to 4 cm wide, depressed to funnel-shaped, thick in the center, thin toward the ascending and somewhat lacerate margin, brown or occasionally more or less rosaceous, with paler tones in the center. **Hymenium** wrinkled, reticulate to almost poroid, pale violet to milky-coffee colored. **Stipe** up to 80 mm long, tapered downward, dilating obconically into the pileus, brown, the

base white tomentose. **Context** pliable, white, then brownish pink on exposure. **Odor** not recorded. **Taste** bitter. **Spore print** brown.

Microscopic characters: **Pileipellis** of scattered to fasciculate, simple hyphae; clamp connections present. **Stipitipellis** of hyaline hyphae up to 2 µm wide; clamp connections present. **Pileus** and **stipe context** of interwoven, hyaline hyphae 2.5-6 µm wide; clamp connections present. **Hymenial trama** of thin-walled hyphae; clamp connections present. **Subhymenial trama** of slightly thickened, hyaline hyphae 3-7 µm wide, with refractive walls; clamp connections present. **Basidia** 50 × 8 µm, with 2-4 sterigmata. Hymenial **cystidia** absent. **Spores** 7.5-10 × 3.5-5 µm, yellow-brown in mass, ellipsoid to obovoid; ornamentation of cyanophilic warts arranged more or less in longitudinal rows (Figure 3.1); apiculus rounded, eccentric.

Habit, habitat and distribution: Terrestrial, in leaf litter, on floor of dry forests of Cameroon (Roberts 1999), the Democratic Republic of Congo, and Uganda (Corner 1966, Roberts 1999).

Collections examined: **DEMOCRATIC REPUBLIC OF CONGO. KINSHASA:** Binga, Province Equateur, April 1928, *P. Heinemann 683* (BR A253 – **holotype**). **UGANDA**: Gunda Forest, May 1918, *T.D. Maitland 275* (K 57307 – as *Gomphus clavatus* var. *parvisporus*).

Discussion: *Gomphus brunneus* is distinguished by its simple basidiomata with smooth pilei, weakly wrinkled hymenia, clamped hyphae, and comparatively small basidiospores. It is unique not only because of its morphology and distribution, but also on molecular grounds (Giachini, chapter 2).

Only two herbarium collections of *G. brunneus* were available for analysis in this study. After studying the type for *G. clavatus* var. *parvisporus* from Uganda, described by Corner (1966) and said to occur in Europe and the western USA, Roberts (1999) considered it a synonym of *G. brunneus*. Both species are macroscopically similar, with unusually small, verrucose spores, and are only known from equatorial Africa. Heinemann (1958, 1959) reported two collections from the forests of the Democratic Republic of Congo, Africa. Roberts (1999) cited

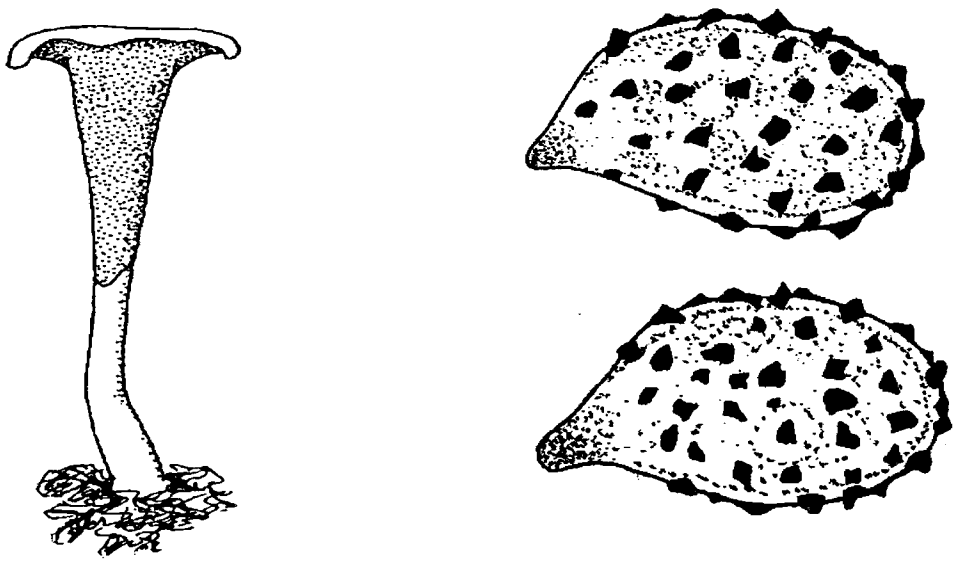


Figure 3.1. *Gomphus brunneus* (Heinem.) Corner: (a) basidioma (× 1); (b) spores (bar = 5 μm). Basidioma drawing from Roberts (1999), with permission.

two collections from Cameroon obtained in 1996, with abundant basidiomata seen at the same location on the following year. Corner (1966) reported a collection of *Gomphus clavatus* var. *parvisporus* from Cameroon. Otherwise, the species appears to be restricted to the Democratic Republic of Congo and Uganda.

For several decades now *Cantharellus pseudoclavatus* A.H. Sm. (Smith and Morse 1947) has been classified under *Gomphus sensu lato* (Corner 1966). After analyzing the type collection (MICH 6916), however, Giachini (chapter 2) concluded that it better fit the description of *Cantharellus*. The main morphological character justifying its removal from *Gomphus sensu lato* was the 8-spored basidia, a feature otherwise never observed in *Gomphus* but occurring in *Cantharellus*. Petersen (1971a) transferred the species to *Pseudocraterellus*, although species in this genus also lack 8-spored sterigmata. Even though Corner (1966) suggested *Gomphus clavatus* var. *parvisporus* (=*Gomphus brunneus*) to occur in Europe and be common in western USA, he only mentioned specimens obtained in Africa in his original description of that variety. *Cantharellus pseudoclavatus*, on the other hand, is common under conifers of the western USA and resembles *G. clavatus* var. *parvisporus*. Corner's (1966) *Gomphus clavatus* var. *parvisporus* from Europe and western USA were undoubtedly *C. pseudoclavatus* rather than true *Gomphus* species.

Gomphus clavatus **(Pers.) Gray, A Natural Arrangement of British Plants 1:638. 1821.** Fig. 3.2

≡*Merulius clavatus* Pers., Observationes Mycologicae 1:21. 1796.

≡*Cantharellus clavatus* (Pers.) Fr., Systema Mycologicum 1:322. 1821.

≡*Craterellus clavatus* (Pers.) Fr., Epicrisis Systema Mycologicum, p. 533. 1838.

≡*Nevrophyllum clavatum* (Fr.) Pat. & Doass., *in* Doassans and Patouillard, Revue Mycologique 8:26. 1886.

≡*Cantharellus clavatus* (Pers.) Lloyd, Mycological Notes 53:762. 1918.

≡*Neurophyllum clavatum* (Pers.) Pat., *in* Petersen, Nova Hedwigia 21:16. 1971a (orthographic variant).

=*Merulius violaceus* Pers., Commentario de Fungis Clavaeformibus, p. 28. 1797b.

=*Gomphus truncatus* Pers., Mycologia Europeae 2:9. 1825.

=*Cantharellus brevipes* Peck, Annual Report of the New York State Museum of Natural History 33:21. 1880.

=*Cantharellus nucleatus* Schröd., Centralblatt für das Gesamte Forstwesen 34:398. 1908.

=*Craterellus carneus* Sacc., Flora Italica Cryptogama, fasc. 14-15:1135. 1916.

Macroscopic characters: **Basidiomata** up to 17 cm tall, unipileate at first and then merismatoid with up to 15 subpilei. **Pileus** up to 15 cm wide, the surface flat, subundulate, fan-shaped, glabrous to covered with brown hyphae that form minute separate and distinct patches toward the margin but merge into a continuous felty tomentum over the disc, orangish brown to overall creamy violet to dark violet; margin crenate (Figure 3.2). **Hymenium** surface wrinkled, generally longitudinally oriented, with or without discrete folds or pits, bright violet at the margin and junction with stipe and overall when immature, at maturity covered with spores and then paler (vinaceous brown). **Stipe** tomentose to hispid toward the base, glabrous above and there blending to pale violet, white at the base and where protected, often pale red-brown where handled. **Context** often with anastomosing cavities, violet around those, off-white to pale rose elsewhere. **Odor** faint or none. **Taste** mild. **Spore print** brown.

Microscopic characters: **Pileipellis** a turf of often crowded, thin-walled, scattered to fasciculate, simple or branched hyphae, usually incrusted apically, with pileocystidia 3-4.5 µm wide, rarely slightly inflated up to 5.5 µm, protruding 50-120 µm from the surface; clamp connections present. Hyphae and bases of pileocystidia often with brown amorphous deposits. **Stipitipellis** of periclinal and parallel, hyaline hyphae 1.5-2 µm wide at the surface, becoming interwoven

beneath, with few projecting hyphae where stipe is glabrous, or fascicles of crowded hyphae where stipe is hispid; clamp connections present. **Pileus** and **stipe context** of thin- to slightly thick-walled, generally oriented on the long axis of the basidioma but profusely interwoven, hyaline hyphae 2.5-6 µm wide, generally uninflated except adjacent to the clamp connections, where it is slightly thick-walled (up to 1 µm thick) and up to 12 µm wide. **Hymenial trama** hyphae more loosely interwoven than the rest of the context, undifferentiated from the **subhymenial trama**. **Basidia** 60-95 × 8.5-12 µm, clavate, collapsing after spore discharge, hyaline, with (2-) 4 slightly divergent, slightly incurved sterigmata up to 10 µm long; clamp connections present at base. Hymenial **cystidia** not observed. **Spores** (9-) 10-15 (-17) × 4-7.5 µm, orange in Melzer's reagent, dark olive in mass (KOH), ellipsoid to obovoid, contents weakly cyanophilic; ornamentation of cyanophilic warts, usually in discrete, raised patches that give an undulate appearance to the spores surface (Figure 3.2); apiculus prominent, eccentric.

Habit, habitat and distribution: Solitary, gregarious to caespitose, when gregarious often separated by a few centimeters, terrestrial. Generally in conifer forests and suggested to form mycorrhizae with species of *Abies* (Pantidou 1980) and *Picea* (Agerer *et al.* 1998), and probably mycorrhizal with other conifer species throughout its range. Known from Austria (Petersen 1971), Canada (East and West), China (Corner 1966), Czech Republic (Kluzák 1994), France (Doassans and Patouillard 1886), Greece (Petersen 1971), Italy (Petersen 1971), Japan (Corner 1966), Lithuania (Urbonas *et al.* 1990), Mexico (Petersen 1971), Pakistan (Corner 1966), Poland (Adamczyk 1996), Russia (Bulakh and Govorova 2000), Spain (Fernando Sanchez, pers. comm.), Sweden, Switzerland (Petersen 1971), Turkey (Sesli 1997), and the USA (especially northwestern/northeastern and into the Appalachian Mountains). Loans were requested from herbaria located in most of these countries but several did not respond, so our examination of specimens is restricted to those listed under collections examined.

Figure 3.2. Basidiomata of *Gomphus clavatus* (Pers.) Gray (× 2).

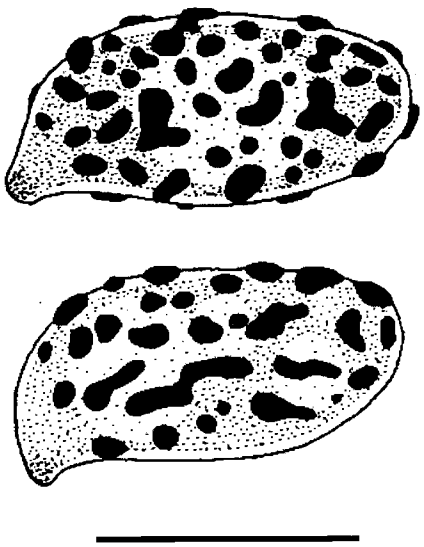


Figure 3.2 (*cont.*). Spores of *Gomphus clavatus* (Pers.) Gray (bar = 10 μm). Drawings from Petersen (1971b), with permission.

Collections examined: **CANADA**. **BRITISH COLUMBIA**: Vancouver Island, 15 October 1962, *M. Pantidou* (DAOM 91369). **QUEBEC**: Duchesnay, 26 August 1938, *H.S. Jackson* (DAOM 8624). **SWEDEN:** Uppsala, Södermanland, Handen, 4 September 1998, *L. Kerwién* (S); Fiby Urskog, 20 September 1998, *A. Taylor* (S). **UNITED STATES**. **CALIFORNIA**: Del Norte Co., Del Norte Coast Redwoods State Park, 9 December 1999, *M.A. Castellano* (OSC 97685); Del Norte Co., Jedediah Smith Redwoods State Park, 17 November 1961, *D. Isely 1479* (WTU), and 12 November 1966, *H.D. Thiers* (SFSU 17740); Del Norte Co., Siskiyou Nat. Forest, Smith River, 30 November 1937, *A.H. Smith 9243* (MICH); El Dorado Co., Pleasant Valley, 22 October 1967, *D.E. Stuntz 14410* (WTU); Mendocino Co., 5 November 1961, *D. Largent 71* (SFSU); Mendocino Co., Aleuria Glenn, 14 November 1967, *R.H. Petersen* (TENN 33256); Mendocino Co., Aleuria Glenn, along Rd. 404, 25 October 1986, *M. Seidl 2120* (WTU); Mendocino Co., Jackson State Forest, 5 November 1967, *R.H. Petersen and H.D. Thiers* (TENN 33174), and 8 December 1999, *A.J. Giachini, M.A. Castellano and E. Nouhra* (OSC 97679, 97680, 97681, 97682, 97683, 97684). **IDAHO**: Bonner Co., Priest River, Binarch Creek, 9 September 1966, *R.H. Petersen* (TENN 32166); Bonner Co., Priest River Experimental Forest, Canyon Creek Road, 11 November 1939, *A.H. Slipp 621* (MICH). **MASSACHUSETTS**: Essex Co., Gloucester, August 1877, *undetermined collector* (FH). **NEW YORK**: Saratoga Co., Ballston Lake, Branch, 1879, *C.H. Peck* (NYS – as *Cantharellus brevipes* – **holotype**). **OREGON**: Benton Co., Siuslaw Nat. Forest, Mary's River, 24 October 1999, *S. Ashkannejhad* (OSC 97622); Clackamas Co., Wemme, 23 September 1946, *A.H. Smith 23644* (MICH); Coos Co., South Slough, 23 September 1985, *C. Ardrey 800* (WTU), and 3 September 1992, *C. Ardrey 1806* (WTU); Lane Co., Cougar Reservoir, Road 19, 27 November 1999, *A.J. Giachini* (OSC 97671, 97672, 97673, 97674, 97675, 97676, 97677); Lane Co., Eugene, 30 October 1999, *undetermined collector* (OSC 97646); Lane Co., H. J. Andrews Experimental Forest, Lookout Mt., Rd. 1506, 23 October 1999, *A.J. Giachini* (OSC 97616, 97620, 97669, 97670, 97678); Lane Co., H. J. Andrews Experimental Forest, 23 October 1999, *A.J. Giachini* (OSC 97617), 5

November 1999, *A.J. Giachini* (OSC 97656), and 7 November 2000, *Y. Yano* (OSC 97694); Lane Co., Oakridge, Road 1934, 15 November 1999, *A.J. Giachini* (OSC 97668); Lane Co., Willamette Nat. Forest, 25 October 1999, *C. Lefevre* (OSC 97623); Linn Co., Sweet Home, 4 November 2000, *A.J. Giachini* (OSC 97696, 97698); Linn Co., Willamette Nat. Forest, Pamelia Lake Trail head, 2 November 1999, *A.J. Giachini* (OSC 97624); Marion Co., Detroit Lake, Road 46, 15 November 1999, *A.J. Giachini* (OSC 97667). **WASHINGTON**: Chelan Co., Lake Wenatchee, 7 November 1980, *D.E. Stuntz 21131* (WTU); Clallam Co., Morse Creek camp, 17 October 1942, *D.E. Stuntz 1245* (WTU); Clallam Co., Olympic Mountains, 30 October 1931, *H.S. Hotson* (WTU); Kings Co., Snoqualmie Nat. Forest, Asahel Curtis Nature Trail, 4 August 1992, *G.R. Walker 10600* (WTU); Lewis Co., Mt. Rainier Nat. Park, Bumping Lake, October 1937, *D.E. Stuntz 759* (WTU); Pierce Co., Mt. Rainier Nat. Park, Lower Tahoma Lake, 23 September 1948, *D.E. Stuntz 4732* (WTU); Pierce Co., Old Tahoma campground, 23 September 1960, *D.E. Stuntz 12000* (WTU); Pierce Co., Mt. Rainier National Park, Tahoma Creek, 18 August 1948, *D.E. Stuntz and A.H. Smith 4003* (WTU); Pierce Co., Mt. Rainier Nat. Park, Tahoma Creek, 23 September 1960, *D. Isely 1257* (WTU).

Discussion: *Gomphus clavatus* has traditionally been placed in its own subgenus on the basis of morphological features (Corner 1966). However, molecular studies by Giachini (chapter 2) support its placement in *Gomphus sensu stricto* together with *G. brunneus* and suggest it to be phylogenetically close related to species of the genus *Gloeocantharellus*. These two genera share several morphological similarities, as pointed out by Petersen (1971). The most striking one, in Petersen's opinion, is that both have the same reaction when 10% KOH is applied to the basidioma pileus. In reference to *G. clavatus* Petersen (1971) adds, "the normal color immediately becomes a most unique salmon-yellow, almost precisely the normal color of the pileus and stipe of *Gloeocantharellus purpurascens*." The pileus surface tomentum of *G. clavatus* is composed of pileocystidia, just as in *G.*

purpurascens, and, even though the pileocystidia of the two species differ in shape and orientation, they have a similar brown agglutinating substance.

The merismatoid habit of *G. clavatus* is shared by other taxa in the Gomphaceae, notably *Phaeoclavulina grandis, P. guadelupensis, P. subclaviformis, P. viridis*, *Gloeocantharellus dingleyae, G. novae-zelandiae,* and *G. pallidus*.

***Gomphus crassipes* (L.M. Dufour) Maire *in* Maire and Werner, Mémoires de la Société des Sciences Naturelles du Maroc 45:81. 1937.** Fig. 3.3

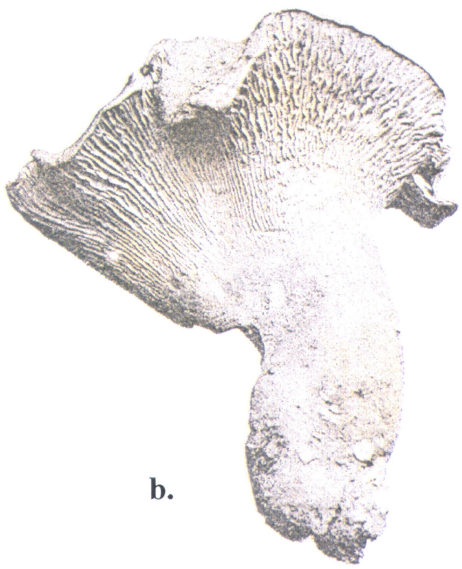
≡*Cantharellus crassipes* L.M. Dufour, Revue Générale de Botanique 1:358. 1889.

≡*Nevrophyllum crassipes* (L.M. Dufour) Maire, Bulletin de la Société Mycologique de France 30:214. 1914.

Macroscopic characters: **Basidiomata** up to 18 cm tall, unipileate or occasionally merismatoid (Figure 3.3). **Pileus** 4-18 cm wide, plane to slightly depressed in the center, funnel-shaped to fan-shaped, non hygrophanous, sordid yellow to orangish brown; margin subundulate. **Hymenium** decurrent, wrinkled, occasionally anastomosing, dichotomous, violet. **Stipe** 40-70 × 25-45 mm, cylindrical to slightly tapering downward, almost entirely underground, central or lateral, nearly black. **Context** firm, pale violet, marbled in the stipe with violet tones. **Odor** sweet. **Taste** not recorded. **Spore print** color not recorded.

Microscopic characters: All **hyphae** 5-8 µm wide; clamp connections present. **Basidia** 70-100 × 8-10 (-12) µm, clavate, with (2-) 4 straight sterigmata. Hymenial **cystidia** absent. **Spores** (11-) 13-15 (-17) × 5.5-6 (-7) µm, pale orange in mass, ellipsoid to obovoid; ornamentation of cyanophilic, fine warts (Figure 3.3); data on apiculus not recorded.

a.



b.

Figure 3.3. *Gomphus crassipes* (L.M. Dufour) Maire: (a) 1 and 2 - basidiomata (× 1), 1s - spores (× 1000), 1b - basidium (× 500), 3 - spores of *G. clavatus* (× 1000); (b) basidioma (× 0.5). Figure **a** from Maire (1914); figure **b** modified from Dufour (1889).

Habit, habitat and distribution: On the ground, generally grouped, in conifer forests in Algeria (Dufour 1889, Maire 1914, Maire and Werner 1937), Morocco (Malençon 1957), and Spain (Miquel À. Pérez-De-Gregorio i Capella, pers. comm.).

Type (epitype): Because the holotype collection of *Gomphus crassipes* was not located, the photograph included with Dufour's original protologue must serve as the holotype (International Code of Botanical Nomenclature, art. 8.1 – Greuter *et al.* 2000). However, that illustration is inadequate to characterize the species. Therefore, Maire's (1914) excellent illustration is hereby designated as the epitype for *G. crassipes*, especially because it is accompanied by a detailed description of the species.

Discussion: The only known collections do not include the type and are at herbarium RAB in Morocco; the loan request was denied due to their fragile condition. Therefore, the description presented here was based on Dufour (1889), Maire (1914), and Maire and Werner (1937). Dufour (1889) did not mention any collection or herbaria for the type species. He stated that "cette espèce est assez voisine du *Cantharellus brevipes* Peck", a synonym of *G. clavatus*. Accordingly, he related it to *G. clavatus*, with similar macro- and microscopic characteristics, differing only by the color of the context, which is violet, off-white to pale rose in *G. clavatus*, and violet to marbled violet in *G. crassipes*. However, overall spore size and its geographic distribution suggest the species to be distinct from *G. clavatus*.

Only a few other references to *G. crassipes* are observed in the literature. Maire (1914) transferred Dufour's *Cantharellus crassipes* to *Nevrophyllum*. He also provided a detailed description and an excellent hand drawing of its basidiomata and spores (Maire 1914). Maire, in Maire and Werner (1937) then transferred *N. crassipes* to *Gomphus*. Later Malençon (1957) called attention to the evident relationship of *G. crassipes* to the coral fungi, especially the genus *Ramaria*. Furthermore, according to this author the drawings by Maire (1914) do not well represent what Dufour (1889) described as *C. crassipes*: its colors are not

those suggested by Dufour (Malençon 1957). It "pulls to much into the yellows and reds" according to Malençon (1957), who described *G. crassipes* as having a pale ocher to rose pileus surface. However, as seen for other species of *Gomphus sensu lato*, for instance *G. clavatus*, the color of the pileus and hymenium surfaces can vary considerably. For *G. clavatus*, for example, the pileus surface can be either creamy violet or completely violet. Maire (Maire and Werner 1937) may have observed a color variant of *G. crassipes*.

DISCUSSION

Gomphus was originally described to include species of cantharelloid-gomphoid[1] fungi that had 'merulioid' (wrinkled) hymenia and verrucose spores. The overall aspect of the basidiomata resembles that of true species of *Cantharellus*, although the configuration of the hymenium and the spores differ considerably.

During the 18th and 19th centuries the only recognized *Gomphus* species was *G. clavatus*, the type for the genus. Persoon (1796) described *G. clavatus* under *Merulius*, and later Gray (1821) transferred it to *Gomphus*. *Gomphus clavatus* was later assigned to *Cantharellus* (Fries 1821), and much later to *Nevrophyllum* (Doassans and Patouillard 1886). By the middle of the 20th century Singer (1945) transferred several species of *Cantharellus* and *Nevrophyllum viride* to *Gomphus*. The foundation for that taxonomic classification was the overall cantharelloid-gomphoid shape of the basidiomata, coupled to the wrinkled 'merulioid' hymenium.

The mere presence of wrinkled hymenia, cantharelloid-gomphoid basidiomata, and verrucose spores was considered sufficient to place a collection in

[1] Basidiomata with the similar shape of a *Cantharellus* species but with decurrent, wrinkled hymenia rather than straight gills.

Gomphus. In the face of the limited resources and technology available until recently, the earlier taxonomic work was quite remarkable.

More recently, the molecular studies of Giachini (chapter 2) sharpened generic and species concepts within the Gomphaceae. He showed *Gomphus sensu lato* to be non-monophyletic and redistributed its species into *Gomphus sensu stricto*, *Gloeocantharellus*, *Phaeoclavulina*, and *Turbinellus*, retaining only three of the original species in *Gomphus sensu stricto*.

In general it is quite straightforward to separate species of *Gomphus* from those of other genera within the Gomphales. Color, which for the most part is vividly violet, violet-brown to orangish brown, and fan-shaped to somewhat funnel-shaped basidiomata pilei are characteristic for the species in the genus.

Gomphus species most resembles some species of the resurrected genus *Phaeoclavulina*. Both have fan- to funnel shaped pilei and clamp connections. However, they mostly differ on the ornamentation of the spores. Most species of *Phaeoclavulina* have echinulate, verrucose, subreticulate or reticulate spores, while those of *Gomphus* are strictly verrucose.

Even though all species of *Turbinellus* were assigned to *Gomphus* until recently, they share only a few morphological characters with the species of *Gomphus sensu stricto*, most notably the spore ornamentation. However, they differ in basidiomata shape and color and presence or absence of clamp connections.

Gomphus and *Gloeocantharellus* species occupy an important position in the evolution of the fungi in the order Gomphales. Common features to these two genera are the shape and ornamentation of the spores and the clamp connections (in some *Gloeocantharellus*). According to the molecular data (Giachini 2001, chapter 2, Humpert *et al.* 2001), *Gloeocantharellus* and *Gomphus* are ancestral genera to *Gautieria*, *Ramaria* (subgenera *Laeticolora* and *Ramaria*), and *Turbinellus*.

Unavailability of samples restricted more in-depth evolutionary inferences of *Gomphus* to other genera in the Gomphales. Additional sampling, especially for *G. crassipes*, is necessary to define if subgeneric arrangements are necessary within *Gomphus sensu stricto* and to infer higher-level relationships to other members of

the Gomphales. A complete discussion on the evolutionary relationships and implications of this taxonomic classification in relation to other members of the Gomphales is presented in chapter 7.

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CHAPTER 4

Systematics of the Gomphales: The Genus *Turbinellus* Earle

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ABSTRACT

The cantharelloid-gomphoid genus *Turbinellus* (Gomphales) was proposed by Earle to accommodate *Cantharellus floccosus*, previously described by Schweinitz. Species under *Turbinellus* were transferred from *Gomphus sensu lato* based on morphology and molecular data. Among the morphological features important for generic level identification of *Turbinellus* are the scaly orange-red or brown pilei, the strongly wrinkled and generally pale yellow to yellow-orange hymenia, the absence of clamp connections, and the verrucose, ellipsoid to obovoid spores. This is the most common and widespread cantharelloid-gomphoid genus in North America and perhaps in the world, with species in almost all continents, except Australia and Antarctica. It occurs in a variety of forest ecosystems, and some, if not all species are presumed to be ectomycorrhizal with members of the Pinaceae. In addition, *T. kauffmanii* is considered rare or threatened in the Pacific northwestern USA due to its limited habitat and low frequency of occurrence. Five species of *Turbinellus* are currently recognized: *T. flabellatus, T. floccosus, T. fujisanensis, T. kauffmanii*, and *T. stereoides*. These represent the result of combining twenty-one previously described species and varieties.

INTRODUCTION

Turbinellus was proposed by Earle (1909) to accommodate *Cantharellus floccosus*, previously described by Schweinitz (1831). Earle (1909) mentioned 3 North American species assigned to the genus but did not provide any names besides *T. floccosus*. He further stated that all three had more in common with the club-shaped species of *Craterellus* than with the species of *Cantharellus*. Species in *Turbinellus* were later transferred to *Gomphus* (Singer 1945), then *Cantharellus* (Smith and Morse 1947), *Nevrophyllum* (Heim 1954), and eventually back to *Gomphus* (Corner 1966).

Species of *Turbinellus* produce aboveground, terrestrial, single to caespitose, and usually large basidiomata. The pilei are cinnamon to red, either funnel- or fan-shaped, and hymenia are somewhat yellow to pale orange, in some species bruising vinaceous. The hymenium is strongly decurrent, and hymenial folds are deeply wrinkled and generally longitudinally oriented. The stipe is robust, tall, and well rooted in the substrate. The hyphae lack clamp connections, and spores have verrucose ornamentation.

This is the most common and widespread cantharelloid-gomphoid[1] genus throughout North America and perhaps the world. Smith and Morse (1947), Corner (1950), and Petersen (1971a) described and studied most of the cantharelloid-gomphoid species currently in *Turbinellus*, especially from the western states of the USA. They proposed a series of special 'forms' to fall under *Cantharellus floccosus* (≡*T. floccosus*) and *C. bonarii* (=*T. floccosus*), most of them differing only on a few plastic morphological features. Corner (1966) and Petersen (1971a) accepted the species proposed by Smith and Morse (1947), transferring them to *Gomphus sensu lato*.

In the 1900's Maire (1902), Singer (1949), Corner (1950), Heim (1954), Heinemann (1958), and Donk (1964) conjectured on the evolutionary relationships of members of the Gomphaceae, then classified in the Aphyllophorales, but

[1] Basidiomata with the similar shape of a *Cantharellus* species with decurrent, wrinkled hymenium.

confusion and disagreement on the precise delimitation of species boundaries persisted. This is particularly evident in the work of Corner (1966, 1969) and Petersen (1971a). These two authorities did most of the work on this section of the Gomphales. They described several species, provided insightful information on evolutionary relationships within the order, and properly delineated the basis for a better understanding of *Gomphus* and related genera. However, most of the molecular biology techniques common nowadays were not available at that time. Allied to the fact that *Gomphus sensu lato* is so large and diverse, the application of morphological techniques alone was problematic, in several cases leading to the description of forms and subspecies, many supported only by one or a few plastic characters. A good example is *Gomphus floccosus* f. *olivaceous*, which was considered to be unique due to the 'ecru olive' (beige orangish) pileus (Petersen 1971a), but aside from that, all other characters perfectly fit the description of *G. floccosus* f. *floccosus*. Still others were described based on site locality, such as *G. bonarii* f. *novamexicanus*, restricted to the southwestern states of the USA, with features similar to those of *G. bonarii* f. *bonarii*.

Based on morphology and molecular data from three combined genomic loci, Giachini (chapter 2) transferred several species of *Gomphus sensu lato* to the genus *Turbinellus*. He also synonymized *G. floccosus*, *G. bonarii*, and all the forms and varieties assigned to these species under the name *T. floccosus*. Those changes and new classification are fundamental to define species boundaries within *Turbinellus* and to aid future ecological and taxonomical studies.

Five species have been assigned to *Turbinellus*: *T. flabellatus, T. floccosus, T. fujisanensis, T. kauffmanii*, and *T. stereoides*, a result of the combination of twenty-one previously described species and varieties (Giachini, chapter 2).

The overall objective of this paper is to present an overview of the important features used to identify species of *Turbinellus*, with a dichotomous key and comprehensive species descriptions. For a complete discussion on the nomenclatural history of *Turbinellus* and allied genera see Giachini (chapter 2).

MATERIAL AND METHODS

Collections examined

Collections of *Turbinellus* analyzed in this study were obtained from the following herbaria: DAOM, FH, K, MICH, PH, OSA, OSC, SFSU, TENN, UC, and WTU (http://www.nybg.org/bsci/ih/ih.html). No collections have been located for *T. stereoides*, so descriptive information was taken from the relevant literature.

In addition to dried herbarium specimens, fresh collections of *T. floccosus* and *T. kauffmanii* from northern California, Idaho, North Carolina, Oregon, and Washington were examined. These were collected mostly in late September to mid December, which in general coincided with the rainy and hence the fruiting season.

Selected collections were photographed and macroscopic features recorded. All were then dried within 24 hours of collection with a forced-air food dehydrator set at 38-40 C and deposited at OSC.

Habitat and fruiting patterns are based on information from the original descriptions or from field observations. Names of authorities are according to Brummit and Powell (1992).

Macroscopic characters

Macroscopic features are based on the original descriptions and notes accompanying herbarium collections supplemented by our own data on fresh or dried specimens. Features of the cap, hymenium, stipe, flesh, odor and taste were recorded whenever possible. Size of basidiomata may vary depending on conditions of the fruiting season, so the ranges of minimum and maximum sizes are presented as the range for 5-10 collections. Several specimens were cut longitudinally through the vertical axis to examine the context and hyphal

arrangement. Application of the various chemicals often used and referred to in the literature in describing species of *Gomphus sensu lato* provided little data of value and therefore were discontinued for this study.

Microscopic characters

Features observed with a compound microscope were described from free-hand sections mounted in Melzer's reagent, 5% KOH, cotton blue, or water. Structures were measured with an optical micrometer at × 1000 magnification, mostly in 5% KOH, water, or Melzer's reagent. The ranges for hypha measurements are thin walls ≤0.5 µm wide, thick walls >0.5 µm wide. The pileipellis and stipitipellis were examined in surface view. When material was available, dimensions of structures were recorded from at least 3 specimens from each of at least 5 collections; both mature and immature specimens were examined for developmental changes. Maturity was judged by the relative abundance of fully ornamented spores.

Spore shape was determined as the length-width ratio of 20-30 randomly selected spores. Dimensions are given as: minlength-maxlength × minwidth-maxwidth, excluding ornamentation and apiculus. Immature or oversized spores were not included in the measurements, though variation was noted.

SYSTEMATICS OF *TURBINELLUS*

Key to species of Turbinellus

1. Spores ≤13 µm long..... 2

1. Spores nearly all longer than 13 µm..... 3

2. Pileus up to 15 cm tall, funnel-shaped, surface initially glabrous then becoming covered with small, subpyramidal to dot-like scales near the margin, larger and heavily rectangular to pyramidal scales downward in the funnel, these becoming reflexed; spores (8.5-) 9.5-11.5 × 5-6 µm; Japan..... *T. fujisanensis*

2. Pileus 10 cm tall, spatula- to fan-shaped, with appressed scales; spores 9-13 × 4.5-6 µm; Africa, Brazil, Malaysia, and Turkey..... *T. stereoides*

3(1). Basidiomata pilei up to 4 cm wide, funnel-shaped when mature, surface minutely innately silky, with minute appressed-floccose scales, dark red-brown; spores 12.5-17 (-19) × (5.5-) 6.5-9 µm; eastern Asia..... *T. flabellatus*

3. Basidiomata pilei up to 35 cm wide, funnel-shaped, surface scaly, pale brown to pale orange, cinnamon, red or orange-red; spores 11-20.5 × (5-) 6-10 µm; northern hemisphere..... 4

4. Basidiomata up to 30 cm tall; pileus surface cinnamon, pale orange, orange-red, red, to scarlet, covered with floccose scales, mostly coarse, appressed to pyramidal or subrectangular, sometimes in a zonate configuration; spores 11-20.5 × (5-) 6-10 µm; northern hemisphere..... *T. floccosus*

4. Basidiomata reaching 40 cm tall; pileus surface pale brown to pale orange, at first almost glabrous at the very margin, then covered with scales which are small, subpyramidal to dot-like near the margin, heavily rectangular to pyramidal, reflexed and larger downward in the funnel; spores 12.5-17.5 (-20.5) × (5-) 6-8 µm; North America..... *T. kauffmanii*

Descriptions

Species are described in alphabetical order. Descriptions include citation of all material examined and the herbarium where the type and other collections are deposited. Phenology and biogeography are based on notes available with collections and the observations made in this study.

Turbinellus Earle, Bulletin of the New York Botanical Garden 5:407. 1909, *emend.* Giachini & Trappe, *emend. prov.*

≡*Chanterel* (Adans.) Murrill, North American Flora 9:168. 1910.

≡*Cantharellus* sect. *Excavatus* A.H. Sm. & Morse, Mycologia 39:500. 1947.

≡*Gomphus* subg. *Gomphus* sect. *Excavatus* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:113. 1966.

≡*Gomphus* subg. *Excavatus* (A.H. Sm. & Morse) R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:381. 1968.

=*Gomphus* subg. *Gomphorellus* Corner, *p. p.*, Annals of Botany Memoir 2:113. 1966.

Type species: *Cantharellus floccosus* Schwein., Transactions of the American Philosophical Society, n.s., 4:153. 1831.

Macroscopic characters: **Basidiomata** up to 40 cm tall, cylindrical when young, rarely merismatoid (composed of several pilei), excavate in some species. **Pileus** 5-35 cm wide, subcylindrical to spatula-like when young becoming fan- to funnel-shaped with age, initially glabrous, then fibrillose, appressed-floccose with heavy reflexed scales, moist, appearing glutinous or gelatinous when wet, especially when water accumulates in the center of the basidioma, colored with various shades of orange, cinnamon, red or brown when fresh, tending toward dark orange, red, dark red-brown or brown with age; scales usually darker than the pileus surface, often weathering loose and then filling the center of the basidioma along with other debris; margin inrolled or recurved, undulate, crenate, generally thin. **Hymenium** of low wrinkles, low ridges or well-developed hymenial folds up to 4 mm tall, either strictly longitudinally arranged or anastomosed into elongate diamond-shaped alveoli, in some species irregularly poroid, yellow to pale brown when young, with a yellow band near the pileus margin in some species, pale orange, orange to pale brown with age, turning brown to violaceous on handling or bruising on some species. **Stipe** up to 150 × 60 mm, initially solid, then often hollow from larval feeding, subcylindrical to slightly tapering somewhat downward, glabrous, often brunnescent where handled, usually white and often hispid below substrate level, concolorous with hymenium or apically brown. **Context** pliable, brittle, firm on pileus and stipe surfaces, off-white, occasionally bruising brown on exposure. **Odor** mild or faintly to obviously aromatic, earthy to sweet. **Taste** mild to acrid, occasionally sweet and sour, but generally not distinctive. **Spore print** cinnamon.

Microscopic characters: **Pileipellis + stipitipellis** of thin- to thick-walled, uninflated to somewhat inflated hyphae, up to 22 μm wide; clamp connections

absent; gleoplerous hyphae occasional to abundant, strongly cyanophilic. **Pileus** and **stipe context** of moderately thin- to thick-walled, parallel, compactly packed, hyaline to yellow hyphae, with occasional to abundant ampulliform swellings; clamp connections absent. **Hymenial trama** of subparallel to interwoven, undifferentiated, narrow, thin-walled hyphae; lacking clamp connections; in general with generative hyphae without skeletal hyphae; gleoplerous hyphae usually present, hyaline and slightly to highly refractive to orange, ampulliform, strongly cyanophilic. **Subhymenial trama** of thin-walled, compactly interwoven hyphae 2-4 µm wide. **Basidia** (45-) 60-90 (-115) × (7.5-) 9-14 (-16), clavate or cylindrical with a somewhat bulbous apex, hyaline, apical contents cyanophilic, with (2-3-) 4, slightly divergent sterigmata up to 9 µm long. Hymenial **cystidia** usually absent, when present elongate-fusiform, 70-90 × 9-11 µm; clamp connections absent. **Spores** (8.5-) 9.5-17 (-20.5) × (4.5-) 5.5-8 (-10) µm, rusty yellow, cinnamon to pale orange in mass, ellipsoid to obovoid; ornamentation of delicate to coarse, scattered strongly cyanophilic warts that can form anastomosed longitudinal ridges; apiculus up to 2 µm long, truncate-rounded, eccentric.

Habit, habitat and distribution: Epigeous, terrestrial, single, gregarious, caespitose, common in parts of the northern hemisphere, but also occurring in Africa and South America. The genus is presumed mycorrhizal with various conifer species.

Discussion: The five species of *Turbinellus* are generally more brightly colored than those in other genera in the Gomphales. *Turbinellus* species also have a moderately to strongly scaly pileus surface, a characteristic not seen in other members of that order. The *Turbinellus* distribution ranges from two species in southeast Asia (*T. flabellatus* and *T. fujisanensis*), one in Africa, Brazil, Malaysia, and Turkey (*T. stereoides*), one restricted to North America (*T. kauffmanii*), and one common in coniferous forests of the northern hemisphere (*T. floccosus*). Suitable habitats made this genus successful in some parts of the world, especially western North America, which Petersen (1971a) considered the center of

distribution for the genus. Some species of *Turbinellus* are also known to be edible, considered a choice edible by some people but causing stomach upsets in others.

Turbinellus floccosus has been suggested to be mycorrhizal with *Abies* (Masui 1926, 1927, Khokhryakov 1956, Valdés-Ramirez 1972, Bulakh 1978, Guzmán and Villarreal 1985), *Pinus* (Masui 1927, Guzmán and Villarreal 1985), *Pseudotsuga menziesii* (Mirb.) Franco (Trappe 1960), and *Tsuga heterophylla* (Raf.) Sarg. (Trappe 1960, Kropp and Trappe 1982). Because other species of *Turbinellus* occupy similar habitats as *T. floccosus*, they presumably also form ectomycorrhizae with the same conifer species.

Turbinellus flabellatus* (Berk.) Giachini, *sp. prov. Fig. 4.1

≡*Cantharellus flabellatus* Berk., Challenger Report 3:50. 1873.

≡*Gomphus flabellatus* (Berk.) Corner, Annals of Botany Memoir 2:119. 1966.

=*Cantharellus glutinosus* Pat., Bulletin de la Société Mycologique de France 25:7. 1909.

≡*Gomphus glutinosus* (Pat.) R.H. Petersen, Nova Hedwigia 21:91. 1971a.

Macroscopic characters: **Basidiomata** up to 7 cm tall, cylindrical, excavate to the base at early stages, unipileate to merismatoid. **Pileus** up to 4 cm wide, funnel-shaped when mature, the surface innately silky, dark red-brown, with minute appressed-floccose scales; margin crenate, thin, not inrolled. **Hymenium** longitudinally ridged above, the ridges up to 1 mm tall, crowded, branching profusely and irregularly, especially toward the margin, extending almost to the substrate, brown when dry. **Stipe** up to 6 mm thick, tapering downward, white, brown when dry. **Context** pliable in the hymenial trama, firm on pileus and stipe surfaces, white. **Odor** and **taste** not recorded. **Spore print** cinnamon.

Microscopic characters: **Pileipellis** of thin- to thick-walled hyphae, strongly constricted at septa, repent, without agglutinating substance, hyaline, 6-30 µm wide; clamp connections absent; gleoplerous hyphae common, strongly cyanophilic

(Figure 4.1). **Hymenial trama** of thin-walled hyphae. **Basidia** 50-80 × 9-16 µm, clavate to apically bulbous, with minute, dense, amorphous, orange to dark orange, crystalline matter, hyaline when young, finally refractive, apical contents strongly cyanophilic, with 4 straight, slightly divergent sterigmata up to 8.5 µm long; clamp connections absent. Hymenial **cystidia** absent. **Spores** 12.5-17 (-19) × (5.5-) 6.5-9 µm, rusty yellow in mass, ellipsoid to obovoid; ornamentation of low, randomly arranged, strongly cyanophilic warts, occasionally anastomosed into ridges (Figure 4.1); apiculus rounded.

Habit, habitat and distribution: Solitary, on the ground under *Pinus* sp. and other conifer species in Japan (Corner 1966) and Vietnam (Patouillard 1909, Petersen 1971a).

Collections examined: **JAPAN**: no location, no date, col. *F.V. Dickens* 1770 (K 63152, as *Gomphus flabellatus* – **holotype**). **VIETNAM**: Tonkin, Plateau de Dalat, July 1909, *L.B.A. Eberhardt 191* (FH).

Discussion: The specimen from Vietnam was first described as *Cantharellus glutinosus*. According to Petersen (1971a), *G. glutinosus* and *G. flabellatus* were supposed to be close related because they share similar morphological characters, such as small to medium-sized basidiomata, abundant and similar gleoplerous hyphae in the pileus as well as on stipe surfaces, and presence of minute, dense, amorphous, orange to dark orange, crystalline matter in the mature basidia. Even though 'flabellatus' means fan-shaped (*flabelliformis* in Latin), a close look at the type specimen shows it to be funnel-shaped rather than totally fan-shaped. Based on morphology and molecular data Giachini (chapter 2) synonymized *G. glutinosus* under *T. flabellatus*.

This species produces the smallest basidiomata in the genus, as pointed out by Petersen (1971a), and according to the colors ascribed by Patouillard (1909) it indeed resembles a miniature *T. floccosus*. The aspect of pileus, basidia, and spores, however, indicate it to be quite different from the former species, a status also supported by the molecular data (Giachini, chapter 2).

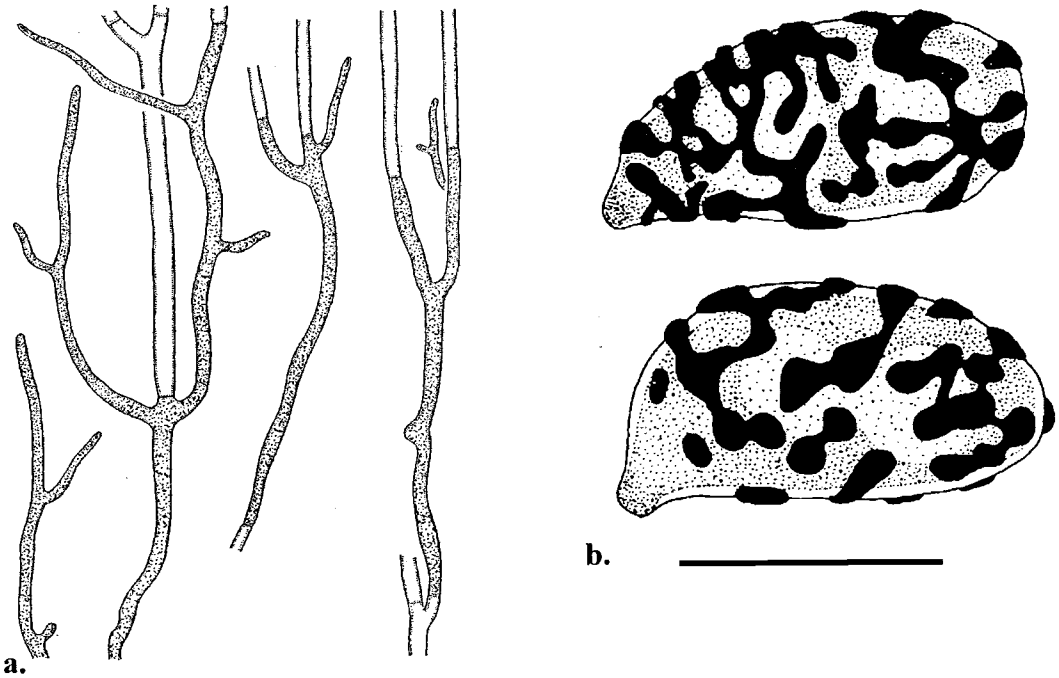


Figure 4.1. *Turbinellus flabellatus* (Berk.) Giachini, *sp. prov.*: (a) gleoplerous hyphae of the context (x 500), from Corner (1966); (b) spores (bar = 10 μm). Spore drawings modified from Petersen (1971b), with permission.

Turbinellus floccosus* (Schwein.) Earle, Bulletin of the New York Botanical Garden 5:407. 1909, *emend.* Giachini & Trappe, *emend. prov. Fig. 4.2

≡*Cantharellus floccosus* Schwein. f. *floccosus*, Transactions of the American Philosophical Society 4:153. 1831.

≡*Craterellus floccosus* Boud., Bulletin de la Societé Botanique de France 24:308. 1877.

≡*Chanterel floccosus* (Schwein.) Murrill, North American Flora 9:168. 1910.

≡*Gomphus floccosus* (Schwein.) Singer f. *floccosus*, Lloydia 8:140. 1945.

≡*Cantharellus floccosus* f. *typicus* A.H. Sm. & Morse, Mycologia 39:521. 1947.

≡*Nevrophyllum floccosum* (Schwein.) R. Heim, Revue Mycologique 19:51. 1954.

=*Cantharellus canadensis* (Klotzsch) Berk., The Annals and Magazine of Natural History 1(3):380. 1839.

≡*Craterellus canadensis* (Klotzsch) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:519. 1888.

≡*Gomphus canadensis* (Klotzsch) Corner, Annals of Botany Memoir 2:116. 1966.

=*Cantharellus princeps* Berk. & M.A. Curtis, The Annals and Magazine of Natural History 3(4):293. 1859.

=*Cantharellus bonarii* Morse, Mycologia 22:219. 1930.

≡*Gomphus bonarii* (Morse) Singer f. *bonarii*, Lloydia 8:140. 1945.

=*Cantharellus floccosus* f. *excavatus* A.H. Sm. & Morse, Mycologia 39:525. 1947.

≡*Gomphus floccosus* f. *excavatus* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:121. 1966.

=*Cantharellus floccosus* f. *rainieriensis* A.H. Sm. & Morse, Mycologia 39:521. 1947.

≡*Gomphus floccosus* f. *rainieriensis* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:121. 1966.

≡*Gomphus floccosus* subsp. *rainieriensis* (A.H. Sm. & Morse) R.H. Petersen, Nova Hedwigia 21:48. 1971a.

=*Cantharellus floccosus* f. *wilsonii* A.H. Sm. & Morse, Mycologia 39:523. 1947.

≡*Gomphus floccosus* f. *wilsonii* (A.H. Sm. & Morse) Corner, Annals of Botany Memoir 2:121. 1966.

≡*Gomphus bonarii* (Morse) Singer f. *wilsonii* (A.H. Sm. & Morse) R.H. Petersen, Nova Hedwigia 21:37. 1971a.

=*Cantharellus wilkinsae* Morse, *in* A.H. Sm. and Morse, Mycologia 39:528. 1947.

≡*Gomphus wilkinsae* (Morse) Corner, Annals of Botany Memoir 2:128. 1966.

≡*Gomphus bonarii* f. *wilkinsae* (Morse) R.H. Petersen, Nova Hedwigia 21:35. 1971a.

=*Gomphus floccosus* f. *cystidiophorus* R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:376. 1968.

=*Gomphus megasporus* Corner, Nova Hedwigia 18:813. 1969.

=*Gomphus bonarii* f. *novamexicanus* R.H. Petersen, Nova Hedwigia 21:44. 1971a.

=*Gomphus floccosus* f. *coccineo-basalis* R.H. Petersen, Nova Hedwigia 21:52. 1971a.

=*Gomphus floccosus* f. *olivaceous* R.H. Petersen, Nova Hedwigia 21:54. 1971a.

=*Gomphus szechwanensis* R.H. Petersen, Nova Hedwigia 21:102. 1971a.

=*Gomphus thiersii* R.H. Petersen, Evolution in the Higher Basidiomycetes, p. 363. 1971b.

Macroscopic characters: **Basidiomata** up to 30 cm tall, unipileate, cylindrical when juvenile, soon becoming truncate, and often with the margin slightly inrolled, enlarging by growth of the peripheral tissue of the truncate pileus primordium into hollow-obconic basidiomata that are funnel-shaped or excavate almost to the ground (Figure 4.2). **Pileus** up to 30 cm wide when mature, funnel-shaped, covered with floccose scales, which are minute to coarse, appressed to pyramidal or

subrectangular, sometimes in a zonate configuration, eventually worn off, possibly by rain, revealing a glabrous surface, cinnamon, pale orange, orange-red, red to scarlet, the scales usually darker than the pileus surface; margin inrolled when young, becoming less so to flat in age. **Hymenium** of wrinkled, distinct hymenial folds up to 4 mm tall, longitudinally oriented below, becoming irregularly anastomosed, longitudinally reticulate to irregularly poroid above, shallow and wrinkled at the pileus margin, dark yellow toward the margin when young, later pale brown to orange, turning brown to violaceous on handling or bruising. **Stipe** up to 33 mm wide, round, white, hispid-tomentose at the base (below substrate level), glabrous above, brunnescent when bruised, pale yellow below the substrate, abruptly becoming darker upward to the hymenium, drying longitudinally ridged and hard (woody). **Context** pliable, brittle, off-white, then white, occasionally bruising brown where exposed. **Odor** earthy and sweet. **Taste** sweet and sour. **Spore print** cinnamon.

Microscopic characters: **Pileipellis + stipitipellis** hyphae thin-walled, parallel, agglutinated to some extent, commonly branching, uninflated to somewhat inflated, pale yellow, 5.5-22 µm wide; clamp connections absent; gleoplerous hyphae occasional to abundant, narrow and interwoven with generative hyphae, pale yellow, strongly cyanophilic. **Pileus context** of generally parallel, crowded, uninflated hyphae 2.5-5.5 µm wide; clamp connections absent. **Stipe context** of thin- to thick-walled (wall up to 1.5 µm thick), compact, parallel, hyaline hyphae 3-9.5 µm wide; clamp connections absent. **Hymenial trama** of thin-walled hyphae. **Subhymenial trama** of compactly interwove, hyaline hyphae 2.5-4.5 µm wide; clamp connections absent. **Basidia** 55-105 × 7-15 µm, clavate, strongly cyanophilic, with cyanophilic granules predominant, with (2-) 4 stout sterigmata, conic when young, becoming slightly bowed in age, up to 9 µm long; clamp connections absent. Hymenial **cystidia** generally absent, when present 70-90 × 9-11 µm, apically rounded to attenuate fusiform; clamp connections absent. **Spores** 11-20.5 × (5-) 6-10 µm, orange in mass, ellipsoid to obovoid; ornamentation of strongly cyanophilic warts up to 0.5 µm tall, often anastomosing into ridges over

relatively large areas of the spore wall (Figure 4.2); apiculus prominent, up to 2 μm long, truncate-rounded, eccentric.

Habit, habitat and distribution: Solitary, gregarious or caespitose, terrestrial in mixed deciduous-conifer to pure conifer forests, rare in pure deciduous forests. *Turbinellus floccosus* is rare in pure deciduous forests. In western North America, where it is abundant (Cifuentes *et al.* 1990, Petersen 1971a, Smith and Morse 1947), *T. floccosus* occurs in most conifer associations with apparently no specific host affinity but generally in stands with *Pseudotsuga menziesii* and *Tsuga* spp. Reported also from China (Corner 1966, 1969), India (Verma *et al.* 1989), Japan (Corner 1966, 1969, Lloyd 1925, Masui 1926, 1927), Nepal (Corner 1966, Smith and Morse 1947), Korea (Wojewoda *et al.* 1993), Pakistan (Corner 1966, Smith and Morse 1947), and Tibet (Corner 1969, Petersen 1971a).

Turbinellus floccosus is presumably mycorrhizal with *Abies* (Masui 1926, 1927, Khokhryakov 1956, Valdés-Ramirez 1972, Bulakh 1978, Guzmán and Villarreal 1985), *Pinus* (Masui 1927, Guzmán and Villarreal 1985), *P. menziesii* (Trappe 1960), and *Tsuga heterophylla* (Trappe 1960, Kropp and Trappe 1982).

Collections examined: Because many collections previously assigned to several species of *Gomphus sensu lato* have been studied here, and for the purpose of clarity, specimens are listed according to their originally described names.

As *Gomphus bonarii* f. *bonarii*: **CANADA. BRITISH COLUMBIA**: Revelstoke, 20 September 1961, *W.G. Ziller* (DAOM 89680). **UNITED STATES. CALIFORNIA:** Butte Co., Butte Meadows, 29 September 1936, *E.B. Copeland* 422 (FH, MICH, WTU); Butte Co., Jonesville, 14 August 1947, *E.B. Copeland* (UC 759902); Mariposa Co., Yosemite Nat. Park, 17 September 1966, *J. Ammirati* (SFSU 265); Mendocino Co., Jackson State Forest, 12 November 1961, *D. Largent* (SFSU 166); Tulare Co., Sequoia Nat. Park, August 1927, *E.E. Morse* (MICH 36441), September 1927, *E.E. Morse* (UC), and 1 October 1945, *S. Pusateri* 1 (MICH). **IDAHO**: Bonner Co., 14 September 1966, *A.H. Smith* (TENN 32175); Bonner Co., Priest River, Priest River Experimental Forest, 9 September 1966, *R.H. Petersen and A.H. Smith* (TENN 32168), and 28 September 1966, *R.H. Petersen* (TENN

32803); Bonner Co., Priest River Experimental Forest, Tago and Tepee Creeks, 13 September 1966, *R.H. Petersen* (TENN 31892). **OREGON**: Clackamas Co., Mt. Hood Nat. Forest, Timothy Lake, 28 August 2001, *A.J. Giachini, M. Castellano and E. Cázares* (OSC 97699, 97700, 97701, 97702, 97703, 97706); Douglas Co., Umpqua National Forest, unit 14 of Chemult Road, Matsutake study, 10 October 1998, *C. Lefevre* (OSC 97574); Hood River Co., Mt. Hood Nat. Forest, Pebble Ford, 14 October 1998, *M. Trappe* (OSC 97576, 97577, 97578); Umatilla Co., Emmigrant Springs, October 1999, *M. Castellano* (OSC 97563, 97564, 97584). **UTAH**: Iron Co., Cedar City, Kaibob, 17-19 August 1973, *D.E. Stuntz 17960* (WTU).

As *Gomphus bonarii* f. *novamexicanus*: **UNITED STATES. ARIZONA**: Pima Co., Tucson, Coronado Nat. Forest, Santa Catalina Mts., Bear Wallow Campground, 18 August 1968, *Sylber* (TENN 34495), and 27 August 1968, *Sylber* (TENN 34502). **NEW MEXICO**: Santa Fe Co., Santa Fe, August 1965, *C.A. Barrows* (MICH 10721).

As *Gomphus bonarii* f. *wilkinsae*: **UNITED STATES. CALIFORNIA**: El Dorado Co., Bryan Creek Tract, 19 October 1941, *E.A. Wilkins* (UC 659985); El Dorado Co., El Dorado National Forest, no date, *E.A. Wilkins* (MICH 10076).

As *Gomphus bonarii* f. *wilsonii*: **UNITED STATES. CALIFORNIA**: Butte Co., Jonesville, 10 September 1937, *E.B. Copeland* (MICH 36447), 11 November 1943, *E.B. Copeland* (MICH 36446), and summer 1945, *E.B. Copeland* (MICH 36445, 36448); Fresno Co., Kings Canyon Nat. Park, 15 October 1945, *Nirlum* (UC 924302); Siskiyou Co., Big Spring Park, Mount Shasta, fall 1958, *R. Scott* (UC 31365); Siskiyou Co., Black Butte, Lava Ridges, 11 October 1958, *R. Scott* (UC 81220).

As *Gomphus canadensis*: **CANADA:** no location, 1867, *W.J. Hooker K-H 3787/69* (K 63157).

As *Gomphus floccosus* f. *coccineo-basalis*: **UNITED STATES. CALIFORNIA**: Mendocino Co., 14 November 1967, *R.H. Petersen* (TENN 33295).

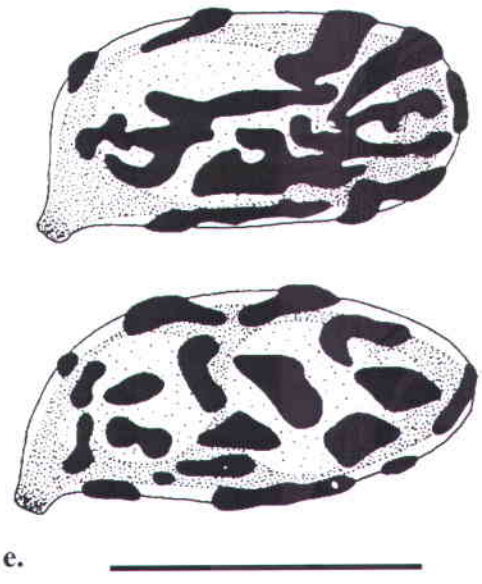
a.

b.

Figure 4.2. *Turbinellus floccosus* (Schwein.) Earle: (a, b) basidiomata (x 5 for a, 1.5 for b).

c.

d.



e.

Figure 4.2 (*cont.*). *Turbinellus floccosus* (Schwein.) Earle: (c) basidiomata (x 2); (d) spores (bar = 10 μm). Spore drawings modified from Petersen (1971b), with permission.

As *Gomphus floccosus* f. *cystidiophorus*: **CANADA. QUEBEC**: L'Islet Co., Elgin Rd., Buval's wood, August 1940, *H.A.C. Jackson* (DAOM 87243). **UNITED STATES. TENNESSEE**: Blount Co., Chilhowee Mountain, Abrams Creek, 6 July 1955, *R.H. Petersen* (TENN 21833).

As *Gomphus floccosus* f. *excavatus*: **UNITED SATES. IDAHO**: Bonner Co., Priest Lake, Beaver Campground, 25 September 1999, *M.A. Castellano* (OSC 97562).

G. floccosus f. *floccosus*: **CANADA. BRITISH COLUMBIA**: Vancouver Island, Oyster Rd., 17 September 1938, *I. Mounce and W. Tougean* (DAOM 9166); Vancouver Island, Quamich, 6 October 1942, *A. Nicholls* (DAOM 11191). **ONTARIO**: Algonquin Peak, Found Lake, 28 July 1975, *J. Ammirati 6994* (WTU), and 20 September 1978, *J. Ammirati 8341* (WTU); WR and Algonquin Peak, Longspur Creek, 5 August 1975, *J. Ammirati 7242* (WTU). **JAPAN:** Aichi Prefecture, no date, *Y. Matsuda* (OSA-MY-1839, OSA-MY-1840); Sendai, 21 September 1913, *A. Yasuda* (WTU). **UNITED STATES. CALIFORNIA:** Mendocino Co., 14 November 1967, *R.H. Petersen* (TENN 33250); Mendocino Co., Aleuria Glen, along Rd. 409, 25 October 1986, *M. Seidl 2119* (WTU); Mendocino Co., Jackson State Forest, 27 October 1961, *J. Jensen 6* (SFSU), and 19 December 1965, *H.D. Thiers* (SFSU 14621); Mendocino Co., Redwood Canyon toward Albion River, 17 November 1947, *M. Kelly* (MICH); Humboldt Co., Arcata, 15 October ?, *H. Lanphere 761* (WTU); Humboldt Co., Redwoods State Park, Prairie Creek, 23 November 1937, *A.H. Smith 9033* (MICH); Tulare Co., Eureka, Sequoia Nat. park, November 1947, *P.C. Richardson* (UC 1139686). **IDAHO**: Bonner Co., Priest Lake, Beaver Campground, 25 September 1999, *M.A. Castellano* (OSC 97560); Bonner Co., Priest River, Priest River Experimental Forest, 28 November 1966, *R.H. Petersen* (TENN 32800). **MAINE:** No location, no date, *Sprague no. 1764* (K 6196). **NEW YORK**: Essex Co., North Elba, Adirondack Mountains, 1896, det. *C.H. Peck* 312 (FH); Tompkins Co., Ithaca, Coy Glen, 9 October 1937, *C. Isely* (WTU); Herkimer Co., Buck Hill Road, 26 September 1979, *Weijek 75-79* (WTU), and 30 August 1983, *Weijek 69-83* (WTU); Warren Co., Warrensburg, August 1932, *Snell* (WTU). **NORTH CAROLINA:** Lenoir Co., Lenoir,

22 June 1939, *D.E. Stuntz 691* (WTU); Macon Co., 11 July 1999, *J. Spatafora* (OSC 69167); Macon Co., Coweeta Hydrol. Lab., 11 August 1966, *R.H. Petersen* (TENN 32099); Oconee Co., Sumter Nat. Forest, 13 July 1999, *J. Spatafora* (OSC 69193). **OREGON**: Benton Co., Corvallis, McDonald Forest, 5 September 1998, *M. Mildner* (OSC 97595); Benton Co., Willamette Nat. Forest, Mary's Peak, 30 September 1999, *A.J. Giachini* (OSC 97553); Clackamas Co., Mt. Hood Nat. Forest, Timothy Lake, 28 August 2001, *A.J. Giachini and M.A. Castellano* (OSC 97704, 97705); Clackamas Co., Mt. Hood Nat. Forest, Timothy Lake, Roads 108 and 104, 23 October 1998, *E. Cázares* (OSC 97581, 97582); Douglas Co., Umpqua Nat. Forest, 5 November 1999, *A.J. Giachini* (OSC 97653, 97654, 97655); Douglas Co., Umpqua Nat. Forest, DEMO study site, 17 October 1998, *D. Luoma* (OSC 97575); Douglas Co., Umpqua Nat. Forest, DEMO study site, Watson Fall Block, 21 October 1998, *D. Luoma and J. Eberhart* (OSC 97583); Douglas Co., Diamond Lake, 27 August 1957, *D. Isely 205* (WTU); Jackson Co., Fish Lake, Butte Creek, 9 September 1960, *D. Isely 1214* (WTU); Jackson Co., Howard Prairie Lake, 25 October 1998, *E. Cázares* (OSC 97593, 97598); Jackson Co., Rogue River Nat. Forest, 16 October 1999, *E. Cázares* (OSC 97559); Jefferson Co., Warm Springs Indian Reservation, junctions Roads 42 and 270, 23 October 1998, *E. Cázares* (OSC 97579); Josephine Co., Rogue River, no date, *D. Isely 602* (WTU); Josephine Co., Grants Pass, 23 November 1956, *D. Isely 497* (WTU); Josephine Co., Williams, 14 December 1998, *M. Trappe* (OSC 97597); Lane Co., Eugene, 30 October 1999, *undetermined collector* (OSC 97648, 97649); Lane Co., Hidden Lake, 25 September 1999, *M. Trappe* (OSC 97552), and 11 October 1998, *M. Trappe* (OSC 97573); Lane Co., H. J. Andrews Experimental Forest, 10 October 1998, *S. Dunham* (OSC 97572); Lane Co., H. J. Andrews Experimental Forest, Crescent Mt. Trail, 23 October 1999, *A.J. Giachini* (OSC 97602, 97603, 97604); Lane Co., H. J. Andrews Experimental Forest, Grass Mtn., 9 September 2000, *S. Dunham* (OSC 97688), and 30 September 2000, *T. O'Dell* (OSC 97689); Lane Co., H. J. Andrews Experimental Forest, Lookout Mt., Rd. 1506, 23 October 1999, *A.J. Giachini* (OSC 97621); Lane Co., H. J. Andrews Experimental Forest, Lost Prairie,

23 October 1999, *A.J. Giachini* (OSC 97606, 97607, 97608, 97609, 97610, 97612, 97613, 97614); Lane Co., McKenzie Pass, 18 November 1937, *A.H. Smith 7924* (MICH); Lane Co., Oakridge, Fall Creek, 20 August 1999, *M. Madsen* (OSC 97551); Lane Co., Slide Creek, 11 October 1999, *M. Trappe* (OSC 97565); Lane Co., Willamette Nat. Forest, 6 October 1999, *S. Holmes* (OSC 97558), 11 October 1999, *M. Trappe* (OSC 97566), and 23 October 1999, *A.J. Giachini* (OSC 97569, 97618); Lane Co., Willamette Nat. Forest, Gold Lake, 3 November 1999, *A.J. Giachini* (OSC 97637, 97638, 97639, 97640, 97642, 97643, 97644); Linn Co., Snow Peak, 14 October 2000, *A.J. Giachini and M. Trappe* (OSC 97690, 97691, 97693); Linn Co., Sweet Home, 4 November 2000, *A.J. Giachini* (OSC 97695, 97697); Linn Co., Sweet Home, Toad Creek Road, 4 November 1999, *F. Sanchez* (OSC 97652); Linn Co., Willamette Nat. Forest, Gordon Lakes Trail, 13 November 1999, *A.J. Giachini* (OSC 97657, 97658, 97660, 97661, 97662, 97663, 97664, 97665, 97666); Linn Co., Willamette Nat. Forest, Pamelia Lake Trail Head, 2 November 1999, *A.J. Giachini* (OSC 97626, 97627, 97628, 97629, 97630, 97631, 97632, 97634, 97635, 97636, 97645); Marion Co., Detroit Road, 17 October 1999, *M. Trappe* (OSC 97568). **PENNSYLVANIA:** No location, no date, *L.D. Schweinitz* (PH – as *Cantharellus floccosus* – **holotype**). **TENNESSEE**: Blount Co., Great Smoky Mountains Nat. Park, Cades Cave, 7 April 1935, *D. Bain and I.R.N.* (TENN 7894); Sevier Co., Great Smoky Mountains Nat. Park, Mount Le Conte, 20 September 1934, *R.H. Petersen* (TENN 5001). **UTAH**: Iron Co., Cedar City, Hailiale, 17-19 August 1973, *V. Bogart 1766* (WTU). **WASHINGTON**: Chelan Co., Glacier Peak Wilderness, Lake Wenatchee Road, Indian Creek Trail, 17 October 1998, *D. Pilz* (OSC 97586); Clallam Co., Mt. Eleanor, August 1912, *S.M. Zeller 116* (WTU); Clallam Co., Olympic Mountains, September 1936, *J. Broadbent 757* (WTU); Kitsap Co., Bainbridge Island, October 1926, *J.W. Hotson* (WTU); Kittitas Co., Lake Kachess Campground, 22 October 1978, *D.E. Stuntz 20471* (WTU); Pend Oreille Co., Sullivan Creek, 3 October 1998, *E. Coulter* (WTU); Skamania Co., Gifford Pinchot Nat. Forest, September 1949, *J. Carlett 5838* (WTU), and 29 September 2000, *D. Luoma* (OSC 97687); Snohomish Co., Barlow Pass, 25 August

1990, *J. Ammirati 10175* (WTU); Snohomish Co., Edmonds, 20 October 1934, *D.E. Stuntz 196* (WTU).

As *Gomphus floccosus* f. *olivaceous*: **UNITED STATES. CALIFORNIA**: Del Norte Co., Jedediah Smith Redwoods State Park, 11 November 1967, *R.H. Petersen* (TENN 33233); Del Norte Co., Jedediah Smith Redwoods State Park, John Stout Grove, 11 November 1967, *R.H. Petersen* (TENN 33231); Mendocino Co., Jackson State Forest, 5 November 1967, *H.D. Thiers* (TENN 33170, 33171). **NORTH CAROLINA:** Jackson Co., Horse Cove Road to Whiteside Cove Road to Summer Chapel, 12 July 1999, *J. Spatafora* (OSC 69180). **OREGON**: Benton Co., Corvallis Watershed, 13 November 1998, *M. Trappe* (OSC 97596). **WASHINGTON**: Thurston Co., Olympia, 6 November 1949, *D.E. Stuntz 5934* (WTU).

As *Gomphus floccosus* f. *rainieriensis*: **CANADA. BRITISH COLUMBIA**: Pitt Island, Union Pass, 28 September 1938, *T.T. McCabe* 82-692989 (UC). **UNITED STATES. CALIFORNIA**: Butte Co., Jonesville, 1 October 1938, *E.B. Copeland* (UC 1407959); El Dorado Co., Blodgett Research Forest, 25 September 2000, *J.M. Trappe* (OSC 97686); Mendocino Co., Jackson State Forest, 5 November 1967, *H.D. Thiers* (TENN 33169), and 14 November 1967, *R.H. Petersen* (TENN 33291). **IDAHO**: Bonner Co., Priest River Experimental Forest, Priest River, 12 September 1966, *R.H. Petersen* (TENN 32285), and 27 September 1966, *R.H. Petersen and A.H. Smith* (TENN 32805). **OREGON**: Clackamas Co., Mt. Hood National Forest, Timothy Lake, Road 5890, 13 October 1998, *D. Pilz* (OSC 97585); Douglas Co., Umpqua Nat. Forest, DEMO study site, 14 October 1999, *D. Luoma and J. Eberhart* (OSC 97567); Jackson Co., Howard Prairie Lake, 25 October 1998, *E. Cázares* (OSC 97592, 97599); Klamath Co., Deschutes Nat. Forest, Summit Lake, Roads 4260 and 42, 23 October 1998, *M.A. Castellano* (OSC 97580); Lane Co., Eugene, 30 October 1999, *undetermined collector* (OSC 97647); Lane Co., H. J. Andrews Experimental Forest, Crescent Mt. Trail, 23 October 1999, *A.J. Giachini* (OSC 97600); Lane Co., Willamette Nat. Forest, Gold Lake, 3 November 1999, *A.J. Giachini* (OSC 97641); Lane Co., H. J. Andrews Experimental Forest, Lost Prairie, 23 October 1999, *A.J. Giachini* (OSC 97605);

Linn Co., Willamette Nat. Forest, Gordon Lakes Trail, 13 November 1999, *A.J. Giachini* (OSC 97659); Linn Co., Willamette Nat. Forest, Pamelia Lake Trail Head, 2 November 1999, *A.J. Giachini* (OSC 97625, 97633); Marion Co., Willamette Nat. Forest, 2 November 1998, *M. Trappe* (OSC 97594); Wasco Co., Skyline Road, 26 September 1946, *A.H. Smith 23734* (MICH). **WASHINGTON:** King Co., Rattlesnake Ridge, 221 November 1980, *V. Bogart 21020* (WTU); Kittitas Co., Easton, 2 October 1955, *D.E. Stuntz 9179* (WTU); Skamania Co., Gifford Pinchot Nat. Forest, Highway 30, Oldman Pass, 15 October 1998, *D. Pilz* (OSC 97587).

As *Gomphus thiersii*: **UNITED STATES. CALIFORNIA:** Calaveras Co., Calavaras Big Tree State Park, 15 October 1967, *J. Jensen* (SFSU 21238).

Discussion: Petersen (1971a) designated the *Cantharellus floccosus* collection cited on Schweinitz's (1831) original description and deposited at PH as the neotype for *G. floccosus* (≡*T. floccosus*). This is not only the most common species of the genus but also one of the more complex problems in taxonomy. Smith and Morse (1947) treated the species as *Cantharellus floccosus* and *C. bonarii*, both with several varieties. Corner (1966) and Petersen (1971a) accepted Smith and Morse's described species and varieties, proposed some of their own, and transferred them to *Gomphus*. Because molecular techniques for evolutionary biology were just being developed at that time, the decisions were based solely on general morphological variation. Petersen's (1971a) decisions, more specifically, were based on macro-morphology: he affirms that the microscopic characters among varieties within *G. floccosus* were much more uniform than the macroscopic ones. An important character used by Petersen (1971a) to delineate species in *Gomphus* was the appearance of the pileus, although he stated "the scaliest forms of *G. floccosus* are distinguished from *G. bonarii* only with difficulty."

A better understanding of interspecific variation among taxa of fungi can be obtained with the application of molecular biology techniques. According to Giachini (chapter 2), *G. floccosus* (including all forms and subspecies) and *G. bonarii* (including all forms) are synonyms under *Turbinellus floccosus*.

The basidiomata of this species have a fibrillose, appressed squamose pileus surface and appear to be distributed conifer forests across the USA. It reaches its center of abundance in the rainy parts of the Pacific northwest (Petersen 1971a). The species is distinguished from other *Turbinellus* species on the scaly, orange colored pileus surface allied with the size of the verrucose spores.

Turbinellus fujisanensis* (S. Imai) Giachini, *sp. prov. Fig. 4.3

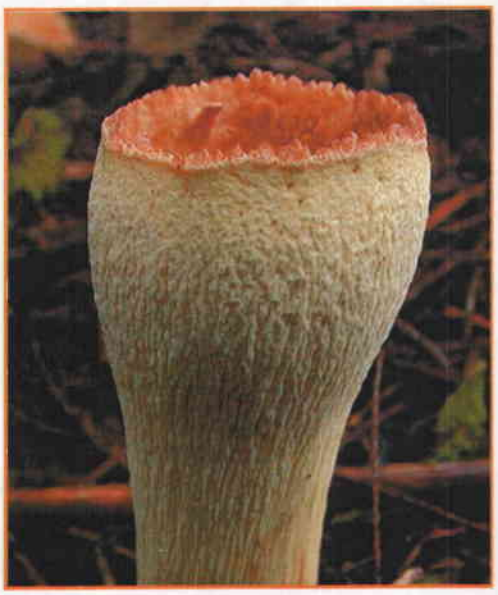
≡*Cantharellus fujisanensis* S. Imai, The Botanical Magazine 55:519. 1941.

≡*Neurophyllum fujisanensis* (S. Imai) S. Ito, Mycological Flora of Japan 2:103. 1955.

Macroscopic characters: **Basidiomata** up to 15 cm tall, unipileate (Figure 4.3). **Pileus** 5-10 cm wide, subcylindrical when juvenile becoming funnel-shaped and squamose in age, initially cinnamon and glabrous, then cinnamon-yellow to pale orange or pale brown; scales larger in the center of the pileus, then dot-like toward the pileus margin (much like *T. kauffmanii*), scales darker than the pileus surface, generally orange with brown tips; margin undulate ornate. **Hymenium** strongly decurrent, hymenial folds strongly forked and up to 1 mm tall, becoming undifferentiated toward the pileus margin, pale yellow to white in young specimens, becoming pale orange to pale brown in age. **Stipe** hollow, glabrous, tapering downward, initially white, then concolorous with the hymenium. **Context** brittle to pliable, white. **Odor** and **taste** not recorded. **Spore print** cinnamon.

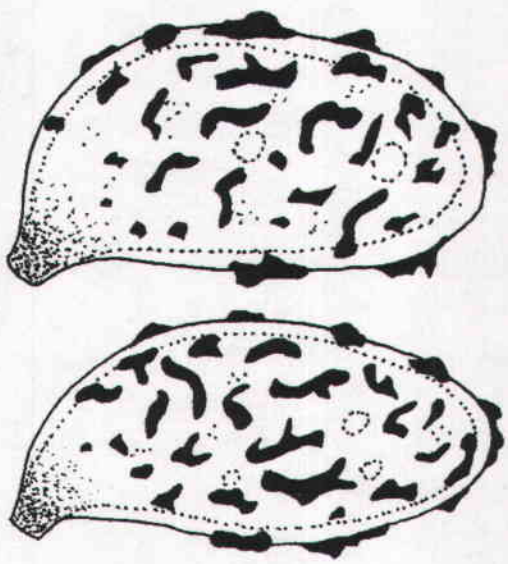
Microscopic characters: All **hyphae** thin-walled, up to 7 µm wide; clamp connections absent; some gleoplerous hyphae seen. **Basidia** clavate, intermixed with gleoplerous end cells, with 4 sterigmata; clamp connections absent. Hymenial **cystidia** absent. **Spores** (8.5-) 9.5-11.5 × 5-6 µm, cinnamon to orange in mass, ellipsoid to obovoid; ornamentation of low, cyanophilic warts (Figure 4.3); apiculus prominent, eccentric.

a.



b.

c.



d.

Figure 4.3. *Turbinellus fujisanensis* (Imai) Giachini, *sp. prov.*: (a, b, c) basidiomata (x 1 to 2); (d) spores (bar = 10 µm).

Habit, habitat and distribution: Gregarious to caespitose, fruiting on soil in mixed conifer forests in Japan (Imai 1941).

Collections examined: **JAPAN:** Aichi Prefecture, 28 September 1995, *Y. Matsuda* (OSA-MY-1841), and 11 September 1996, *Y. Matsuda* (OSA-MY-1842 – **neotype** here designated). No collection has ever been assigned as the type for this species. Therefore, OSA-MY-1842 is here designated as the neotype for *T. fujisanensis*.

Discussion: Imai (1941) first described the species as *Cantharellus* but did not cite any collection nor designated a holotype. Ito (1955) transferred *C. fujisanensis* to *Neurophyllum*, and again no collection was mention and no type designated. Recently Giachini (chapter 2) transferred it to *Turbinellus*, and now OSA-MY-1842 is here designated as the neotype for *T. fujisanensis*.

The species is endemic to Japan. It resembles and is close related to the North American species *T. kauffmanii*. Both have similar overall morphological features, with especially similar scaly pileus. The Japanese counterpart however produces smaller basidiomata with smaller spores than *T. kauffmanii*.

Corner (1966) considered it to be a synonym of *T. floccosus*. However, morphology and genetics show it to be unique and more closely related to *T. kauffmanii* than to *T. floccosus* (Giachini, chapter 2).

Turbinellus kauffmanii* (A.H. Sm.) Giachini, *sp. prov. Fig. 4.4

≡*Cantharellus kauffmanii* A.H. Sm., *in* Smith and Morse, Mycologia 39:516. 1947.

≡*Gomphus kauffmanii* (A.H. Sm.) Corner, Annals of Botany Memoir 2:122. 1966.

Macroscopic characters: **Basidiomata** maturing up to 40 × 35 cm, unipileate, solid and fleshy when young (Figure 4.4). **Pileus** up to 35 cm wide, initially cylindrical-truncate, expanding above and becoming progressively depressed, funnel-shaped and finally excavate, surface pale brown to pale orange, usually with insect damage

or decay inside lower portion of the cavity, surface almost glabrous at the margin, then covered with small scales which are subpyramidal to dot-like near the margin, heavily rectangular to pyramidal downward in the cone and there becoming reflexed so that in fleshy, slightly immature basidiomata the lower scales often block the pileus cavity; scales pale toward the margin, darker below, usually decaying in age before general decay of the basidioma, or weathering loose to expose the cavity of the pileus which is otherwise covered with debris. **Hymenium** deeply decurrent, composed of anastomosing and deeply wrinkled ridges up to 3 mm tall, especially wrinkled in older specimens, pale yellow to pale cinnamon, then pink-yellow, occasionally bruising vinaceous. **Stipe** up to 150 × 60 mm wide, solid for some time, finally hollow most of the length, faintly rough, tapering downward, the base up to 20 mm thick and blunt, curved in the soil at times, often covered with minute white mycelial felts below the substrate level, concolorous with hymenium above and occasionally bruising vinaceous. **Context** pliable, generally with cavities made by insects, off-white or white. **Odor** mild or often faintly to obviously aromatic. **Taste** mild, sometimes acrid but usually not distinctive. **Spore print** cinnamon.

Microscopic characters: **Pileipellis + stipitipellis** consisting of a layer of thick-walled hyphae, sometimes finely granulated, more irregularly interwoven than the hyphae bellow, rarely with ampulliform swellings, 3-4 µm wide, the cells rather sausage shaped, individual hyphae yellow in water, brown in KOH; clamp connections absent; gleoplerous hyphae present. **Context** hyphae moderately thin-walled, parallel to the long axis of the basidioma, becoming more interwoven toward the hymenium surface, hyaline to pale yellow, with occasional to abundant ampulliform swellings, less common toward the pileus surface and margin; clamp connections absent. **Hymenial trama** of thin-walled, subparallel to interwoven, hyaline hyphae 2.5-5 µm wide. **Subhymenial trama** of thin-walled, compactly interwoven hyphae 3-4 µm wide. **Basidia** (45-) 60-90 (-115) × (7.5-) 9-11.5 (-13) µm, clavate or cylindrical with somewhat bulbous apex, hyaline, with 2 and 4 slender, straight, not divergent sterigmata up to 8.5 µm long; clamp connections

absent. Hymenial **cystidia** absent. **Spores** 12.5-17.5 (-20.5) × (5-) 6-8 μm, orange in mass, ellipsoid to obovoid; ornamentation of verrucose, with low, somewhat anastomosed cyanophilic ridges (Figure 4.4); apiculus rounded, somewhat obscure, eccentric.

Habit, habitat and distribution: Solitary, gregarious or loosely caespitose in rich soil in conifer forests. Known only from North America, especially eastern and western USA (Cifuentes *et al.* 1990, Petersen 1971a, Smith and Morse 1947).

Collections examined: **CANADA. BRITISH COLUMBIA**: Vancouver Island, Sooke, 18 October 1962, *M. Pantidou* (DAOM 91371). **UNITED STATES. CALIFORNIA**: Del Norte Co., Jedediah Smith Redwoods State Park, Stout Grove, 11 November 1967, *R.H. Petersen* (TENN 33220); Mendocino Co., Jackson State Forest, 16 January 1967, *H.D. Thiers* (SFSU 18476), and 5 November 1967, *H.D. Thiers* (TENN 33167); Sierra Co., Yuba Pass, 26 October 1965, *H.D. Thiers* (SFSU 13852). **NORTH CAROLINA**: Macon Co., Nantahala Nat. Forest, Standing Indian State Park, 16 July 1999, *J. Spatafora* (OSC 69257). **OREGON**: Clackamas Co., Mt. Hood Nat. Forest, East Fork Salmon River, 6 October 1944, *A.H. Smith 19457* (MICH); Clackamas Co., Mt. Hood Nat. Forest, Salmon River, 12 October 1946, *A. H. Smith 24444* (MICH); Coos Co., South Slough, 9 September 1986, *C. Ardrey 1016* (WTU), 23 September 1985, *C. Ardrey 801* (WTU), and 3 October 1987, *C. Ardrey 1185* (WTU); Lane Co., Eugene, 30 October 1999, *collector unknown* (OSC 97650, 97651); Lane Co., H. J. Andrews Experimental Forest, 10 October 1998, *E. Muench* (OSC 97571); Lane Co., H. J. Andrews Experimental Forest, Lost Prairie, 23 October 1999, *A.J. Giachini* (OSC 97615); Lane Co., Willamette Nat. Forest, Waldo Lake, 17 October 1999, *C. Lefevre* (OSC 97561); Linn Co., Snow Peak, 14 October 2000, *A.J. Giachini and M. Trappe* (OSC 97692); Multnomah Co., Portland, 8 October 1966, *R.H. Petersen* (TENN 32276). **TENNESSEE**: Sevier Co., Great Smoky Nat. Park, 14 August 1968, *R.H. Petersen* (TENN 33824). **WASHINGTON**: King Co., Moore's Fall, 14 August 1976, *D.E. Stuntz 19654* (WTU); Pierce Co., Mount Rainier Nat. Park, Mowich Lake, 8 September 1990, *collector unknown* (WTU); San Juan Co., Matia Island, 20 July 1980, *D.E. Stuntz*

20973 (WTU); Skamania Co., Mt. Adams Recreation, Takhlakh Meadows, 22 September 1986, *W.B. and V.G. Cooke 63377* (WTU); Snohomish Co., Hyak Ski, Twin Lakes, 1 October 1994, *P. Slimperi* (WTU); Snohomish Co., Snoqualmie Nat. Forest, Annette Lake Trail, 5 September 1994, *G.R. Walker 771* (WTU); Snoqualmie Co., Mt. Baker Recreation, Shuksan Inn, no date, *A.H. Smith 16156* (MICH 10069 – as *Cantharellus kauffmanii* – **holotype**).

Discussion: This is the largest *Turbinellus* species. It can be spectacular with its large pale brown to pale orange basidiomata. This species was considered close to *T. floccosus* by virtue of the coarsely scaly pileus and the solid stipe that gradually becomes hollowed by the breaking up of the interior scales (Smith and Morse 1947). The molecular data corroborate this observation but shows that it is more closely related to *T. fujisanensis* than to *T. floccosus* (Giachini, chapter 2).

Turbinellus kauffmanii is easily separated from other *Turbinellus* species by several characters. It tends to have the pileus covered with scales that become smaller and smaller (dot-like) toward the margin of the pileus, a phenomenon also seen in *T. fujisanensis*. However, *T. fujisanensis* is known only from Japan, while *T. kauffmanii* is known only to North America. In addition, the spore sizes of the two species do not overlap, and the basidiomata of *T. kauffmanii* are much larger. The spores of *T. kauffmanii* are more delicately ornamented and in general longer than those of other *Turbinellus* species.

Turbinellus kauffmanii resembles *T. floccosus*, especially in early stages of basidioma development. However, the size and arrangement of scales in the pileus surface separate these two species. *Turbinellus kauffmanii* may have large, reflexed scales on the pileus surface, invariably in the center of the pileus and never on the margin. Generally pale brown, small, dot-like scales cover the margin of the pileus of *T. kauffmanii*, a condition never observed in *T. floccosus*.

The vinaceous bruising reaction of *T. kauffmanii* is common to other species of *Turbinellus* and species of *Ramaria* and *Phaeoclavulina,* suggesting and supporting the evolutionary relationships shared among these genera of fungi.

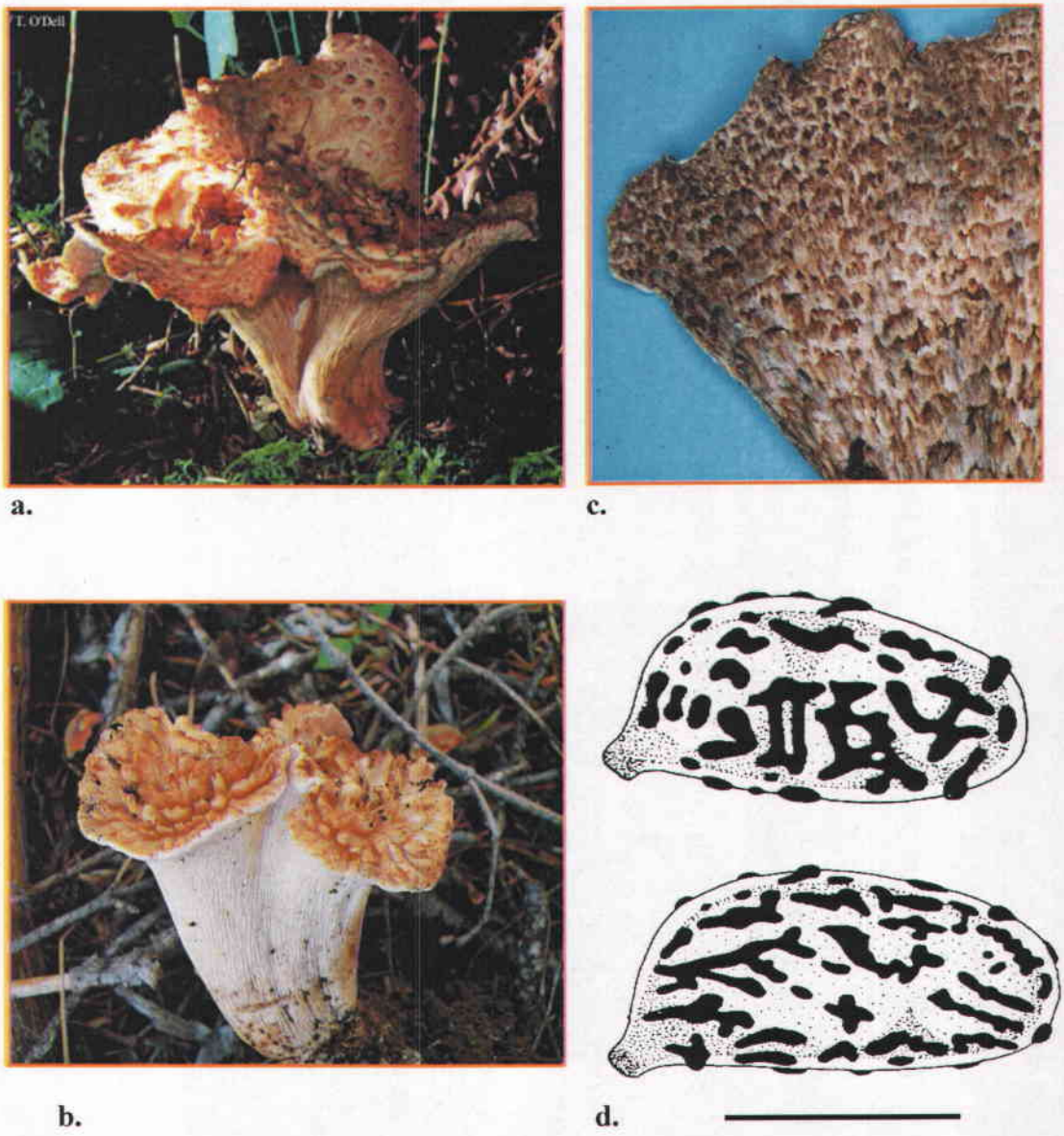


Figure 4.4. *Turbinellus kauffmanii* (A.H. Sm.) Giachini, *sp. prov.*: (a, b) basidiomata (x 3); (c) close-up of pileus surface (x 1.5); (d) spores (bar = 10 µm). Spore drawings modified from Petersen (1971b), with permission.

Turbinellus stereoides* (Corner) Giachini, *sp. prov. Fig. 4.5

≡*Gomphus stereoides* Corner, Annals of Botany Memoir 2:124. 1966.

=*Gomphus brasiliensis* Corner, Nova Hedwigia 18:807. 1969.

Macroscopic characters: **Basidiomata** 10 cm tall, merismatoid, pilei arising from a common stipe, overall pale orange (Figure 4.5). **Pileus** 6 cm wide, spatula-like at first, then fan-shaped, surface with appressed scales, pale orange; margin recurved. **Hymenium** decurrent, rugulose with folds up to 1 mm tall, bifurcating especially toward the margin of the pileus, orange. **Stipe** 10-80 × 3-15 mm, solid, subcylindrical to slightly tapering downward, with white mycelium covering the base of the stipe. Data on **context** not recorded. **Odor** mild. **Taste** not recorded. **Spore print** cinnamon.

Microscopic characters: **Pileipellis, stipitipellis,** and **pileus** and **stipe context** of parallel and compact, septate hyphae 2-10 (-15) µm wide, slightly inflated at the tips; clamp connections absent; gleoplerous hyphae interwoven, frequently branched, minutely inflated, up 3-15 µm wide (Figure 4.5). **Hymenial trama** of thin-walled hyphae. **Subhymenial trama** hyphae 2-4 µm wide (Figure 4.5). **Basidia** 60-85 × 8-11 µm, clavate, with (2-3-) 4 straight sterigmata, 6-8 µm long; clamp connections absent (Figure 4.5). Hymenial **cystidia** absent. **Spores** 9-13 × 4.5-6 µm, orange in mass, ellipsoid to obovoid (Figure 4.5); ornamentation of cyanophilic warts 0.5 µm tall; apiculus up to 1 µm long.

Habit, habitat and distribution: Solitary to gregarious, on soil in Africa (Corner 1966), Brazil (Corner 1969), Malaysia (Corner 1966), and Turkey (Sesli and Türkekul 2000).

Type (holotype): **MALAYSIA:** Perak, Slim River, 10 May 1930, *E.J.H. Corner* (CGE – as *Gomphus stereoides*).

Discussion: Personnel at CGE were contacted, but loan of the type for *T. stereoides* was denied because of the specimen's fragile condition. Therefore, the description presented here is based on notes from Corner (1966).

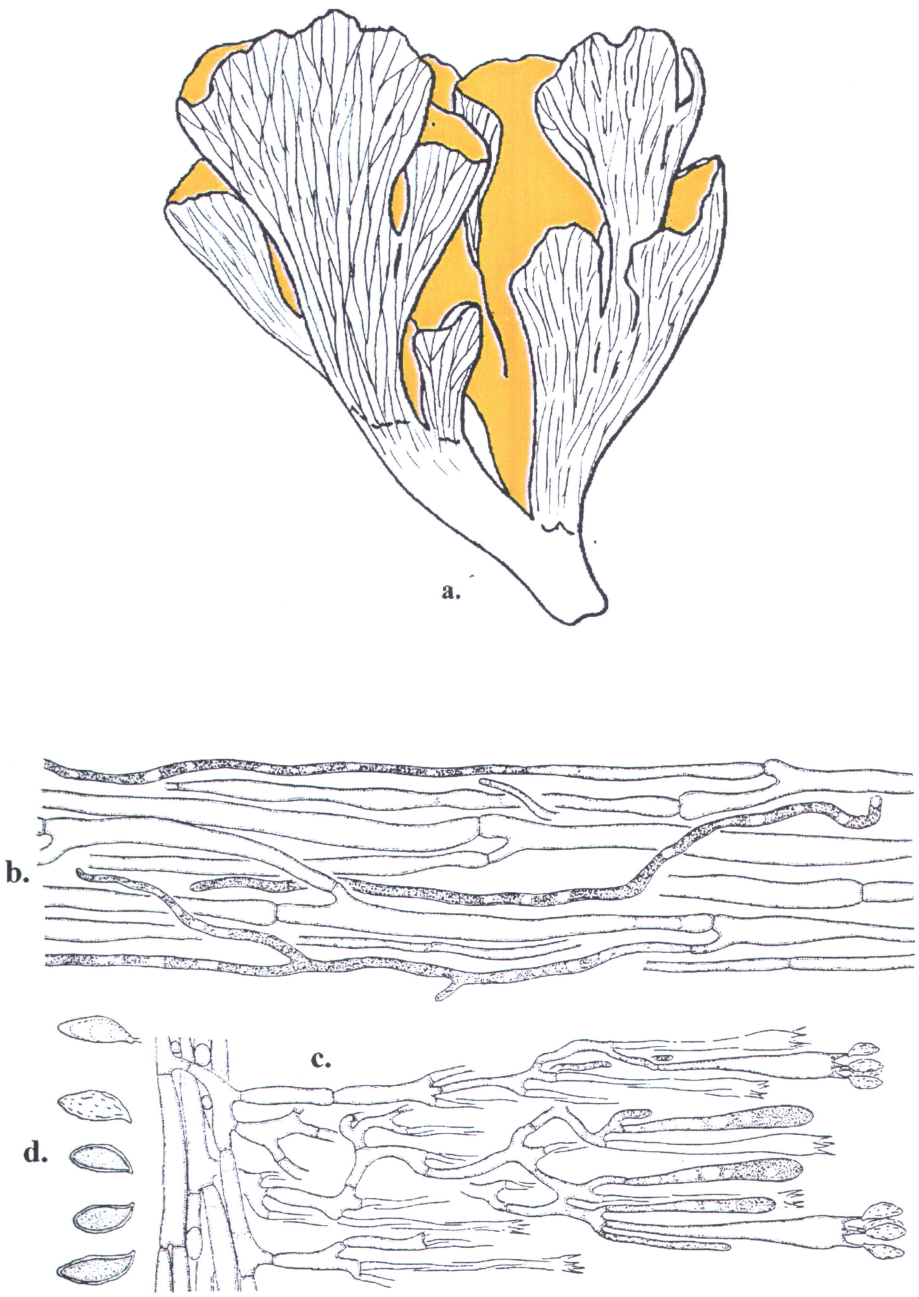


Figure 4.5. *Turbinellus stereoides* (Corner) Giachini, *sp. prov.*: (a) basidioma (x 0.5); (b) gleoplerous hyphae (x 500); (c) hymenium (x 500); (d) spores (x 100). Modified from Corner (1966).

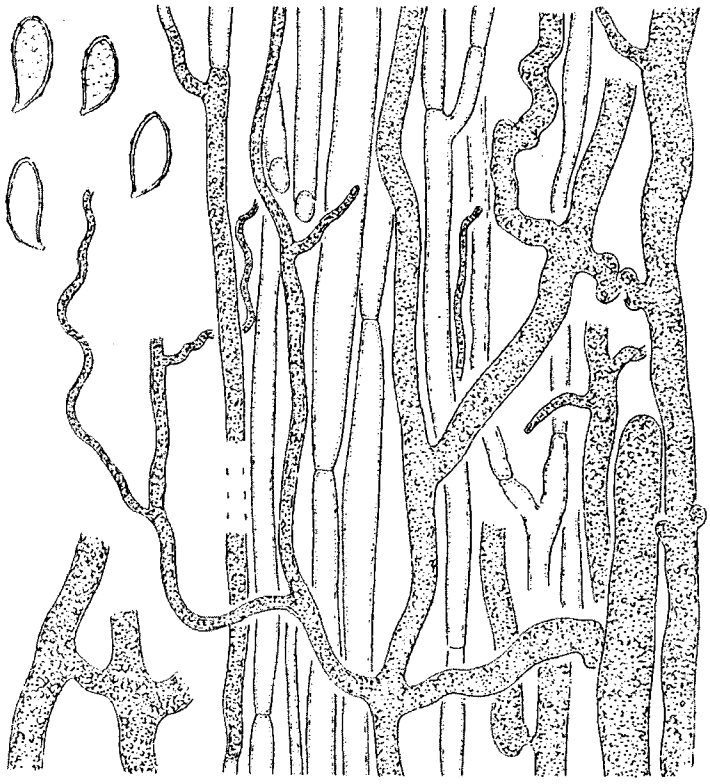


Figure 4.5 (*cont.*). *Turbinellus stereoides* (Corner) Giachini, *sp. prov.*: spores (x 1000) and hyphae of the subhymenium (x 500). Modified from Corner (1969).

Corner (1966) described *G. brasiliensis*, which resembles *Phaeoclavulina subclaviformis*. However, the absence of clamp connections and the much wider gleoplerous hyphae confirmed the evidence of the rather strongly lamellate hymenium that makes it distinct and not a member of that genus. Giachini (chapter 2), after verifying Corner's description for *G. brasiliensis* also at CGE but unavailable for loan, considered it a synonym of *T. stereoides*. According to Corner (1966), the basidiomata of *T. stereoides* appear regularly every season in Malaysia, but are not evident until several weeks after the rains begin. They grow slowly and seem to last for many days.

DISCUSSION

The name *Turbinellus* was recently resurrected to accommodate species of *Gomphus sensu lato* that present unique morphological features not observed in other member of the Gomphales (Giachini, chapter 2). The genus originally proposed by Earle (1909) contained only 3 species, although only *T. floccosus* was cited. Singer (1945) adopted the overall characteristics of the pileus and hymenium to combine some species of *Cantharellus, Chloroneuron,* and *Turbinellus* into *Gomphus sensu lato*. Subsequent workers accepted Singer's classification, and even though some species were transferred to *Cantharellus* and *Gloeocantharellus* over the years, many retained their placement in *Gomphus* until recently.

This fascinating and widely distributed genus of fungi has recently been genetically characterized and its evolutionary history delineated within the order Gomphales (Giachini, chapter 2). In addition, molecular data provided a basis for delimitating species boundaries. Combined morphology and molecular techniques showed *Gomphus sensu lato* to be non-monophyletic, suggesting the segregation of *Gomphus sensu lato* species into 4 genera: *Gomphus sensu stricto, Gloeocantharellus, Phaeoclavulina,* and *Turbinellus* (Giachini, chapter 2).

The need for a general taxonomic and nomenclatural revision of the genera within Gomphales was clear. A good example is *Gomphus bonarii* (=*T. floccosus*), long known for its occurrence and alleged rarity in the Pacific northwestern USA. In 1994 *G. bonarii* and *G. floccosus* (≡*T. floccosus*) acquired special status due to the reduced number of populations predicted for the forests of that region, and general surveys were to be conducted before any forest management activities were approved for federally owned properties (U.S.D.A. and U.S.D.I. 1994ab). In 2000 and 2001, after intensive surveys on occurrence and abundance of those species, *T. floccosus* lost its 'endangered status' because it was considered to be underestimated rather than rare (U.S.D.A. and U.S.D.I. 2000, 2001). However, the current classification for *Turbinellus* shows that *G. bonarii* is a synonym of *T. floccosus* (Giachini, chapter 2). *Gomphus bonarii* should, for that reason, not receive special status, and therefore should be removed from the list of special concern.

Turbinellus is distinguished from other genera in the Gomphales by molecular as well as morphological characters (Giachini, chapter 2). Among the morphological characters important for genus level identification are the scaly yellow, orange, brown to red pileus, the strongly wrinkled and generally pale yellow hymenium, the absence of clamp connections, and the verrucose spores.

Turbinellus species occur on four continents in a variety of forest ecosystems. Some species are presumed to be ectomycorrhizal with major species of conifers (Masui 1926, Masui 1927, Khokhryakov 1956, Trappe 1960, Valdés-Ramirez 1972, Bulakh 1978, Kropp and Trappe 1982, Guzmán and Villarreal 1985).

The largest abundance of *Turbinellus* basidiomata appears in North America, more specifically in the Pacific northwestern USA. In that region species fruit in the fall, with occasional fruiting events during wet, warm springs, and tend to occur in abundant clusters of several basidiomata.

Even though some species of *Turbinellus* received considerable attention in the past, much still needs to be known regarding its evolution and ecology. Further

studies focusing on these topics are necessary to expand the knowledge on this well-distributed but understudied genus.

A complete discussion on the evolutionary history and the relationships of *Turbinellus* to other members of the Gomphales is provided in chapter 7.

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CHAPTER 5

Systematics of the Gomphales: The Genus *Gloeocantharellus* Singer

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ABSTRACT

The aboveground fruiting, agaricoid-gomphoid genus *Gloeocantharellus* is currently composed of ten species distributed primarily in tropical and subtropical regions of Bolivia, Borneo, Brazil, Guam, Hawaii, Malaysia, Papua New Guinea, the Solomon Islands, and Sri Lanka. Some species also occur in Japan, New Zealand, Russia, and the USA. *Gloeocantharellus* species are characterized by relatively small basidiomata with wrinkled to lamellate hymenium and presence of large numbers of gleoplerous hyphae. Main features used to separate species within *Gloeocantharellus* are the size and ornamentation of the spores, presence or absence of clamp connections, presence or absence of gleocystidia, habitat, and distribution. All species of *Gloeocantharellus* are terrestrial and generally occur in places where well-known ectomycorrhizal tree species are common. *Gloeocantharellus* is composed of multiple derived evolutionary lineages, which may represent distinct subgenera composed of one to several species.

INTRODUCTION

Gomphus sensu lato and *Gloeocantharellus* have historically been separated by the presence or absence of gleocystidia (gleoplerous cystidia). *Gomphus sensu lato* has been characterized by often rather large basidiomata, fan-shaped to funnel-shaped pilei, with longitudinally wrinkled hymenia. *Gloeocantharellus*, on the other hand, of which *Linderomyces* is a synonym, is paxilloid[1] but differs from the Paxillaceae in the presence of gleoplerous cystidia and ornamented spores. However, not all *Gloeocantharellus* species have gleocystidia, but all have many more gleoplerous hyphae than the species of *Gomphus sensu lato*. *Gloeocantharellus* also differs from *Gomphus sensu lato* in its more agaricoid[2] habit and by having species with lamellate hymenia.

Singer (1945) transferred *Cantharellus purpurascens* to *Gloeocantharellus* on the basis of gleocystidia in *Gloeocantharellus*, as opposed to the coscinocystidia in *Linderomyces*, which are identified as cystidia projecting as pseudocystidia. Singer (according to Petersen 1971a), in the discussion of a paper by Petersen (1971b), agreed that *Gloeocantharellus lateritius, G. purpurascens*, and *Linderomyces corneri* (≡*Gloeocantharellus corneri*) possess coscinocystidia, but that *L. corneri* could be separated from the other two on the basis of a bilateral hymenophoral trama, even though this character is never mentioned in the description of *Linderomyces*. After studying the holotype of *L. lateritius* (≡*Gloeocantharellus lateritius*), which was the type for *Linderomyces*, Petersen (1968, 1969) discussed the proper placement of the three aforementioned species within the order Gomphales. Later, after having seen no evidence for the bilateral hymenophoral trama seen by Singer in *L. corneri*, Petersen (1971a) proposed the three species to be classified under *Gloeocantharellus*.

Gloeocantharellus species are recorded from South America (Bolivia, Brazil), the South Pacific (Borneo, Guam, Hawaii, Papua New Guinea, the

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[1] Basidiomata with the similar shape of a *Paxillus* species.
[2] Basidiomata with the similar shape of an *Agaricus* species.

Solomon Islands), and southeast Asia (Malaysia, Singapore, Sri Lanka). Some species also occur in Japan, New Zealand, Russia, and the USA.

All species of *Gloeocantharellus* are terrestrial and generally found where ectomycorrhizal tree species are common. *Gloeocantharellus pallidus*, for example, was suggested to be ectotrophic with fagaceous trees in Japan. In Hawaii, on the other hand, it is restricted to growth in association with *Psidium* in the Myrtaceae. (http://www.mycena.sfsu.edu/hawaiian/Alien_Wet_Forests/G_pallidus.html). Both host and fungus have been introduced to the archipelago from elsewhere. *Gloeocantharellus dingleyae* and *G. novae-zelandiae* occur in the podocarp-broadleaf forests of New Zealand (Segedin 1984), while *G. papuanus* fruits in the *Castanopsis-Lithocarpus* forests near Lae, in Papua New Guinea. Even though these species fruit near ectomycorrhizal tree species, direct evidence for the mycorrhizal status of *Gloeocantharellus* is lacking.

A molecular phylogeny for the Gomphales has been proposed by Giachini (chapter 2), who showed *Gloeocantharellus* to be monophyletic and composed of ten species. Because of its basal (ancestral) phylogenetic placement, a better knowledge of the characters that make *Gloeocantharellus* unique is critical to understand the evolution of other members in the order Gomphales. This topic will be extensively discussed in chapter 8 of this dissertation.

The objective of this study is to present an overview of the important features used to identify species of *Gloeocantharellus*, with a dichotomous key and species descriptions.

MATERIAL AND METHODS

Collections examined

Collections of *Gloeocantharellus* analyzed in this study were obtained from the following herbaria: BPI, F, K, OSC, PDD, PERTH, and TENN (http://www.nybg.org/bsci/ih/ih.html). No specimens of *G. corneri* were located. *Gloeocantharellus echinosporus* and *G. okapaensis* were not examined because loan of the only known collections was denied because of their fragile condition, so the descriptions had to based on the literature.

Habitat and fruiting patterns are from the original descriptions or collection packets. Names of authorities are according to Brummit and Powell (1992).

Macroscopic characters

Macroscopic features are based on the original descriptions and notes accompanying herbarium collections supplemented by my own data on dried specimens when available. Features of the cap, hymenium, stipe, flesh, odor and taste were recorded when possible. Color terms, except for *G. papuanus*, were mostly taken from Corner (1966, 1969), Petersen (1968), Segedin (1984), and Singer *et al.* (1983). Size of basidiomata may vary depending on conditions of the fruiting season, so ranges of minimum and maximum sizes are presented. Some specimens were cut longitudinally through the vertical axis to examine the context and hyphal arrangement. Application of the various chemicals often used and referred to in the literature in describing species of *Gomphus sensu lato* provided little data of value and therefore were discontinued in this study.

Microscopic characters

Features observed with a compound microscope were described from free-hand sections mounted in Melzer's reagent, 5% KOH, cotton blue, or water. Structures were measured with an optical micrometer at × 1000 magnification, mostly in 5% KOH, water, or Melzer's reagent. The ranges for hypha measurements are thin walls ≤0.5 µm wide, thick walls >0.5 µm wide. The pileipellis and stipitipellis were examined in surface view. When material was available, dimensions of structures were recorded from at least 3 specimens from each of at least 5 collections; both mature and immature specimens were examined for developmental changes. Maturity was judged by the relative abundance of fully ornamented spores.

Spore shape was determined as the length-width ratio of 20-30 randomly selected spores. Dimensions are given as: minlength-maxlength × minwidth-maxwidth, excluding ornamentation and apiculus. Immature or oversized spores were not included in the measurements, though variation was noted.

SYSTEMATICS OF *GLOEOCANTHARELLUS*

Key to species of Gloeocantharellus

1. Pileus viscid..... 2

1. Pileus dry..... 3

    2. Spores echinulate..... *G. echinosporus*

2. Spores verrucose..... *G. corneri*

3(1). Hymenial cystidia present..... 4

3. Hymenial cystidia absent..... 8

4. Hymenial cystidia with bent tips..... *G. okapaensis*

4. Hymenial cystidia without bent tips..... 5

5. Cystidia apically attenuated; spores (7-) 8-11 (-13.5) × 3.5-5.5 µm; USA..... *G. purpurascens*

5. Cystidia obtuse; spores 9-16 × 5-7 µm; New Zealand, Papua New Guinea, and Sri Lanka..... 6

6. Spores 9-10.5 (-11.5) × 5.5-7 µm; Sri Lanka..... *G. lateritius*

6. Spores 9-14 (-16) × 4-5.5 (-6.5) µm; New Zealand and Papua New Guinea..... 7

7. Spores 9-10 (-11.5) × 4-5 µm; pileus pale orange to pink; New Zealand..... *G. novae-zelandiae*

7. Spores 12-15 (-16) × 5-5.5 (-6.5) µm; pileus creamy yellow when fresh, pale yellow, pale brown with yellow spots when dry; Papua New Guinea..... *G. papuanus*

8(3). Clamp connections present; spores 12-16 (-19.5) × (3-) 4-7 µm..... *G. mamorensis*

8. Clamp connections absent; spores 9-12 (-13) × 3-6.5 µm..... 9

9. Hymenium strongly wrinkled; spores 9-10.5 (-12.5) × 3.5-5 µm; Guam, Hawaii, Japan, and Russia..... *G. pallidus*

9. Hymenium with distinctly forked, broad, hymenial folds; spores 9.5-12 (-13) × 4.5-6.5 µm; New Zealand..... *G. dingleyae*

Descriptions

Species are described in alphabetical order. Descriptions include citation of all material examined and the herbarium where the type and other collections are deposited. Phenology and biogeography are based on notes available with collections and the observations made in this study.

Gloeocantharellus Singer, Lloydia 8:140. 1945, *emend.* Giachini, *emend. prov.*

=*Linderomyces* Singer, Farlowia 3:156. 1947.

Type species: *Cantharellus purpurascens* Hesler, *in* Smith and Hesler, Lloydia 6(4):248. 1943.

***Macroscopic characters*: Basidiomata** up to 15 cm tall, agaricoid-gomphoid, unipileate to merismatoid. **Pileus** 1-13.5 cm wide, hemispherical when young, convex then flat to slightly concave when mature, in some species with irregular lobes, funnel- or fan-shaped, surface glabrous to the naked eye, minutely tomentose, squamulose or velvety under 100 × magnification, fibrillose, dry or

viscid, off-white, pale to creamy yellow, pale yellow-brown, pale to livid orange, orange-pink, pink, pale brown, dark yellow-orange, dark rusty brown to reddish, one becoming violet when bruised (*G. purpurascens*); margin thin, acute, incurved, even to subcrenate, more or less undulate, inrolled when young, lacerate with age (*G. dingleyae*). **Hymenium** deeply decurrent, supported by either true lamellae, bifurcating broad hymenial folds that become labyrinthine (anastomosed or veined) toward the stipe, or of wrinkled hymenial folds up to 2 mm tall, ranging from white, creamy yellow, pale orange, orange, pale cinnamon to brown, in one species pink to violet near the stipe surface, the margin of the pileus and the young gills (*G. echinosporus*), slightly violet when bruised. **Stipe** up to 120 × 50 mm, slender to stout, solid or hollow, fibrous, equal to tapering downward, cylindrical, subcylindrical to flattened or grooved, glabrous to velvety, creamy yellow when young, white, pale yellow, orange-pink, pink or concolorous with the rest of the basidioma with age, orange below substrate level, pale vinescent to red where bruised. **Context** pliable to somewhat firm, off-white then white, occasionally bruising vinaceous or red when cut or exposed, dark yellow-orange when dry. **Odor** none, mild, sour, or occasionally of anise. **Taste** sometimes mildly bitter. **Spore print** in general brown.

Microscopic characters: **Pileipellis + stipitipellis** of thin-walled, parallel to interwoven, flexuous, hyaline to pale orange hyphae 2.5-5 µm wide, appressed toward the margin, gelatinous in some species, slightly inflated in others, with pileocystidia in *G. purpurascens*; clamp connections present or absent; gleoplerous hyphae present or absent. **Pileus context** of thin-walled, parallel to closely interwoven hyphae with occasional ampulliform swellings up to 22 µm, a few terminating among basidia; clamp connections present or absent; gleoplerous hyphae scarce or frequent, tortuous, rarely branched, rarely septate, cyanophilic. **Stipe context** of parallel to interwoven, narrow hyphae; clamp connections present or absent; gleoplerous hyphae generally abundant. **Hymenial trama** with well-developed mediostratum (in *G. purpurascens*) of generally parallel, compactly arranged hyphae identical to those of pileus surface; gleoplerous hyphae tortuous,

uninflated, somewhat interwoven, with cyanophilic contents, 2.5-10 µm wide. Basidiomata of generative hyphae without skeletal hyphae; clamp connections absent only in *G. dingleyae* and *G. pallidus*. Generative hyphae usually uninflated, hyaline to pale yellow; clamp connections present or absent; gleoplerous hyphae generally abundant and conspicuous, tortuous, rarely branching, with occasional ampulliform swellings, cyanophilic, interweaving with the generative hyphal system, some ending among basidia to form tortuous pseudocystidia. **Basidia** 24-80 × 5-12 µm, clavate, hyaline, with 1 to 4 sterigmata up to 11 µm long; clamp connections basal or absent. Hymenial **cystidia** when present up to 160 × 12 µm, subcylindrical to clavate, obtuse or attenuated, with or without bent tips; clamp connections basal or absent; most cystidia gleoplerous (gleocystidia). **Spores** (7-) 8.5-14 (-19.5) × (3-) 4.5-7 µm, yellow to cinnamon-brown in mass, ellipsoid, obovoid to lacrimoid; ornamentation of delicate, cyanophilic low warts and spines that eventually can form small anastomosing ridges up to 2 µm tall; apiculus 1-2 µm long, eccentric.

Habit, habitat and distribution: Epigeous, terrestrial, solitary, gregarious, or caespitose. *Gloeocantharellus corneri* is only known from Brazil. *Gloeocantharellus dingleyae* and *G. novae-zelandiae* occur in mixed podocarp-broadleaf forests in New Zealand (Segedin 1984); *G. echinosporus* in Borneo, Malaysia, Singapore, and the Solomon Islands; *G. lateritius* in Sri Lanka; *G. mamorensis* in the Bolivian Amazon; and *G. okapaensis* in Papua New Guinea and the Solomon Islands. *Gloeocantharellus pallidus* is the most widespread of all, occurring with Myrtaceae and/or Fagaceae in Guam, Hawaii, Japan, and Russia. *Gloeocantharellus papuanus* is from moist Myrtaceae-dominated forests in Papua New Guinea. *Gloeocantharellus purpurascens* is the only species endemic to the United States.

Discussion: Basidiomata of *Gloeocantharellus* appear superficially paxilloid for some of the species, but the ornamented spores and the gleoplerous hyphal system separate the genus from the Paxillaceae. Presence of generally veined to lamellar

folds rather than completely wrinkled hymenia (except for *G. pallidus* and *G. mamorensis*) separates *Gloeocantharellus* from other close related genera.

***Gloeocantharellus corneri* (Singer) Corner, Nova Hedwigia 18:799. 1969.** Fig. 5.1

≡*Linderomyces corneri* Singer, Vellozia 1:14. 1961 (not located, *fide* Corner, Nova Hedwigia 18: 799. 1969).

Macroscopic characters: **Basidiomata** agaricoid-gomphoid, unipileate. **Pileus** 5-7 cm wide, convex then flat, viscid, often glabrous, livid orange with concolorous gluten, becoming pale yellow-brown; margin incurved, white. **Hymenium** deeply decurrent, gills crowded, rather narrow, often forked, slightly folded at the base toward the margin, white then pale orange, and finally orange to pale cinnamon. **Stipe** 40-90 × 6-12 mm, subcylindrical, tapered at the deeply rooted base, often curved, apex often ribbed from the decurrent gills, the base scurfy pruinose, surface pale orange, more or less dark pink or orange-pink downward to the white base. **Context** 6-14 mm thick in the center of the pileus, white then vinaceous on the stipe and gills when bruised. **Odor** slightly sour. **Taste** not recorded. **Spore print color** not recorded.

Microscopic characters: **Pileipellis** of thin-walled, flexuous hyphae appressed toward the margin. **Stipitipellis** of slightly thick-walled, parallel hyphae 2-4 (-5) µm wide. **Context** of thin-walled hyphae; clamp connections present; gleoplerous hyphae closely interwoven, up to 16 µm wide in the stipe, 25 µm wide in the pileus, and 2-6 µm wide in the hymenium. **Basidia** 60-80 × 10-12 µm, clavate, with 4 slender, straight sterigmata 7-11 µm long (Figure 5.1); clamp connections present at base. Hymenial **cystidia** 55-105 × 6-8 µm, thin-walled, lanceolate, smooth; clamp connections present at base. **Spores** 9-15 × 6-7 µm, pale cinnamon in mass, somewhat ellipsoid to lacrimoid with a blunt apex; ornamentation irregularly

verrucose with flat, rounded or elongated, cyanophilic, sometimes with subreticulate patches up to 0.5 μm tall (Figure 5.1); apiculus 1-1.5 μm long.

Habit, habitat, and distribution: Scattered on the forest floor, deeply rooted in the soil in the Corcovado Mountain of Rio de Janeiro, Brazil (Corner 1969).

Type (holotype): **BRAZIL. RIO DE JANEIRO**: Corcovado Mtn., 500 meters up, 4 December 1948, *E.J.H. Corner* (No herbarium mentioned – as *Gloeocantharellus corneri*).

Discussion: The type collection for this species was not located and therefore this description was based on notes from Corner (1969).

Gloeocantharellus corneri is distinguished by its livid orange pileus that becomes pale yellow-brown with age. According to Corner (1969), the viscid pellicle allies it with *G. echinosporus*, but the echinulate versus verrucose spores separate the two species.

Gloeocantharellus dingleyae* (Segedin) Giachini, *sp. prov. Fig. 5.2

≡*Gomphus dingleyi* Segedin, New Zealand Journal of Botany 22:536. 1984.

Macroscopic characters: **Basidiomata** up to 7 cm tall, agaricoid-gomphoid, occasionally merismatoid (Figure 5.2). **Pileus** up to 7 cm wide, flat at first, becoming mainly funnel-shaped or occasionally fan-shaped and with irregular lobes, dry, downy fibrillose, pink to orange; margin lacerate with age. **Hymenium** deeply decurrent, with distinct bifurcating, broad, hymenial folds that become labyrinthine (anastomosed) toward the stipe. **Stipe** 6-15 mm thick, solid, grooved, dry, velvety, with white patches especially toward the base, otherwise concolorous. **Context** firm, orange. **Odor** not noticeable. **Taste** bitter. **Spore print color** not recorded.

Microscopic characters: **Pileipellis + stipitipellis** of thin-walled hyphae; clamp connections present. **Pileus context** of thin-walled, parallel to closely interwoven hyphae; clamp connections absent; gleoplerous hyphae frequent, tortuous, rarely

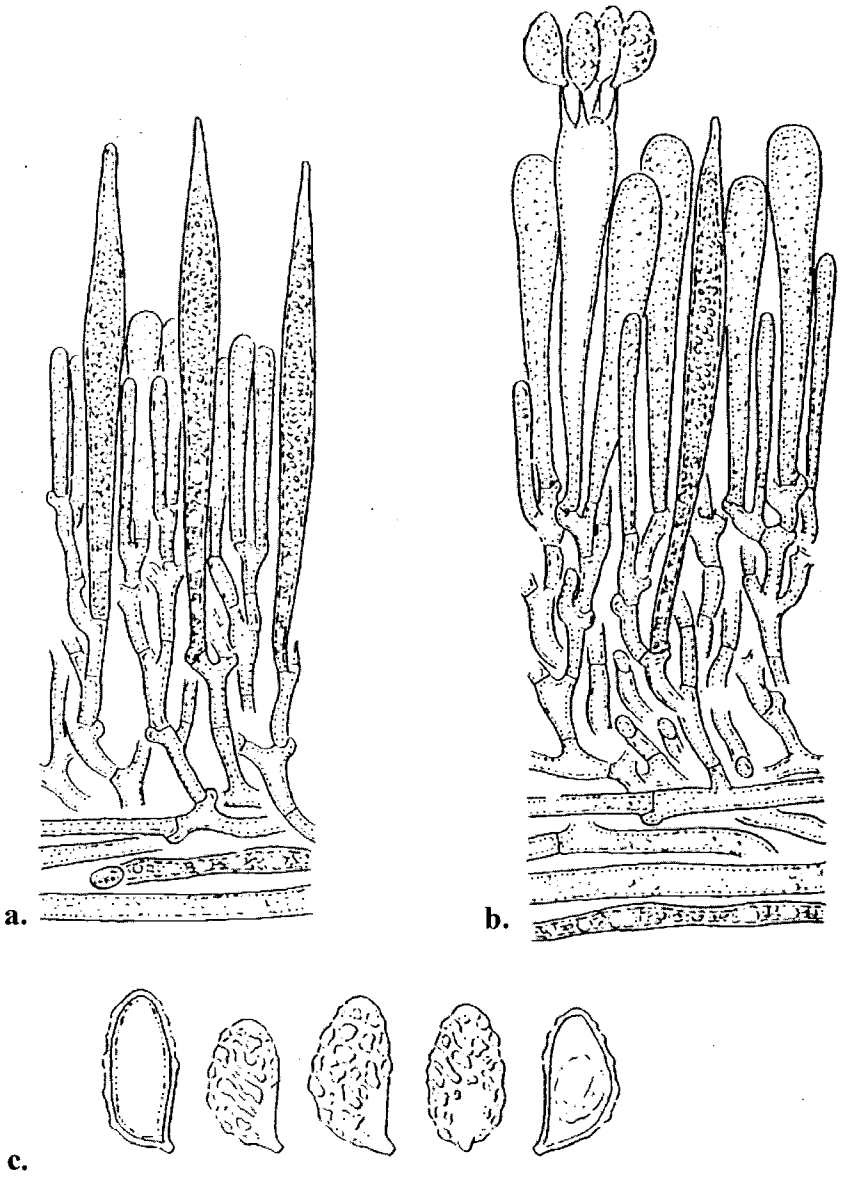


Figure 5.1. *Gloeocantharellus corneri* (Singer) Corner: (a) immature hymenium; (b) mature hymenium (× 500); (c) spores (× 1000). Reproduced from Corner (1969).

branched, rarely septate, cyanophilic, with occasional ampulliform swellings up to 20 µm, a few terminating among basidia. **Stipe context** of parallel hyphae with branched, hyaline caulocystidia; clamp connections absent. **Basidia** 60-70 × 7-9 µm, clavate, with 2-4 sterigmata; clamp connections absent. Hymenial **cystidia** not observed. **Spores** 9.5-12 (-13) × 4.5-6.5 µm, ellipsoid; ornamentation of cyanophilic, coarse warts (Figure 5.2); apiculus prominent.

Habit, habitat and distribution: In mixed podocarp-broadleaf forests in New Zealand (Segedin 1984).

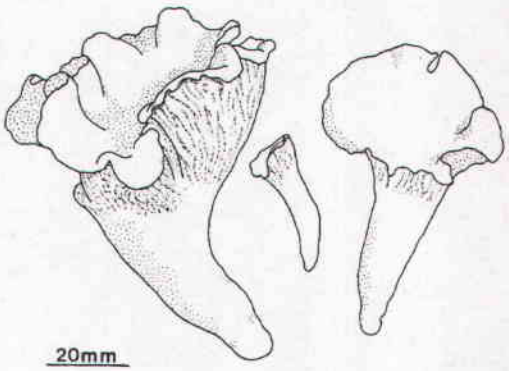
Collections examined. **NEW ZEALAND:** Auckland, Waiatarua, Waitakere Road, 26 June 1972, *J.M. Dingley* (PDD 30179 – as *Gomphus dingleyi* – **holotype**).

Discussion: This species differs from *G. novae-zelandiae* by its larger size, broader hymenial folds, solid stipe, and margin becoming lacerate with age. Both species share the same habitat under the same tree species. In addition both species have only been recorded from near Auckland.

***Gloeocantharellus echinosporus* Corner, Nova Hedwigia 18:801. 1969.** Fig. 5.3

Macroscopic characters: **Basidiomata** up to 10 cm tall, agaricoid, unipileate (Figure 5.3). **Pileus** 4-13.5 cm wide, convex then flat, glabrous but innately squamulose over the center, viscid, yellowish orange to red, margin incurved at first. **Hymenium** decurrent, gills often attenuate, crowded, often furcated, especially near the margin, not reticulate at the base or slightly veined near the margin, thin, easily separable from pileus, firm, white when dry, pink to violet near the stipe, the margin of the pileus and the young gills. **Stipe** 30-100 × 7-22 mm, solid, fibrous, minutely scurfy pruinose, tapering downward, often shortly rooting, pale white to pale yellow or pale pink. Data on **context**, **odor**, **taste**, and **spore print color** not recorded.

a.



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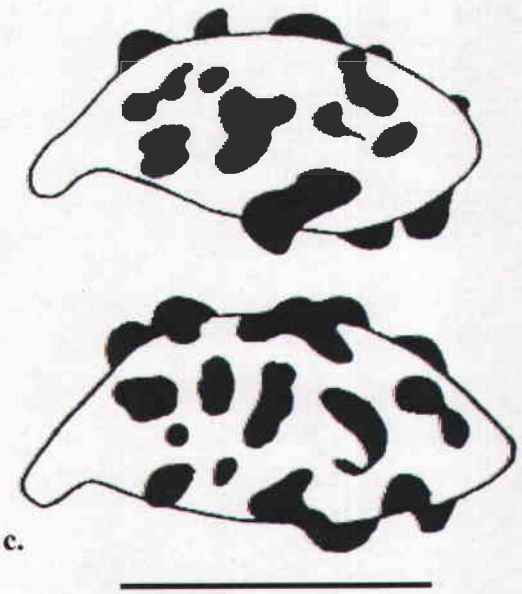


c.

Figure 5.2. *Gloeocantharellus dingleyae* (Segedin) Giachini, *sp. prov.*: (a, b) basidiomata (× 1); (c) spores (bar = 5 µm). Drawings and photograph from Segedin (1984), with permission.

Microscopic characters: **Pileipellis + stipitipellis** of interwoven, gelatinous, pale orange hyphae 2.5-5 µm wide. **Stipe context** of parallel, cylindrical, inflated hyphae 4-22 µm wide, more interwoven in the **pileus context**; clamp connections present; gleoplerous hyphae scarce or absent in the stipe and pileus, 3-6 µm wide. **Hymenial trama** of parallel, somewhat interwoven hyphae 2.5-10 µm wide; gleoplerous hyphae scarce or absent. **Basidia** 48-60 × 9-11 µm, with (2-) 4 sterigmata 6-10 µm long (Figure 5.3); clamp connections present at base. Hymenial **cystidia** 45-160 × 5-12 µm, thin-walled, lanceolate to subclavate, smooth; clamp connections present at base. **Spores** 9-11.5 (-13) × 5-7 µm, yellow-cinnamon in mass, ellipsoid to somewhat lacrimoid; ornamentation of cyanophilic spines 0.5-2 µm tall (Figure 5.3); apiculus 1-2 µm long.

Habit, habitat, and distribution: Solitary or gregarious, on the ground in forests, often rooting. In Borneo, Malaysia, Singapore, and the Solomon Islands (Corner 1969).

Type (holotype): **SINGAPORE:** Bukit Timah, 19 August 1939, *E.J.H. Corner* (CGE – as *Gloeocantharellus echinosporus*).

Discussion: Only the type collection is known. The loan of the type was denied due to its fragile conditions, and therefore this description was based on notes from Corner (1969).

This is the only *Gloeocantharellus* species with echinulate spores and orangish to red basidiomata.

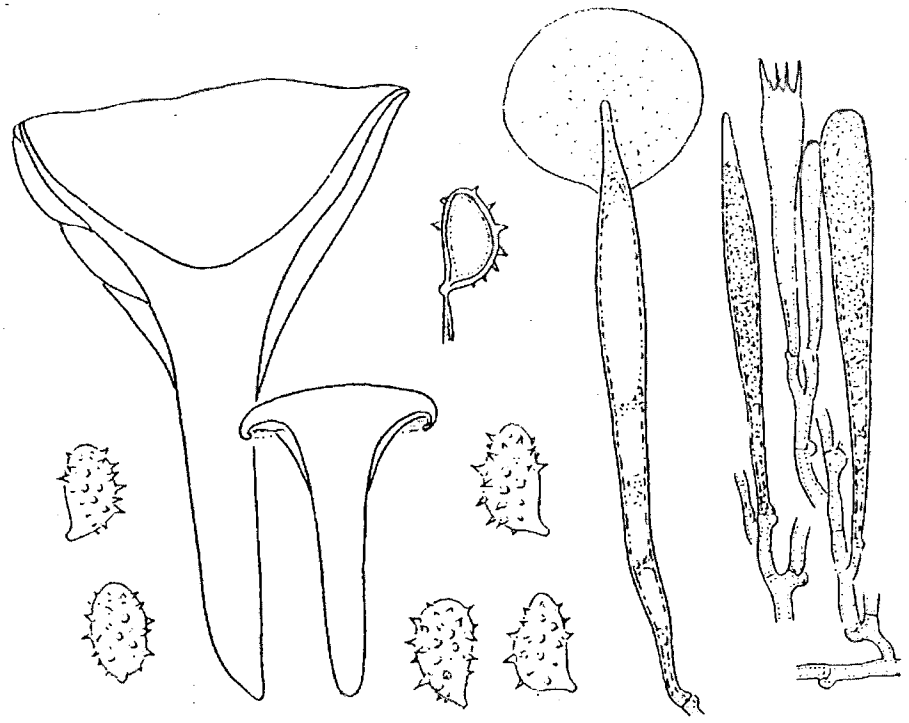


Figure 5.3. *Gloeocantharellus echinosporus* Corner: basidiomata (× 0.5); hymenium (× 500); spores (× 1000). Reproduced from Corner (1969).

Gloeocantharellus lateritius **(Petch) Corner, Nova Hedwigia 18:803. 1969.**

Fig. 5.4

≡*Paxillus lateritius* Petch, Annals of the Royal Botanic Gardens, Peradeniya 6:202. 1917.

≡*Linderomyces lateritius* (Petch) Singer, Farlowia 3:157. 1947.

≡*Gomphus lateritius* (Petch) R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:380. 1968.

Macroscopic characters: **Basidiomata** up to 5 cm tall, agaricoid, unipileate. **Pileus** concave, funnel-shaped, minutely felty, dry; margin inrolled. **Hymenium** with decurrent lamellae 1.5-2 mm tall, not crowded, rarely forking dichotomously toward the margin. **Stipe** glabrous, equal to tapering slightly downward, and constricted at the base below substrate surface. **Context** firm, homogenous, dark yellow-orange when dry. **Odor**, **taste**, and **spore print color** not recorded.

Microscopic characters: All **hyphae** agglutinated, poorly rehydrating and therefore shattering irregularly, difficult to measure; clamp connections present. **Basidia** with 4 sterigmata. Hymenial **cystidia** about 90-100 µm long, obtuse, brown; cystidia gleoplerous, strongly cyanophilic, without bent tips. **Spores** 9-10.5 (-11.5) × 5.5-7 µm, hyaline singly, pale yellow in mass, ellipsoid to obovoid (Figure 5.4); ornamentation of small, non-anastomosing, strongly cyanophilic warts; apiculus prominent, eccentric.

Habit, habitat and distribution: Terrestrial, known from Sri Lanka (Petersen 1971a).

Collections examined: **SRI LANKA:** Peradeniya, 1 November 1914, *T. Petch 4230* (K 63156 – as *Paxillus lateritius* – **lectotype** – Petersen 1971a).

Discussion: According to Petersen (1971a) the basidiomata of *G. lateritius* are close to those of *Cantharellus cibarius* and not like those of *G. purpurascens*. The spore size differs, and cystidia are obtuse versus apically attenuated like those of *G. purpurascens*. The poor condition of the lectotype for *G. lateritius* limited the amount of information that could be obtained for this species.

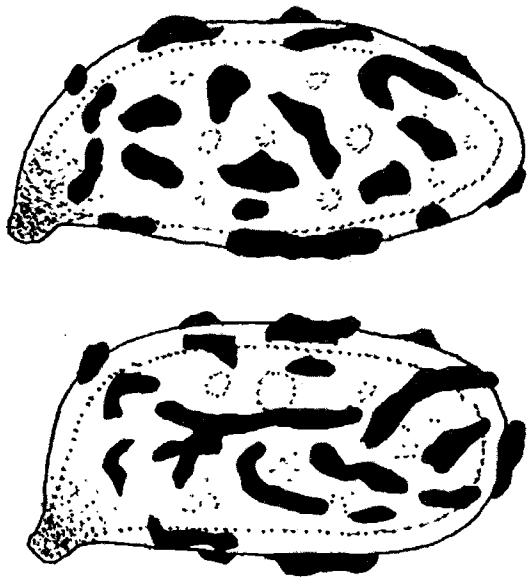


Figure 5.4. Spores (bar = 10 μm) of *Gloeocantharellus lateritius* (Petch) Corner.

Gloeocantharellus mamorensis* (Singer) Giachini, *sp. prov. Fig. 5.5

≡*Gomphus mamorensis* Singer, *in* Singer *et al.*, Beihefte zur Nova Hedwigia 77:17. 1983.

Macroscopic characters: **Basidiomata** up to 15 cm tall, agaricoid-gomphoid, unipileate. **Pileus** up to 11.5 cm wide, funnel-shaped, dry, glabrous to the naked eye but with innate brown fibrils and zones, appressedly silky, later fibrillose to subglabrous with appressed pale fibrils near the margin, off-white where glabrous becoming paler and more sordid in age; margin thin, acute. **Hymenium** surface radially wrinkled with somewhat anastomosing or forking low and obtuse, pale orange folds. **Stipe** 27-65 × 10-14 mm, equal, glabrous, hollow, white. **Context** white, unchanging when exposed or bruised. **Odor** none. **Taste** mild. **Spore print** brown.

Microscopic characters: **Hymenial trama** of thin-walled, compact and non-gelatinous, inamyloid hyphae 2-7 µm wide; clamp connections present. **Basidia** 24-32 (-70) × 5-11 µm, with 4 sterigmata. Hymenial **cystidia** absent. **Spores** 12-16 (-19.5) × (3-) 4-7 µm, yellow in mass, ellipsoid to obovoid; ornamentation of low, cyanophilic warts, sometimes in longitudinal rows or longitudinal ridges, but not reticulate (Figure 5.5); apiculus rounded or subacute.

Habit, habitat and distribution: Gregarious, on the ground in tropical forests in the Bolivian Amazon (Singer *et al.* 1983).

Collections examined. **BOLIVIA.** **BENI**: Vaca Diez, Guayaramerin, 6 March 1956, *R. Singer B 1614* (F – as *Gomphus mamorensis* – **holotype**).

Discussion: This species is similar to *G. corneri*, found in the Atlantic forest of Brazil. The basidioma shape is similar, although it does not present the livid orange to yellow-brown pilei as seen in *G. corneri*. *Gloeocantharellus corneri* also has somewhat smaller spores and possesses cystidia, structures not observed in *G. mamorensis*.

Figure 5.5. Spores (bar = 10 μm) of *Gloeocantharellus mamorensis* (Singer) Giachini, *sp. prov.*

Gloeocantharellus novae-zelandiae* (Segedin) Giachini, *sp. prov. Fig. 5.6

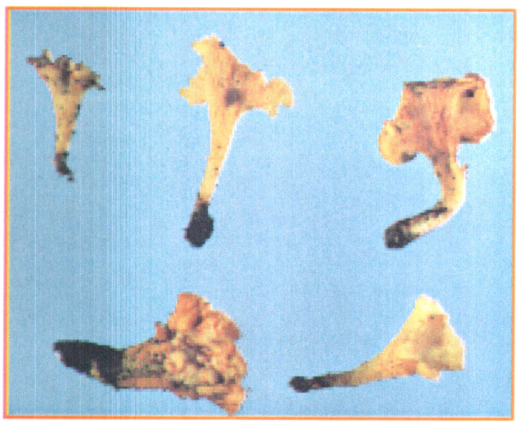
≡*Gomphus novae-zelandiae* Segedin, New Zealand Journal of Botany 22:533. 1984.

Macroscopic characters: **Basidiomata** 3.5-7 cm tall, agaricoid-gomphoid, occasionally tending toward merismatoid (Figure 5.6). **Pileus** 1-3 cm wide, concave to funnel-shaped, dry, thin, matted to velvety pale orange to pink; margin straight to slightly incurved, more or less undulate. **Hymenium** decurrent, smooth or with slightly separated, shallow hymenial folds, darker than the pileus. **Stipe** 5-50 mm tall, thin, cylindrical to flattened or grooved, occasionally tapering downward, hollow, velvety, concolorous with pileus, turning red when bruised. **Context** pliable, orange, context of pileus turns red on cutting but not on bruising. **Odor** not noticeable. **Taste** slightly bitter. **Spore print** brown.

Microscopic characters: **Pileipellis** of thin-walled hyphae; clamp connections present. **Pileus context** of thin-walled, parallel to compactly interwoven, not inflated hyphae up to 10 µm wide; clamp connections strongly cyanophilic; gleoplerous hyphae tortuous, occasionally branched, rarely septate, scattered but more frequent near the hymenium. **Stipe context** of parallel, narrow hyphae; clamp connections present; gleoplerous hyphae occasional. **Basidia** 70 × 6-10 µm, clavate, with 1-2-4 sterigmata up to 8 µm long; clamp connections present at base. Hymenial **cystidia** frequent, 30 × 5-6 µm, clavate, hyaline, obtuse, without bent tips. **Spores** 9-10 (-11.5) × 4-5 µm, ellipsoid to lacrimoid (Figure 5.6); ornamentation of strongly cyanophilic warts; apiculus prominent, rounded.

Habit, habitat and distribution: Gregarious, in mixed podocarp-broadleaf forests in New Zealand (Segedin 1984).

Collections examined. **NEW ZEALAND**: Auckland, Titirangi, Atkinson's Park, 19 June 1980, *B.P. Segedin* (PDD 44960 – as *Gomphus novae-zelandiae* – **holotype**).



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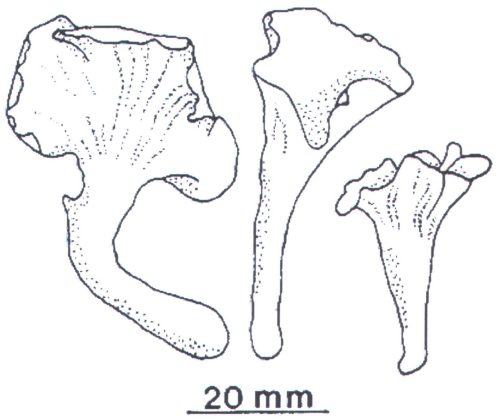

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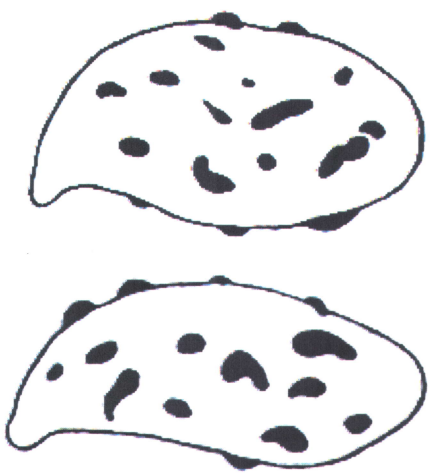


c.

Figure 5.6. *Gloeocantharellus novae-zelandiae* (Segedin) Giachini, *sp. prov.*: (a, b) basidiomata (× 1); (c) spores (bar = 5 µm). Drawings and photograph from Segedin (1984), with permission.

Discussion: This species has small, fragile basidiomata with a somewhat smooth hymenium. *Gloeocantharellus novae-zelandiae* differs from other *Gloeocantharellus* species by its smooth hymenium and spore characteristics. It is endemic to New Zealand. It additionally differs from *G. dingleyae*, the other New Zealand *Gloeocantharellus* species, in the presence of gleocystidia and clamp connections.

***Gloeocantharellus okapaensis* Corner, Nova Hedwigia 18:803. 1969.** Fig. 5.7

≡*Gomphus okapaensis* Corner, Annals of Botany Memoir 2:123. 1966.

Macroscopic characters: **Basidiomata** relatively small, agaricoid, unipileate (Figure 5.7). **Pileus** up to 10 cm wide, plano-convex to concave and widely funnel-shaped, dry, subtomentose, then cracking into minute, scurfy squamules, orange-pink, paler with age; margin incurved. **Hymenium** decurrent, crowded, in some areas forking dichotomously, wrinkled, pale white, then brown. **Stipe** 40-120 × 9-14 mm, attenuated downward to subcylindrical, minutely scurfy-pruinose, concolorous, pale orange below, apex off-white. **Context** firm, subfloccose, white, all parts turning dingy vinaceous on bruising. **Odor** sour. **Taste** and **spore print color** not recorded.

Microscopic characters: **Pileipellis** + **stipitipellis** hyphae 6-11 µm wide; gleoplerous hyphae abundant (Figure 5.7). **Stipe context** of interwoven hyphae 3-7 µm wide. Other hyphae thick-walled, 3-14 µm wide; clamp connections present; gleoplerous hyphae scattered and generally unbranched, up to 5 µm wide. **Basidia** 55-70 × 8.5-10 µm, clavate, with (2-) 3 slender, straight sterigmata 6-10 µm long (Figure 5.7); clamp connections present at base. Hymenial **cystidia**, gleoplerous, subcylindrical, rarely subclavate, occasional with a short branch, rarely bifurcated, 2-5 (-6) µm wide, generally exceeding the young basidia in the immature hymenium, with bent tips. **Spores** 9-12 × 5-7 µm, cinnamon-brown in mass,

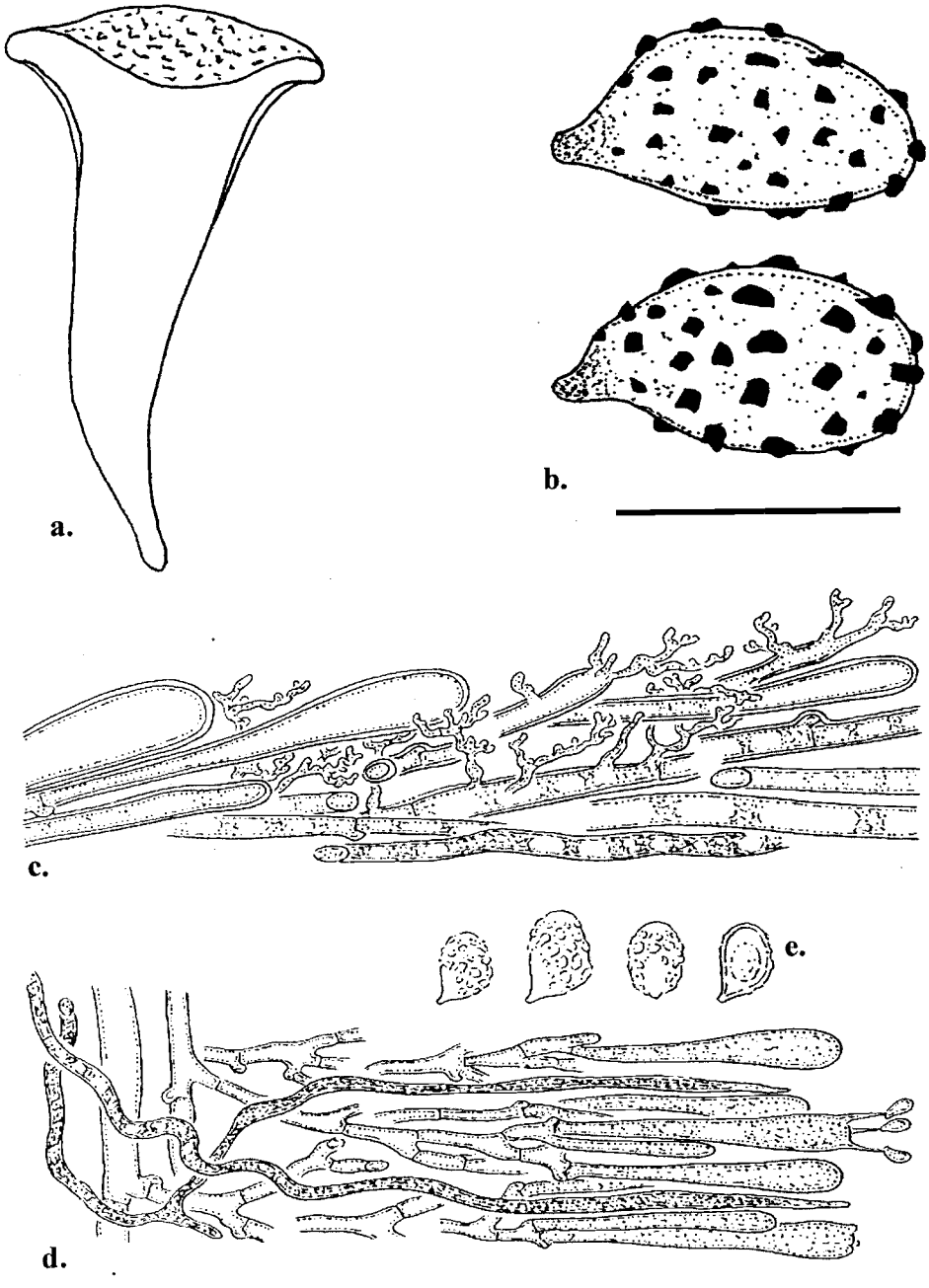


Figure 5.7. *Gloeocantharellus okapaensis* Corner: (a) basidioma (× 1); (b) spores (bar = 10 μm); (c) pileipellis; (d) hymenium (× 500); (e) spores (× 1000). Modified from Corner (1966, 1969).

ellipsoid to lacrimoid; ornamentation of flat, rounded to ellipsoid, cyanophilic warts (Figure 5.7); apiculus 1 μm long.

Habit, habitat and distribution: Solitary or gregarious, on the ground in the forest. Found in Papua New Guinea and the Solomon Islands (Corner 1969).

Type (holotype): **PAPUA NEW GUINEA:** Okapa, about 1800 meters of altitude, 10 October 1960, *E.J.H. Corner* (CGE – as *Gomphus okapaensis*).

Discussion: I was unable to obtain the loan of the type collection because of its fragile conditions. Therefore, this description was based on notes from Corner (1966, 1969).

Gloeocantharellus okapaensis has similar macroscopic and microscopic features of *G. corneri, G. echinosporus, G. lateritius, G. papuanus,* and *G. purpurascens*. Overall morphological features that separate *G. okapaensis* from the aforementioned species are the bent-tipped hymenial cystidia and the 3-spored basidia. *Gloeocantharellus okapaensis* shares close similarities and distribution to *G. echinosporus* and *G. papuanus*. However, *G. echinosporus* has echinulate spores while *G. okapaensis* has verrucose spores. *Gloeocantharellus okapaensis* differs from *G. novae-zelandiae* n the size of basidiomata and spores, and number of sterigmata per basidium.

Gloeocantharellus pallidus* (Lloyd) Giachini, *sp. prov. Fig. 5.8

≡*Cantharellus pallidus* Lloyd, Mycological Notes 47:661. 1917.

≡*Gomphus pallidus* (Lloyd) Corner, Annals of Botany Memoir 2:123. 1966.

Macroscopic characters: **Basidiomata** up to 10 cm tall, gomphoid, unipileate or merismatoid, when merismatoid with up to 6 tongue-like, petaloid or lacerated pilei (Figure 5.8). **Pileus** 9 cm wide, appearing funnel-shaped or fan-shaped, becoming funnel-shaped with reflexed sides, lobed, dry, surface barely velvety, dark yellow-orange to dark rusty brown. **Hymenium** of low, strongly wrinkled, generally longitudinally oriented and irregularly anastomosed hymenial folds, with no

geometrical pattern, creamy yellow. **Stipe** irregular in length, 10-50 mm thick, wrinkled below, glabrous upward, hard to woody, sometimes branched and when so each branch with a pileus, usually rooting, orange below the substrate level, white elsewhere. Data on **context**, **odor**, **taste**, and **spore print color** not recorded.

Microscopic characters: **Pileipellis + stipitipellis** of thin-walled, parallel, slightly inflated, hyaline to yellow hyphae up to 7 µm wide, with ampulliform swellings; clamp connections absent; gleoplerous hyphae common. **Pileus context** of slender, interwoven hyphae; gleoplerous hyphae strongly cyanophilic. **Basidia** not rehydrating. Hymenial **cystidia** absent. **Spores** 9-10.5 (-12.5) × 3.5-5 µm, yellow in mass, ellipsoid (Figure 5.8); ornamentation of coarse, low, non-anastomosing, strongly cyanophilic warts; apiculus prominent, eccentric.

Habit, habitat and distribution: Gregarious or caespitose, in humus or soil in Guam (Francisco Camacho, pers. comm.), Hawaii (http://www.mycena.sfsu.edu/), Japan (Lloyd 1917), and Russia (Bulakh and Govorova 2000).

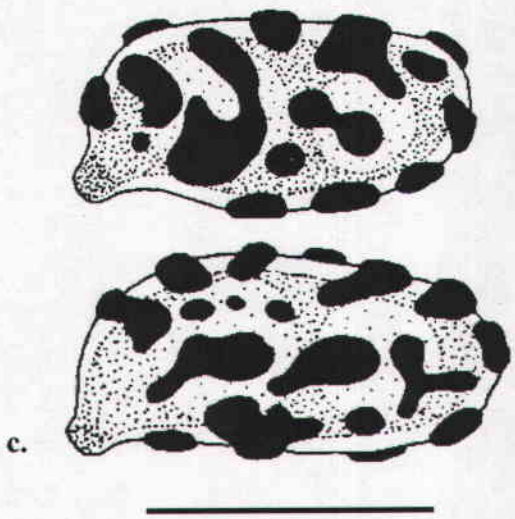
Collections examined. **JAPAN**: Sendai, Honshu, Hokkaido, 16 August 1916, *A. Yasuda* (BPI 54197 – as *Gloeocantharellus pallidus* – **holotype**).

Discussion: *Gloeocantharellus pallidus* is Hawaii's only gomphoid species. It is arguably the most common fleshy basidiomycete encountered in guava thickets throughout the Hawaiian Islands (http://www.mycena.sfsu.edu/hawaiian/Alien_Wet_Forests/G_pallidus.html). First described from Japan, the species was probably introduced into the Islands along with Japanese vascular plants. Although the species is believed to be mycorrhizal with fagaceous trees in Japan, in Hawaii it is restricted to growth in association with *Psidium* in the Myrtaceae.

Gloeocantharellus pallidus shares only a few morphological features with other species of *Gloeocantharellus*. The combination of strongly wrinkled creamy yellow hymenium, absence of gleoplerous cystidia, and absence of clamp connections, is not seen in other *Gloeocantharellus* species.

a.

b.



c.

Figure 5.8. *Gloeocantharellus pallidus* (Lloyd) Giachini, *sp. prov.*: (a, b) basidiomata (× 2); (c) spores (bar = 10 μm). Spore drawings from Petersen (1971b), with permission.

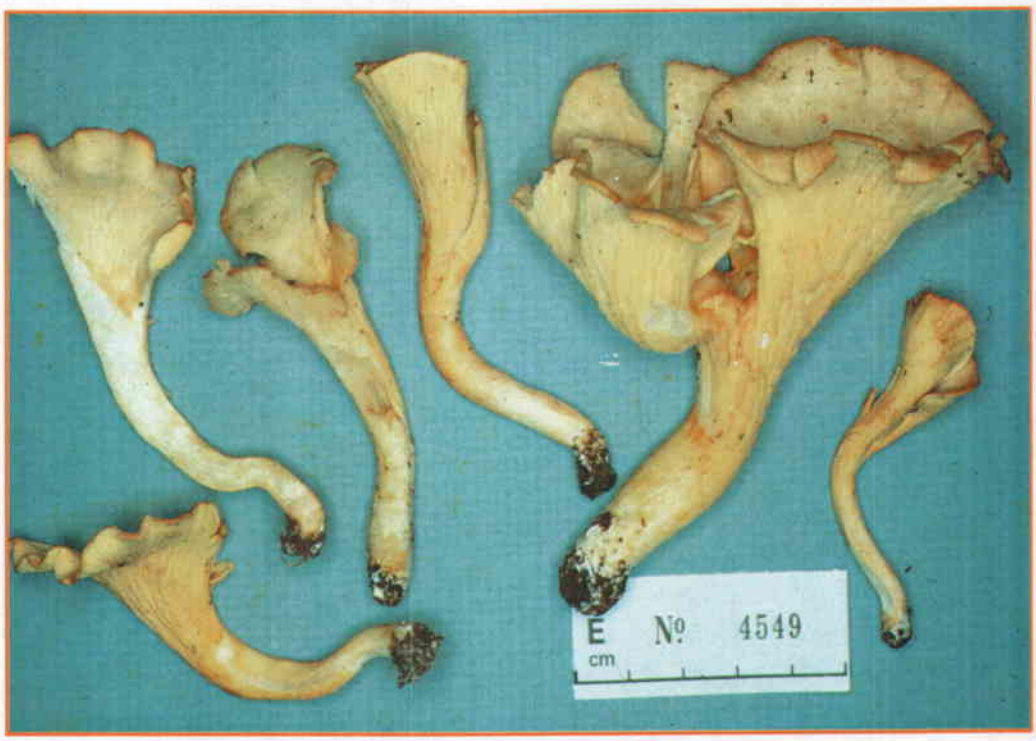
Gloeocantharellus papuanus* Giachini, Bougher, Castellano et Trappe, *nom. ined. Fig. 5.9

A G. novae-zelandiae hymenio rugosioreque sporis longioribus et a G. dingleyae possessione fibularum differt.

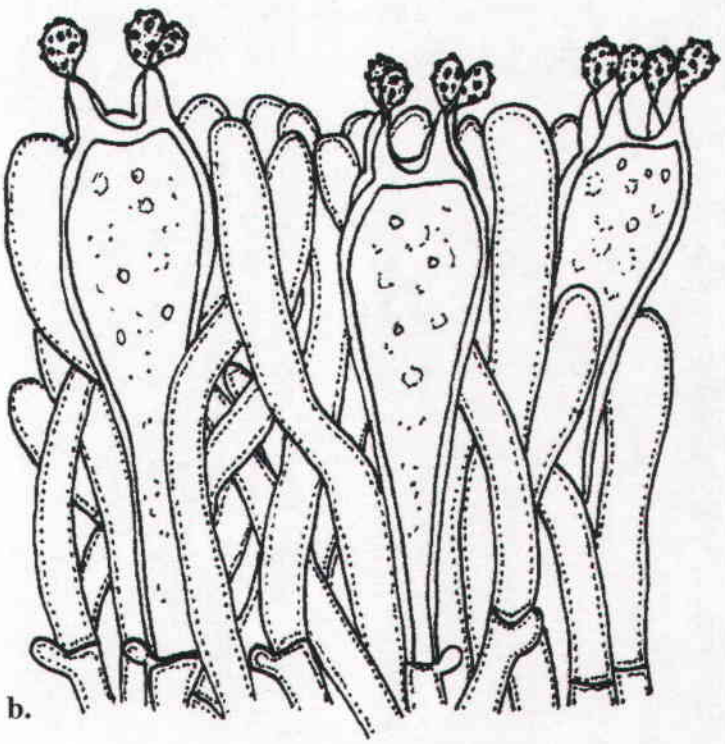
Holotypus hic designatus E4549 (PERTH).

Macroscopic characters: **Basidiomata** up to 7.5 cm tall, agaricoid-gomphoid, commonly tending toward merismatoid (Figure 5.9). **Pileus** up to 4 cm wide, funnel- to fan-shaped, upturned, dry, tomentose to glabrous but not scaly, creamy yellow when fresh, pale yellow, pale brown with yellow spots when dry; margin strongly undulated, incurved at first. **Hymenium** decurrent, of longitudinally arranged folds that extend down to half the length of the stipe, where it becomes smooth and inconspicuous and extends almost to the substrate level, multi forked, especially toward the margin of the pileus, folds shallow (up to 2 mm tall), creamy yellow in fresh basidiomata, pale yellow to pale or dark brown when dry. **Stipe** up to 50 × 15 mm, solid, cylindrical to flattened or grooved, slightly tapered downward, tomentose to glabrous, concolorous with the hymenium above, cream colored below. **Context** white, unchanging when cut or bruised. **Odor** not distinctive. **Taste** not recorded. **Spore print** brown, paler when dried.

Microscopic characters: **Pileipellis** of thin-walled, compactly arranged, interwoven, occasionally inflated, hyaline hyphae; clamp connections present; gleoplerous hyphae not seen. **Stipitipellis** of thin-walled, interwoven, septate, mucilaginous appearing, hyaline, moderately cyanophilic hyphae, a few with agglutinating materials, inflated up to 8 µm; clamp connections present; gleoplerous hyphae thin-walled, long and tortuous, interspersed among other hyphae (Figure 5.9). **Basidia** 50-70 × 5-6 µm, clavate, hyaline, tips commonly inflated up to 12 µm, with 4 stout, straight, not divergent sterigmata up to 8 µm long (Figure 5.9); clamp connections present at base. Hymenial **cystidia** 70-90 × 5-7.5 µm, gleoplerous, obtuse, dispersed among basidia, hyaline (Figure 5.9). **Spores**

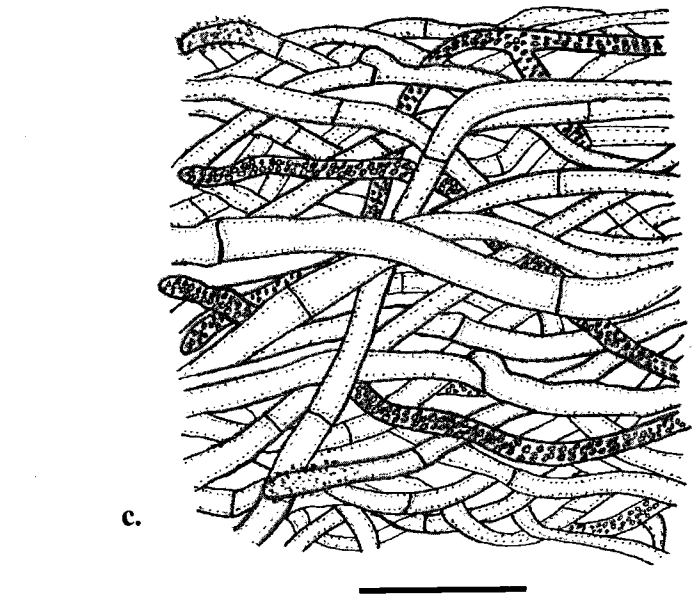


a.

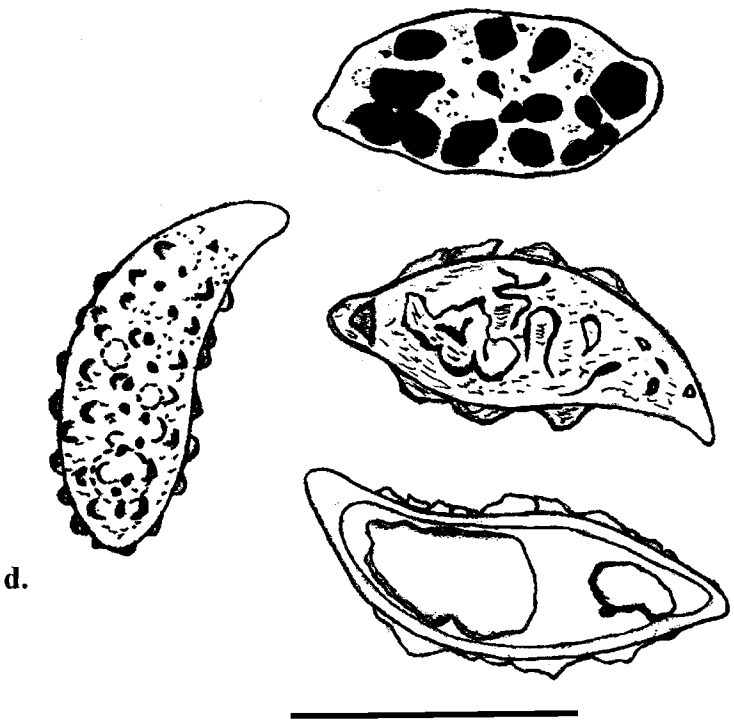


b.

Figure 5.9. *Gloeocantharellus Gloeocantharellus papuanus* Giachini, Bougher, Castellano et Trappe, *sp. prov.*: (a) basidiomata (× 1); (b) mature hymenium showing basidia and intermingled cystidia (× 500) – spores are × 2000.



c.



d.

Figure 5.9 (*cont.*). *Gloeocantharellus papuanus* Giachini, Bougher, Castellano et Trappe, *sp. prov.*: (c) hyphae of the stipitopellis showing intermixed gloeoplerous hyphae (bar = 20 μm); (d) spores (bar = 10 μm).

12-15 (-16) × 5-5.5 (-6.5) µm, yellow in mass, ellipsoid in face view, elongate lacrimoid in profile (Figure 5.9); ornamentation of coarse, non-anastomosed, cyanophilic warts; apiculus prominent, eccentric.

Etymology: Latin, *papuanus*, for Papua New Guinea where the type was collected.

Habit, habitat, and distribution: Solitary to gregarious but not caespitose, on soil under *Castanopsis* and *Lithocarpus* near Lae, Papua New Guinea.

Collections examined. **PAPUA NEW GUINEA:** Morobe province, about 40 km southwest of Lae, Oomsis regeneration plots, 6° 45'S, 146° 47'E, 13 February 1992, *N.L. Bougher and M.A. Castellano E4549* (PERTH 06707114– **holotype** here designated; Isotype OSC 107808).

Discussion: Only known from the type collection from Papua New Guinea. The macroscopic and microscopic characteristics of *G. papuanus* resemble those of *G. novae-zelandiae* and *G. dingleyae*. *Gloeocantharellus papuanus* differs from *G. novae-zelandiae* by having a more wrinkled versus smooth hymenium and larger spores, and from *G. dingleyae* by the possession of clamp connections. All three species from Oceania produce small basidiomata compared to the northern hemisphere *Gloeocantharellus* species. The southern hemisphere species seem to be restricted to Myrtaceae-Podocarpaceae-Fagaceae dominated forests.

Gloeocantharellus purpurascens **(Hesler) Singer, Lloydia 8:140. 1945.**
Fig. 5.10

≡*Cantharellus purpurascens* Hesler, *in* Smith and Hesler, Lloydia 6:248. 1943.

≡*Gomphus purpurascens* (Hesler) R.H. Petersen, The Journal of the Elisha Mitchell Scientific Society 84:380. 1968.

Macroscopic characters: **Basidiomata** up to 10 cm tall, agaricoid-gomphoid, unipileate (Figure 5.10). **Pileus** up to 12 cm wide, flat to concave, dry, appressedly fibrillose, yellow-orange to orange-pink, violet where bruised; margin thin, even to subcrenate, inrolled when young. **Hymenium** surface in well-developed, thin

hymenial folds up to 3 mm tall, decurrent, narrow, regularly longitudinal at the stipe, forking irregularly 1-3 times upward, white, violet where bruised. **Stipe** 40-100 × 8-20 mm, solid, dry, fibrillose, rounded at base, attenuate downward, creamy yellow when young, concolorous in age with the rest of the basidioma, pale vinescent where bruised. **Context** pliable above and more compact below, off-white. **Odor** mild, of anise. **Taste** sometimes mildly bitter. **Spore print** brown.

Microscopic characters: **Pileipellis** of a compact layer of hyphae often with elongate-fusiform or sickle-shaped cells, with abundant pileocystidia 25-110 × 4-7 µm long, of two types: (1) gleoplerous, yellow, with strongly cyanophilic contents, and (2) thin-walled, interwoven, hyaline, with clamp connections. **Stipitipellis** of densely interwoven hyphae embedded in agglutinating substance, with abundant gleoplerous hyphae, some ending in gleoplerous caulocystidia identical to hymenium cystidia. **Pileus context** of abundantly branched hyphae 3-4.5 µm wide, occasionally inflated to 7 µm, of two types: (1) gleoplerous, yellow, and (2) thin-walled, interwoven, hyaline, with agglutinating substances; clamp connections present. **Stipe context** of packed hyphae of two types: (1) thin-walled, parallel, hyaline, with clamp connections, and (2) gleoplerous, tortuous, aseptate, interwoven, yellow, common but not abundant. **Hymenial trama** with well-developed mediostratum of generally parallel, compactly arranged hyphae identical to those of pileus surface; gleoplerous hyphae tortuous, uninflated, with cyanophilic contents. **Basidia** 55-70 × 8.5-10.5 µm, clavate, collapsing after spore discharge, hyaline, with 4 straight, stout sterigmata up to 7.5 µm long; clamp connections present. Hymenial **cystidia** 60-130 × 7-12 µm, elongate-fusiform, apically attenuated, strongly cyanophilic, mostly gleoplerous and without bent tips, arising from gleoplerous hyphae in the hymenial mediostratum and penetrating the hymenium. **Spores** (7-) 8-11 (-13.5) × 3.5-5.5 µm, ellipsoid to obovoid (Figure 5.10); ornamentation of low, uneven, weakly cyanophilic warts; apiculus eccentric.

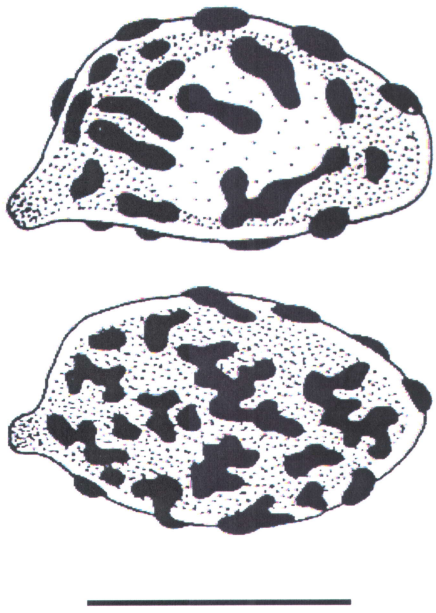


Figure 5.10. *Gloeocantharellus purpurascens* (Hesler) Singer: (a) basidiomata (× 1); (b) spores (bar = 5 µm). Spore drawings From Petersen (1971b), with permission.

Habit, habitat, and distribution: Solitary to gregarious, not caespitose, terrestrial, in moist *Acer-Tsuga* forests on the East coast of the USA (Petersen 1968, Smith and Hesler 1943).

Collections examined. **UNITED STATES. NORTH CAROLINA:** Yancey Co., Indian Creek, 11 August 1940, *L.R. Hesler* (TENN 12793 – **holotype**), 2 May 1942, *L.R. Hesler* (TENN 14265), and 20 August 1959, *L.R. Hesler* (TENN 23225).

Discussion: This species is quite distinct compared to other species of *Gloeocantharellus* because of the differentiated lamellar mediostratum, commonly accepted as an agaricoid feature (Petersen 1971a). *Gloeocantharellus purpurascens* shares morphological features with *G. corneri, G. echinosporus, G. lateritius, G. papuanus,* and *G. okapaensis*. Similar features of these species are the presence of gleocystidia and clamp connections. *Gloeocantharellus purpurascens* is, however, uncommon and only reported from the eastern USA.

DISCUSSION

Interest in the systematics and evolutionary biology of *Gloeocantharellus*, and its involvement in the history and evolution of the Gomphales arose when Singer (1945) transferred *Cantharellus purpurascens* to *Gloeocantharellus* on the basis of gleoplerous cystidia, moving the species from the Cantharellales to the Gomphales. This was the only species of *Gloeocantharellus* until Petersen (1971a) accepted *Linderomyces corneri* (≡*Gloeocantharellus corneri*) and *L. lateritius* (≡*Gloeocantharellus lateritius*) as members of the genus.

Currently *Gloeocantharellus* contains species distributed primarily in the tropics and subtropics plus a few in temperate locations. Only *G. purpurascens* occurs in the USA and represents the link between the tropics and the low elevation temperate region of the Appalachian Mountains.

As mentioned by Petersen (1976), ample examples show that the lower elevations of the southern Appalachian Mountains contain representatives of a tropical flora. Among them are species of *Amanita*, *Hydnum*, and *Tulasnella* indigenous to the Pacific tropics, species of *Echinoramaria* and *Clavicorona* from tropical South and Central America, tropical Indochina, and the tropical Pacific, and species of *Clavulinopsis*, with a large distributional crescent from Japan through Indochina and subtropical India, northern Australia and New Zealand, tropical South America and Africa, and eastern North America, but most commonly in the southern Appalachians. By its occurrence, *Gloeocantharellus* is evidently another genus with a pantropical distribution, with *G. pallidus* and *G. purpurascens* as the only two North temperate representatives.

Gloeocantharellus basidiomata are generally found in similar habitats as for many other species of the Gomphales. They are always terrestrial and have been seen fruiting under forested areas containing *Acer*, Fagaceous, *Podocarpus*-broadleaf, *Psidium*, and *Tsuga* species. Based on the assortment of plant species with which *Gloeocantharellus* is found, it is possible the genus is ectomycorrhizal. However, studies on the nutritional status and substrate affinity for *Gloeocantharellus* are still lacking. Further studies on molecular analysis of roots and basidiomata (Gardes *et al.* 1991, Bruns and Gardes 1993, Bruns *et al.* 1998), pure culture synthesis (Molina 1979, Molina and Trappe 1994), and/or $^{12}C - {}^{13}C$ (Hobbie *et al.* 2001) isotope ratio are necessary to determine the substrate affinity of the genus.

Gloeocantharellus species are characterized by relatively small agaricoid-gomphoid basidiomata, with folded (wrinkled) to lamellate hymenium, and presence of large numbers of gleoplerous hyphae. Main features used to separate species within *Gloeocantharellus* are the size and ornamentation of the spores, presence or absence of clamp connections and gleocystidia, the habitat, and the distribution.

This diversity of characters is reflected in the recent phylogenetic analyzes for the Gomphales, which included 5 species of *Gloeocantharellus* (Giachini,

chapter 2). The results of that study suggested a unique arrangement within *Gloeocantharellus* that deserves further investigation. Based on the overall morphological differences and the phylogenetic arrangement, five distinct clades can be detected, but further investigation is necessary to verify if they truly represent five unique lineages. The largest of these lineages encompasses *G. corneri, G. echinosporus, G. lateritius, G. okapaensis, G. papuanus,* and *G. purpurascens* (only the latter two were genetically sampled). This lineage is characterized by the presence of massive numbers of gleoplerous hyphae, presence of gleocystidia, presence of clamp connections, and an agaricoid (lamellate) to slightly wrinkled hymenium.

The remaining lineages are all monotypic for now, a conclusion based mainly on their unique morphological features and/or exclusive distribution reflected in the phylogenetic analyzes. One of these lineages is represented by the pantropical species *G. pallidus*: it has unique morphological features, such as strongly wrinkled hymenia, not seen in other species of the genus. In addition, it lacks clamp connections or gleocystidia but does have gleoplerous hyphae.

A third lineage consists of *G. mamorensis*, only known from tropical Bolivia. This species produces small, fleshy, terrestrial basidiomata in the Bolivian Amazon. Morphological features unique to this species, in addition to the exclusive South American distribution, include presence of gleoplerous hyphae and clamp connections, smooth or widely separated, shallowly folded hymenia, and absence of gleocystidia. *Gloeocantharellus mamorensis* seems to have intermediate characteristics between *G. novae-zelandiae* and *G. dingleyae*.

Even though *G. novae-zelandiae* and *G. dingleyae* occur in similar habitats in New Zealand, microscopic features seem to separate them into two unique lineages. Both possess gleoplerous hyphae and clamp connections, but the similarities in hyphal tissue end there. *Gloeocantharellus novae-zelandiae*, for example, possesses gleocystidia, a feature not observed in *G. dingleyae*.

Not all species of *Gloeocantharellus* possess gleocystidia. Among other uniquely derived characters, this may be responsible for the multiple derived

evolutionary lineages observed in the genus. These lineages may represent re-arrangements into distinct subgenera or even distinct genera and further studies are necessary to delimit their subgeneric or generic boundaries. Additional collecting is also essential for a better understanding of the distribution of *Gloeocantharellus*, focusing primarily in the diversity-rich tropical areas. Furthermore, investigation with molecular tools is necessary to identify the proper placement of species and to resolve the systematics of this poorly studied genus.

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CHAPTER 6

Systematics of the Gomphales: The Genus *Phaeoclavulina* Brinkmann

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ABSTRACT

The genus *Phaeoclavulina* has 41 species characterized macroscopically by pileate or ramarioid, greenish violaceous, brown, or orange-red basidiomata, and wrinkled to smooth hymenia. Microscopic features include monomitic hyphae, presence of clamp connections, and echinulate to verrucose, subreticulate or reticulate spores. The six pileate species are transfers from *Gomphus sensu lato.* These have funnel- to fan-shaped basidiomata and strictly tropical to subtropical distribution. The ramarioid section of *Phaeoclavulina* includes species transferred from *Ramaria* subgenus *Echinoramaria.* A remarkable characteristic of many *Phaeoclavulina* species is a cosmopolitan distribution. *Phaeoclavulina* species range from tropical to temperate regions, but are more abundant in the tropics and subtropics. A few species present a pantropical distribution, occurring in tropical places and with a refugium in the Appalachian Mountains of the USA. No *Phaeoclavulina* species has been confirmed as either mycorrhizal or saprotrophic, although the wood inhabiting tendency of many species indicate the genus may be saprotrophic. Additional studies on ecological and evolutionary aspects are necessary to better understand the placement and role of this diverse fungal genus.

INTRODUCTION

The nomenclatural history of species in *Phaeoclavulina*, as for many others in the Gomphales, has been unsettled over the years. For the pileate species, it started when Patouillard (Doassans and Patouillard 1886) coined the name *Nevrophyllum* to accommodate *N. clavatum* (≡*Cantharellus/Gomphus clavatus)*, later including *N. viride* (Patouillard 1888). The two species were grouped together because of their fan-shaped pilei. *Nevrophyllum clavatum* was separated from *N. viride* primarily by spore morphology: *N. clavatum* was claimed to have 'smooth spores', while *N. viride* had rough spores. *Nevrophyllum viride* differed from *N. clavatum* not only in general microscopic aspects but also by its tropical distribution.

On the basis of Patouillard's descriptions of *N. clavatum* and *N. viride*, Murrill (1910) transferred the latter to *Chlorophyllum*, with *C. viride* as the type. After discovering the name *Chlorophyllum* was preempted (Massee 1898), Murrill (1911) coined the name *Chloroneuron* to accommodate *C. viride*. Later species of *Nevrophyllum* and *Chloroneuron* were accommodated under *Gomphus*.

The history of the ramarioid species of *Phaeoclavulina* had a similar trajectory, although with an earlier start than the pileate ones. Formal cognizance of a coralloid member of this group came when Persoon (1794) described *Clavaria abietina*, a name that, although popular for a time, was misapplied by Fries (1821).

Reliance on the literature of Fries on the coral fungi persisted longer than for the agarics, except for the writings of Karsten (Petersen 1981). Over the years many taxonomists overlooked the works of Karsten. One problem recognized with the works of Karsten is the listing of species. Karsten's (1882, 1889) use of asterisks preceding some but not all species names made it confusing whether he was referring to species or varieties when employing such symbols.

After Fries the next taxonomic progress with the coral fungi came from Junghuhn (1830), who introduced the name *C. ochraceo-virens* as a substitute for Persoon's *C. abietina.* According to Petersen (1981), Junghuhn's species

represented a very different taxon from *C. abietina*. Later Brinkmann (1897) erected the genus *Phaeoclavulina* to include *P. macrospora*, which, according to him was to be related to *Clavaria testaceoflava*, *C. spinulosa*, and *C. abietina*. Brinkmann (1897) assigned *Phaeoclavulina* to the Clavariaceae, which also included *Clavaria, Clavariella, Clavulina,* and *Typhula*. Unable to recognize Fries' concept of *C. abietina*, and aware that Persoon's description antedated the newly imposed starting point, Cotton and Wakefield (1919) introduced a new name, *Clavaria invalii*, for the Friesian concept of *C. abietina* (Petersen 1981). Besides the genera mentioned above, species of *Phaeoclavulina* were also accommodated under *Cladaria, Cnazonaria, Dendrocladium, Lachnocladium, Penicillaria, Phaeopterula, Pistillaria, Pterula, Ramaria* and *Thelephora*.

Others contributed to increase the list and knowledge of coralloid fungi, providing more in-depth clarification of the natural classification within the group. Among them are Léveillé, Patouillard, Hennings, Berkeley, Overeem, Cleland, Imai, Atkinson, and Spegazzini, just to name a few. However, one of the more important pieces on the direct relatives of *Phaeoclavulina*, the 'Ramarias', came in 1923 with Coker's "*The Clavarias of the United Sates and Canada*." Others (Corner, Fawcet, Overeem, Petersen) followed Coker's compendium as a base for the identification and new descriptions to come.

The next step on the historical nomenclature and taxonomy of coralloid fungi came with Corner's (1950) book "*A monograph of Clavaria and allied genera*." In his publication Corner recognized almost 30 ramarioid taxa, mostly from the tropics, widening the concept of 'clavarioid' to a new breadth.

Doty (1944) published on the clavarioides of Oregon, subsequently (Doty 1948) providing a key to genera similar to that proposed by Corner.

Over the following years new interest on clavarioid/coralloid/ramarioid fungi re-appeared around the world, especially on the genus *Ramaria*. Corner (1970) proposed to subdivide *Ramaria* into subgenera *Ramaria, Echinoramaria*, and *Lentoramaria*, each composed of several *series nova*. Marr and Stuntz (1973) proposed *Laeticolora* as a 4th subgenus of *Ramaria*. Marr (1968), Olexia (1968),

Dodd (1970), Marr and Stuntz (1973), and McAfee (1978) made important contributions on the North American taxa. Parmasto (1965) and Schild (1975, 1978) expanded on the European and Scandinavian taxa. Yokoyama and Sagara (1973) studied the Japanese species, and Singh (1977) and Rattan and Khurana (1978) circumscribed the Indian taxa.

The literature for this group continued into the late 1900's. In the 1970's and 80's Petersen produced fundamental compilations for the genus *Ramaria*. He produced monographs on *Ramaria* subgenus *Lentoramaria* (Petersen 1975) and subgenus *Echinoramaria* – to which *Phaeoclavulina* was a synonym (Petersen 1981). He also published several articles on species of *Ramaria* around the world, with an inclusive manuscript on the clavarioid fungi of New Zealand (Petersen 1988).

However, even while the literature continued to add information it revealed the complexity of the group. As pointed out by Petersen (1981), detailed treatment of the group was still lacking for large members of taxa around the world; modern examination of many species and their phylogenetic relationships with other members of the Gomphales is still missing.

Recently taxonomists have employed molecular methods to determine intergeneric and interspecific boundaries for taxa assigned to *Ramaria* and other allied genera in the Gomphales. Humpert *et al.* (2001) and others have shown the genus *Ramaria* to be non-monophyletic. Based on morphology and molecular sequences of three combined genomic regions, Giachini (chapter 2) showed, among other things, that a few species of the pileate *Gomphus sensu lato* formed a monophyletic group with the coralloid species of *Ramaria* subgenus *Echinoramaria*. Detailed morphological analyses of those species indicated distinctive combinations of morphological features, which resulted in the resurrection of the genus *Phaeoclavulina* Brinkmann (Brinkmann 1897). *Phaeoclavulina* was long recognized as a synonym of *Ramaria* subgenus *Echinoramaria* section *Dendrocladium* (Giachini, chapter 2). Two main basidiomata shapes are now recognized in *Phaeoclavulina*: pileate and ramarioid.

Pileate forms are shared by species formerly in *Gomphus sensu lato*. Those formerly in *Ramaria* subgenus *Echinoramaria* share the ramarioid shape.

The pileate species of *Phaeoclavulina* are characterized by cantharelloid-gomphoid[1] and unipileate to merismatoid (composed of several pilei) basidiomata that display some green or violaceous color on pileus and hymenium, and by fan- to funnel-shaped pilei. Pilei are glabrous to subtomentose, and hymenia decurrent with hymenial folds rather than gills. Basidiomata vary in size, and species are known only from the tropics and subtropics. Micromorphological features include presence of clamp connections and echinulate, verrucose, subreticulate or reticulate spores. Known pileate species of *Phaeoclavulina* are *P. africana* (Borneo), *P. grandis* (Borneo), *P. guadelupensis* (Guadeloupe, in the Lesser Antilles), *P. retispora* (Malaysia and the Solomon Islands), *P. subclaviformis* (Brazil and Trinidad and Tobago), and *P. viridis* (Australia, Belize, French Guiana, and Martinique).

Ramaria subgenus *Echinoramaria* was originally proposed to include species of spiny-spored *Ramaria*, which were also alleged to be saprotrophic (Corner 1970). Today, ramarioid species of *Phaeoclavulina* are recognized to have greenish violaceous, brown, or orange-red basidiomata and to occur on soil or wood, mainly in the tropics and subtropics but also in temperate regions. Micro morphological features include monomitic hyphae, presence of clamp connections, presence of gleoplerous hyphae, and ornamented spores. The ornamentation is either echinulate or verrucose, and the spore apiculus is generally prominent. Species of *Ramaria* subgenus *Echinoramaria* have long been alleged to be saprotrophic (Corner 1970, Petersen 1981), but the substrate affinity has not yet been verified by scientific investigation.

The objective of this study is to describe important morphological features used to identify species of *Phaeoclavulina* and present a dichotomous key followed

[1] Basidiomata with the similar shape of a *Cantharellus* species but with decurrent, wrinkled hymenia rather than straight gills.

by detailed species descriptions. For a complete discussion on the nomenclatural history of *Phaeoclavulina* see Giachini (chapter 2).

MATERIAL AND METHODS

Collections examined

Collections of *Phaeoclavulina* examined in this study were obtained from the following herbaria: BPI, BR, CANB, DAR, FH, GH, H, K, LPS, M, NCU, NY, NYS, OSC, OULU, PERTH, PDD, S, TENN, and TNS (http://www.nybg.org/bsci/ih/ih.html). Holotypes of synonyms were examined whenever available. Habitat and fruiting patterns are based on the original descriptions and other relevant literature. Names of authorities are according to Brummit and Powell (1992).

Macroscopic characters

Macroscopic features are based on the original descriptions and notes accompanying herbarium collections supplemented by my own data on dried specimens. Features of the cap, hymenium, stipe, flesh, odor and taste were recorded whenever possible. Dimensions of basidiomata are given as the range (min-max) from all collections examined. Application of the various chemicals often used and referred to in the literature in describing species of *Gomphus sensu lato* provided little data of value and therefore were discontinued in this study.

Microscopic characters

Features observed with a compound microscope were described from free-hand sections mounted in Melzer's reagent, 5% KOH, cotton blue, or water. Structures were measured with an optical micrometer at × 1000 magnification, mostly in 5% KOH, water, or Melzer's reagent. The ranges for hypha measurements are thin walls ≤0.5 µm wide, thick walls >0.5 µm wide. The pileipellis and stipitipellis were examined in surface view. When material was available, dimensions of structures were recorded from at least 3 specimens from each of at least 5 collections; both mature and immature specimens were examined for developmental changes. Maturity was judged by the relative abundance of fully ornamented spores.

Spore shape was determined as the length-width ratio of 20-30 randomly selected spores. Dimensions are given as: minlength-maxlength × minwidth-maxwidth, excluding ornamentation and apiculus. Immature or oversized spores were not included in the measurements, though variation was noted.

SYSTEMATICS OF *PHAEOCLAVULINA*

Key to pileate species of Phaeoclavulina

1. Base of stipe significantly expanded and bulbous below substrate; pileus creamy brown; uncommon, Uganda..... *P. africana*

1. Base of stipe not expanded or bulbous below substrate..... 2

2. Pileus funnel-shaped; spores partially reticulate to reticulate..... 3

2. Pileus fan-shaped; spores echinulate, verrucose or partially reticulate..... 4

3. Hymenial cystidia absent; basidiomata frequently merismatoid, on soil or humus; pileus pale sordid olivaceous, pale yellow-brown toward the margin..... *P. retispora*

3. Hymenial cystidia 90-140 × 8-10 µm long, thin-walled, cylindrical, hyaline, acyanophilic; basidiomata unipileate, on soil or wood; pileus dark sordid green, olive-green or gray-olive, becoming dark yellow-brown at the center of the pileus with age..... *P. viridis*

4(2). Spores <13 µm long; basidiomata up to 9 cm tall; gleoplerous hyphae thin-walled, up to 6 µm wide; Brazil, Trinidad and Tobago..... *P. subclaviformis*

4. Spores >14 µm long; basidiomata >10 cm tall; gleoplerous hyphae inflated to 22 µm or more often absent; Borneo and the Caribbean..... 5

5. Gleoplerous hyphae absent; spores (14-) 16-17.5 × 5.5-7 µm; basidiomata up to 30 × 22 cm; hymenium with tall wrinkled folds, pale olivaceous to violet in age, all parts bruising vinaceous; Borneo..... *P. grandis*

5. Gleoplerous hyphae rare, aseptate, cyanophilic, in some places inflated up to 22 µm; spores 15-18 (-25.5) × 7.5-10.5 (-12) µm; basidiomata up to 15 × 10 cm; hymenium smooth to wrinkled, orange to brown or slightly darker; Guadeloupe..... *P. guadelupensis*

***Key to ramarioid species of* Phaeoclavulina**

1. Spores ornamented with discrete spines at distal and proximal ends and mixed discrete spines and spines connected into circular to semi-circular ridges in median area, the ornamentation sometimes covering the entire surface of the spores..... *P. decolor*

1. Spores echinulate or verrucose, not ornamented with spines connected into circular to semi-circular ridges in median area..... 2

2. Branch axils[2] with narrow, sterile webbing[3]..... *P. articulotela*

2. Branch axils without sterile webbing..... 3

3. Crystals present in trama or adhered to rhizomorph hyphae..... 4

3. Crystals absent in trama or rhizomorphs hyphae..... 5

4. Basidiomata green to orange-green, bruising green..... 6

4. Basidiomata not bruising green; apices not becoming greenish; spores without distinct oblique apiculus..... 7

5. Spores verrucose, ornamentation eventually connected into randomly located ridges..... 8

5. Spores echinulate..... 9

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[2] The area at the junction of two or more branches.
[3] Resembling the foot of a waterfowl.

6(4). Branch apices greenish; spores 5-9 × 2.5-5.5 µm, with a distinctly oblique apiculus; basidia ≤45 µm long..... *P. flaccida*

6. Branch apices yellow to creamy yellow; spores 8-11.5 × 4-5.5 µm, without a distinct oblique apiculus, but often somewhat curved; basidia >50 µm long..... *P. glauco-aromatica*

7. Crystal aggregates only present in trama; basidia ≥45 µm long..... *P. eumorpha*

7. Crystal aggregates present in trama and/or rhizomorphs; basidia < 45 µm long..... 33

8(5). Basidiomata bruising olive, green or blue-green on handling or weathering..... 10

8. Basidiomata not bruising olive, green or blue-green on handling or weathering, but rather remaining yellow-orange to brown..... 11

9(5). Hyphae with H-connections..... 14

9. Hyphae without H-connections..... 15

10(8). Spores 6-12 × (3-) 4-4.5 (-5.5) µm, ornamented with cyanophilic, fine to rough warts..... *P. ochraceo-virens*

10. Spores 8-12 × 6-8.5 µm, ornamented with cyanophilic, forked or lobed, stout, blunt or truncate warts and longitudinal ridges up to 2.5 µm tall..... *P. pancaribbea*

11(8). Spores nearly all longer than 9 µm..... 12

11. Spores <9 µm long..... 13

12. Basidia <50 µm long; basidiomata up to 5 × 2.5 cm; stipe up to 3 mm thick; southern South America..... *P. campoi*

12. Basidia ≥60 µm long; basidiomata up to 17 × 5.5 cm; stipe up to 15 mm thick; India..... *P. sikkimia*

13(11). Spores 10.5-14 × 4.5-6 µm, ornamented with blunt, scattered, cyanophilic warts <1 µm tall; hymenium generally amphigenous[4]; India..... *P. echinovirens*

13. Spores 8-11 × 6.5-8 µm, ornamented with cyanophilic blunt warts and longitudinal ridges up to 3 µm tall; hymenium unilateral; New Zealand..... *P. zealandica*

14(9). Spores 10-15.5 × 6-10 (-11) µm..... *P. zippelii*

14. Spores 18-20 (-24) × 9-11 µm..... *P. angustata*

15(9). Basidiomata branches or tips with tints of olive or green when fresh or dry..... 16

15. Basidiomata branches or tips without tints of olive or green when fresh or dry, but rather gray, yellow, orange, cinnamon, red or brown..... 17

[4] All around as opposed to unilateral (generally fertile on the outside facing side of the branch).

16. Spores >10 µm long..... *P. cyanocephala*

16. Spores <9 µm long..... 18

17(15). Spores nearly all longer than 15 µm..... 19

17. Spores <15 µm long..... 20

18(16). Branch apices about 1 mm long and wide, straight, digitate, creamy yellow-green to orange; basidiomata up to 16 cm tall; basidia 40-55 × 5-6 µm..... *P. mutabilis*

18. Branch apices waxy, dichotomous, awl-shaped, pale yellow; basidiomata up to 5.5 cm tall; basidia 30 × 7 µm..... *P. ochracea*

19(17). Basidia with 2 sterigmata; branch apices slightly thickened and shortly dentate or subcristate, intensely brick red to nearly scarlet; spores 15-18 × 8-10 µm; Brazil..... *P. apiahyna*

19. Basidia with (2-) 4 sterigmata; branch apices orange to cinnamon; spores (12.5-) 14-20 (-22) × 4.5-8 µm; Europe, Japan, and the USA..... *P. macrospora*

20(17). Branch apices orange to vivid red..... 21

20. Branch apices white to silvery, gray-yellow, gray-brown, dark olive-yellow, yellow to brown, cinnamon, orange vinaceous..... 22

21. Spores 7-9.5 × 3-4.5 µm, ornamented with small, sparsely scattered, cyanophilic spines <0.5 µm tall; basidia <40 µm long; basidiomata up to 5.3 cm tall, delicate..... *P. camellia*

21. Spores 9-16 × 4-7.5 µm, ornamented with acute, hyaline, strongly cyanophilic spines 1-2 µm tall; basidia >45 µm long; basidiomata up to 13 cm tall..... *P. cokeri*

22(20). Basidiomata >11 cm tall..... 23

22. Basidiomata ≤11 cm tall..... 26

23. Basidiomata cauliflower-like; branches up to 3 cm long..... *P. campestris*

23. Basidiomata not cauliflower-like; branches >5 cm long..... 24

24. Hymenium unilateral..... *P. insignis*

24. Hymenium amphigenous..... 25

25. Basidia >80 cm long; branch apices up to 20 mm long, slender, bifurcating with subacute axils, abruptly tapered, abruptly white; spores 7-10 (-14) × 4.5-6.5 (-8.5) µm..... *P. gigantea*

25. Basidia <60 cm long; branch apices up to 3 mm long, rounded-acute, golden yellow to orange; spores 9.5-11.5 × 4.5-6 µm, spore aberrations common, usually of spores up to 17 µm long and slender to a maximum of 4.5 µm wide, these usually much less highly ornamented than normal.... *P. tropicalis*

26(22). Spores 12-15 µm long..... *P. griseobrunnea*

26. Spores ≤11 µm long..... 27

27. Hymenium amphigenous[5]..... 28

27. Hymenium unilateral..... 31

28. Hymenium surface velutinose-pruinose..... *P. cervicornis*

28. Hymenium surface rugulose..... 29

29. Branch apices minute, acute, irregular and congested when young, becoming flattened and irregularly digitate in age, awl-shaped, usually drying off-white, white to silvery..... *P. argentea*

29. Branch apices dichotomous to trichotomous, not divergent, yellow, orange, orange vinaceous to brown..... 30

30. Spores 5-6 × 3-4 µm; odor pleasant, slightly of anise; taste acrid to almost salty; on the ground near bamboo in southeast Asia..... *P. capucina*

30. Spores 5-9.5 × 2.5-5.5 µm; odor slightly earthy; taste more or less earthy, somewhat bitter; under *Quercus ilex*, Italy..... *P. quercus-ilicis*

31. Spores (3.5-) 4.5-6.5 (-8) µm long; basidia 25-36 µm long..... *P. curta*

31. Spores 7-11 µm long; basidia 40-50 µm long..... 32

[5] All around as opposed to unilateral (generally fertile on the outside facing side of the branch).

32. Branches not over 2 mm thick; stipe 20-30 × 1.5-2 mm; basidia with 2 stout, slightly curved sterigmata; Brazil, French Guiana, Guadeloupe, Jamaica, and Panama..... *P. guyanensis*

32. Branches up to 5 mm thick; stipe up to 70 × 7 mm; basidia with (2-3-) 4 stout, slightly incurved sterigmata; USA..... *P. longicaulis*

33(7). Branch apices usually in two thin lash-like branchlets; basidiomata >6 cm tall..... *P. vinaceipes*

33(7). Branch apices without two thin lash-like branchlets, but rather dentate, acute to rounded; basidiomata <5 cm tall..... 34

34. Crystal aggregates 1.5-5.5 μm, more rarely connected into larger bodies of 8-14.5 μm; branches 3.5-7 mm thick above, subclavate, rarely 2-4-branched; apices 3-7 dentate..... *P. clavarioides*

34. Crystal aggregates abundant, minute; branches up to 2 mm thick, sparsely to repeatedly branched up to 4 ranks; apices acute to rounded... *P. roellinii*

Descriptions

Species are described in alphabetical order. Descriptions include citation of all material examined and the herbarium where the type and other collections are deposited. Phenology and biogeography are based on notes available with collections and the observations made in this study.

Phaeoclavulina **Brinkmann, Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst 25:197. 1897,** ***emend.*** **Giachini,** ***emend. prov.***

≡*Clavaria* sect. *Phaeoclavulina* (Brinkmann) Killerm., *in* Engler and Prantl, Die Natürlichen Pflanzenfamilien 6:155. 1928 (not located, *fide* Petersen, Bibliotheca Mycologica 79:44. 1981).

=*Lachnocladium* sect. *Dendrocladium* Pat., Journal de Botanique 3:26. 1889.

≡*Dendrocladium* (Pat.) Lloyd, Mycological Notes 60:870. 1919.

≡*Ramaria* subg. *Echinoramaria* sect. *Dendrocladium* (Pat.) R.H. Petersen, Bibliotheca Mycologica 79:44. 1981.

=*Chloroneuron* Murrill, Mycologia 3:25. 1911.

≡*Chlorophyllum* (Pat.) Murrill, *nom. illeg.*, North American Flora 9:172. 1910.

=*Clavaria* sect. *Clavariella* subsect. *Terrestres* Killerm., *in* Engler and Prantl, Die Natürlichen Pflanzenfamilien 6:154. 1928 (not located, *fide* Petersen, Bibliotheca Mycologica 79:100. 1981).

=*Neurophyllum* subg. *Chloroneuron* Heim., Revue Mycologique 19:51. 1954.

=*Ramaria* subg. *Echinoramaria* Corner, Beihefte zur Nova Hedwigia 33:238. 1970.

≡*Ramaria* subg. *Echinoramaria* ser. *Grandisporae* Corner, Beihefte zur Nova Hedwigia 33:239. 1970.

=*Ramaria* subg. *Echinoramaria* ser. *Flaccidae* Corner, Beihefte zur Nova Hedwigia 33:239. 1970.

≡*Ramaria* subg. *Echinoramaria* sect. *Flaccidae* (Corner) R.H. Petersen, Bibliotheca Mycologica 79:100. 1981.

=*Ramaria* subg. *Echinoramaria* ser. *Virescentes* Corner, Beihefte zur Nova Hedwigia 33:239. 1970.

=*Gomphus* subg. *Phaeoclavulinoides* R.H. Petersen, Mycologia 68:432. 1976a.

Type species: *Phaeoclavulina macrospora* Brinkmann, Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst 25:198. 1897.

Macroscopic characters: **Basidiomata** up to 1.5-30 × 1.5-22 cm, solid, cantharelloid-gomphoid, unipileate, merismatoid or ramarioid. **Pileate** species pilei up to 22 cm wide, flat to depressed, fan- to funnel-shaped, glabrous to subtomentose or floccose-squamose (*P. retispora*), white, pale orange, orange to sordid olivaceous, sordid green to olive-green, yellow-brown, brown with age; margin incurved, crenate, lobed or inrolled when young, undulate to straight with age. **Ramarioid** species of wide branches below, cylindrical, subcylindrical to flattened or with small grooves or ridges, sometimes palmate, erect, crowded to openly spaced, sometimes spreading, stout to fragile, dichotomous to irregularly branched (up to 6 ranks), velutinous-pruinose (*P. cervicornis*) to rugulose, in general sterile and subtomentose on the inner surfaces and on the uppersides of the axils, forked or cristate near the apices, pale pink, gray, olivaceous, olive-green, blue-green, creamy yellow, orange, brown, cinnamon to red, in general bruising vinaceous brown to olive-green (*P. ochraceo-virens*); internodes short to generally elongated, especially at the primary axes[6], length diminishing gradually distally, forked or single near the apices, blue-green, creamy white to pale yellow, yellow-brown to dark brown, golden yellow to orange, olive-orange, cinnamon, brick red; axils subacute, acute to rounded, in general U-shaped, branches subparallel to slightly divergent, with narrow, sterile 'webbing'[7] (*P. articulotela*), gray-yellow, brick red to reddish brown, cinnamon when dry (*P. eumorpha*); apices waxy, acute, subacute to rounded, dentate, digitate, subcristate, Y-shaped to awl-shaped in some species, composed of two thin lash-like branchlets in *P. vinaceipes*, white to various shades of gray, olive, green, yellow, brown or red. **Hymenium: pileate species** – smooth in some species, lamellate to sublamellate or irregularly wrinkled with decurrent hymenial folds in others, generally longitudinally oriented,

[6] First branches observed from the stipe.
[7] Resembling the foot of a waterfowl.

dichotomously forked, anastomosing in some species, pale to dark orange, pale to sordid olivaceous, brown, sometimes violet in age (*P. grandis*) or bruising vinaceous; **ramarioid species** – amphigenous or unilateral, with regular decurrent folds sometimes extending to the substrate level, smooth to rugulose, with wrinkles forking regularly, waxy where fertile, minutely felty and ferruginous where sterile, but in general concolorous with branches. **Stipe** (2-) 30-90 (-150) × (0.6-) 6-30 (-45) mm, firm, solid to partially hollow, slender or stout, simple to fused, cylindrical, subcylindrical to flattened, ridged or grooved, more or less equal to generally slightly tapered downward, significantly expanded (up to 25 mm tall and 15 mm thick) below the substrate level to a bulbous shape in *P. africana*, in general coriaceous to brittle, surface glabrous to tomentose, especially at the base, frequently covered with hymenium, in general concolorous with pileus and branches, white below the substrate level, sometimes bruising blue-green, vinaceous, lavender-brown, brick-red or red-brown. **Context** firm, tender to tough, generally pliable and moist when fresh, gelatinous, punky pliable to fibrous when dry, white, creamy yellow to orange, in some species bruising vinaceous to brighter/darker colors than original color. **Odor** none to anise-like, earthy, spicy and aromatic, sweet to farinaceous, or paracresol-like. **Taste** none to bitter, musty, sour, mildly earthy, starchy, occasionally astringent, acrid to almost salty in *P. capucina*. **Spore print** cinnamon brown, yellow-brown, ferruginous.

Microscopic characters: **Pileipellis** up to 100 µm thick, of thin- to slightly thick-walled, compact to loosely parallel or compactly interwoven, undifferentiated, agglutinated or smooth, in general cyanophilic hyphae 1.5-16 µm wide, eventually with ampulliform swellings; clamp connections present; gleoplerous hyphae present or absent. **Stipitipellis** of thick-walled, parallel to compactly interwoven, branched, hyaline, moderately cyanophilic hyphae up to 14 µm wide, with ampulliform swelling in some species; clamp connections present; gleoplerous hyphae common. **Context** of thin- to slightly thick-walled, parallel to compactly interwoven hyphae 2-13.5 µm wide, inflated up to 15 µm in others, generally smooth, with adherent amorphous crystals (*P. eumorpha*), H-connections present in

P. angustata and *P. zippelii*; clamp connections present; gloeoplerous hyphae, either present, cyanophilic, not inflated or inflated to 25 µm, yellow. **Subhymenial trama** of irregular, more or less parallel to interwoven, generally narrow, indistinctly defined hyphae. **Rhizomorphic strands**, when present, more or less parallel, with hyphae between 1-3.5 µm thick, usually flattened, moderately pliable, easily broken when dry, white, in some species scattered with polymorph crystaloid elements of 1.5-14.5 µm. **Basidia** (19-) 40-100 (-140) × 4-16 µm, clavate, cyanophilic, with (1-) 2 (-3-) 4 stout, slightly divergent, slightly incurved to straight sterigmata up to 11 µm long, persisting or not after spore discharge; clamp connections generally present at base. Hymenial **cystidia** present only in *P. viridis*. **Spores** (3.5-) 8-17.5 (-25.5) × (2.5-) 3.5-9 (-12) µm, golden yellow, yellow-brown, orange-brown to ferruginous in mass, ellipsoid, ovoid, obovoid, subglobose, lacrimoid (tear-drop-shaped) to fusoid; ornamentation of cyanophilic warts and spines up to 3.5 µm tall, occasionally anastomosing at base of ornamentation to form subreticulate to reticulate ridges; apiculus prominent, eccentric.

Habit, habitat and distribution: Epigeous, single to gregarious or sometimes caespitose, on soil or wood on forest floors or in gardens, from tropical to temperate regions.

Discussion: Giachini (chapter 2) showed *Ramaria* subgenus *Echinoramaria* (monomitic hyphae and mostly echinulate spores) to group in a separate clade from other ramarioid species (non-monomitic hyphae and verrucose to smooth spores). A few gomphoid species were seen nested among the ramarioid species. This culminated with the resurrection of *Phaeoclavulina*. Forty-one species are known for the genus: 6 pileate and 35 ramarioid. The basidiomata of these species display a great breath of sizes, shapes, and colors.

Common characteristics of pileate and ramarioid species of *Phaeoclavulina* include: (a) echinulate to verrucose (anastomosed into subreticulate to reticulate ridges in some species) basidiospores, (b) presence of clamp connections, and (c) terrestrial and/or lignicolous substrate affinity. No species in this genus has been

proved to be mycorrhizal, perhaps due to the lack of investigation, although some have been suggested to be saprotrophic.

Both Corner (1970) and Petersen (1981) recognized several sections and series within *Ramaria* subgenus *Echinoramaria*. Because not all taxa could be molecularly sampled for this subgenus, Giachini (chapter 2) did not adopt Corner or Petersen's concepts of sections and series for *Phaeoclavulina*.

Even tough shape of the basidiomata wouldn't suggest an evolutionary link between ramarioid and pileate lineages, molecular genetics shows them to be evolutionarily more closely related than had been suspected. In light of the recent discoveries, more collecting needs to be done, especially in tropical and subtropical regions, to increase the knowledge for these gomphoid-ramarioid lineages of Gomphales. This will enhance understanding of species distributions, diversity and substrate requirements.

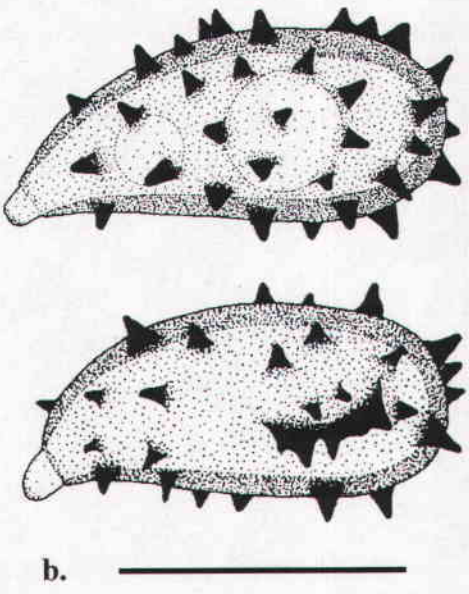
Pileate species

Phaeoclavulina africana* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.1

≡*Gomphus africanus* R.H. Petersen, Mycologia 68:429. 1976a.

Macroscopic characters: **Basidiomata** up to 4.5 cm tall, cantharelloid-gomphoid, unipileate (Figure 6.1). **Pileus** up to 2.5 cm wide, funnel-shaped, flat when young, depressed when mature, yellow-brown; margin thin and shiny when young, eventually crenate. **Hymenium** decurrent, with regular wrinkled hymenial folds extending to the substrate level, forking regularly, brown when dry. **Stipe** solid, significantly expanded with a subsurface bulb up to 25 mm tall and 15 mm thick, white, covered with a tomentum incorporating much sand (see figure 6.1). Data on **context**, **odor**, and **taste** not recorded. **Spore print** brown.

a.



b.

Figure 6.1. *Phaeoclavulina africana* (R.H. Petersen) Giachini, *sp. prov.*: (a) basidiomata (× 0.4); (b) spores (bar = 10 μm). Spore drawings modified from Petersen (1976b), with permission.

Microscopic characters: **Pileipellis** of thin-walled, compactly interwoven, agglutinated hyphae, yellow to a depth of 50 µm, often with adherent spores and minute debris; clamp connections present; gleoplerous hyphae often clavate, not inflated, strongly cyanophilic, yellow. **Pileus context** of compactly interwoven hyphae 2-4 µm wide, with adherent amorphous crystalline material; clamp connections present; gloeoplerous hyphae not inflated, yellow. **Basidia** 70-72 × 8-10 µm, clavate, gleoplerous, with agglutinated material, yellow, with 2 sterigmata that are stout below and abruptly narrow above; hyaline; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 12.5-18 × 6.5-8 µm, thin-walled, ferruginous in mass, ellipsoid to obovoid, contents moderately cyanophilic; ornamentation of acute, moderately cyanophilic cones up to 1 µm tall, occasionally anastomosing at the base to form short ridges (Figure 6.1); apiculus rounded.

Habit, habitat and distribution: The only known specimen was collected on grassland in Uganda (Petersen 1976a).

Collections examined: **UGANDA:** Bukoto Co., Masal District, Bale, Lake Nabugabb, 17 May 1972, *K. Lye* (TENN 36291 – as *Gomphus africanus* – **holotype**).

Discussion: As noted by Petersen (1971, 1976a), the morphological characters of *Gomphus africanus* (≡*P. africana*) are strikingly similar to those of some species formerly in *Ramaria* subgenus *Echinoramaria*, a condition corroborated by the molecular data (Giachini, chapter 2). Moreover, for those species previously in *Ramaria* subgenus *Echinoramaria* bearing heavily ornamented spores, sterigmata number is often 2, and basidia are normally gleoplerous and agglutinated, as observed for *P. africana*.

The most obvious characters that link *P. africana* to other species of *Phaeoclavulina* are the size and ornamentation of the spores and presence of clamp connections. Indeed, it would be difficult to distinguish between a microscope mount of hymenium and spores of *Ramaria zippelii* (≡*P. zippelii*) and *Gomphus africanus* (≡*P. africana*) (Petersen 1976a).

Phaeoclavulina grandis* (Corner) Giachini, *sp. prov. Fig. 6.2

≡*Gomphus grandis* Corner, Nova Hedwigia 18:812. 1969.

Macroscopic characters: **Basidiomata** up to 30 × 22 cm, merismatoid (Figure 6.2). **Pileus** up to 22 cm wide, fan-shaped, glabrous, pale orange and then orange; margin blunt, inrolled when young, undulate with age. **Hymenium** decurrent, with tall, wrinkled hymenial folds running down the stipe to the substrate level, forked occasionally, less crowded and smooth to sublamellate toward the margin than in the center of the pileus, pale olivaceous to violet in age, all parts bruising vinaceous. **Stipe** up to 150 × 45 mm, tapering downward, fibrillose to tomentose, especially at the base, pale brown to concolorous with pileus. **Context** pliable and moist when fresh, gelatinous, off-white to creamy yellow; context of stipe stringy, pale orange. **Odor** strong, resembling that of *Ganoderma* (paracresol). **Taste** not recorded. **Spore print color** not recorded.

Microscopic characters: **Pileipellis** 50-100 µm thick, of loosely interwoven hyphae 2-4 (-5) µm wide. **Stipitipellis** a stratum 100-500 µm thick, with hyphae 2-3 µm wide. **Context** of parallel, inflated hyphae 3-12 µm wide; clamp connections present; gleoplerous hyphae absent. **Basidia** 95-140 × 11-14 µm, clavate, with (3-) 4 sterigmata 7-8 µm long. Hymenial **cystidia** absent. **Spores** (14-) 16-17.5 × 5.5-7 µm, ellipsoid; ornamentation of irregular, cyanophilic warts up to 1.5 µm tall (Figure 6.2); apiculus prominent, straight.

Habit, habitat and distribution: This large fungus is known from a single collection by Corner in a dense forest of *Agathis* and Fagaceae at the mid-slopes of Kinabalu, North Borneo.

Collections examined: **BORNEO:** Kota Kinabalu, 26 April 1964, *E.J.H. Corner RSBN 8448* (BR 079158-06 – as *Gomphus grandis* – **holotype**).

Discussion: Corner (1969) stated that *G. grandis* is close to *G. guadelupensis* in possessing clamp connections and lacking gleoplerous hyphae. His pictures show a

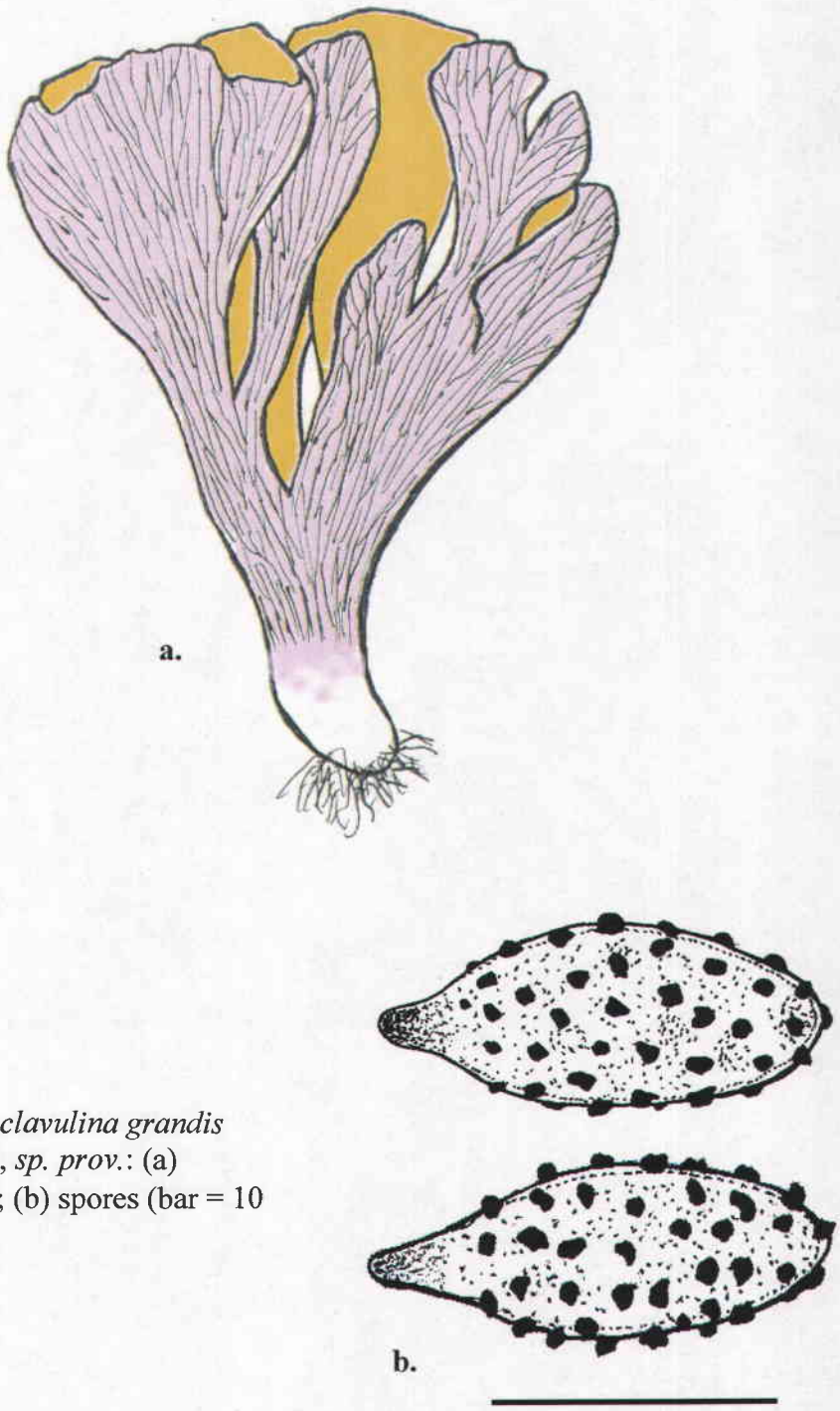


Figure 6.2. *Phaeoclavulina grandis* (Corner) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 10 µm).

resemblance to *Gomphus clavatus*, although overall size of the hymenial folds and size and shape of the spores immediately distinguish it from *G. clavatus*.

Phaeoclavulina guadelupensis* (Pat.) Giachini, *sp. prov. Fig. 6.3

≡*Stereum guadelupense* Pat., Bulletin de la Société Mycologique de France 15:201. 1899.

≡*Gomphus guadelupensis* (Pat.) D.A. Reid, Persoonia 2:134. 1962.

=*Nevrophyllum ochraceum* Pat., *in* Duss, Flore Cryptogamique de Antilles Françaises, p. 38. 1903.

≡*Cantharellus ochraceus* (Pat.) Sacc. & D. Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 17:36. 1905.

≡*Gomphus ochraceus* (Pat.) Singer, Lloydia 8:140. 1945.

Macroscopic characters: **Basidiomata** 10-15 cm tall, unipileate at first and then merismatoid. **Pileus** up to 10 cm wide, fan-shaped, lobed, flattened to subundulate, sometimes depressed at the center, with a tomentum of hyphae over the disc, velvety, orange when fresh, becoming brown with age, crenate at margin. **Hymenium** decurrent nearly to the base of the stipe, smooth to wrinkled, with low, shallow, crowded, simple or branched hymenial folds, commonly anastomosing downward to form irregular diamond patterns, concolorous with pileus or slightly darker. **Stipe** 30-70 × 30 mm, firm, glabrous, concolorous with pileus and hymenium. **Context** orange. **Odor** and **taste** not recorded. **Spore print** cinnamon brown.

Microscopic characters: **Pileipellis** of thin- to slightly thick-walled, parallel to interwoven, undifferentiated hyphae 2-10 µm wide, inflated away from the surface of the pileus, stipe, and hymenium into the context; clamp connections present, large; gleoplerous hyphae absent. **Stipitipellis** of undifferentiated hyphae covered with abundant spores. **Stipe context** of generally parallel, agglutinated, slightly cyanophilic hyphae; gleoplerous hyphae rare, aseptate, cyanophilic, in some places inflated up to 22 µm. **Basidia** 65-110 × 14-16 µm, clavate, strongly cyanophilic,

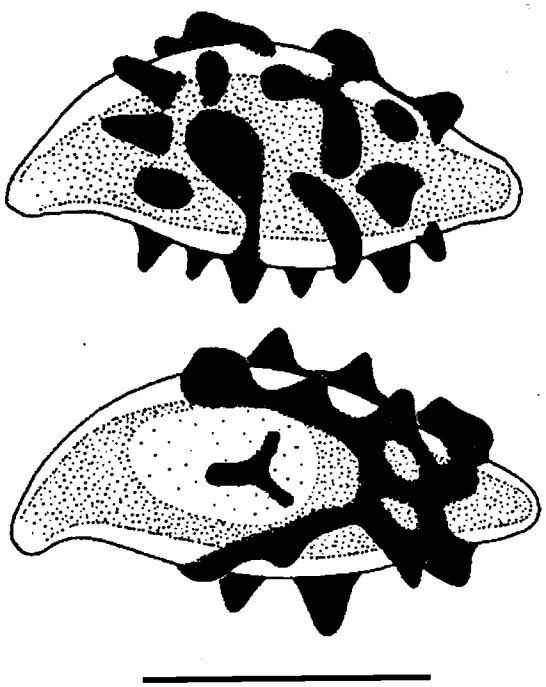


Figure 6.3. Spores (bar = 10 μm) of *Phaeoclavulina guadelupensis* (Pat.) Giachini, *sp. prov.* Spore drawings modified from Petersen (1971b), with permission.

with 2-3-4 stout, slightly divergent, slightly incurved sterigmata up to 8 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 15-18 (-25.5) × 7.5-10.5 (-12) µm, cinnamon in mass, ellipsoid to lacrimoid or fusoid; ornamentation of coarse, slightly cyanophilic warts up to 2.5 µm tall, partially reticulate (Figure 6.3); apiculus prominent, conical, eccentric.

Habit, habitat and distribution: Solitary to gregarious or subcaespitose. Two specimens are known, both on wood from Guadeloupe in the Lesser Antilles. This species likely occurs on other Caribbean islands and on the nearby mainland of South and Central America (Petersen 1971).

Collections examined: **GUADELOUPE:** Camp Jacob, February 1898, *A. Duss 120* (FH – as *Stereum guadelupense* – **holotype**).

Discussion: This remarkable species needs to be redescribed from living material (Corner 1966). It is evidently closely related to *P. grandis*, *P. subclaviformis*, and *P. viridis* on the basis of spore morphology, biogeography, and molecular data (Giachini, chapter 2). Its large basidioma size and coarse spore ornamentation resemble *P. viridis* (Petersen 1968, 1971). Petersen (1968) has also drawn analogies between *Gomphus guadelupensis* (≡*P. guadelupensis*) and the spiny-spored species of *Ramaria*, especially between *P. guadelupensis* and *P. zippellii*.

Phaeoclavulina retispora* (Corner) Giachini, *sp. prov. Fig. 6.4

≡*Gomphus retisporus* Corner, Annals of Botany Memoir 2:124. 1966.

Macroscopic characters: **Basidiomata** merismatoid (Figure 6.4). **Pileus** 7-11 cm wide, funnel-shaped, floccose-squamose to nearly glabrous, pale sordid olivaceous, pale yellow-brown toward the margin, in some specimens yellow toward the margin; margin incurved at first, then lobate-undulate, minutely subvillose. **Hymenium** decurrent, with distinct gill-folds up to 1 cm tall, dichotomous near the margin, transversely wrinkled in the interstices, sordid olivaceous, pale orange toward margin. **Stipe** 40-90 × 8-18 mm, concolorous, bruising vinaceous. **Context**

soft, paler concolorous with the surface, with watery zones in the pileus and watery-marbled zones in the stipe, unchanging color on exposure. **Odor** none. **Taste** not recorded. **Spore print color** not recorded.

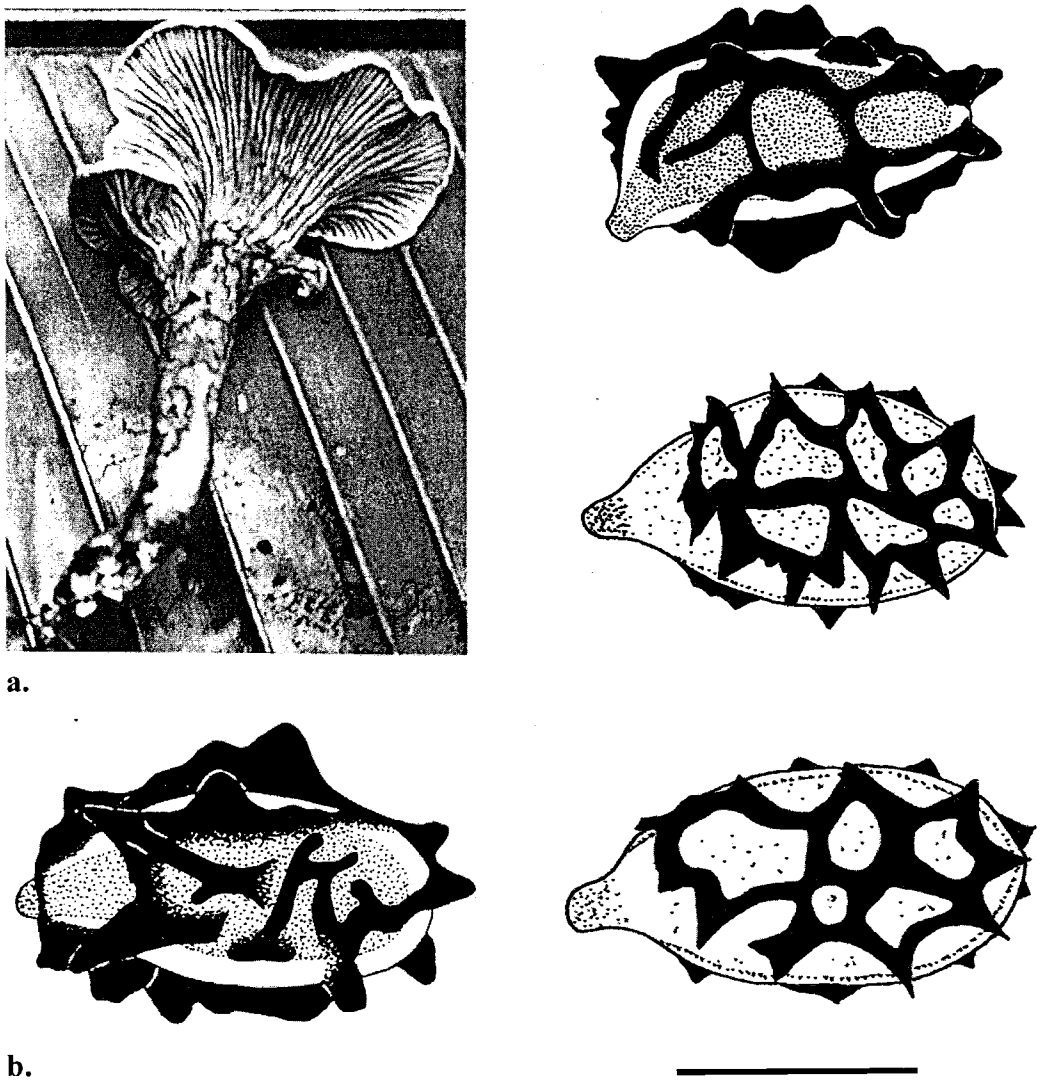
Microscopic characters: **Pileipellis** of distinctly thick-walled, compact, heavily agglutinated hyphae. **Stipitipellis** a tomentum 500 µm thick, composed of more or less entangled hyphae 4-7 µm wide. Other **hyphae** thin-walled, 17-25 µm wide, inflated; clamp connections present. **Basidia** 60-125 × (7-) 10-13 µm, clavate, with (2-) 3-4 straight sterigmata 8-11 µm long. Hymenial **cystidia** absent. **Spores** (11.5-) 14-17 (-20) × (5.5-) 6.5-7.5 µm, cinnamon in mass, ellipsoid to ovoid; ornamentation of irregularly oriented, strongly cyanophilic, subreticulate to reticulate ridges varying in height along their length up to 3 µm tall (Figure 6.4); notes on apiculus not recorded.

Habit, habitat and distribution: Fruiting gregariously on soil and humus in Malaysia and the Solomon Islands (Corner 1966, 1969).

Type (holotype): **MALAYSIA. BATU BALAI:** Pahang, Flum. Cheka, 13 November 1930, *E.J.H. Corner* (CGE – as *Gomphus retisporus*).

Discussion: The present description was based on notes from Corner (1966, 1969) and Petersen (1971). Corner (1966) described the species from a collection obtained in Pahang, Malaysia. Later Corner (1969) mentioned two more collections from the Solomon Islands. Petersen (1971) examined the isotype deposited at the National Herbarium Nederland (L) and concluded that it has "subreticulate rather than reticulate spores, and that the ornamentation anastomosed, often giving the impression of a reticulum." The species has affinities with *Phaeoclavulina viridis*, although closer in color and agglutination of hyphae to *P. guadelupensis*.

No collection was available for analysis in this study. Loan of the type was denied due to the specimen's fragile condition, and we were unable to obtain loan of the isotype deposited at L.



a.

b.

Figure 6.4. *Phaeoclavulina retispora* (Corner) Giachini, *sp. prov.*: (a) basidioma (× 1); (b) spores (bar = 10 μm). Basidioma photo from Corner (1969).

Phaeoclavulina subclaviformis* (Berk.) Giachini, *sp. prov. Fig. 6.5

≡*Thelephora subclavaeformis*[8] Berk., Bulletin of Miscellaneous Information 8:238. 1856.

≡*Gomphus subclavaeformis* (Berk.) Corner, Nova Hedwigia 18:815. 1969.

=*Gomphus cavipes* Corner, Nova Hedwigia 18:808. 1969.

Macroscopic characters: **Basidiomata** up to 9 cm tall, unipileate to merismatoid (Figure 6.5). **Pileus** around 5 cm wide, fan-shaped, often lobed and becoming concrescent around the stipe, finally appearing slightly funnel-shaped, glabrous, pale orange to white; margin straight. **Hymenium** initially smooth, then more or less radially and irregularly wrinkled with shallow hymenial folds of about 0.3 mm tall, pale orange when immature, dark orange with age. **Stipe** 40 × 2-9 mm, tapering downward, glabrous, concolorous. **Context** moist-fibrous, bruising vinaceous. **Odor** slightly sour. **Taste** not recorded. **Spore print color** not recorded.

Microscopic characters: **Pileipellis** of compact hyphae up to 10 µm wide; clamp connections present. **Stipitipellis** of thick-walled, parallel, branched, slightly inflated hyphae 2-7 µm wide; clamp connections present; gleoplerous hyphae thin-walled, aseptate, up to 6 µm wide (Figure 6.5). Generative hyphae often coiled, rarely branched. **Basidia** 52-85 × 8-10 µm, clavate, with 4 straight sterigmata up to 8 µm long; clamp connections present at base (Figure 6.5). Hymenial **cystidia** absent. **Spores** 10.5-12.5 × 5.5-7 µm, cinnamon in mass, ellipsoid to fusoid; ornamentation of round to irregular, non-anastomosed, cyanophilic warts up to 1 µm tall (Figure 6.5); apiculus up to 1.5 µm tall, eccentric.

Habit, habitat and distribution: Solitary or gregarious, not caespitose, on the ground in closed forest in Amazonas (Panuré) and Mato Grosso States, Brazil, and Arima, in Trinidad and Tobago (Corner 1969).

Collections examined: **BRAZIL. MATO GROSSO**: Chavantina, 1 February 1966, *E.J.H. Corner K-969* (BR 079159-07 – as *Gomphus subclavaeformis* – **holotype**).

[8] The 'ae' connective is an orthographic error (International Code of Botanical Nomenclature, article 60G.1) to be replaced with an 'i' (Greuter *et al.* 2000).

a.

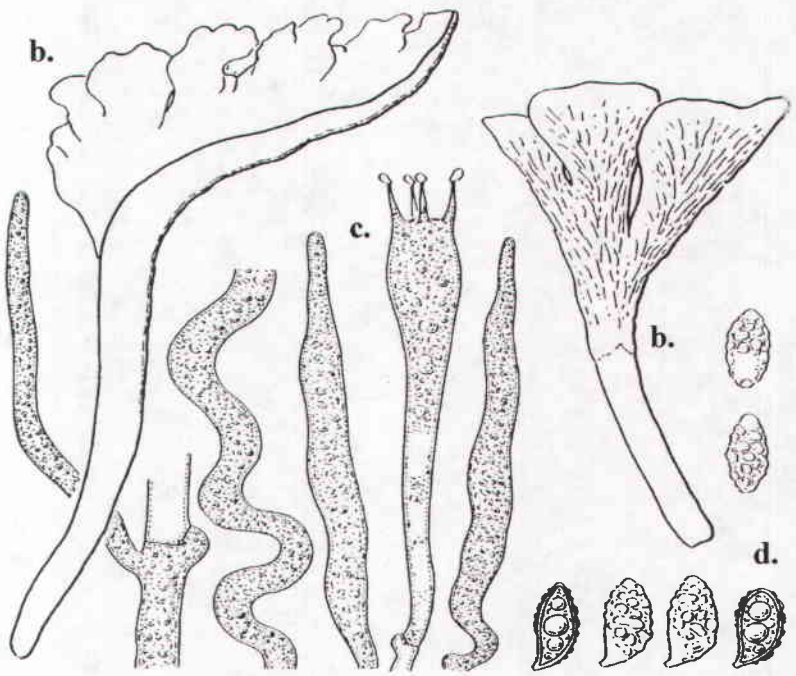
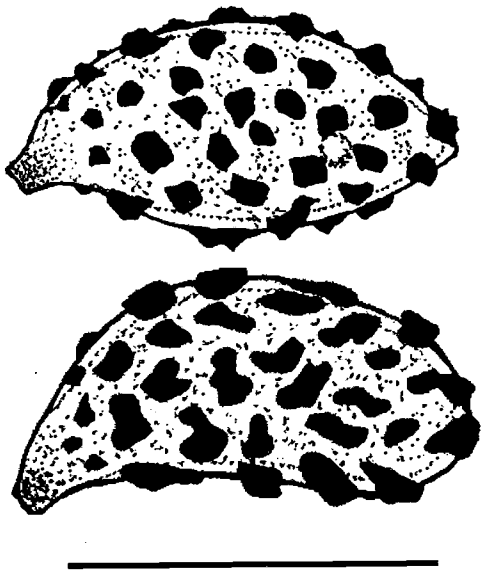


Figure 6.5. *Phaeoclavulina subclaviformis* (Berk.) Giachini, *sp. prov.*: (a, b) basidiomata (× 1); (c) basidium and gleoplerous hyphae (× 1000); (d) spores (× 1000). Figures b, c, and d modified from Corner (1969).

Figure 6.5 (*cont.*). Spores (bar = 10 μm) of *Phaeoclavulina subclaviformis* (Berk.) Giachini, *sp. prov.*



Discussion: Berkeley (1856) described *Thelephora subclavaeformis* from Panuré, from the northern regions of Brazil. Later Corner (1969) elaborated on the correct identity of this species and transferred it to *Gomphus*. Even though only one collection was reported, he regarded this as a common species in the forests North of Chavantina, Mato Grosso, in Central-West Brazil. It also occurs in Arima, in Trinidad and Tobago. The basidiomata resemble *G. clavatus*, although the similarities end there. Giachini (chapter 2) studied Corner's (1969) description of *Gomphus cavipes* from Trinidad and Tobago (the loan of the type from CGE was denied because of its fragile condition) and synonymized it with *P. subclaviformis* because of the overall morphology and spore shape and size.

Phaeoclavulina viridis* (Pat.) Giachini, *sp. prov. Fig. 6.6

≡*Nevrophyllum viride* Pat., Journal de Botanique 2:406. 1888.

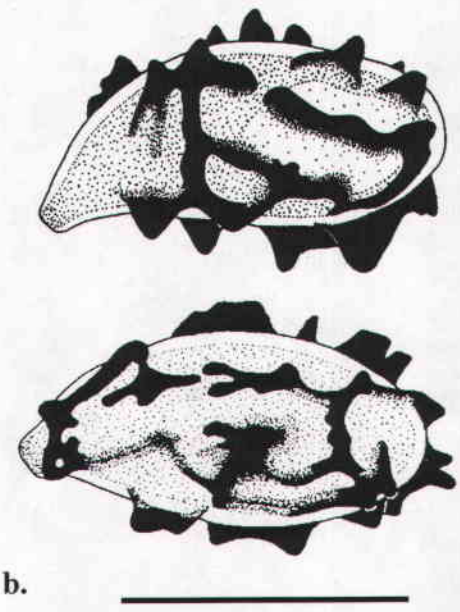
≡*Chlorophyllum viride* (Pat.) Murrill, *nom. illeg.*, North American Flora 9:172. 1910.

≡*Gomphus viridis* (Pat.) Singer, Lloydia 8:140. 1945.

=*Cantharellus patouillardii* Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 9:65. 1891.

Macroscopic characters: **Basidiomata** up to 12 cm tall, unipileate (Figure 6.6). **Pileus** flat to depressed, funnel-shaped, fleshy-coriaceous, minutely velvety or felty, dark sordid green, olive-green or gray-olive, becoming dark yellow-brown at the center of the pileus with age; margin deeply lobed to crenate. **Hymenium** with wrinkled, decurrent hymenial folds, generally longitudinally oriented, dichotomously forked toward the pileus margin, suppressed below on stipe, olivaceous. **Stipe** 6-9 mm thick, glabrous, tapering downward, concolorous with pileus, paler below substrate level. Data on **context** not recorded. **Odor** none. **Taste** sour. **Spore print color** not recorded.

a.



b.

Figure 6.6. *Phaeoclavulina viridis* (Pat.) Giachini: (a) basidiomata (× 0.8); (b) spores (bar = 10 μm). Figure **a** modified from Neale Bougher. Drawings modified from Petersen (1971b), with permission.

Microscopic characters: **Pileipellis** of thin-walled, compactly interwoven, undifferentiated hyphae 4.5-6.5 µm wide; clamp connections present. **Stipitipellis** of hyphae identical to those of pileipellis, up to 14 µm wide, with ampulliform thin-walled swellings. **Stipe context** of thin- to slightly thick-walled, interwoven, closely packed, moderately cyanophilic hyphae, yellow-green in mass, 8.5-12.5 µm wide, with thin-walled ampulliform swellings up to 15 µm; clamp connections present; gleoplerous hyphae hyaline, strongly cyanophilic. **Basidia** 90-110 × 6-8 µm, clavate, with 2-4 stout, divergent, straight sterigmata; clamp connections present at base. Hymenial **cystidia** 90-140 × 8-10 µm long, thin-walled, cylindrical, hyaline, acyanophilic; clamp connections present at the base. **Spores** 13-16 (-21.5) × 6.5-8 (-12) µm, cinnamon in mass, ellipsoid to lacrimoid; ornamentation of irregularly oriented, strongly cyanophilic, subreticulate to reticulate ridges varying in height along their length from <0.5 to 3.5 µm tall (Figure 6.6); apiculus prominent, eccentric.

Habit, habitat and distribution: Single or gregarious, occasionally caespitose, on soil or rotting wood under *Agathis robusta, Allocasuarina littoralis, Angophora* sp., and *Eucalyptus grandis* in Australia, and *Coccoloba belizensis* and *Pinus* sp. in Belize. Also known from French Guiana and Martinique.

Collections examined. **AUSTRALIA. QUEENSLAND**: Kennedy Road to Kirrama, 28 April 1990, *N.L. Bougher and M.A. Castellano E4302* and *E4303* (PERTH). **BELIZE**: Mountain Pine Ridge, Lower Nature Trail, Five Sisters Lodge, 20 November 2001, *K.K. Nakasare and D.J. Lodge* (OSC 97708), and 23 November 2001, *D.J. Lodge and B. Ortiz-Santana* (OSC 97707). **FRENCH GUIANA**: no location, no date, *N.T. Patouillard* (FH – as *Nevrophyllum viride* – **holotype**). **MARTINIQUE**: Marne Larcher, Pres du Camp Balata', August 1900, *A. Duss 1853* (FH).

Discussion: The vegetation at the type locality was not described. Corner (1966) reported the species fruiting on the ground in swampy woods in French Guiana (one collection – type) and Martinique (one collection). In 2001, Dr. Jean Lodge collected it twice in Belize under *Coccoloba* and *Pinus* sp.

This species has an unusual distribution in Australia, Belize, and Central and South America and has been never reported elsewhere. It occurs in mixed forests containing Araucariaceae (*Agathis*), Casuarinaceae (*Allocasuarina*), and Myrtaceae (*Angophora* and *Eucalyptus*) in Australia, and under species of the Pinaceae (*Pinus*) and Polygonaceae in Belize.

As noted by Corner (1966), the species has affinities with *P. retispora* and is brownish olive rather than truly green as described by Patouillard (1888).

Ramarioid species

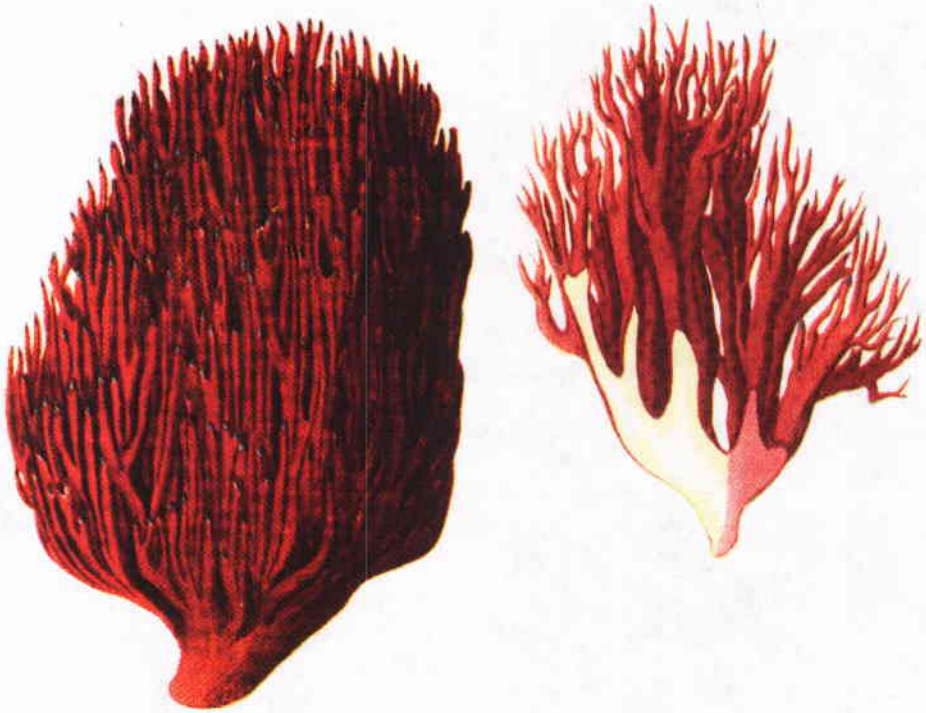
Phaeoclavulina angustata* (Lév.) Giachini, *sp. prov. Fig. 6.7

≡*Merisma angustatum* Lév., Annales des Sciences Naturelles Botanique 3(5):158. 1846.

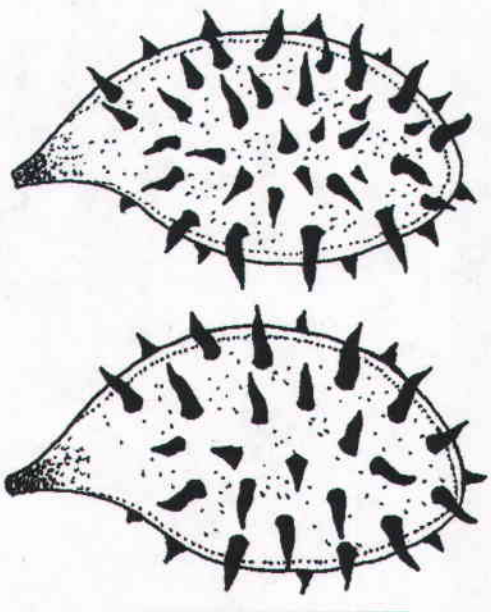
≡*Thelephora angustata* Fr., Nova Acta Regiae Societatis Scientiarum Upsaliensis 3:116. 1854.

≡*Ramaria angustata* (Fr.) Corner, Beihefte zur Nova Hedwigia 33:242. 1970.

Macroscopic characters: **Basidiomata** 6-30 × 5-15 cm, ramarioid, repeatedly branched (Figure 6.7). **Branches** 5-15 mm wide below, cylindrical, erect, crowded, sometimes spreading, generally regularly dichotomous with successive branching more or less at right angles, the branching sometimes more irregular, some times 3-4-chotomous below, sterile and subtomentose on the adaxial surfaces and on the uppersides of the axils, pale pink, then more or less dark yellow, orange to brown, often tinged cinnamon to orange from the spores, all parts soon turning sordid vinaceous on bruising; internodes gradually more elongated distally, short and obscure proximally, 1.5-2.5 mm wide at the tips; tips subacute, intensely blue or blue-green, or in some specimens white or creamy white. **Hymenium** unilateral.



a.



b.

Figure 6.7. *Phaeoclavulina angustata* (R.H. Petersen) Giachini, *sp. prov.*: (a) basidiomata (× 0.4); (b) spores (bar = 10 μm). Basidioma drawings modified from Corner (1950).

Stipe 6-65 × 3-16 mm, cylindrical, relatively slender, slightly tapering downward, generally attenuate at the subvillose base, with white mycelium, concolorous elsewhere. **Context** rather dry but fibrous-brittle, breaking when bent, white or pale yellow, dark yellow near the hymenium, soon turning sordid vinaceous on exposure. **Odor** slight to none. **Taste** slightly bitter and astringent. **Spore print** brown.

Microscopic characters: All **hyphae** parallel, compact, smooth; H-connections frequent, with pale yellow walls, dark yellow-brown and with blue tones at the tips, often rather unevenly inflated, 2.5-10 µm wide; clamp connections present. **Basidia** 55-75 × 9-11 µm, subclavate, generally constricted below the sterigmata, with a long narrow base 3 µm wide, with (1-) 2 (-3) sterigmata 6-8 (-10) µm long. Hymenial **cystidia** absent. **Spores** 18-20 (-24) × 9-11 µm, orange to golden yellow in mass, lacrimoid, rather densely echinulate with conical, acute, hyaline, cyanophilic spines 1-3.5 µm tall (Figure 6.7); data on apiculus not recorded.

Habit, habitat and distribution: Gregarious or rarely caespitose, on the ground in forests of tropical America (Petersen 1981), Malaysia (Corner 1950), and perhaps tropical Africa.

Collections examined: **COSTA RICA**: Location unknown, no date, *A.D. Oersted* (BPI – as *Thelephora angustata* – **holotype**).

Discussion: Corner (1950) considered this the most common species of *Ramaria* subgenus *Echinoramaria* in Malaysia. Its large size plus distinctive dark yellow-brown branches with blue, or blue-green tips makes it one of the more striking ramarioid species in the genus.

Phaeoclavulina apiahyna* (Speg.) Giachini, *sp. prov. Fig. 6.8

≡*Clavaria apiahyna* Speg., Boletin de la Academia Nacional de Ciencias de Córdoba 23:435. 1918.

≡*Ramaria apiahyana* (Speg.) Corner, Annals of Botany Memoir 1:555. 1950.

Macroscopic characters: **Basidiomata** 5-8 cm tall, ramarioid. **Branches** subcylindrical, glabrous, white below, orange above; apices slightly thickened and shortly dentate or subcristate, intensely brick red to nearly scarlet. Data on **hymenium** configuration and features of the **stipe** not recorded. **Context** white. **Odor** and **taste** not recorded. **Spore print** ferruginous.

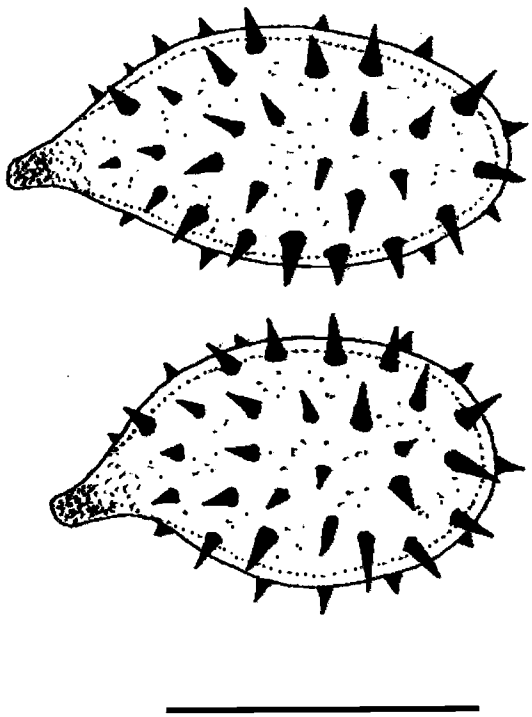
Microscopic characters: **Context** hyphae with agglutinating material, yellowish; clamp connections present. **Basidia** with 2 sterigmata. Hymenial **cystidia** absent. **Spores** 15-18 × 8-10 µm, orange in mass, ellipsoid obovoid; ornamentation of densely and minutely dispersed, cyanophilic spines 1-3 µm tall, 1-2.5 µm wide at the base, often flattened and generally in longitudinal rows (Figure 6.8); apiculus blunt.

Habit, habitat and distribution: On the ground in forests in Brazil (Petersen 1981).

Collections examined: **BRAZIL. SÃO PAULO:** Apiaí, January 1891, *Puiggari 307* (LPS 13259 – as *Clavaria apiahyna* – **holotype**).

Discussion: The species is near *P. macrospora* but seems more brilliantly colored (Corner 1970). It is also similar to *P. camellia*, which is said to have similarly colored basidiomata, similar distribution, but much smaller spores.

Figure 6.8. Spores (bar = 10 µm) of *Phaeoclavulina apiahyna* (Speg.) Giachini, *sp. prov.*



Phaeoclavulina argentea* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.9

≡*Ramaria argentea* R.H. Petersen, Bibliotheca Mycologica 79:111. 1981.

=*Ramaria incognita* R.H. Petersen, Bibliotheca Mycologica 79:145. 1981.

=*Ramaria incongrua* R.H. Petersen, Bibliotheca Mycologica 79:147. 1981.

Macroscopic characters: **Basidiomata** up to 7 × 5 cm, ramarioid, repeatedly and irregularly branched (Figure 6.9). Major **branches** up to 6 mm wide, usually flattened or with small grooves, sometimes palmate, pale olivaceous to dark yellow; secondary branches flattened, subcartilaginous on drying, dark yellow, orange, moderately olivaceous to dark brown; axils rounded; apices minute, acute, irregular and congested when young, becoming flattened and irregularly digitate in age, awl-shaped, usually drying off-white to white or silvery. **Hymenium** amphigenous, rugulose. **Stipe** single to usually complex, off-white when fresh, bruising brown, drying white; basal mycelium off-white to white, with ill-defined rhizomorphs extending at least 30 mm from the base of the basidiomata. **Context** white when fresh. **Odor** mild to none or weakly of anise when dry. **Taste** mild to none. **Spore print color** not recorded.

Microscopic characters: **Peridiopellis** of thin-walled hyphae 1.5-2.5 µm wide; clamp connections present. **Context** of thin-walled, generally parallel, easily separated hyphae 1.5-13 µm wide, generally inflated up to 15 µm; clamp connections present. Rhizomorphs less than 2 mm thick, usually flattened, moderately pliable, easily broken when dry, white. **Basidia** 35-45 × 5.5-8 µm, clavate, with 4 short, spindly sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 4.5-8.5 × 3-4.5 µm, ellipsoid lacrimoid; ornamentation of densely scattered, blunt, cyanophilic spines up to 1 (-2) µm tall (Figure 6.9); apiculus obscure.

Habit, habitat and distribution: On humus or woody debris under *Abies, Cupressus*, *Populus*, and *Pseudotsuga*. The species is known from the western states of the USA, perhaps East to Arizona and western Texas, as well as parts of

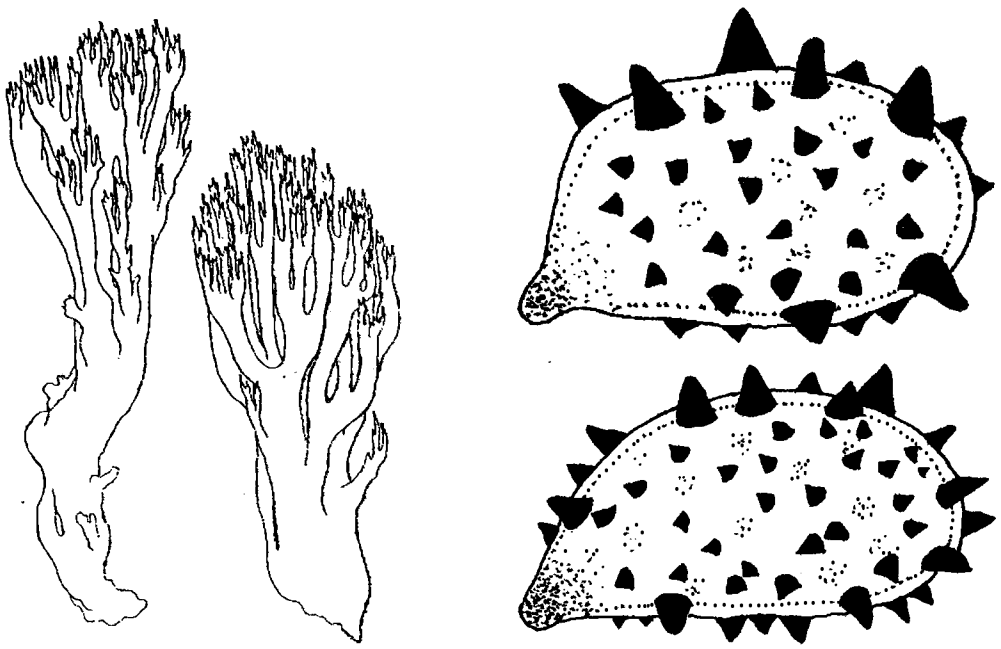


Figure 6.9. *Phaeoclavulina argentea* (R.H. Petersen) Giachini, *sp. prov.*: (a) basidiomata (× 0.5); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

Nevada, and eastern states of Canada and the USA (Petersen 1981). It is also known from Sweden (Petersen 1981).

Collections examined: **SWEDEN.** Biludden, 30 August 1974, *R.H Petersen* (TENN 39810, 39815). **UNITED STATES. ARIZONA:** Cochise Co., Coronado Nat. Forest, 1 September 1958 (TENN 32034 – as *R. incognita*). **COLORADO:** Alamosa Co., Mosca Pass Trail, 17 July 1964 (TENN 31777 – as *R. incognita*); San Miguel Co., Ophir, 7 August 1956, *A.H. Smith 51939* (TENN 41373). **IDAHO:** Valley Co., McCall, Boulder Creek, 26 July 1958, *A.H. Smith* (TENN 41370 – as *Ramaria argentea* – **holotype**). **NEW MEXICO**: Bernalillo Co., Sandia Mts., 21 August 1968, *Gilbertson 8068* (TENN 34493 – as *R. incognita*). **OHIO**: Greene Co., John Bryan St. Park, 10 August 1966, *W.C. Cooke 37921* (TENN 32422 – as *R. incongrua*); Hamilton Co., Sgaron Woods Co. Pk., 24 September 1966, *W.C. Cooke 37754* (TENN 32430 – as *R. incongrua*; Highland Co., 4 September 1965, *W.C. Cooke 35675* (TENN – as *R. incongrua*. **WASHINGTON:** Pierce Co., Mount Rainier Nat. Park, Lower Tahoma Creek, 28 July 1948, *A.H. Smith 29575* (TENN – as *R. incognita*).

Discussion: Obvious brown bruises on the off-white stipe surface easily separate this species from others. It also has minute, congested apices, which often become silvery or off-white on drying.

Phaeoclavulina articulotela* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.10

≡*Ramaria articulotela* R.H. Petersen, Bibliotheca Mycologica 79:115. 1981.

Macroscopic characters: **Basidiomata** up to 7 × 3 cm, ramarioid. **Branches** slender, up to 2 mm thick, ascending, in 2-4 ranks, flattened, especially below axils, orange to dark orange; axils rounded, with narrow, sterile 'webbing'[9] (Petersen 1981) (Figure 6.10); apices up to 7 mm long, straight, erect, awl-shaped, pale

[9] Resembling the foot of a waterfowl.

yellow. **Hymenium** amphigenous at upper internodes, becoming unilateral just above axils, absent from intra-axillary 'web', with fertile portion smooth. **Stipe** 25 × 2 mm, discrete, slender, flattened, glabrous, pale yellow to off-white where protected, pale orange upward. Data on **context**, **odor**, **taste,** and **spore print color** not recorded.

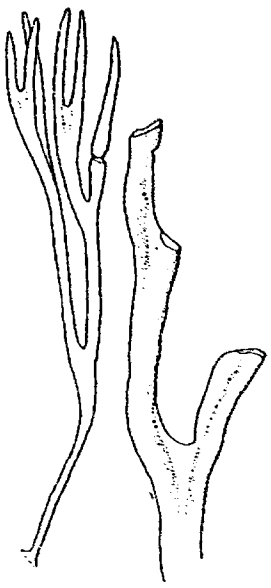
Microscopic characters: **Context** of thin-walled, parallel, hyaline hyphae up to 3 µm wide; clamp connections present. **Basidia** short, hyaline, with 4 straight, narrow, spindly sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 6-9.5 × 3-5 µm, ellipsoid lacrimoid; ornamentation of scattered, cyanophilic, acute and blunt spines ≤1 µm tall (Figure 6.10); apiculus short, eccentric.

Habit, habitat and distribution: On litter and wood in Bolivia and Brazil (Petersen 1981).

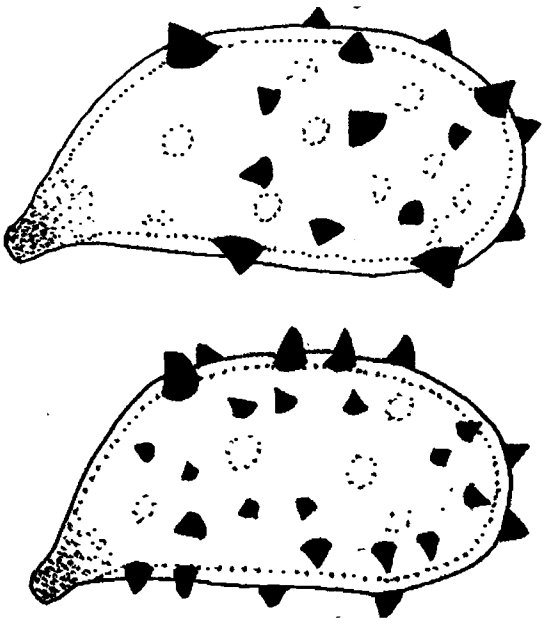
Type (holotype): **BOLIVIA**. **BENI**: Provincia Vaca Diez, Arroyo Florida, 22 km East of Riberalta, 7 April 1956, *R. Singer B-2550* (BAFC – as *Ramaria articulotela*). **BRAZIL**. **BRASILIA**: 1914, *Torrend* (S – as *Lachnocladium ochraceum*).

Discussion: The herbarium BAFC was contacted for loan of the type for this species but no answer was obtained. Therefore, this description was based on notes from Petersen (1981).

Two important characteristics identify this tropical species: the habitat, on rotten wood, and the 'webbed' axils, similar to a foot of a waterfowl. The species resembles *P. camellia*, another species with the same general distribution, differing primarily in the color of the basidiomata, which is red for *P. camellia* and orange for *P. articulotela*. The spores are also similar to those of *P. flaccida*, although smaller and with less pronounced spines.



a.



b.

Figure 6.10. *Phaeoclavulina articulotela* (R.H. Petersen) Giachini, *sp. prov.*: (a) basidioma branches showing sterile 'webbing' (× 0.3); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

Phaeoclavulina camellia* (Corner) Giachini, *sp. prov. Fig. 6.11

≡*Ramaria camellia* Corner, Darwiniana 11:200. 1957.

Macroscopic characters: **Basidiomata** up to 5.3 cm tall, delicate, ramarioid (Figure 6.11). Major **branches** few, ascending, upper branches slender, <1 mm thick, erect, branched dichotomously in up to 6 ranks, overall camellia red; internode length diminishing gradually distally; axils rounded to narrowly rounded; apices waxy, erect, red. **Hymenium** mostly amphigenous. **Stipe** 5-20 × 1.5-3 mm, tapering downward into a small tangle of white mycelium and slender rhizomorphs, off-white to white, not changing color upon picking. Data on **context**, **odor**, and **taste** not recorded. **Spore print** brown.

Microscopic characters: **Context** of slightly thick-walled, not agglutinated, hyaline hyphae 2.5-16 µm wide; clamp connections present, with occasional ampulliform clamps up to 15 µm. **Basidia** 30-40 × 6-7 µm, clavate, with 4 sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 7-9.5 × 3-4.5 µm, lacrimoid; ornamentation of small, sparsely scattered, cyanophilic spines <0.5 µm tall (Figure 6.11); data on apiculus not recorded.

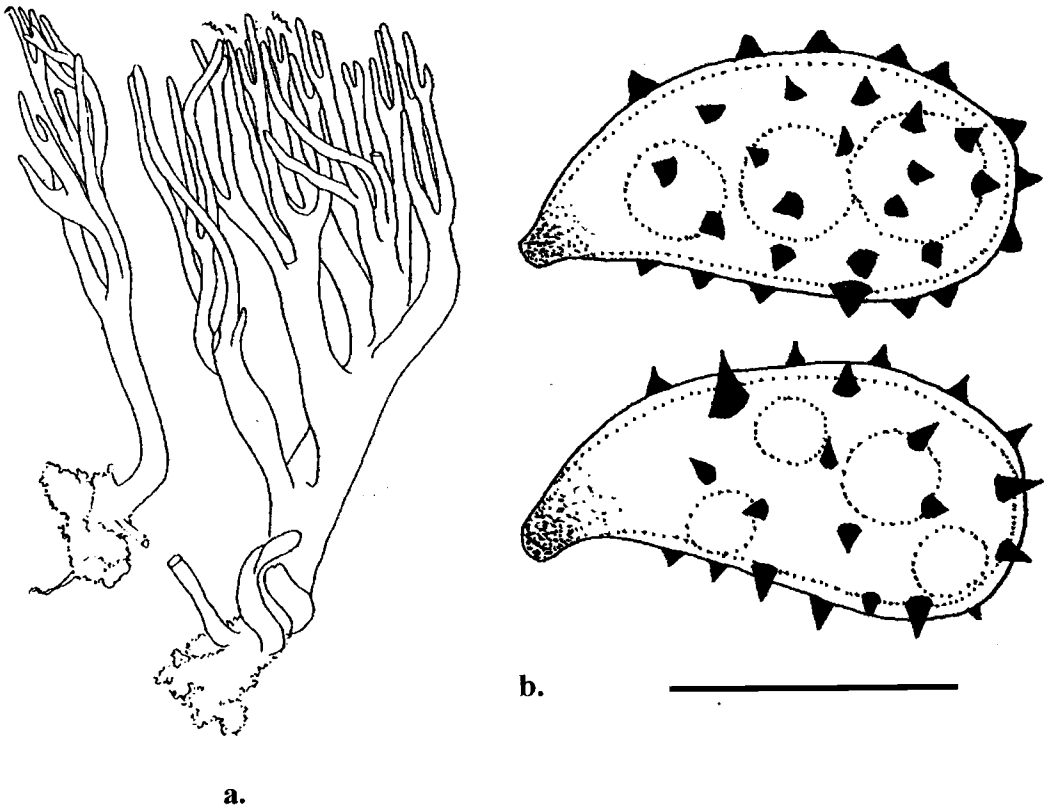
Habit, habitat and distribution: On well-rotted wood and litter in Argentina, Bolivia, and temperate Brazil (Petersen 1981).

Type (holotype): **ARGENTINA. CATAMAICA:** between Alto de la Junta and Mesada, 16 January 1952, *R. Singer T1735* (LIL – as *Ramaria camellia*).

Discussion: The herbarium LIL was contacted for loan of the type for this species but no answer was received. Therefore, this description was based on Corner (1957, 1970) and Petersen (1981).

Small, delicate basidiomata with red tones characterize this species. Species with delicate basidiomata and small spores are taxonomically difficult to place (Petersen 1981). However, the red color of the upper branches, especially when young, is a diagnostic feature for this species.

Corner (1970) considered this species a synonym of *Ramaria flaccida* (≡*P. flaccida*) because its overall features resemble those of *R. flaccida*. He regarded the



a.

Figure 6.11. *Phaeoclavulina camellia* (Corner) Giachini, *sp. prov.*: (a) basidiomata (× 0.3); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

red color as a variant under that name. We agree with Petersen (1981) when saying that it should be considered distinct because of the spore size and the distribution.

Phaeoclavulina campestris **(K. Yokoy. & Sagara) Giachini,** ***sp. prov.*** Fig. 6.12

≡*Ramaria zippelii* var. *campestris* K. Yokoy. & Sagara, Transactions of the Mycological Society of Japan 14:302. 1973.

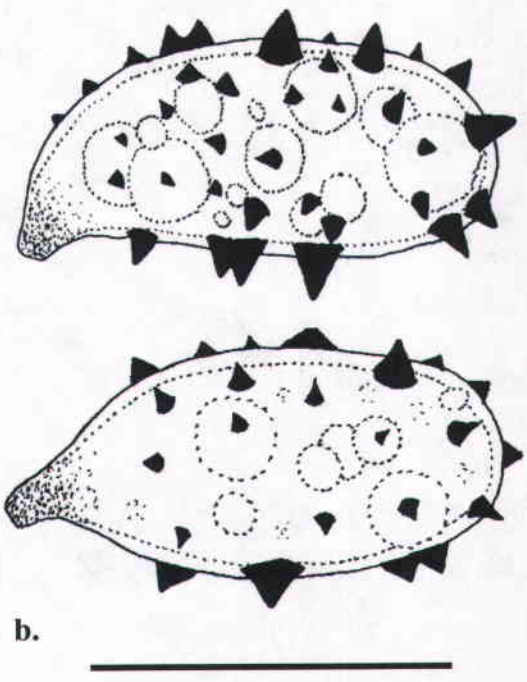
≡*Ramaria campestris* (K. Yokoy. & Sagara) R.H. Petersen, Bibliotheca Mycologica 79:57. 1981.

Macroscopic characters: **Basidiomata** up to 15 cm tall, cauliflower-like, massive, ramarioid, branched up to 5 times (Figure 6.12). Major **branches** numerous, up to 30 × 10-25 mm, upper branches yellow to orange when young, finally darkening to olivaceous brown at maturity; internodes short; axils rounded; apices coarse, dentate to digitate, dark olive-yellow at maturity. Data on **hymenium** configuration, **stipe**, and **context** not recorded. **Odor** faint. **Taste** bitter. **Spore print** pale brown.

Microscopic characters: **Branch context** of thick-walled, pale yellow hyphae up to 16 µm wide; clamp connections present. **Basidia** up to 75 × 13 µm, clavate, hyaline, with (2-) 3-4 conical, spindly sterigmata up to 8 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 11.5-14 × 5.5-7 µm, pale orange to orange in mass, ellipsoid obovoid; ornamentation of acute, cyanophilic spines up to 1.5 µm tall (Figure 6.12); apiculus wide.

Habit, habitat and distribution: Forming fairy rings up to 10 meters in diameter, on the ground in grassland dominated by *Pleioblastus distichus* var. *nezasa* and rarely in plantations of *Cryptomeria japonica* that has been raised on the grassland (Petersen 1981, Yokoyama and Sagara 1973). Known from the Kuju Highlands and adjacent areas (500-100 m above sea-level) of Kyushu, Japan.

a.



b.

Figure 6.12. *Phaeoclavulina campestris* (K. Yokoy. & Sagara) Giachini, *sp. prov.*: (a) basidiomata and habitat; (b) spores (bar = 10 µm). Photographs modified from Yokoyama and Sagara (1973).

Collections examined: **JAPAN:** Yufuin-machi, Oita Prefecture, Kyushu, 6 September 1968, *collected by residents – N. Sagara 1502* (TNS – as *Ramaria zippelii* var. *campestris* – **holotype**).

Discussion: The spores and the typically 4-spored basidia of this species resemble *P. cokeri*. Basidioma stature and color, however, differ. As shown in the color illustrations of Yokoyama and Sagara (1973), immature basidiomata of *P. campestris* are stout, stocky, and yellow to orange. Those of *P. cokeri* are more slender and brick red, especially toward the tips. Moreover, *P. cokeri* occurs in forests, whereas *P. campestris* occurs in grasslands.

According to Yokoyama and Sagara (1973), the grasses whiten in winter and are burned March every year, but the thick mycelia of this fungus develop perennially in the soil. In 1970, probably for the first time in the century, the bamboo grass *P. distichus* var. *nezasa* burst into flowers and died to its rhizomes and roots over almost all the area of distribution. This triggered the fungus to stop fruiting in most of the grassland: "the mycelia seemed to be dying" (Yokoyama and Sagara 1973).

Phaeoclavulina campoi* (Speg.) Giachini, *sp. prov. Fig. 6.13

≡*Clavaria campoi* Speg., Boletin de la Academia Nacional de Ciencias de Córdoba 25:28. 1921.

Macroscopic characters: **Basidiomata** up to 5 × 2.5 cm, ramarioid, repeatedly branched (Figure 6.13). **Branches** arising at substrate level to give a caespitose appearance, short, pale orange; internode length diminishing abruptly distally; axils rounded; apices short-digitate, polychotomous, dark yellow. Data on **hymenium** configuration not recorded. **Stipe** up to 3 mm thick where exposed, irregularly grooved longitudinally, dissipating into a tangle of white rhizomorphs, white downward. Data on **context**, **odor**, **taste** and **spore print color** not recorded.

Microscopic characters: **Branch context** of thin-walled, parallel, hyaline hyphae up to 6.5 µm wide; clamp connections present. Hyphae of basal mycelium up to 3 µm wide, with occasional ampulliform swellings up to 6 µm wide; clamp connections present. **Basidia** 38-43 × 5.5-7.5 µm, almost cylindrical above, tapering below, with 4 straight, slender sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 5.5-8 × 3-4.5 µm, pale orange in mass, lacrimoid; ornamentation of sparse, cyanophilic warts <1 µm tall and are occasionally connected by low ridges (Figure 6.13); data on apiculus not recorded.

Habit, habitat and distribution: Mainly under *Nothofagus* in southern South America (Argentina), but also in other forest types of southern Brazil (Petersen 1981).

Collections examined: **ARGENTINA:** Victoria, Marihuan, 20 May 1918, *G.A. Campo 39622* (LPS – as *Clavaria campoi* – **holotype**). **BRAZIL. RIO GRANDE DO SUL:** Cerro Azul, 1928, Farlow herb. Exp., ex herb. Doty (TENN 32266).

Discussion: The type is the largest basidioma ever found for this species. Singer (on specimen labels) drew attention to a possible association of this species with *Nothofagus*. Petersen (1981) mentioned that the species has also been collected in southern Brazil. However, the range of distribution for *Nothofagus* in South America does not reach Brazil, suggesting that the range of distribution is outside that of pure *Nothofagus* forests.

According to Petersen (1981), Lazo's (1972) *R. flaccida* var. *chilensis* could well be *P. campoi*. After studying the type for that species, however, Giachini (chapter 2) considered it a synonym of *P. ochracea*.

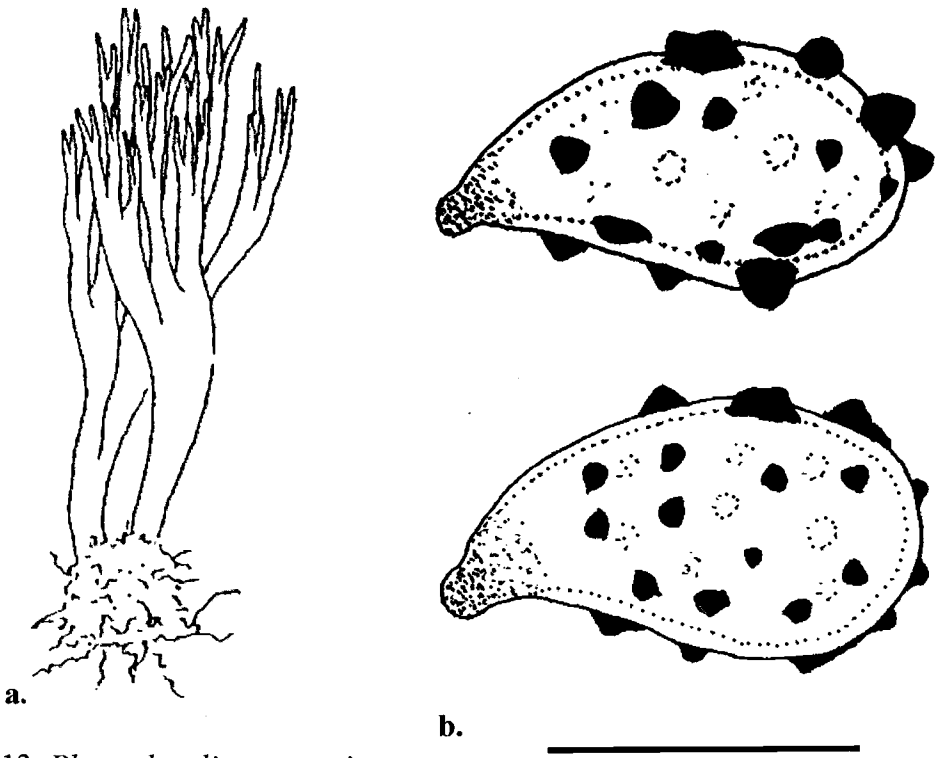


Figure 6.13. *Phaeoclavulina campoi* (Speg.) Giachini, *sp. prov.*: (a) basidiomata (× 0.3); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

Phaeoclavulina capucina* (Pat.) Giachini, *sp. prov. Fig. 6.14

≡*Clavaria capucina* Pat., Bulletin de la Société Mycologique de France 33:50. 1917.

≡*Ramaria capucina* (Pat.) Corner, Annals of Botany Memoir 1:565. 1950.

Macroscopic characters: **Basidiomata** up to 4 × 2.5 cm, ramarioid, repeatedly branched (Figure 6.14). **Branches** erect, slender, fragile, in 3-5 ranks, orange to brown; internode length diminishing gradually distally; axils rounded; apices dichotomous, not divergent, dark yellow to brown. **Hymenium** amphigenous, rugulose. **Stipe** up to 15 × 3 mm, discrete, brown upward, white near the substrate, basal mycelium not discrete. Data on **context** not recorded. **Odor** pleasant, slightly of anise. **Taste** acrid to almost salty. **Spore print** brown.

Microscopic characters: **Context** of thin-walled, compactly parallel, hyaline hyphae up to 7 µm wide; clamp connections present. **Basidia** with 4 sterigmata. Hymenial **cystidia** absent. **Spores** 5-6 × 3-4 µm, ellipsoid to obovoid; ornamentation of scattered, acute, cyanophilic spines up to 1 µm tall (Figure 6.14); apiculus rounded, eccentric.

Habit, habitat and distribution: On the ground near bamboo in southeast Asia (Corner 1950, Petersen 1981).

Collections examined: **VIETNAM**: Hanoi, 2 February 1908, *M. Demange 288* (GH – as *Clavaria capucina* – **holotype**).

Discussion: Corner (1950) considered this species similar to *Lentaria byssiseda*, but the resemblance is only superficial. According to both Corner (1950) and Petersen (1981), this is Indochina's version of *P. flaccida*. Spores are small, mycelium copious, basidiomata small and delicate, and the habitat is quite distinct from other ramarioid species. Spore ornamentation is also somewhat coarser than observed in other small-spored *Phaeoclavulina* species.

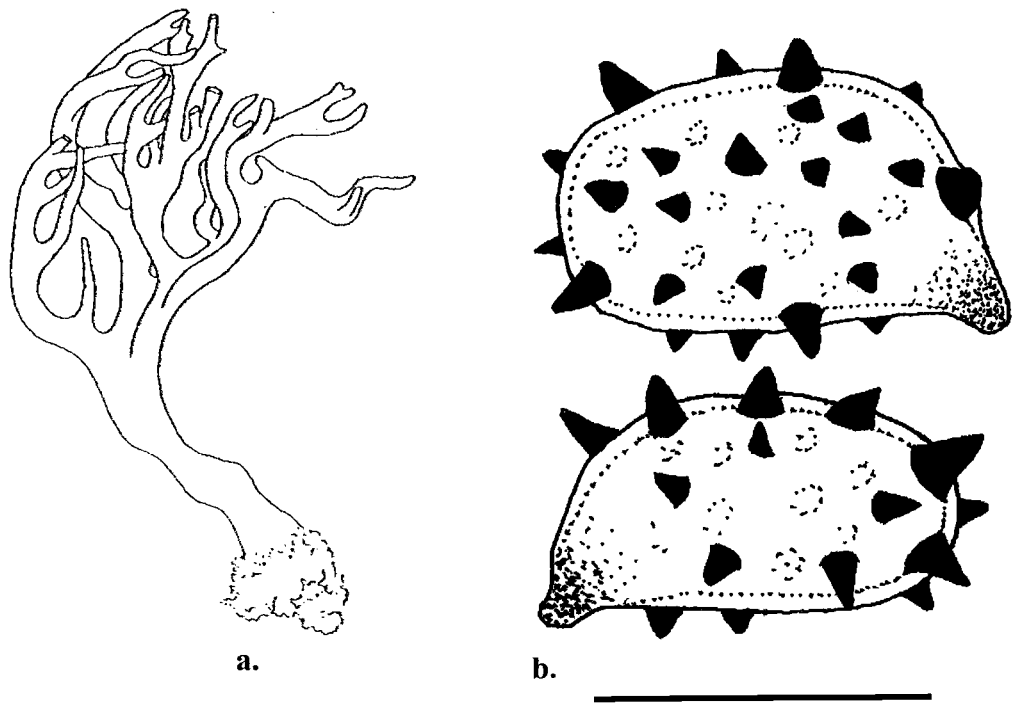


Figure 6.14. *Phaeoclavulina capucina* (Pat.) Giachini, *sp. prov.*: (a) basidioma (× 0.2); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

Phaeoclavulina cervicornis* (A.L. Sm.) Giachini, *sp. prov. Fig. 6.15

≡*Clavaria cervicornis* A.L. Sm., Journal of the Linnean Society of London. Botany 35:10. 1901.

≡*Ramaria cervicornis* (A.L. Sm.) Corner, Annals of Botany Memoir 1:565. 1950.

Macroscopic characters: **Basidiomata** 8 cm tall, ramarioid, repeatedly branched. **Branches** compressed, flattened, dichotomous, polychotomous upward, velutinous-pruinose (*sensu* A.L. Sm.), pale yellow then cinnamon, not bruising on handling or picking; apices concolorous. **Hymenium** amphigenous, velutinous-pruinose (*sensu* A.L. Sm.). **Stipe** 20 mm tall, subcylindrical. Data on **context**, **odor**, **taste** and **spore print color** not recorded.

Microscopic characters: Data on **hyphal** construction not recorded. **Basidia** not observed. Hymenial **cystidia** absent. **Spores** 8 × 6 µm, yellow-brown in mass, ellipsoid to obovoid; ornamentation of acute, cyanophilic spines ≤1 µm tall (Figure 6.15); data on apiculus not recorded.

Habit, habitat and distribution: On rotten wood and leaves in the Dominican Republic and Saint Vincent (Smith 1901).

Type (holotype): **DOMINICAN REPUBLICAN**: Prince Rupert's, March 1894, *A.L. Smith 917* (No herbarium located – as *Clavaria cervicornis*).

Discussion: Because the type for this species was not located, this description was based on notes from Smith (1901) and Corner (1950). According to these authors, this resembles a *Thelephora* species in the flattened branches and brown echinulate spores, but the hymenium covers all sides of the branches, unlike any species of *Thelephora*.

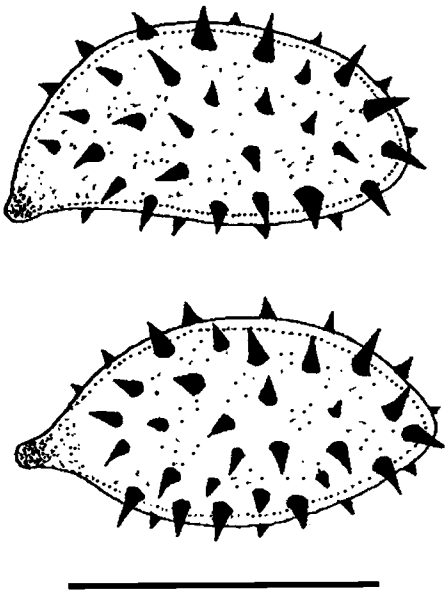


Figure 6.15. Spores (bar = 5 μm) of *Phaeoclavulina cervicornis* (A.L. Sm.) Giachini, *sp. prov.*

Phaeoclavulina clavarioides* (Schild) Giachini, *sp. prov. Fig. 6.16

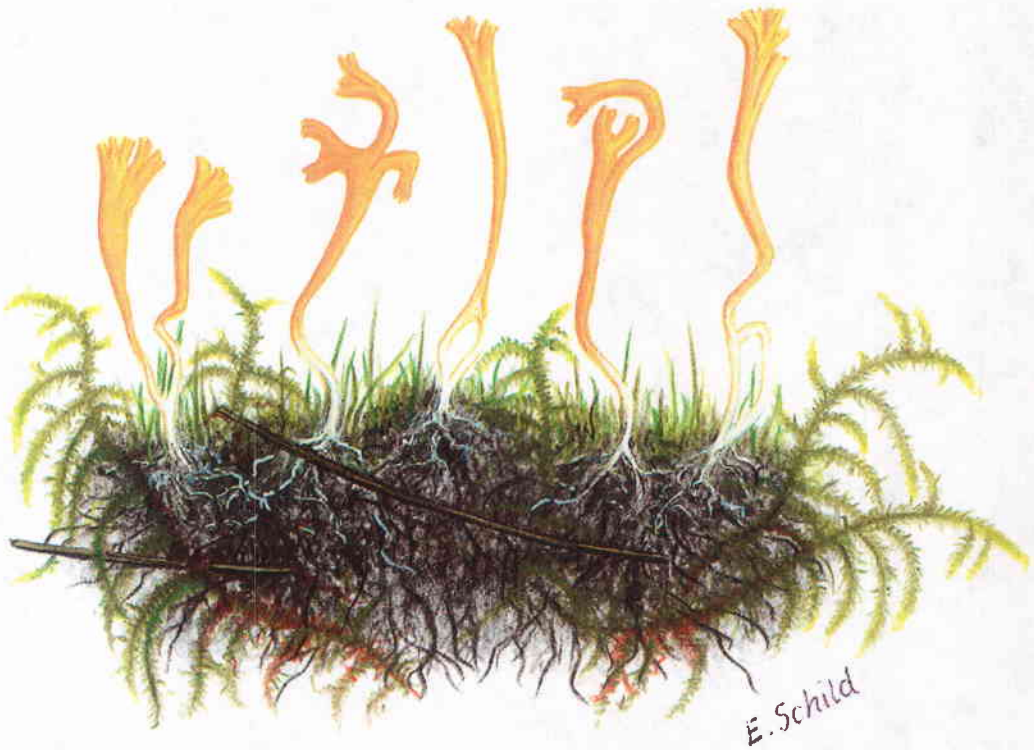
≡*Ramaria clavarioides* Schild, Zeitschrift für Mykologie 64:60. 1998.

Macroscopic characters: **Basidiomata** 3-5 cm tall, ramarioid, sparsely branched, resembling a species of *Ramariopsis* or *Clavulinopsis* (Figure 6.16). **Branches** 3.5-7 mm thick above, subclavate, rarely 2-4-branched, pale orange when young, later orange; apices 3-7 dentate, concolorous. Data on **hymenium** configuration not recorded. **Stipe** 10-15 × 1.2-1.4 mm, more or less equal. **Context** white, then pale orange, unchanging when bruised or exposed. **Odor** slightly unpleasant. **Taste** mildly bitter to mildly earthy. **Spore print color** not recorded.

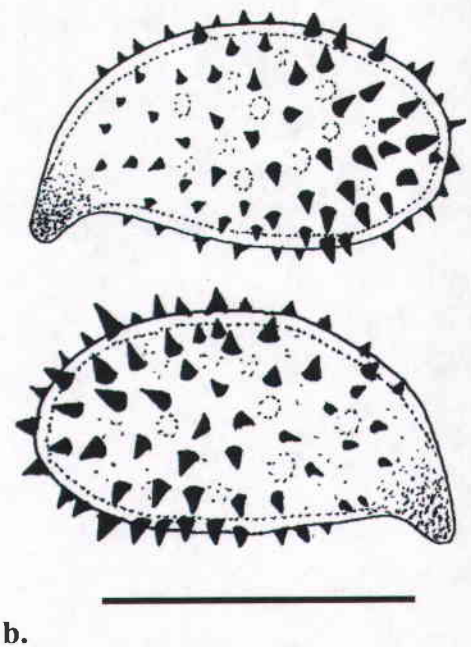
Microscopic characters: **Branch context** of irregularly arranged hyphae 1.5-6.5 (-8) µm wide; clamp connections present; gleoplerous hyphae rare, cyanophilic, 3 (-7.5) µm wide. **Stipe context** hyphae also irregularly arranged, just like in the upper basidioma; clamp connections present and up to 4.5-8 µm wide. **Subhymenial trama** of irregular, generally narrow, indistinctly defined hyphae. Rhizomorphs more or less parallel, between 1-3.5 µm thick, the hyphae scattered with small polymorph crystaloid elements of approximately 1.5-5.5 µm, more rarely connected to larger bodies of 8-14.5 µm around; clamp connections often present but not at all septa. **Basidia** 28-42 × 5.5-6.5 µm, clavate, with (3-) 4 sterigmata 4-5 µm long. Hymenial **cystidia** absent. **Spores** 4.5-8.5 (-9.5) × 3-4.5 µm, pale orange in mass, usually more or less lacrimoid; ornamentation of cyanophilic, more or less pronounced spines 0.5 (-1) µm tall, (Figure 6.16); apiculus 0.5-1 µm long, often laterally oriented.

Habit, habitat and distribution: In coniferous forests in Sardinia, Italy (Schild 1998).

Collections examined: **ITALY**. **SARDINIA**: NU, Oliena, 11 November 1994, *A. Errico 2107* (ZT – as *Ramaria clavarioides* – **holotype**).



a.



b.

Figure 6.16. *Phaeoclavulina clavarioides* (Schild) Giachini, *sp. prov.*: (a) basidiomata (× 0.5); (b) spores (bar = 5 μm). Basidiomata drawing modified from Schild (1998), with permission.

Discussion: This species has shape and habit unique in the genus *Phaeoclavulina*. In habit it can easily be confused with species of *Ramariopsis* or *Clavulinopsis*, although the latter has pale gray-green or hyaline single spores, white to pale in mass, and the former has much more finely ornamented spores. The pale orange, echinulate spores indicate the genus *Phaeoclavulina*. The color of the basidiomata resembles that of *P. flaccida* or *P. roellinii*, but *P. clavarioides* is more vividly yellow-orange. The spore's size and ornamentation are similar to *P. flaccida*, although the apiculus is laterally positioned in *P. clavarioides*.

Phaeoclavulina cokeri* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.17

≡*Ramaria cokeri* R.H. Petersen, The Distributional History of the Biota of the Southern Appalachians, p. 291. 1976b.

=*Clavaria echinospora* Berk. & Broome, Journal of the Linnean Society of London. Botany 14:75. 1875.

=*Clavaria echinospora* Henn., *nom. illeg.*, Monsunia 1:141. 1899.

=*Clavaria fragillima* Sacc. & P. Syd., Sylloge Fungorum Omnium Hucusque Cognitorum 16:206. 1902.

≡*Clavariella fragillima* (Sacc. & Syd.) Overeem, *in* Overeem and Weese, Icones Fungorum Malayensium I-IV. 1923.

≡*Ramaria fragillima* (Sacc. & Syd.) Corner, Annals of Botany Memoir 1:588. 1950.

Macroscopic characters: **Basidiomata** 3-14 cm tall, ramarioid, repeatedly branched from a substantial stipe, generally with irregular, alternating branching, sometimes rather irregular. **Branches** numerous, stout, crowded, cylindrical, erect, parallel, polychotomous with short internodes below, becoming dichotomous with more elongate internodes above, 1.5-2.5 mm wide, cinnamon to pink-yellow, becoming orange or dark red-brown, pale orange toward the tips (Figure 6.17); tips blunt or subacute, orange to brick red. Data on **hymenium** configuration not

recorded. **Stipe** 10-40 × 2.5-20 mm, often with a rooting base, sometimes divided from the base, flesh color to cinnamon, villous with white mycelium at the base. **Context** pliable, brittle, white, all parts slowly turning sordid vinaceous when cut or bruised. **Odor** strong, of *Ganoderma* (paracresol). **Taste** not recorded. **Spore print color** not recorded.

Microscopic characters: All **hyphae** thin-walled, 4-12 µm wide; clamp connections present; gleoplerous hyphae represented by short segments, 2.5-5.5 µm wide, often swelling at septa up to 14 µm. **Basidia** 45-80 × 7.5-12 µm, clavate to subcylindrical, yellow-brown, with (1-2-3-) 4 sterigmata, often of unequal length or with 1-3 abortive and sterile ends, (3-) 6-8.5 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 9-16 × 4-7.5 µm, orange in mass, ellipsoid to slightly obovoid, variable in size and shape, with acute, hyaline, strongly cyanophilic spines 1-2 µm tall (Figure 6.17); data on apiculus not recorded.

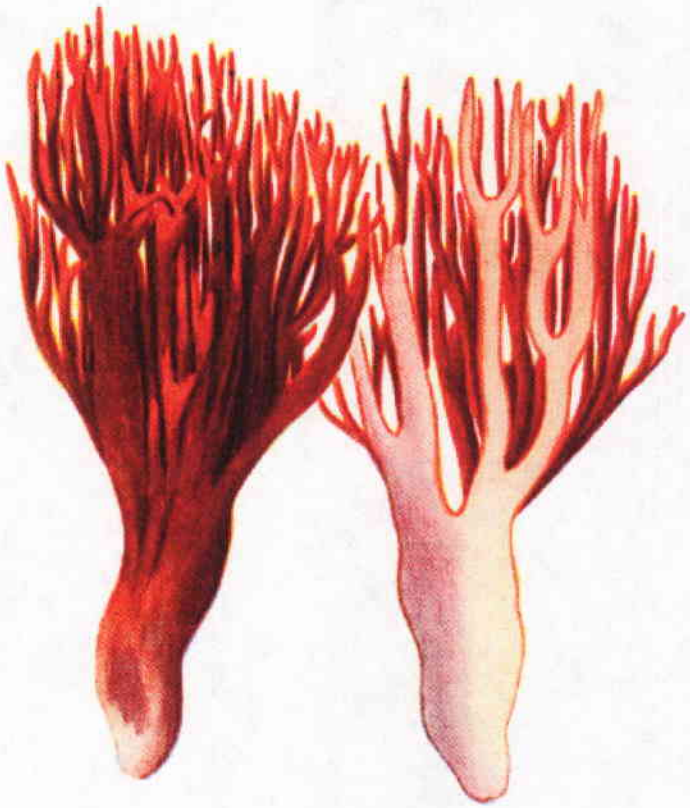
Habit, habitat and distribution: Solitary, on the ground in forest, or under trees in gardens. Known from Colombia (Petersen 1981), Java (Corner 1950), Malaysia (Corner 1950), Sri Lanka (Corner 1950, Petch 1925), Papua New Guinea (Petersen 1981), and Solomon Islands (Petersen 1981). Also known from southern portions of the Appalachian Mountains (USA) and South America (Petersen 1976b, 1981).

Collections examined: **UNITED STATES. TENNESSEE**: Blount Co., Great Smoky Mountains National Park, near Cades Cove, one mile West of Crib Gap, 10 July 1969, *R.H. Petersen* (TENN 34653), 2 July 1971, *R.H. Petersen* (TENN 36030 – as *Ramaria cokeri* – **holotype**), 16 July 1971, *R.H. Petersen* (TENN 36064), and 25 July 1972, *R.H. Petersen* (TENN 36436).

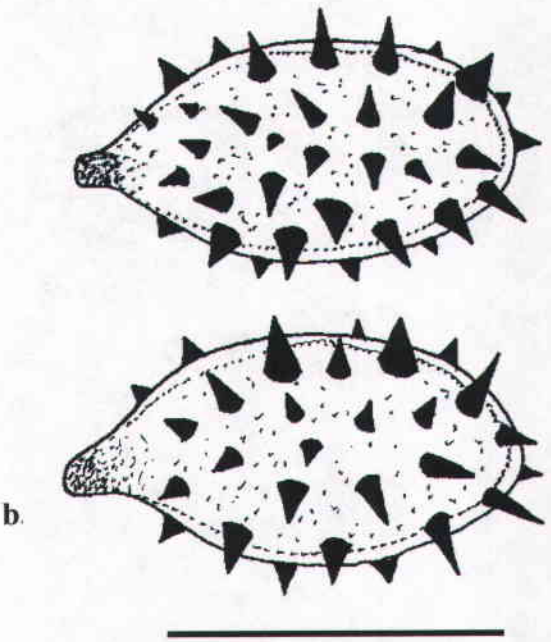
Discussion: According to Corner (1950), this seems to be closely related to *P. guyanensis*. *Phaeoclavulina cokeri* also resembles the North temperate, 2-spored species *P. macrospora*. When compared to the latter, *P. cokeri* has slightly smaller spores and larger, non-blackening basidiomata.

Petersen (1981) considered *C. fragillima* a *nomina miscellanea deposita.* His decision was based on the fact that the type specimen for the then unique *Clavaria fragillima*, described by Hennings (1899) is apparently destroyed, leaving no type collection to be designated under that epithet. Additionally, *Clavaria echinospora sensu* Henn. was considered illegitimate as a later homonym, being supplanted by Saccardo and Sydow (1902). Later Overeem, in Overeem and Weese (1923), used *Clavariella fragillima* apparently in a different sense from that of Hennings (1899). Corner (1950) used the name in the sense of Overeem. According to Petersen (1981), therefore, the true sense has been obscured and cannot be buttressed with an adequate type specimen. Additionally, Berkeley and Broome (1875) did not mention a type specimen or a herbarium name when describing *Clavaria echinospora.* Petersen (1981) further suggested using *Ramaria cokeri* R.H. Petersen to accommodate *C. fragillima sensu* Overeem and *sensu* Corner.

Phaeoclavulina cokeri occurs in a belt from Borneo through Papua New Guinea to the Solomon Islands. It is also known from the Appalachian Mountains in the USA. Just how the species has a tropical distribution and also occurs in the Appalachian Mountains is unknown, but it well resembles other cases of such a pantropical distribution within the fungi. Ample examples have become available to show that the lower elevations of the southern Appalachian chain contain representatives of a tropical flora, and that it very well represents a refugium for tropical basidiomycetes (Petersen 1976b). Other examples include species of *Amanita, Clavicorona, Clavulinopsis, Gloeocantharellus, Hydnum, Multiclavulina,* and *Tulasnella* (Petersen 1976b).



a.



b.

Figure 6.17. *Phaeoclavulina cokeri* (R.H. Petersen) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 10 µm). Drawing of basidiomata modified from Corner (1950).

Phaeoclavulina curta* (Fr.) Giachini, *sp. prov. Fig. 6.18

≡*Clavaria curta* Fr., Monographia Hymenomycetum Sueciae 2(69):281. 1863.

≡*Ramariopsis curta* (Fr.) Corner, Annals of Botany Memoir 1:639. 1950.

=*Clavaria pusilla* Peck, Bulletin of the Buffalo Society of Natural Science 1:62. 1873 (*non C. pusilla* (Pers.:Fr.) Pers., Mycologia Europeae 1:187. 1822).

≡*Ramaria pusilla* (Peck) Corner var. *pusilla*, Annals of Botany Memoir 1:617. 1950.

=*Clavaria myceliosa* Peck, Bulletin of the Torrey Botanical Club 31(4):182. 1904.

≡*Ramaria myceliosa* (Peck) Corner var. *myceliosa*, Annals of Botany Memoir 1:607. 1950.

≡*Ramaria myceliosa* var. *microspora* R.H. Petersen, Bibliotheca Mycologica 79:157. 1981.

=*Clavaria decurrens* var. *australis* Coker, The Clavarias of the United States and Canada, p. 177. 1923.

≡*Ramaria pusilla* var. *australis* (Coker) Corner, Annals of Botany Memoir 1:618. 1950.

≡*Ramaria decurrens* var. *australis* (Coker) R.H. Petersen, Bibliotheca Mycologica 79:127. 1981.

=*Ramaria subdecurrens* var. *burnhami* R.H. Petersen, Bibliotheca Mycologica 79:171. 1981.

Macroscopic characters: **Basidiomata** 1.5-5 × 1.5-3 cm, rarely 7 × 5 cm, ramarioid. **Branches** dichotomous to submonopodial, slightly flattened, flabellate-spreading at the nodes, minutely forked to cristate near the apices, gray-yellow to olive-brown when dry; internodes short, usually ≤10 mm long; axils U-shaped and branches widely parallel or slightly divergent at right angles, gray-yellow; apices minute, acute, awl-shaped, gray-yellow. **Hymenium** unilateral, fertile area olive when dry, sterile area brown. **Stipe** 5 × 2 mm, slender, coriaceous-pliable when fresh, drying brittle, arising from mycelial strands and a felty basal tomental mat,

pale creamy white to pale yellow, often with pink stains. **Context** drying friable or soft, pale yellowish, bruising pink then brownish. **Odor** faintly sweet. **Taste** bitter. **Spore print** yellow-brown.

Microscopic characters: **Branch context** of slightly thick-walled, parallel, hyaline hyphae up to 8 µm wide, with occasional ampulliform swellings. Other **hyphae** thin-walled, parallel to slightly interwoven, non inflated, moderately cyanophilic, 3-4 (-8) µm wide; clamp connections swelling near septa common and up to 7-10 µm; gleoplerous hyphae not observed. Hyphae of rhizomorphs of two types: (a) outer hyphae thin- to slightly thick-walled, hyaline, up to 3.5 µm wide; ampulliform clamps abundant, up to 12 µm wide; and (b) inner hyphae usually refringent, golden yellow, with gleoplerous contents. Hyphae of both the rhizomorphs and tomentum 1.5-2.5 µm wide. **Basidia** 25-36 × 4-8.5 µm, clavate, with 2-4 straight to slightly incurved, erect sterigmata 3-5.5 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** (3.5-) 4.5-6.5 (-8) × 2.5-4 µm, ellipsoid obovoid; ornamentation of fine, cyanophilic spines (Figure 6.18); data on apiculus not recorded.

Habit, habitat and distribution: Corner (1950) cites it from humus under *Pinus, Sequoia,* and *Tsuga* in Canada (Ottawa) and the USA (New York, North Carolina, and Oregon). *Phaeoclavulina curta* is also known from Scandinavia (Killermann 1922, Schild 1975), some places in Europe (Corner 1950, Petersen 1981), and India (Thind 1961). Because the same habitat is found across Russia and at high elevations in China, it is predicted the species to be present there as well.

Collections examined: **CANADA. ONTARIO:** Paird Park, 9 July 1968, *Larsen 3332* (TENN 34629 – as *Ramaria decurrens* var. *australis*). **FINLAND**. Tammela, Mustiala, 18 August 1866, *P.A. Karsten 2113* (H – as *R. myceliosa*). **INDIA**. Himachal Pradesh, Mahasu, Narkanda, 12 August 1965, *Pui 4526* (TENN 37645 – as *R. myceliosa*). **JAVA**. No location, no date, *Clautrian* (FH – as *C. aeruginosa*). **SWEDEN**. Uppsala, Uppland, Barby, 3 September 1930, *Lundell* (TENN 36395 – as *R. myceliosa*); Uppsala, Backen vid Helsobrunnen, 18 October 1856, *E.P. Fries* (K – as *Clavaria curta* – **holotype**). Umea, 3 September 1974 (TENN 39766 – as

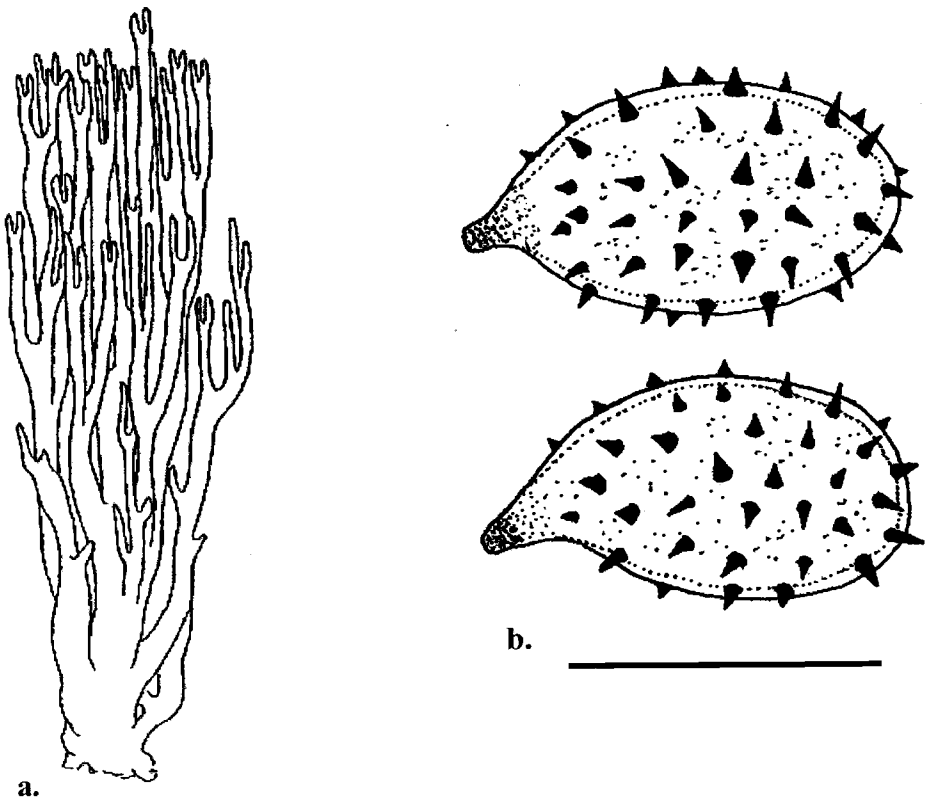


Figure 6.18. *Phaeoclavulina curta* (Peck) Giachini, *sp. prov.*: (a) basidiomata (× 0.2); (b) spores (bar = 5 μm). Basidioma drawings modified from Petersen (1981), with permission.

R. myceliosa). **UNITED STATES: CALIFORNIA:** Mendocino Co., Jackson St. Forest, 16 January 1967 (TENN 33199 – as *R. myceliosa*); Santa Clara Co., Mountains behind Stanford University, 4 July 1902, *E.B. Copeland* (NYS – holotype of *Clavaria myceliosa*). **IDAHO**: Bonner Co., Priest River Experimental Forest, 26 September 1964, *A.H. Smith 70824* (TENN – as *R. myceliosa*); Bonner Co., Binarch Creek, 14 September 1966 (TENN 31916 – as *R. myceliosa*); Bonner Co., Tule Bay, 27 September 1968 (TENN 36285, 36393, 36396, 36398, 36400 – as *R. myceliosa*). **NEW YORK:** Essex Co., Newcomb, August, *C.H. Peck* (NYS – as *Clavaria pusilla*); Essex Co., North Elba, Adirondack Mountains, July, *C.H. Peck* (NYS – holotype of *C. pusilla*), and August, *C.H. Peck* (NYS as *C. pusilla* – 3 collections); Franklin Co., Floodwood, August 1918, *C.H. Peck* (NYS – as *C. pusilla*); Washington Co., Vaughn's, Burnham's Woods, 7 September 1917, *W.C. Coker and R.C. Burnham 102* (TENN – as *R. subdecurrens* var. *burnhami*). **NORTH CAROLINA:** Macon Co., Norton Community, August 1964 (TENN 31398 – as *R. decurrens* var. *australis*); Orange Co., Chapel Hill, 25 July 1917, *W.C. Coker 2769* (NCU – holotype of *C. decurrens* var. *australis*; isotype at NY). **TENNEESSEE:** Unicoi Co., Unaka Springs, 18-24 August 1904, *W.A. Murrill 907* (NCU – holotype of *C. murrillii*). **WASHINGTON**: King Co., Seattle, 10 November 1911, *W.A. Murrill 174* (TENN 32297 – as *R. myceliosa*); Pend Oreille Co., Cusick, 24 September 1964, *A.H. Smith 70764, 70765* (TENN – as *R. myceliosa*).

Discussion: This description was partially based on notes from Coker (1923), Corner (1950, 1970), Marr and Stuntz (1973), Petersen (1981), and Schild (1975). *Phaeoclavulina curta, P. flaccida,* and *P. ochraceo-virens* have similar spore ornamentation and general habitat, but *P. curta* is easily distinguished from the other two by its considerably shorter spores. Coker (1923) described *C. decurrens* var. *australis*, which later was considered a variety of *R. pusilla* based on overall morphological features, especially the size and ornamentation of the spores (Corner 1950). Giachini (chapter 2) considered *R. pusilla* var. *australis* a synonym of *P. curta*, since the overall morphological characters are the same.

When describing *Clavaria myceliosa,* Peck (1904) recognized the close relationship of this species to that of *C. pusilla* (≡*P. curta*). After studying both types, Marr and Stuntz (1973) regarded *Ramaria myceliosa* as a variety of *R. pusilla*. The basis for this combination is the divaricated form of the basidiomata, the echinulate spores, and the habitat of both species on redwood litter.

Later Petersen (1981) proposed *Ramaria myceliosa* var. *microspora*, which, at first, seems as a perfectly legitimate new species. After examining the type for both *Ramaria myceliosa* var. *microspora* and *R. myceliosa,* and the descriptions proposed by Petersen (1981), Giachini (chapter 2) strongly believed that Petersen was dealing with another specimen of *R. pusilla* when referring to var. *microspora*. The shape of the basidiomata, and the shape, size, and ornamentation of the spores match those observed for the aforementioned species.

Petersen (1981) also considered *Clavaria corrugata* Karst. as a synonym of *R. pusilla*. *Clavaria corrugata* has similar basidioma features but the spores are larger, as seen for *P. flaccida*. Therefore, the former is placed as synonymy with *P. flaccida* (Giachini, chapter 2).

Phaeoclavulina cyanocephala* (Berk. & M.A. Curtis) Giachini, *sp. prov.

Fig. 6.19

≡*Clavaria cyanocephala* Berk. & M.A. Curtis, The Journal of the Linnean Society of London. Botany 10:338. 1869.

≡*Ramaria cyanocephala* (Berk. & M.A. Curtis) Corner, Annals of Botany Memoir 1:568. 1950.

≡*Ramaria grandis* f. *cyanocephala* (Berk. & M.A. Curtis) R.H. Petersen, Bibliotheca Mycologica 79:71. 1981.

=*Clavaria grandis* Peck, Bulletin of the Torrey Botanical Club 29(2):73. 1902.

≡*Ramaria grandis* (Peck) Corner f. *grandis*, Annals of Botany Memoir 1:595. 1950.

=*Clavaria spiculospora* G.F. Atk., Annales Mycologici 7:368. 1909.

≡*Clavaria spiculisperma* (G.F. Atk.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 21:426. 1912 (*lapsus calamitus*).

=*Ramaria zippelii* f. *aeruginosa* R.H. Petersen, Bibliotheca Mycologica 79:96. 1981.

Macroscopic characters: **Basidiomata** up to 30 × 15 cm, ramarioid, repeatedly branched (Figure 6.19). **Branches** up to 1.2 mm thick, erect, re-branching in 2-4 ranks, overall reddish-brown, all parts bruising vinaceous; axils narrowly to openly rounded, brick red to reddish brown; tips subacute, blue or greenish blue. **Hymenium** unilateral. **Stipe** up to 6 × 2 cm, stout, cylindrical, slightly tapering downward, attached to mycelium by a few small delicate, brownish lavender, white rhizomorphic strands at the very base, white or whitish below substrate level, soon bruising brick red to lavender brown. **Context** firm but tender, whitish or pale yellowish, darker yellow next to the hymenium, bruising vinaceous brown on exposure. **Odor** faintly sweet, of anise. **Taste** bitter, astringent. **Spore print** brown.

Microscopic characters: **Context** of thin-walled, densely interwoven, hyaline hyphae 2-11 µm wide; clamp connections present. **Subhymenial trama** of slightly inflated hyphae 3-6 µm wide. **Basidia** 55-75 × 9-11 µm, clavate, gleoplerous, with (1-) 2 (-3) obconical, stout, persistent sterigmata up to 10 µm long; clamp connections present. Hymenial **cystidia** not observed. **Spores** (10-) 12.5-18.5 × (5.5-) 7.5-10.5 µm, ferruginous in mass, obovoid; ornamentation of acute, hyaline, weak to strongly cyanophilic spines 1-3.5 µm long (Figure 6.19); apiculus prominent.

Habit, habitat and distribution: On the ground in the forest, Africa, the Americas, and tropical Asia (Corner 1950, Petersen 1981, Teng 1939). It is said to occur in the Appalachian Mountains of the USA (Petersen 1981).

Collections examined: **CUBA:** No location, Fungi Cubensis Wrightiana, June, Exsiccati no. 458, *C. Wright 261* (K – as *Clavaria cyanocephala* – **holotype**; isotype at FH). **GUATEMALA. LOS AMANTES:** Finca, Alsacia, 17 July 1936 (FH

– as *Ramaria grandis* f. *grandis*). **UNITED STATES. MARYLAND:** No location, no date, *F.J. Braendle* (NYS – as *C. grandis* – holotype of *C. grandis*). **NORTH CAROLINA:** Macon Co., Coweeta Hydrol. Lab., 15 August 1971 (TENN 36164 – as *R. grandis* f. *cyanocephala*). **TENNESSEE:** Blount Co., Great Smoky Mountains Nat. Park, Commentary Trail, Roaring Fork, 4 August 1971, *R.H. Petersen* (TENN 36114 – as *R. grandis* f. *grandis*); Blount Co., Great Smoky Mountains Nat. Park, 2 August 1966 (TENN 31815 – as *R. grandis* f. *cyanocephala*), and 19 September 1966 (TENN 32324, 36033 – as *R. grandis* f. *cyanocephala*); Blount Co., Montvale Springs, 23 August 1934 (TENN 6279 – as *R. grandis* f. *grandis*), and 30 August 1936 (TENN 9410); Sevier Co., Great Smoky Mountains Nat. Park, October 1965 (TENN 31785 – as *R. grandis* f. *grandis*), and 26 July 1969 (TENN 34682 – as *R. grandis* f. *grandis*).

Discussion: *Ramaria cyanocephala* has been regarded as synonym of *R. zippelii* (Bresadola, v. Hoehnel, Coker and Overeem, *in* Corner 1950), but there is no proof that the two intergrade, nor have the differences between them been clearly stated. Corner (1950) stated that *R. cyanocephala* was the most common of the two in Malaysia, distinguished by reddish brown basidiomata and bluish green tips. *Ramaria zippelii* has generally smaller basidiomata of brown color and white tips. It also has smaller basidia, narrower hypha, and more often polychotomous branching. Petersen (1981) accepted *R. zippelii* and *R. grandis* as separate species, but reduced *R. cyanocephala* to a form of *R. grandis*. It is important to note that Petersen's *R. grandis* f. *cyanocephala* and *R. grandis* don't differ morphologically according to their descriptions (Petersen 1981). After examining the types, Petersen (1981) concluded that the latter almost always has larger and fleshier basidiomata than the former. One important feature to separate species according to Petersen is, among other things, the color of the tips. Apparently, bluish green tips are only to be seen in *R. grandis* (=*R. cyanocephala*). *Ramaria zippelii* is separated from the former in larger stature of the basidiomata, but also because of the white tips. In his seminal work of 1981, Petersen, however, describes *R. zippelii* as having "white, cream colored, or pale blue-green" tips. In addition, his *R. zippelii* f. *aeruginosa* is

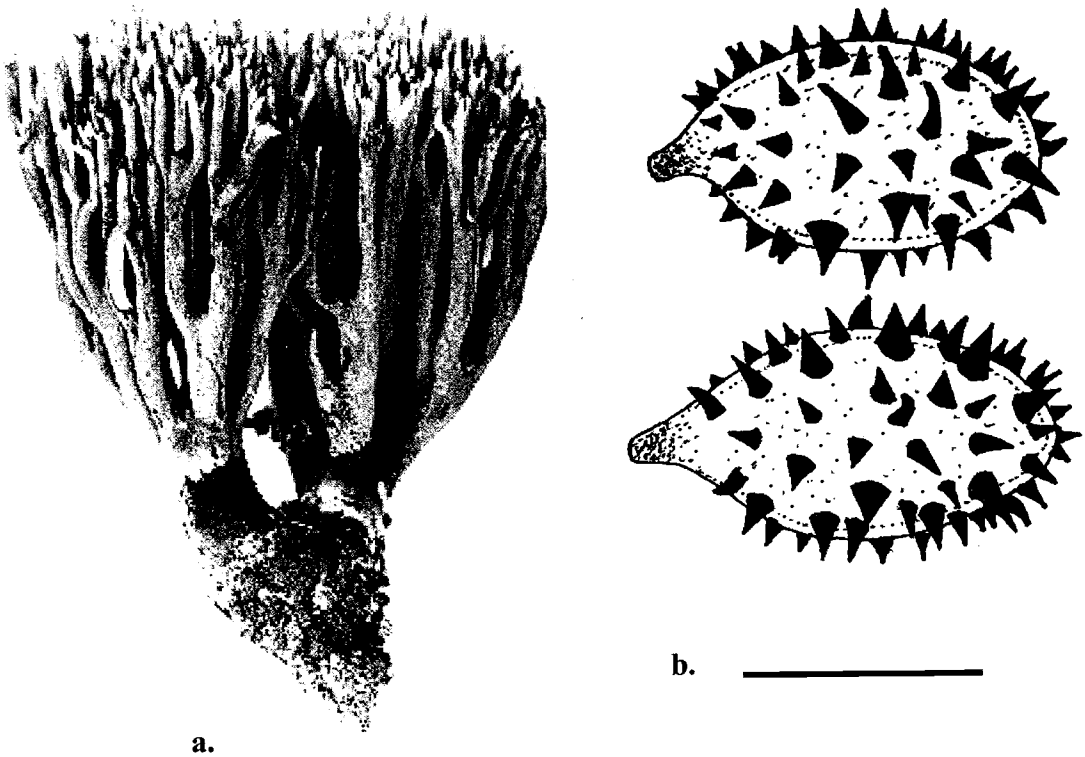


Figure 6.19. *Phaeoclavulina cyanocephala* (Berk. & M.A. Curtis) Giachini, *sp. prov.*: (a) basidiomata (× 0.5); (b) spores (bar = 10 µm). Photograph of basidiomata modified from Coker (1923).

supposed to closely resemble *R. zippelii*, except for the "pale to neutral blue or blue-green" apices (Petersen 1981). As can be seen, trying to delimit species boundaries for this group is time consuming and frustrating. Molecular analysis, however, indicates that *R. grandis* and *R. zippelii* do not group, but rather come in separate clades in all phylogenetic analyses (Giachini, chapter 2). After examining the types and descriptions for these species, it seems that the best arrangement for now is to group the blue-tipped forms into one species and the white-tipped forms into another. Illustrations of *R. zippelii* almost invariably show the elongate stature of the branches and slenderer stipe portion than in *R. grandis*.

Ramaria grandis, Ramaria cyanocephala, and *R. zippelii* are said to occur in the tropics as well as in the Appalachian Mountains (Corner 1950, Petersen 1981). Based on this and other examples it is clear that the southern Appalachian Mountains represent the northernmost refugium of a tropical flora and, as such, offer an area where the circumboreal fungal flora is interfaced with a tropical element (Petersen 1976b).

Phaeoclavulina decolor* (Berk. & M.A. Curtis) Giachini, *sp. prov. Fig. 6.20

≡*Clavaria decolor* Berk. & M.A. Curtis, Proceedings of the American Academy of Arts and Sciences 4:124. 1858.

≡*Ramaria decolor* (Berk. & M.A. Curtis) R.H. Petersen, Persoonia 12(3):231. 1984.

=*Ramaria zippelii* var. *cristatospora* Corner, Proceedings of the Linnean Society of London 178:103. 1967.

≡*Ramaria cristatospora* (Corner) R.H. Petersen, Bibliotheca Mycologica 79:64. 1981.

Macroscopic characters: **Basidiomata** up to 10 cm tall, ramarioid, repeatedly branched (Figure 6.20). **Branches** ascending, sordid pale orange; apices acute, white. Data on **hymenium** configuration and **stipe** not recorded. **Context** off-

white, vinaceous upon exposure or bruising. **Odor, taste** and **spore print color** not recorded.

Microscopic characters: **Branch context** of thin- to thick-walled, parallel, yellowish, 3-8 µm wide hyphae; clamp connections present. **Stipe context** of thin-walled, interwoven hyphae up to 5 µm wide, with agglutinating material; clamp connections present; crystal aggregates abundant and up to 11 µm long. **Basidia** with 2-3-4 sterigmata. Hymenial **cystidia** absent. **Spores** 11-16 × 4.5-7 µm, ellipsoid to obovoid; ornamentation of discrete, cyanophilic, spines 1.5 to 2 µm tall at distal and proximal ends, and mixed discrete spines and spines connected into circular to semi-circular ridges in the median area, the ornamentation sometimes covering the entire surface of the spores (Figure 6.20); apiculus pronounced, straight.

Habit, habitat and distribution: On soil in Hong Kong (Corner 1950), Malaysia (Corner 1967), New Caledonia (Perreau-Bertrand 1967), Papua New Guinea, and the Solomon Islands (Corner 1967, Petersen 1981).

Collections examined: **CHINA. HONG KONG**: Ringgold and Rodgers Experiment, 14 August 1854, *C. Wright* (FH – as *Clavaria decolor* – **holotype**). **PAPUA NEW GUINEA. GULF DISTRICT**: Hill Crest, ca. 1 mile NE of junction of Vailala and Lohiki Rivers, 7° 40' S, 145° 30' E, 245 m alt., 26 January 1966, *R. Schodde and L.A. Craven* (CANB – as *Ramaria* sp., dupl. at LAE). **NEW BRITAIN**: Epap River, Nakanai Mts., 45 km SE of Hoskins, 5° 45' S, 150° 44' E, 300 m alt., 20 February 1989, *H. Streimann 40710* (CBG – as *Ramaria* sp.). **SOLOMON ISLANDS. SAN CRISTOBAL**: Sarawak, Bau, Kuching, 11 January 1964, *E.J.H. Corner* (PC – as *Ramaria cristatospora*); Warahito River, 22 July 1965, *E.J.H. Corner RSS 719* (PC – as *Ramaria cristatospora*).

Discussion: Berkeley and Curtis (1858) described *Clavaria decolor*. Later, Corner (1967) described *Ramaria zippelii* var. *cristatospora* to differentiate from all other species of *Ramaria* on spore ornamentation alone. In 1984, Petersen considered Corner's *R. zippelii* var. *cristatospora* to be unique rather than a variety under *R. zippelii* and further described *R. cristatospora*. Spore shape and the 2-4 sterigmata

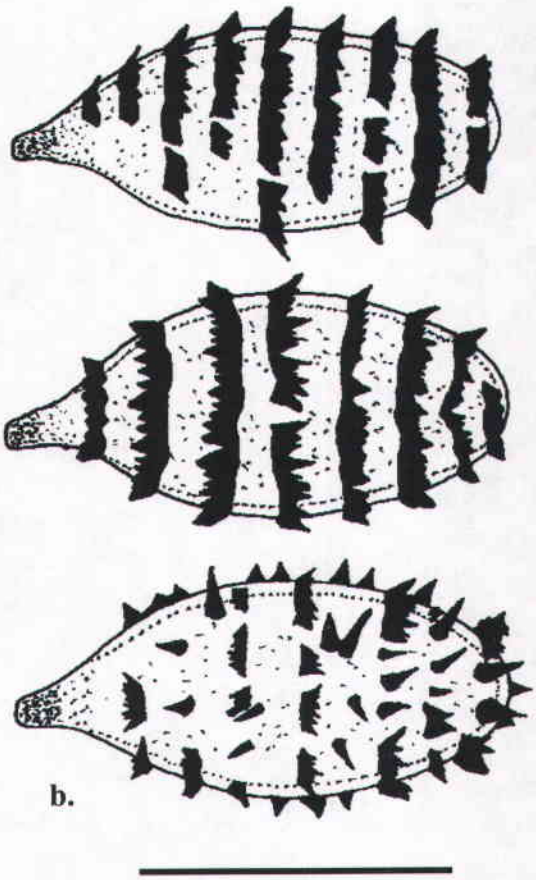


Figure 6.20. *Phaeoclavulina decolor* (Berk. & M.A. Curtis) Giachini, *sp. prov.*: (a) basidiomata (bar = 1 cm); (b) spores (bar = 10 μm).

basidia removed the species from *R. zippelii* (Petersen 1981). Spore shape and size immediately relate the species to *P. cokeri*, but the branch apices in that species are cinnamon to dark red-brown, and the basidiomata somewhat larger and more robust than those of *P. decolor*.

Phaeoclavulina echinovirens* (Corner, K.S. Thind & Dev) Giachini, *sp. prov.

Fig. 6.21

≡*Ramaria echinovirens* Corner, K.S. Thind & Dev, Transactions of the British Mycological Society 40:473. 1957.

Macroscopic characters: **Basidiomata** up to 13 × 7.5 cm, ramarioid, repeatedly branched. **Branches** ascending, polychotomous below, dichotomous above, orange-yellow, concolorous with stipe downward, brighter upward; axils rounded; apices 1-4 mm long, digitate, orange-yellow. **Hymenium** generally amphigenous. **Stipe** up to 40 × 25 mm, simple to fused, white below, unchanging on drying, with a basal mat of white rhizomorphs, dark where unprotected, pale yellow-brown elsewhere; surface and context slowly dark green where handled or when cut. **Context** pliable when fresh. **Odor** not recorded. **Taste** starchy. **Spore print color** not recorded.

Microscopic characters: **Branch context** of thin-walled, parallel hyphae; clamp connections present; gleoplerous hyphae uncommon, 1.5-5 µm wide. **Basidia** 40-50 × 7-9 µm, thin-walled, clavate, with (2-) 4 short, stout, straight sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 10.5-14 × 4.5-6 µm, ellipsoid to lacrimoid; ornamentation of blunt, scattered, cyanophilic warts <1 µm tall (Figure 6.21); apiculus short, gradual.

Habit, habitat and distribution: In *Quercus* forest in the Himalayan Mountains of India (Petersen 1981).

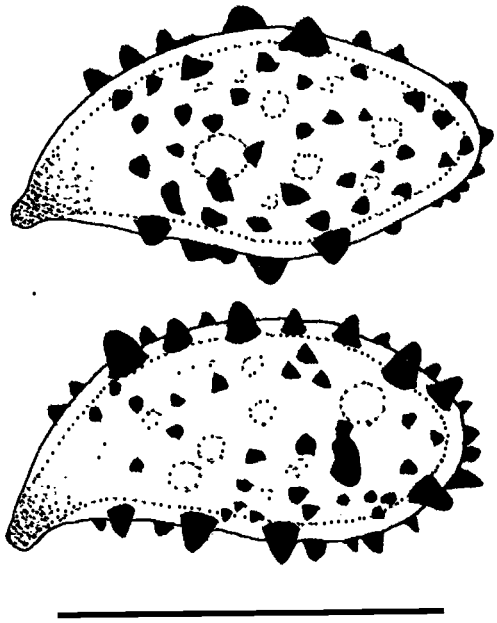


Figure 6.21. Spores (bar = 10 μm) of *Phaeoclavulina echinovirens* (Corner, K.S. Thind & Dev) Giachini, *sp. prov.* Modified from Petersen (1981), with permission.

Type (holotype): **INDIA**: Musoorie, U.P., Sarkunda Road, 12 September 1954, *K.S. Thind and S. Dev 121* (PAN – as *Ramaria echinovirens*). **UTTAR PRADESH:** Nainital, Cheena Park, 6 August 1968, *S.S. Rattan 4639* (TENN 37619); Lariah Kauta, 10 August 1968, *S.S. Rattan 4645* (TENN 36997).

Discussion: The herbarium PAN was contacted for loan of the type for this species but no answer was obtained. Therefore, this description was based on notes from Corner *et al.* (1957).

This is a robust fleshy look-a-like of *P. ochraceo-virens* with longer and more strongly echinulate spores. Petersen (1981) suggested the species could be easily separated from others on at least two characters: (a) the large spores, and (b) the orange-yellow tips, which are quite distinct, especially in relation to *P. ochraceo-virens*.

Phaeoclavulina eumorpha* (P. Karst.) Giachini, *sp. prov. Fig. 6.22

≡*Clavariella spinulosa* subsp. *eumorpha* P. Karst., Bidrag till Kännedom af Finlands Natur och Folk 37:185. 1882.

≡*Clavaria eumorpha* (P. Karst.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:701. 1888.

≡*Clavaria spinulosa* subsp. *eumorpha* (P. Karst.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:701. 1888.

≡*Clavariella eumorpha* (P. Karst.) P. Karst., Bidrag till Kännedom af Finlands Natur och Folk 48:388. 1889.

≡*Ramaria eumorpha* (P. Karst.) Corner, Annals of Botany Memoir 1:575. 1950.

=*Clavaria patagonica* Speg., Flora Patagonica 11:19. 1887.

≡*Clavulinopsis patagonica* (Speg.) Corner, Annals of Botany Memoir 1:383. 1950.

≡*Ramaria patagonica* (Speg.) Corner, Darwiniana 11:203. 1957.

=*Clavaria invalii* Cotton & Wakef., Transactions of the British Mycological Society 6:176. 1919.

≡*Ramaria invalii* (Cotton & Wakef.) Donk, Bibliotheca Mycologica 29:113. 1933.

≡*Clavaria flaccida* subsp. *invalii* (Cotton & Wakef.) Konrad & Maubl., Icones Selectae Fungorum, p. 7. 1935.

≡*Clavaria flaccida* var. *invalii* (Cotton & Wakef.) J. Favre, Matériaux pour la Flore Cryptogamique Suisse 10(3):32. 1948.

=*Clavaria murrillii* Coker, The Clavarias of the United Sates and Canada, p. 190. 1923.

≡*Ramaria murrillii* (Coker) Corner, Annals of Botany Memoir 1:607. 1950.

Macroscopic characters: **Basidiomata** up to 8 × 6 cm, ramarioid, generally fusiform to subspherical in outline, repeatedly branched. **Branches** cylindrical, crowded, commonly anastomosed, erect, in 2-5 ranks, generally dichotomous, always with central branches longer (higher) than outer branches to render a variety of basidiomata shapes, brown to yellow-brown, branches generally paler when young; axils narrowly rounded, cinnamon when dry; tips up to 2 cm long, rounded, acute to awl-shaped, often curled when dry, golden yellow, paler with age. **Hymenium** amphigenous to clearly unilateral, especially decurrent from axils, dark brown to yellow-brown when dry. **Stipe** up to 5 cm long, up to 3 cm thick below, absent in some specimens (branches occurring at substrate level, or more than one short stipe arising in a densely caespitose habit), white, becoming red-brown to olive-brown in some areas, then chocolate brown on exposure or bruising (*fide* Petersen 1981), beset by copious lateral rhizomorphs at base; rhizomorphs ephemerally bright yellow in 15% KOH (Petersen 1981). **Context** soft when fresh, not brittle, drying friable. **Odor** mild, fresh, faintly sweet, perhaps farinaceous in some specimens (*fide* Petersen 1981). **Taste** musty to mildly bitter (*fide* Petersen 1981). **Spore print** pale brown to yellow-brown.

Microscopic characters: **Branch context** of thin-walled, parallel, tightly packed, inflated, hyaline hyphae 2-8 μm wide; ampulliform clamp connections present; gleoplerous hyphae present; crystals irregularly quadrilateral to amorphous, only

present in the **trama**. **Basidia** 30-60 × 6.5-9 µm, clavate, with (2-) 4, straight, acute, narrow sterigmata not persistent after spore discharge; clamp connections present. Hymenial **cystidia** absent. **Spores** 6.5-10 × 3.5-5 µm, yellow brown in mass, ellipsoid to lacrimoid; ornamentation of short (up to 1.5 µm long), cyanophilic, conical, acute spines scattered randomly over the spore surface (Figure 6.22); data on apiculus not recorded.

Habit, habitat and distribution: Solitary, gregarious to caespitose. Under conifers (*Abies, Picea, Pinus*) and broad-leaved (*Fagus, Quercus*) forests; northern Europe and Scandinavia, eastern North America (mostly under conifers), southern Appalachian Mountains (Petersen 1981).

Collections examined: **AUSTRIA.** Tirol, Ötztal, Königstal, 26 August 1969, *Kankainen* (OULU – as *Ramaria invalii*), and 29 August 1969, *Kankainen* (OULU – as *R. invalii*). **CANADA. QUEBEC:** No location, 14 September 1898, Herb. Ellis, *2 and 5a* (NY). **CZECHOSLOVAKIA.** Loucky, Konstantinovy Lazne, 25 October 69, *Pilat* (NY). **DENMARK.** Kristiansmind, Soro, 21 September 70 (TENN 36521, 36522, 36523, 36529). **ENGLAND.** Carlisle, no date, *G. Massee* (NY – as *Clavaria abietina*). **FINLAND:** Tammela, Mustiala, 1881, *P.A. Karsten* (H – as *Clavariella spinulosa* subsp. *eumorpha* – **holotype**); Tammela, Mustiala, 15 August 1889, *P.A. Karsten 2112* (H – as *C. corrugata*); Tammela, Myllypera, 26 September 1889, *P.A. Karsten 1313* (H – as *C. corrugata*). **GERMANY.** Berlin, 25 September 1896, *P. Hennings* (NY – as *C. abietina*). **POLAND.** Swieta Katarzyna, Mt. Lysica, 8 September 1966, *M. Geesteranus 14925* (OULU – as *R. invalii*). **SWEDEN.** Biludden, 30 August 74 (TENN 39759, 39765, 39823); Stockholm, Värta Station, 28 August 1888, *L. Romell 5655, 5656* (S – as *C. abietina*); Uppsala, 10 September 1888, *L. Romell 5651* (S – as *C. abietina*). **SWITZERLAND.** Brienz, 20 August 69, *E. Schild* (TENN). **UNITED STATES. CALIFORNIA**: Del Norte Co., Jedediah Smith Redwood St. Park, 11 November 1967, *Lum. 39* (TENN 36383); Humboldt Co., Patrick's Point State Park, 11 December 1967 (TENN 36390, 33225). **NEW YORK:** Essex Co., Lake Placid, Adirondacks, 3-14 October 1912, *W.A. Murrill and E.L. Murrill 895* (NY – as *C.*

gracilis). **NORTH CAROLINA:** Macon Co., Coweeta Hydrol. Lab., 11 July 1967 (TENN 32604 – as *R. murrillii*); Macon Co., Highlands, 3 July 1963 (TENN 31080) and 31 July 1963, *Bursdall* (TENN 32907); Macon Co., Horse Cove, 10 August 1966 (TENN 32089 – as *R. murrillii*); Macon Co., Wayah Bald, August 1964 (TENN 31454, 31469 – as *Ramaria murrillii*). **TENNESSEE:** Blount Co., Great Smoky Mountains Nat. Park, Ekanetlee Trail, 8 September 1965 (TENN 32006 – as *R. murrillii*), and 15 September 1965 (TENN 32777 – as *R. murrillii*); Union Co., Unaka Springs, 18-24, July 1904, *W.A. Murrill 907* (NCU – as *Clavaria murrillii*). **WASHINGTON:** Pierce Co., Mount Rainier Nat. Park, 28 July 1948, *A.H. Smith 29576* (TENN), and 15 October 1968 (TENN 34413, 34454).

Discussion: According to Petersen (1981), the prolonged apices seem to relate it to more tropical taxa, where economy of basidiomata development is not as pressing as in temperate climate. The basidiomata produced under *Pinus* and *Fagus* seem to be larger and more fusiform than those under *Picea* or *Abies*. Basidiomata under hardwoods show little basal felt, but more rhizomorphic strands of paler color (off-white). The larger basidiomata also have a tendency to produce longer spores without changes in the width.

A suite of characters marks the species. Basidioma stature is always stocky, even though shape seems to vary with substrate. Under *Picea* the stature is short, with congested branches and more or less spherical profile (Cotton and Wakefield 1919). Under *Pinus* its branches are much longer, and basidioma profile is almost fusiform. Additionally, basidiomata are always accompanied by a basal tomentum. The mat may be off-white (usually) to yellowish, and may dissipate into ill-defined rhizomorphic strands. The context is soft when fresh, not brittle, drying friable. The basidiomata are lightweight compared to other taxa. The reason may be the inflated hyphae. Even small basidiomata of *P. eumorpha* don't have the bluish green bruising reaction seen in the similar *P. ochraceo-virens*. Even poor basidiomata of *P. eumorpha* can be distinguished both fresh and dried from those of *P. ochraceo-virens*.

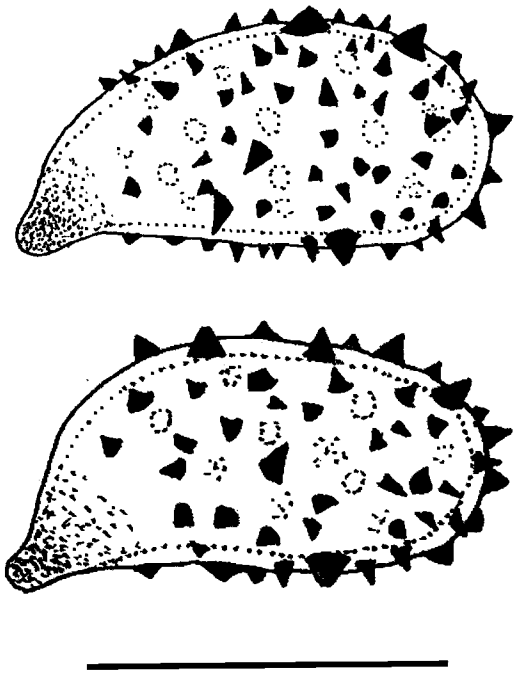


Figure 6.22. Spores (bar = 5 μm) of *Phaeoclavulina eumorpha* (P. Karst.) Giachini, *sp. prov.*

Phaeoclavulina flaccida* (Fr.) Giachini, *sp. prov. Fig. 6.23

≡*Clavaria flaccida* Fr., Systema Mycologicum 1:471. 1821.

≡*Clavariella flaccida* (Fr.) P. Karst. var. *flaccida*, Revue Mycologique 3:21. 1880.

≡*Ramaria flaccida* (Fr.) Bourdot var. *flaccida*, Revue Scientifique du Bourbonnais et du Centre de la France 11:235. 1898.

=*Clavaria abietina* Fr. f. *abietina*, Systema Mycologicum 1:469. 1821 (*non Clavaria abietina* Pers., Mycologia Europeae 1:164. 1822).

=*Clavaria crispula* Fr., Systema Mycologicum 1:470. 1821.

≡*Clavariella crispula* (Fr.) P. Karst., Revue Mycologique 3:21. 1880.

≡*Ramaria crispula* (Fr.) Quél., Flore Mycologique de la France, p. 464. 1888.

=*Clavaria decurrens* Pers. Mycologia Europeae 1:164. 1822.

≡*Ramaria decurrens* (Pers.) R.H. Petersen var. *decurrens*, Bibliotheca Mycologica 79:124. 1981.

=*Clavaria corrugata* P. Karst., Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar 9:371. 1868.

≡*Clavariella corrugata* P. Karst., Revue Mycologique 3:21. 1880.

≡*Clavaria abietina* f. *corrugata* (P. Karst.) Killerm., Denkschriften der Königlichen Bayrischen Botanischen Gesellschaft in Regensburg 15:113. 1922.

≡*Ramaria corrugata* (P. Karst.) Schild, Schweizerische Zeitschrift für Pilzkunde 53:130. 1975.

=*Clavariella flaccida* var. *dendroides* P. Karst., Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar 9:372. 1868.

=*Clavaria muscigena* P. Karst., Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar 9:373. 1868.

=*Clavaria abietina* f. *personii* Fr., Hymenomycetes Europaei Epicriseos Systematis Mycologici, 2 ed., p. 671. 1874.

=*Clavaria subdecurrens* Coker var. *subdecurrens*, The Clavarias of the United Sates and Canada, p. 172. 1923.

≡*Ramaria subdecurrens* (Coker) Corner var. *subdecurrens*, Annals of Botany Memoir 1:626. 1950.

=*Ramaria ligustri* Velen., Novitates Mycologicae, p. 162. 1939.

=*Ramaria fuscobrunnea* Corner, *in* Balfour-Browne, Bulletin of the British Museum of Natural History 1:200. 1955.

=*Ramaria flaccida* var. *longiramosa* Corner, Beihefte zur Nova Hedwigia 33:250. 1970.

=*Ramaria perfluo-punicea* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:100. 1988.

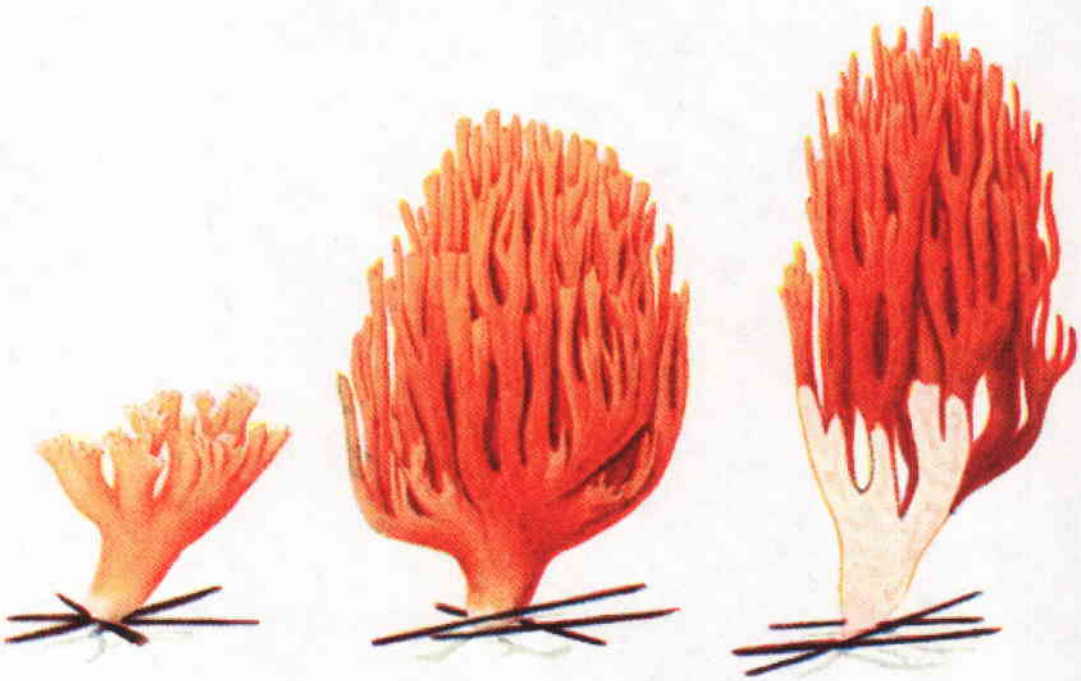
Macroscopic characters: **Basidiomata** 2.5-9 × 1.5-3.5 cm, ramarioid, repeatedly branched (Figure 6.23). **Branches** 1-2 mm thick, slender, erect, single or forked near apices, nodes mostly dichotomous, branches and apices golden yellow, orange, bruising green; axils subacute to narrowly rounded; apices awl-shaped, up to 20 × 1-3 mm, rounded to acute, generally dichotomous, golden yellow when young, finally paler to greenish. **Hymenium** decurrent, clearly unilateral, olive-brown. **Stipe** 10-30 × 6 mm, single, slender, ridged or grooved, white, becoming red-brown, then dark brown on exposure or bruising, with a conspicuous yellow-white to pale yellow basal tomental mat and mycelial strands, dried specimens pale yellow near the stipe base, otherwise entirely olive-brown. **Context** of branches coriaceous when fresh, drying brittle, paler than respective surface. **Odor** faintly earthy to sweet, fragrant when dry (*fide* Petersen 1981). **Taste** not distinctive to mildly bitter. **Spore print** brown.

Microscopic characters: **Branch context** of thin- to thick-walled, parallel, smooth, inflated, slightly cyanophilic hyphae 2.5-8 µm wide; clamp connections commonly swollen up to 8 µm, except in localized regions where they can enlarge up to 15 µm; gleoplerous hyphae present. **Stipe context** of interwoven hyphae, subparallel near the surface. Hyphae of both the rhizomorphs and tomentum up to 3 µm wide. **Subhymenial trama** of thin-walled, interwoven hyphae 2.5-3.5 µm wide; clamp connections present. Stellate aggregates present in trama. **Basidia** 25-45 × 5-6.5

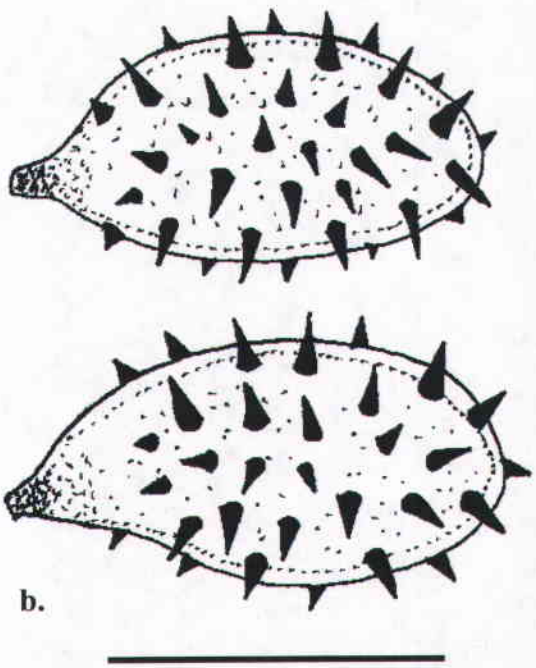
µm, clavate, with 4 straight, erect, long sterigmata not persisting after spore discharge; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 5-9 × 2.5-5.5 µm, golden yellow to pale orange in mass, obovoid to lacrimoid; ornamentation of cyanophilic spines 0.3-2 µm tall (Figure 6.23); apiculus distinctly oblique.

Habit, habitat and distribution: Growing solitary or gregarious on humus, litter or well-rotted wood in Argentina (Corner 1970), Australia, Austria (Corner 1970, Petersen 1981), Canada (Coker 1923, Petersen 1981), Congo (Corner 1970), Denmark (Petersen 1981), East Africa (Corner 1970), Finland (Karsten 1880, 1881, Petersen 1981), France (Bourdot 1898, Petersen 1981), Germany (Brinkmann 1897, Killermann 1922, Petersen 1981), Great Britain (Petersen 1981), Java (Corner 1970), New Zealand (Petersen 1988), Norway (Petersen 1981), Poland (Adamczyk 1996), Sweden (Petersen 1981), Switzerland (Schild 1975), and the USA (Coker 1923, Corner 1970, Petersen 1981).

Collections examined: **AUSTRALIA. NEW SOUTH WALES:** Riverina, Ashleigh Park Farm, North of Cobram, 3 June 2000, *R. Strömmer* (DAR 75197 – as *Ramaria* sp.); Riverina, Ringwood State Forest, N of Mulwala, SAND site 25, 4 June 2000, *J.M. Trappe 23179* (CANB – as *Ramaria abietina*); Wahgunyah State Forest Roadside, 26 June 2000, *J.M. Trappe 25334* (CANB – as *Ramaria abietina*). **AUSTRIA**. Salzburg, Ullandorf, 28 July 1904, *B578* (FH); Wiesenbei Hasissfaf, 6 October 1909, *B578* (FH); Vienna, Minningswald, 28 October 1906, *von Höhnel B569* (FH – as *Clavaria crispula*); Vienna, Trenensal, 4 September 1913, *v. Höhnel B580* (FH – as *R. abietina*), and 6 September 1903, *von Höhnel B580* (FH – as *C. abietina*). **BELGIUM**. Eastern Belgium, no location, 21 October 1972 (TENN 36912 – as *R. abietina*). **CANADA. NOVA SCOTIA:** Baddeck, 7 September 1963, *Harrison 63-2* (TENN – as *R. abietina*). No location, 14 September 1898 (NY). **DENMARK**. Allindelille Fredskov, 24 September 1970 (TENN 36528 – as *R. decurrens*); Aunstrup, Aunstrup Forest, 22 September 1970 (TENN 36563 – as *R. abietina*); Kristiansminde, Soro, 21 September 1970 (TENN 36527). **FINLAND**. Mustiala, November 1878, *P.A. Karsten* (NY); Mustiala, September 1890, *P.A.*



a.



b.

Figure 6.23. *Phaeoclavulina flaccida* (Fr.) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 5 μm). Drawings of basidiomata modified from Corner (1950).

Karsten (NY). **FRANCE.** Caen, no date, ex. Herb. Curtis, *Lenormand* (FH – as *C. abietina*); Jura, Poligny, October 1882, *N.T. Patouillard 2416* (NY). **SWEDEN:** Location unknown, no date, *E.M. Fries* (FH – as *Clavaria flaccida*). **STOCKHOLM:** Starrbäcken, 3 September 1889, *L. Romell* (S – as *R. abietina*); Ugglevіksskogen, 8 December 1907, *L. Romell 5811* (S – as *R. abietina*); Uppsala, no date, *E.M. Fries*, ex Herb. Berkeley (FH - photograph). **SWITZERLAND**. Brienz, 9 September 1972 (TENN 36809 – as *R. abietina*). **UNITED STATES. MAINE:** No location, no date, *Sprague 276,900* (FH – as *C. abietina*). **NEW YORK:** Washington Co., Vaughn's, Burnham's woods, 2 September 1917, *W.C. Coker and R.C. Burnham 101* (NCU – holotype of *C. subdecurrens*). **WASHINGTON**: Pierce Co., Mt. Rainier Nat. Park, Lower Tahoma Creek, 17 October 1954, *A.H. Smith 49081* (TENN – as *R. abietina*).

Discussion: Besides the collections examined this description was also based on notes from Balfour-Browne (1955), Bourdot (1898), Coker (1923), Corner (1950, 1957, 1970), and Petersen (1981, 1988). The type collection for *Ramaria flaccida* is missing, as pointed out by Petersen (1981). However, one collection made by Fries is still available and is deposited at the Farlow Herbarium (FH) at Harvard University, and is here designated as the neotype for *P. flaccida* (FH – as *Clavaria flaccida* – **neotype**).

This species has 13 different synonyms (Giachini, chapter 2). Fries (1821) described *Clavaria flaccida, Clavaria crispula,* and *Clavaria abietina*, thereby sanctioning all three epithets. The question now lies on which one to use. Even though Corner (1950) and Petersen (1981) did not consider the 3 above-mentioned names to be the same species, they provided insightful discussions regarding the nomenclatural history associated with those names. Corner (1950) explained the reason why the epithet '*abietina*' could not be used for this species (for further details see the description of *P. ochraceo-virens*). Petersen (1981) presented his reasoning behind rejecting '*crispula*' as the correct epithet for the species. His explanation basically revolved around the fact that what Fries (1821) called '*crispula*' could easily embrace several taxa, including *Clavaria flaccida* (≡*P.*

flaccida), *C. myceliosa* (=*P. curta*), *C. decurrens* (=*P. flaccida*), and *Ramaria roellinii* (≡*P. roellinii*). Moreover, in light of the ambiguity of the species concepts of *C. flaccida* and *C. abietina*, it would be surprising if only one taxon was represented by the name *C. crispula*. Petersen (1981) treated the name as a *nomen dubium*. Giachini (chapter 2) considered the above names to be synonyms, and for reasons of priority in accordance with the International Code of Botanical Nomenclature (Greuter *et al.* 2000) adopted the epithet '*flaccida*' as the accepted name for the species, therefore rejecting *'abietina'* and '*crispula*' for the reasons explained above.

Phaeoclavulina flaccida is distinguished from *P. ochraceo-virens* and *P. curta* by its golden yellow to orange, non-bruising basidiomata and its more grossly spiny spores.

Phaeoclavulina gigantea* (Pat.) Giachini, *sp. prov. Fig. 6.24

≡*Lachnocladium giganteum* Pat., Journal de Botanique 3:34. 1889.

≡*Ramaria gigantea* (Pat.) R.H. Petersen f. *gigantea*, Bibliotheca Mycologica 79:66. 1981.

=*Lachnocladium olivaceum* Henn., Hedwigia 36:196. 1897a.

=*Lachnocladium echinosporum* Bres., Annales Mycologici 9:551. 1911.

=*Ramaria zippelii* var. *gracilis* Corner, Annals of Botany Memoir 1:635. 1950.

=*Ramaria gigantea* f. *tenuispora* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:97. 1988.

Macroscopic characters: **Basidiomata** up to 16 × 7 cm, ramarioid, repeatedly branched (Figure 6.24). **Branches** up to 10 cm long, 1-7 mm thick below, ascending, generally dichotomous at first, generally rather loose and spreading, cinnamon to olive-brown; internode length diminishing gradually distally; axils rounded, usually dichotomous, especially above; apices slender, up to 20 mm long, bifurcating with subacute axils, abruptly tapered, abruptly white. **Hymenium**

amphigenous. **Stipe** 5-80 × 2-8 mm, tapering downward, tomentose throughout its length, grooved upward. **Context** white, bruising vinaceous (not in all specimens), in some cases black-brown. **Odor** in general absent. **Taste** weakly bitter. **Spore print color** not recorded.

Microscopic characters: **Branch context** of thin-walled, parallel, agglutinated hyphae; clamp connections present. **Basidia** up to 100 × 8-11 μm, clavate, with (2-) 3-4 stout, conical and incurved sterigmata 6-7 μm long and persistent after spore discharge. Hymenial **cystidia** absent. **Spores** 7-10 (-14) × 4.5-6.5 (-8.5) μm, cinnamon to orange in mass, ellipsoid to obovoid; ornamentation of cyanophilic spines 0.5-1.0 (-2.5) μm tall (Figure 6.24); data on apiculus absent.

Habit, habitat and distribution: On the ground in forests in Borneo (Corner 1950, Petersen 1981), Brazil (Petersen 1981), French Guiana (Petersen 1981), Gabon (Petersen 1981), Malaysia (Corner 1950, Petersen 1981), Martinique (Petersen 1981), New Zealand (Petersen 1988), Puerto Rico (Petersen 1981), Singapore (Corner 1950), and the USA (Petersen 1981).

Collections examined: **BRAZIL. RIO DE JANEIRO:** no location, March 1884, *E. Ule 114* (S – as *Lachnocladium olivaceum*). **BAHAMA ISLANDS. NASSAU:** New Providence, no date, *J.K. Brace* (NY – as *Clavaria abietina*). **FRENCH GUIANA:** Maroni, no date, *Melinon 109* (FH – as *Lachnocladium giganteum* – **holotype**). **GABON. LIBREVILLE:** no location, 7 September 1971, *G. Gilles 68* (PC), and no location, no date, *G. Gilles 86* (PC). **MARTINIQUE:** No location, July 1972, ex. Herb. LY (TENN).

Discussion: This species resembles *P. zippelii*. The only morphological difference appears in the spores, which are smaller than those of *P. zippelii*, and on the number of sterigmata, mostly 2 for *P. zippelii* while mostly 4 for *P. gigantea*.

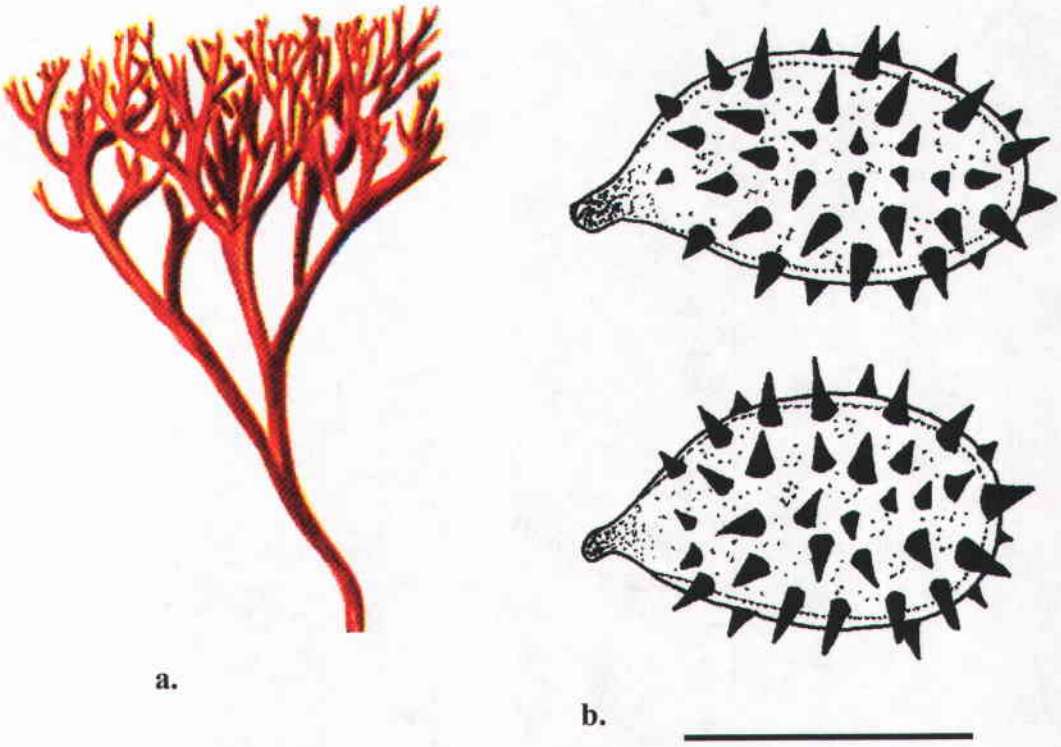


Figure 6.24. *Phaeoclavulina gigantea* (Pat.) Giachini, *sp. prov.*: (a) basidiomata (× 0.5); (b) spores (bar = 10 μm). Drawings of basidiomata modified from Corner.

Phaeoclavulina glauco-aromatica* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.25

≡*Ramaria glauco-aromatica* R.H. Petersen, Bibliotheca Mycologica 79:141. 1981.

Macroscopic characters: **Basidiomata** up to 15 × 5 cm, ramarioid, repeatedly branched. **Branches** ascending, re-branched into 3-6 ranks, orange-green when fresh, becoming watery where handled and then changing color to olive-green, remaining olive-green on drying; axils acute; apices acute, dichotomous to trichotomous, yellow to creamy yellow. Data on **hymenium** configuration not recorded. **Stipe** up to 15 mm thick, white and cottony below substrate level, remaining so after drying, upward orange-olive, staining intense blue-green when handled, slowly changing to dark olive on exposure. Data on **context** not recorded. **Odor** none to moderate, occasionally strong, resembling that of anise on drying. **Taste** mildly bitter. **Spore print** yellow-brown.

Microscopic characters: **Branch context** of thin-walled, generally parallel, hyaline hyphae 2.5 µm wide; clamp connections present, ampulliform clamps up to 15 µm. Basal tomentum of thin-walled, hyaline hyphae 1.5-2.5 µm wide; clamp connections present, ampulliform clamps up to 12 µm. Complicated stellate crystalline material often found in basal tomentum. **Basidia** 55-65 × 6.5-7.5 µm, clavate, hyaline when immature, with (3-) 4 delicate, divergent, sometimes incurved sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 8-11.5 × 4-5.5 µm, orange in mass, ellipsoid to obovoid; ornamentation of numerous, scattered, cyanophilic warts or blunt spines up to 1 µm tall but normally shorter, usually about 0.5-1 µm tall (Figure 6.25); apiculus slender, often somewhat curved.

Habit, habitat and distribution: On conifer litter in western North America, from New Mexico to Alberta – Canada (Petersen 1981).

Collections examined: **CANADA. ALBERTA**: Calgary, Brown Lowery Nat. Area, 26 August 1973, Daniels 1111 (TENN). **UNITED STATES. IDAHO**: Boundary Co., 3.5 miles North of upper Priest River, 25 September 1968, *R.H. Petersen*

(TENN 34144). **NEW MEXICO:** Otero Co., Lincoln Nat. Forest, Silver Springs Canyon, 24 August 1968, *Larsen 2993* (TENN 34625).

Discussion: The loan of the type for this species was not granted. Therefore, this description was based on other collections examined and the notes from Petersen (1981).

This species is readily recognizable by its intense blue-green stains at the base of the basidiomata, usually right above the white stipe base. Only a few minutes after picking the entire basidioma stains dark green-olive, except for the stipe base, which remains white. The stipe base is quite large but not as pronounced as for *P. africana.*

Corner (1950) and Petersen (1981) suggested the species to be closely related to *P. ochraceo-virens* and *P. echinovirens.* It differs from those two species based on three main characters: (a) the basidiomata context of *P. glauco-aromatica* is not especially virescent, only the stipe and branch surfaces; (b) *P. echinovirens* is reported from *Quercus*, while *P. glauco-aromatica* is known from coniferous forests; and lastly (c) the spores of *P. echinovirens* are slightly larger but narrower than those of *P. glauco-aromatica.* Petersen (1981) added that these species, which are obviously close related, make up an interesting distributional pattern, ranging from the Himalayas to the European Alps, all the way to the North American Rockies.

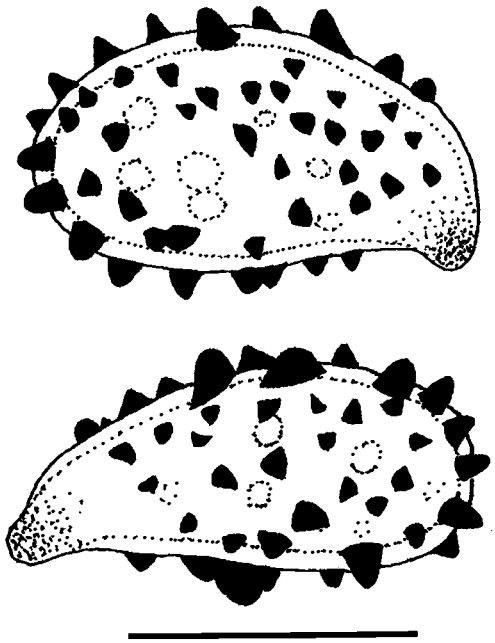


Figure 6.25. Spores (bar = 5 µm) of *Phaeoclavulina glauco-aromatica* (R.H. Petersen) Giachini, *sp. prov.* Modified from Petersen (1981), with permission.

Phaeoclavulina griseobrunnea* (Singer) Giachini, *sp. prov. Fig. 6.26

≡*Ramaria griseobrunnea* Singer, *in* Singer *et al.*, Beihefte zur Nova Hedwigia 77:19. 1983.

Macroscopic characters: **Basidiomata** up to 11 cm tall, ramarioid, repeatedly branched. **Branches** erect, repeatedly and dichotomously branched, branches cylindrical or slightly flattened with membranous extensions (*fide* Singer *et al.* 1983), gray; tips acute, gray. Data on **hymenium** configuration and **stipe** not recorded. **Context** tough. **Odor** none. **Taste** not recorded. **Spore print color** not recorded.

Microscopic characters: **Branch context** of thin-walled, parallel hyphae; clamp connections present. **Basidia** (19-) 30-46 × (6.5-) 8-10 µm, with 2 sterigmata 8 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 12-15 × 8-9.5 µm, orange in mass, obovoid, cyanophilic; ornamentation of cyanophilic spines 1-2 µm tall (Figure 6.26); data on apiculus not recorded.

Habit, habitat and distribution: With caespitosely aggregate bases, on sandy soil in tropical forest in Pará, in the Brazilian Amazon (Singer *et al.* 1983).

Type (holotype): **BRAZIL. PARÁ:** Estância Pirelli, 7 June 1966, *R. Singer B 4216* (BAFC – as *Ramaria griseobrunnea*).

Discussion: The herbarium BAFC was contacted for loan of the type for this species but no answer was ever obtained. Therefore, this description was based on notes from Singer *et al.* (1983).

This species is close to *P. zippelii*. They share same overall characteristics, such as 2-spored basidia, but the basidiomata, and more importantly, the tips of *P. griseobrunnea* are not white as in *P. zippelii*. *Phaeoclavulina zippelii* also has larger spores than *P. griseobrunnea*. According to Singer (Singer *et al.* 1983), who described the species, it may be ectomycorrhizal with unknown tree hosts in the Brazilian Amazon forests of the igapó type – forests that are flooded by typically black-water rivers for extended periods (4-10 months).

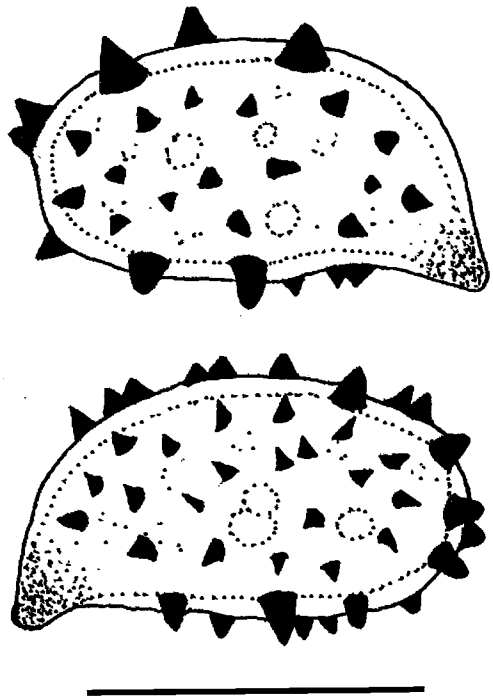


Figure 6.26. Spores (bar = 10 µm) of *Phaeoclavulina griseobrunnea* (Singer) Giachini, *sp. prov.*

Phaeoclavulina guyanensis* (Pat.) Giachini, *sp. prov. Fig. 6.27

≡*Lachnocladium guyanense* Pat., Journal de Botanique 3:35. 1889.

≡*Ramaria guyanensis* (Pat.) Corner, Annals of Botany Memoir 1:596. 1950.

=*Lachnocladium leucoceras* Pat., Journal de Botanique 3:33. 1889.

≡*Ramaria leucoceras* (Pat.) Corner, Annals of Botany Memoir 1:600. 1950.

Macroscopic characters: **Basidiomata** 5-10 × 4 cm, ramarioid, repeatedly branched (Figure 6.27). **Branches** not over 2 mm thick, upright, extremely slender and gracile, flattened, dichotomous to irregularly branched, surface rugulose, pale yellow-brown then dark brown to cinnamon; internodes up to 15 mm long; axils rounded; tips erect, rounded, prolonged, divergent, whitish. **Hymenium** clearly unilateral, rugulose. **Stipe** 20-30 × 1.5-2 mm, slender, probably straight when fresh and then also probably rooting (*fide* Petersen 1981). Data on **context**, **odor**, and **taste** not recorded. **Spore print** brown.

Microscopic characters: **Context** of thin- to slightly thick-walled, compactly parallel, closely packed hyphae 3-8 µm wide, slightly inflated, especially near the septum; clamp connections present. **Basidia** 40-50 × 5.5-11 µm, with 2 stout, slightly divergent, slightly curved sterigmata 6-8 µm long. Hymenial **cystidia** absent. **Spores** 7-10 × 4-6.5 µm, orange in mass, obovoid; ornamentation of rounded, cyanophilic spines up to 1.5 µm tall (Figure 6.27); data on apiculus not recorded.

Habit, habitat and distribution: Solitary, gregarious or caespitose, on the ground in forests in Brazil (Corner 1970, Rick 1931), French Guiana (Corner 1950), Guadeloupe (Corner 1950), Jamaica (Corner 1970), and Panama (Corner 1970).

Collections examined: **FRENCH GUIANA:** Maroni, no date, *Melinon 84* (FH – as *Lachnocladium guyanense* – **holotype**).

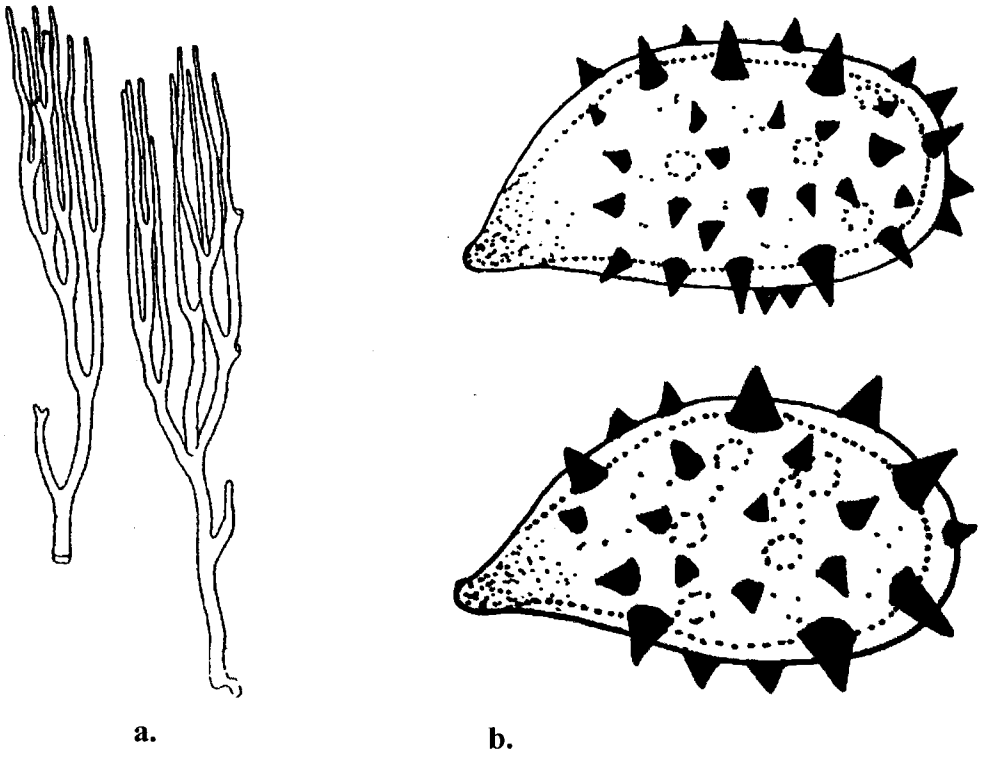


Figure 6.27. *Phaeoclavulina guyanensis* (Pat.) Giachini, *sp. prov.*: (a) basidiomata (× 0.5); (b) spores (bar = 10 μm). Basidioma drawings modified from Petersen (1981), with permission.

Discussion: Corner (1950) described *Ramaria guyanensis, R. leucoceras*, and *R. longicaulis*. Later he synonymized *R. longicaulis* to *R. guyanensis*, but doubted in doing so for *R. leucoceras* (Corner 1970). Further analyses of the species descriptions suggested *R. guyanensis* and *R. leucoceras* to be synonyms, and *R. longicaulis* to be a separate species (Giachini, chapter 2). Both *Lachnocladium leucoceras* (≡*R. leucoceras*) and *L. guyanense* (≡*R. guyanensis*) were proposed by Patouillard (1889) in the same volume of the 'Journal of Botanique.' Therefore, the adopted epithet for the species could be either *guyanensis* or *leucoceras*. The slender stature, unilateral hymenium and slender branches suggest it to be close related to *P. gigantea*, *P. insignis,* and *P. longicaulis*.

Phaeoclavulina insignis* (Pat.) Giachini, *sp. prov. Fig. 6.28

≡*Lachnocladium insigne* Pat., Journal de Botanique 3:34. 1889.

≡*Ramaria insigne* (Pat.) R.H. Petersen, Bibliotheca Mycologica 79:77. 1981.

Macroscopic characters: **Basidiomata** up to 15 × 6 cm, ramarioid, repeatedly and usually dichotomously branched, all parts slender (Figure 6.28). **Branches** up to 7 cm long, 3 mm thick, branching dichotomously, brown, nearly black when dry; axils rounded; apices prolonged (up to 15 mm long), slender, ascending, pale yellow. **Hymenium** unilateral, fertile surface smooth, brown, sterile inner surface ferruginous. **Stipe** up to 70 × 3 mm, slender, curved, tomentose, off-white where protected, brown elsewhere. Data on **context**, **odor**, **taste,** and **spore print color** not recorded.

Microscopic characters: **Branch context** of thin-walled, compactly parallel, agglutinated hyphae; clamp connections present. **Basidia** with 2 stout, conical, divergent sterigmata. Hymenial **cystidia** absent. **Spores** 9.5-11 × 6-7.5 μm, obovoid; ornamentation of acute, conical, cyanophilic spines up to 1.5 μm tall, usually scattered on the surface of the spores but sometimes in spiraling rows (Figure 6.28); apiculus prominent, conical-rounded, eccentric.

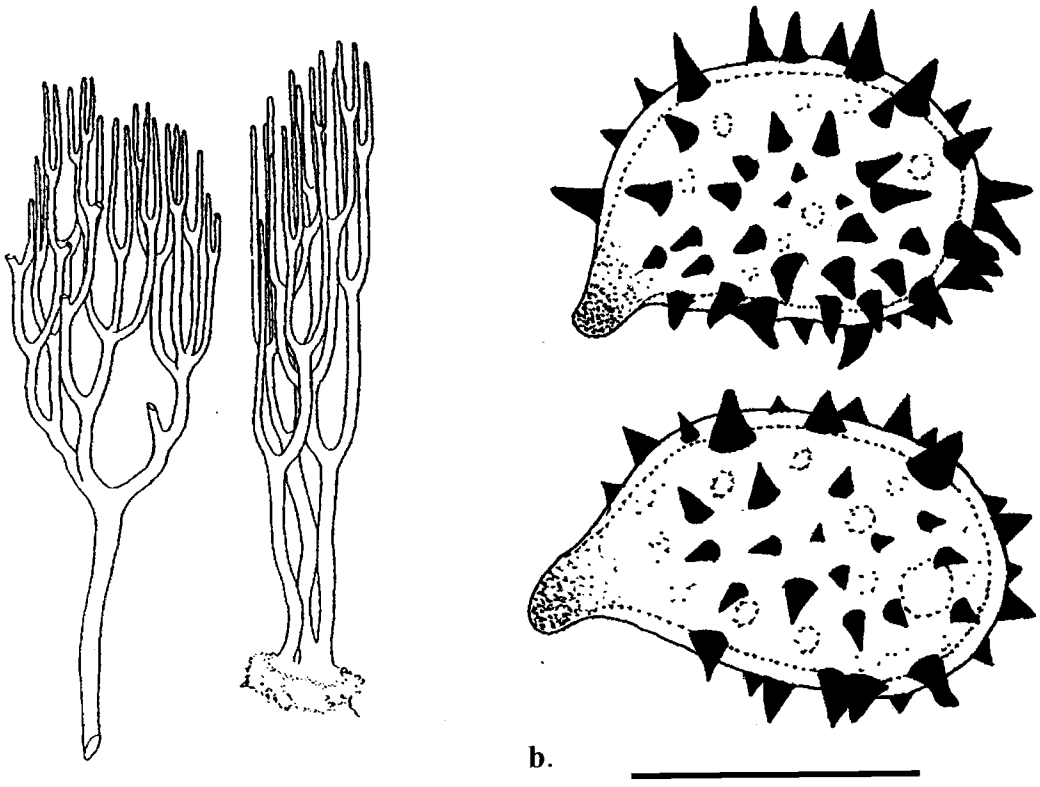


Figure 6.28. *Phaeoclavulina insignis* (Pat.) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 5 μm). Drawing of basidiomata and spores modified from Petersen (1981), with permission.

Habit, habitat and distribution: On moist soil and litter in the Caribbean and tropical Central and South America (Petersen 1981).

Collections examined: **COSTA RICA:** Koreai, January 1924, ex. herb. Doty (TENN 31760, 32303 – as *Ramaria insigne*). **FRENCH GUIANA**: Maroni, no date, *Melinon 104* (FH – as *Lachnocladium insigne* – **holotype**).

Discussion: According to Petersen (1981) this species is similar to *Ramaria leucoceras* (≡*P. guyanensis*), from which it differs in larger spores and larger basidiomata. Both species are denoted by their slender parts, including the stipe, which hardly appears adequate to hold up the basidioma. Corner (1950) synonymized Patouillard's *Lachnocladium insigne* to *Ramaria cyanocephala* probably due to the slender stature of the basidiomata. However, the characteristic pale yellow apices have never been attributed to *L. insigne*, and the type bears little resemblance to *R. cyanocephala*.

Phaeoclavulina longicaulis* (Peck) Giachini, *sp. prov. Fig. 6.29

≡*Clavaria longicaulis* Peck, Bulletin of the Torrey Botanical Club 25:371. 1898.

≡*Ramaria longicaulis* (Peck) Corner, Annals of Botany Memoir 1:600. 1950.

Macroscopic characters: **Basidiomata** up to 10 × 4 cm, ramarioid, repeatedly branched (Figure 6.29). **Branches** up to 5 mm thick, in 2-5 ranks, divergent then erect, cylindrical, gray-brown, becoming paler upward; axils rounded; tips rounded-acute, divergent, up to 1 cm long at maturity, often Y-shaped, creamy brown when young, concolorous with branches when mature. **Hymenium** obscurely unilateral when fresh (*fide* Petersen 1981), obscurely to obviously unilateral when dry; fertile area smooth, waxy; sterile areas randomly scattered above, more regularly on inner sides of branches and decurrent from axils below, darker than fertile areas, often appearing minutely wooly or granular from adhered spores (*fide* Petersen 1981). **Stipe** up to 70 × 7 mm, solid, often rooting up to 3 cm

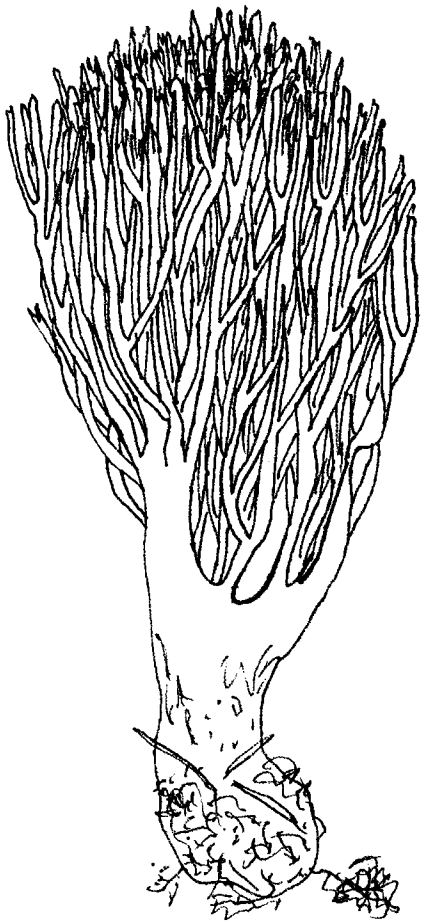
deep, arising from thread-like, white rhizomorphs, white where protected, bruising vinaceous brown. **Context** whitish or cinnamon, in some cases bruising vinaceous. **Odor** none to very mild, sweet, like *Ramaria stricta*. **Taste** bitter, astringent. **Spore print** yellow-brown.

Microscopic characters: **Context** of thin-walled, strictly parallel, closely packed hyphae 1.5-6 µm wide; ampulliform clamps thin-walled, common, up to 12 µm wide; gleoplerous hyphae occasional, generally swollen distally, not delimited by clamps. **Basidia** 42-50 × 6.5-7.5 µm, clavate, with (2-3-) 4 stout, slightly divergent, slightly incurved sterigmata, 5.5 µm long and persisting after spore discharge; clamp connections present. Hymenial **cystidia** not observed. **Spores** 7.5-11 × 4.5-7 µm, yellow-brown in mass, ellipsoid to obovoid; ornamentation of scattered long (up to 3 µm long), acute, cyanophilic spines becoming smaller toward the apiculus (Figure 6.29); apiculus a short, thin-walled extension of endosporium protruding from an eccentric collar of exosporium (*fide* Petersen 1981).

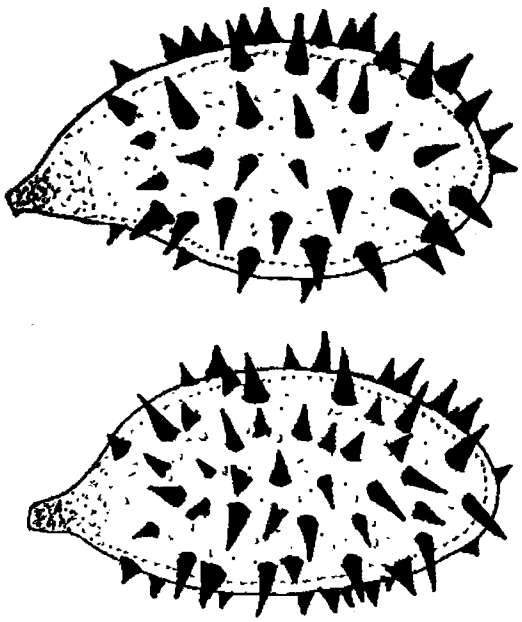
Habit, habitat and distribution: In humus under deciduous and conifer forests in the USA (Alabama, Colorado, Massachusetts, and the southern Appalachian Mountains).

Collections examined: **UNITED STATES. ALABAMA:** Commission Co., Auburn, no date, ex. Herb. Peck, *F.S. Earle* (NYS – as *Clavaria longicaulis* – **holotype**; isotype at CUP). **NORTH CAROLINA:** Macon Co., Coweeta Hydrol. Lab., 15 August 1971 (TENN 36154). **TENNESSEE:** Blount Co., Great Smoky Mountains Nat. Park, Ekanetlee Trail, 20 August 1968 (TENN 33826), and 12 August 1969 (TENN 34660).

Discussion: Superficially, *P. longicaulis, P. eumorpha,* and *P. pancaribbea* appear similar in the field (Petersen 1981). The first, however, exhibits gray-brown branches and tips and usually a white pseudorhiza that bruises vinaceous brown. *Phaeoclavulina eumorpha* shows golden yellow to brown branch tips. *Phaeoclavulina pancaribbea* has brown branch tips, often with blue or blue-green tones.



a.



b.

Figure 6.29. *Phaeoclavulina longicaulis* (Peck) Giachini, *sp. prov.*: (a) basidiomata (× 2); (b) spores (bar = 10 μm).

With its long-stemmed stature, unilateral hymenium and slender branches, supported by geographical data, *P. longicaulis* likely is a relative of some of the neotropical taxa, i.e. *P. insignis, P. gigantea, P. pancaribbea*, etc.

Corner (1970) synonymized *R. longicaulis* with *R. guyanensis* (≡*P. guyanensis*). However, the type of *P. guyanensis* has basidia with only 2 sterigmata. Additionally, the basidiomata of *P. guyanensis* are relatively much more gracile than those of *P. longicaulis*. Accordingly, Petersen (1981) stated, "when the two are viewed at the same time, there is no difficulty with their separation." The species also resemble *P. zippelii* (Corner 1950).

Phaeoclavulina macrospora **Brinkmann,** Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst 25:198. 1897, *emend.* Giachini, *emend. prov.* Fig. 6.30

≡*Ramaria macrospora* (Brinkmann) Corner, Annals of Botany Memoir 1:603. 1950 (*non Ramaria macrospora* Velen., Opera Botanica Čechica 4:90. 1947).

=*Clavaria broomei* Cotton & Wakef., Transactions of the British Mycological Society 6:170. 1919.

≡*Phaeoclavulina broomei* (Cotton & Wakef.) Overeem, Bulletin du Jardin Botanique de Buitenzorg 3(5):277. 1923.

≡*Ramaria broomei* (Cotton & Wakef.) R.H. Petersen, Bibliotheca Mycologica 79:53. 1981.

=*Ramaria nigrescens* (Brinkmann) Donk var. *nigrescens*, Bibliotheca Mycologica 21:104. 1933 [*nom. illeg.*, *sensu* Coker, The Clavarias of the United States and Canada, p. 187, *in. obs.* 1923].

=*Ramaria nigrescens* var. *americana* Corner, Annals of Botany Memoir 1:608. 1950.

≡*Ramaria americana* (Corner) R.H. Petersen, Bibliotheca Mycologica 79:48. 1981.

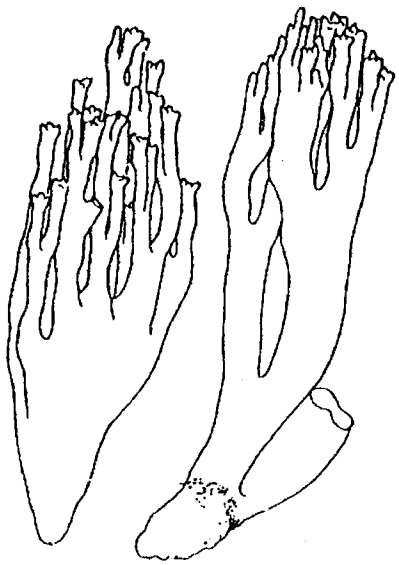
Macroscopic characters: **Basidiomata** 3-8 × 2-4 cm, ramarioid, repeatedly branched (Figure 6.30). **Branches** numerous, irregular, suberect, the larger branches rugulose, orange, cinnamon with age, turning brown soon after bruising; axil tips flattened; tips orange to cinnamon. **Hymenium** amphigenous, smooth. **Stipe** 20-50 × 2-4 mm, white, with white mycelium at the base. **Context** rather tough, white, becoming vinaceous on bruising, especially in the stipe, blackening on drying. **Odor** not recorded. **Taste** bitter. **Spore print** ferruginous.

Microscopic characters: **Branch context** of tightly parallel hyphae 1.5-3 µm wide, yellow in mass; clamp connections present. Other **hyphae** thin-walled, compactly parallel, 3-6 µm wide, with inflated ends up to 12 µm; clamp connections present. **Basidia** 32-50 × 6.5-9 µm, with (2-) 4 slender, straight, slightly divergent sterigmata; clamp connections present at base. Hymenial **cystidia** absent. **Spores** (12.5-) 14-20 (-22) × 4.5-8 µm, dark orange in mass, obovoid to lacrimoid; ornamentation of discrete, cyanophilic spines up to 2.5 µm tall (Figure 6.30); data on apiculus not recorded.

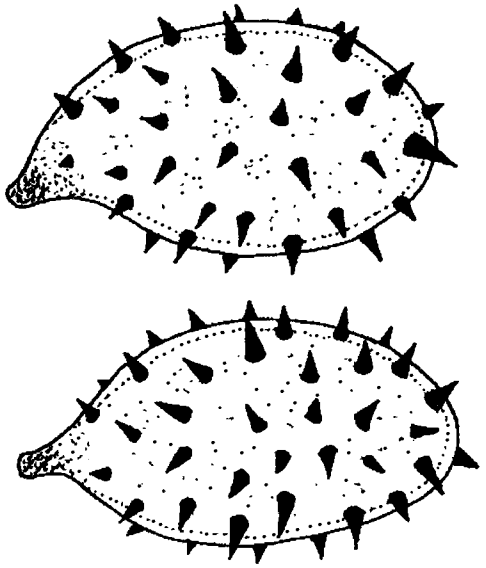
Habit, habitat and distribution: Solitary or gregarious, on the ground in forests in Europe (Brinkmann 1897, Cotton and Wakefield 1919, Donk 1933), Japan (Corner 1950), and the USA (Coker 1923, Corner 1950, Petersen 1981).

Collections examined: **GERMANY. WESTFALIA**: Lenginisch, no date, ex. Herb. Bresadola, no. 16 (NCU – as *Ramaria macrospora* – **holotype**). **SWITZERLAND**: Brienz, 25 August 1974, *E. Schild and R.H. Petersen* (TENN 39938). **UNITED STATES. NEW YORK:** Washington Co., Vaughn's Woods, 1 October 1911, *R.C. Burnham* (NCU – as *Clavaria broomei*), 13 August 1915, *R.C. Burnham 74* (NCU – holotype of *C. broomei*; portion at NY and CUP 28485), and 13 September 1919, *R.C. Burnham* (CUP 28456). No location, 15 October 1909, *H. Murray 287* (K – as *C. broomei*; portion at NY).

Discussion: This description was also based on notes from Corner (1950), Cotton and Wakefield (1919), Overeem (1923), and Petersen (1981).



a.



b.

Figure 6.30. *Phaeoclavulina macrospora* (Brinkmann) Giachini, *sp. prov.*: (a) basidiomata (× 0.2); (b) spores (bar = 10 μm). Drawing of basidiomata modified from Petersen (1981), with permission.

Corner (1950) separated *Ramaria nigrescens* var. *americana* from *R. nigrescens* by having 4 instead of 2 sterigmata. Later Petersen (1981) used the description of Corner (1950) and raised the rank of the variety to species. After carefully examining the descriptions for those species, Giachini (chapter 2) considered them to be synonyms because of the overall similar microscopic characteristics, such as size and shape of the spores, and hyphal construction. Main features unique to this species are the brown to red basidiomata in conjunction with the large echinulate spores.

Phaeoclavulina mutabilis* (Schild & R.H. Petersen) Giachini, *sp. prov. Fig. 6.31

=*Ramaria mutabilis* Schild & R.H. Petersen, *in* R.H. Petersen, Bibliotheca Mycologica 79:149. 1981.

Macroscopic characters: **Basidiomata** up to 16 × 10 cm, ramarioid, repeatedly branched, of variable stature, from fusiform to wide ovate in profile. **Branches** in several ranks, up to 5 mm thick, ascending to erect, usually flattened laterally or with longitudinal grooves or ridges, all branches extremely fragile on drying, pale yellow-brown, olive-brown to green; axils rounded; apices about 1 mm long and wide, straight, digitate, creamy yellow-green to orange. **Hymenium** irregularly unilateral, sterile areas on inner or upper branch surfaces, especially above axils. **Stipe** 2-20 mm long, usually grooved or ridged longitudinally as continuations of the major branches, white below from basal mycelium, brown to olive-brown above, occasionally with definite green tones, especially in large basidiomata, slowly bruising red-brown when handled; base 3-30 mm wide, dissipating into a mass of white mycelium and rhizomorphs extending up to a few centimeters from the basidioma; rhizomorphs and mycelium fragile, occasionally discrete and rope-like, remaining off-white after drying, bruising brown in limited areas. Data on **context** not recorded. **Odor** mild, farinaceous to fragrant. **Taste** variable, from musty to bitter or acrid. **Spore print** yellow-brown.

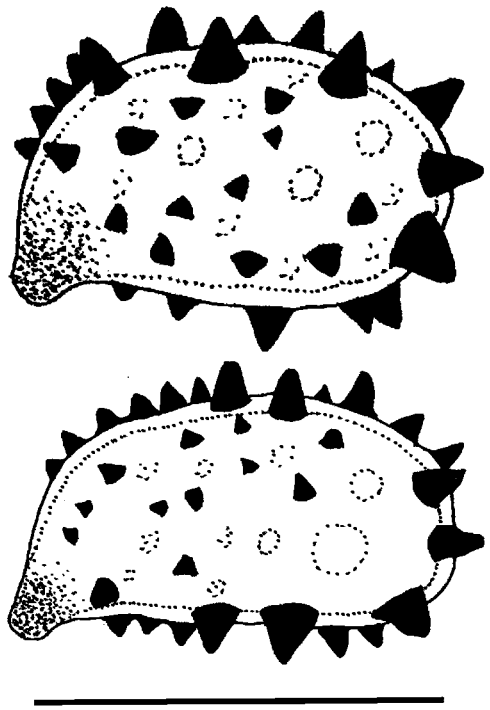


Figure 6.31. Spores (bar = 5 µm) of *Phaeoclavulina mutabilis* (Schild & R.H. Petersen) Giachini, *sp. prov.* Spore drawings modified from Petersen (1981), with permission.

Microscopic characters: **Branch context** of thin-walled, loosely parallel, inflated, hyaline hyphae 1.5-7 µm wide; clamp connections present. Hyphae of rhizomorphs thin-walled, 1.5-3 µm wide; clamp connections present, with thin- to thick-walled ampulliform clamp connections up to 12 µm. **Basidia** 40-55 × 5-6 µm, narrowly clavate, hyaline to pale yellow, not persistent after spore discharge; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 5.5-7.5 × 3-4 µm, dark yellow in mass, ellipsoid to obovoid; ornamentation of scattered, acute, cyanophilic spines ≤0.5 µm tall (Figure 6.31); apiculus eccentric, rounded.

Habit, habitat and distribution: In conifer forests from western and northern North America to central Europe (Petersen 1981). Possibly also in similar habitats in the Himalayas.

Collections examined: **CANADA. BRITISH COLUMBIA**: Sheep Lake, 3 October 1966 (TENN 32231). **INDIA.** Himachal Pradesh, Dharamsala, McLeon Ganj, 7 September 1966, *Pui 4951, 4952* (TENN 37647, 37671 – as *R. flaccida*); Himachal Pradesh, Dalhousie, Lakkarmandi, 8 September 1963, *Pui 233* (TENN 36965 – as *R. flaccida*); Jammu and Kashmir, Sanasar, 10 August 1967, (TENN 36985, 37673 – as *Ramaria flaccida*). **SWITZERLAND**: Brienz, Bauwald, Axalp, 10 September 1974, *E. Schild and R.H. Petersen 787* (TENN 39893 – as *Ramaria mutabilis* – **Isotype**). **UNITED STATES. CALIFORNIA:** Santa Cruz Co., San Lorenzo Valley, 18 January 1967 (SFSU 1109, TENN 36411). **IDAHO**: Boundary Co., 1.5 mi. S Upper Priest River Rd., 1 October 1968 (TENN 34237, 34239, 34240, 34241, 34273. **OREGON**: Benton Co., Wren, 21 February 1938, *W.C. Cooke 9985* (TENN); Linn Co., Peoria Road, 30 January 1938, *W.C. Cooke 9947* (TENN – as *Clavaria myceliosa*). **WASHINGTON**: Mason Co., Baker Lake, 1 September 1941, *A.H. Smith 16562* (TENN).

Discussion: This seasonal fruiter of the northern countries has probably been classified under other names in the past. It resembles *P. flaccida*, with hyphae virtually the same, although spores are slightly smaller. The fresh basidiomata of *P. mutabilis* always include some olivaceous tones with the basic brown coloration, which can be maintained or lost upon drying. The hymenium configuration is

unique. In all other species the sterile portions are most pronounced in the axils, proceeding down the branches, often narrowing downward as fertile tissue encroaches. In *P. mutabilis*, however, the sterile area often proceeds up the branches from the axils until closed gradually by fertile tissue. According to Petersen (1981) this is by no means invariable, but it is unexplained.

Hyphal construction, hymenium configuration, and spore features all seem to relate *P. mutabilis* to *P. curta*. *Phaeoclavulina curta*, however, has smaller spores and basidiomata growing on angiosperm substrate, although it seems to share the same distribution as *P. mutabilis* in northern Europe and northeastern North America.

Phaeoclavulina ochracea* (Bres.) Giachini, *sp. prov. Fig. 6.32

≡*Lachnocladium ochraceum* Bres., *in* Bresadola and Saccardo, Bulletin de la Société Royale de Botanique de Belgique 38:157. 1899.

≡*Ramaria ochracea* (Bres.) Corner var. *ochracea*, Annals of Botany Memoir 1:610. 1950.

=*Clavaria intricatissima* Speg., Anales del Museo Nacional de Buenos Aires 19:279. 1909.

≡*Ramaria intricatissima* (Speg.) Corner, Annals of Botany Memoir 1:598. 1950.

=*Ramaria luteo-flaccida* Corner, Annals of Botany Memoir 1:601. 1950.

=*Ramaria flaccida* var. *chilensis* Lazo, Mycologia 64:73. 1972.

=*Ramaria ochracea* var. *sicco-olivacea* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:98. 1988.

Macroscopic characters: **Basidiomata** up to 5.5 × 3.5 cm, ramarioid, delicately branched (Figure 6.32). Major and minor **branches** all less than 3 mm thick, ascending, in 5-6 ranks, orange when young, slowly darkening in age to cinnamon or brown, in some specimens drying olive-green; internode length diminishing

gradually distally; axils rounded; apices waxy, dichotomous, awl-shaped, pale yellow. **Hymenium** clearly unilateral, waxy where fertile, minutely felty and ferruginous where sterile. **Stipe** distinct, up to 3 mm thick, erect, white downward when fresh, inserted in a small ball of mycelium, which extends about 3 mm up the stipe as a pruinose tomentum. Data on **context** not recorded. **Odor** faint or earthy. **Taste** bitter. **Spore print color** not recorded.

Microscopic characters: **Branch context** of thin- to thick-walled, parallel, hyaline hyphae 4-7 µm wide; clamp connections present. **Basidia** about 30 × 7 µm, yellow, with 4 sterigmata. Hymenial **cystidia** absent. **Spores** 4.5-6 × 3-3.5 µm, pale olive in mass, lacrimoid to obovoid; ornamentation of sparse, cyanophilic spines <1 µm tall (Figure 6.32); apiculus inconspicuous, eccentric.

Habit, habitat and distribution: Gregarious, on rotten wood in forests of Africa – Democratic Republic of Congo (Corner 1950), Sumatra (Corner 1970), New Zealand (Petersen 1988), and South America (Spegazzini 1909, Corner 1950, Lazo 1972). Also in parts of Europe (Schild 1990).

Collections examined: **BRAZIL. RIO GRANDE DO SUL**: Sao Leopoldo, 1900, *J.E. Rick* (FH – as *Lachnocladium guyanensis*), and 1907 and 1908, *J.E. Rick* (FH – as *L. guyanensis*). **CHILE. ACONCAGUA:** Limache, 30 September 1927, *A. Garaventa 1009* (FH – as *C. longicaulis*). **DEMOCRATIC REPUBLIC OF CONGO:** Location unknown, no date, ex herb. Bresadola, *A. Dewèvre* (S – as *Lachnocladium ochraceum* – **holotype**; isotype at FH).

Discussion: This species is characterized by slender and delicate basidiomata. The spores are small and sparsely echinulate. Corner (1950) first accepted the name but later (Corner 1970) synonymized it with *Ramaria flaccida*. It differs from the latter in the smaller spores, basidiomata color, and tropical rather than temperate distribution.

Petersen (1988) described *Ramaria ochracea* var. *sicco-olivacea* as differing from *R. ochracea* because the basidiomata of the former dry with an olive coloration whereas those of the latter do not. A detailed examination of Petersen's description revealed, however, that the two differ little and the olive coloration seen

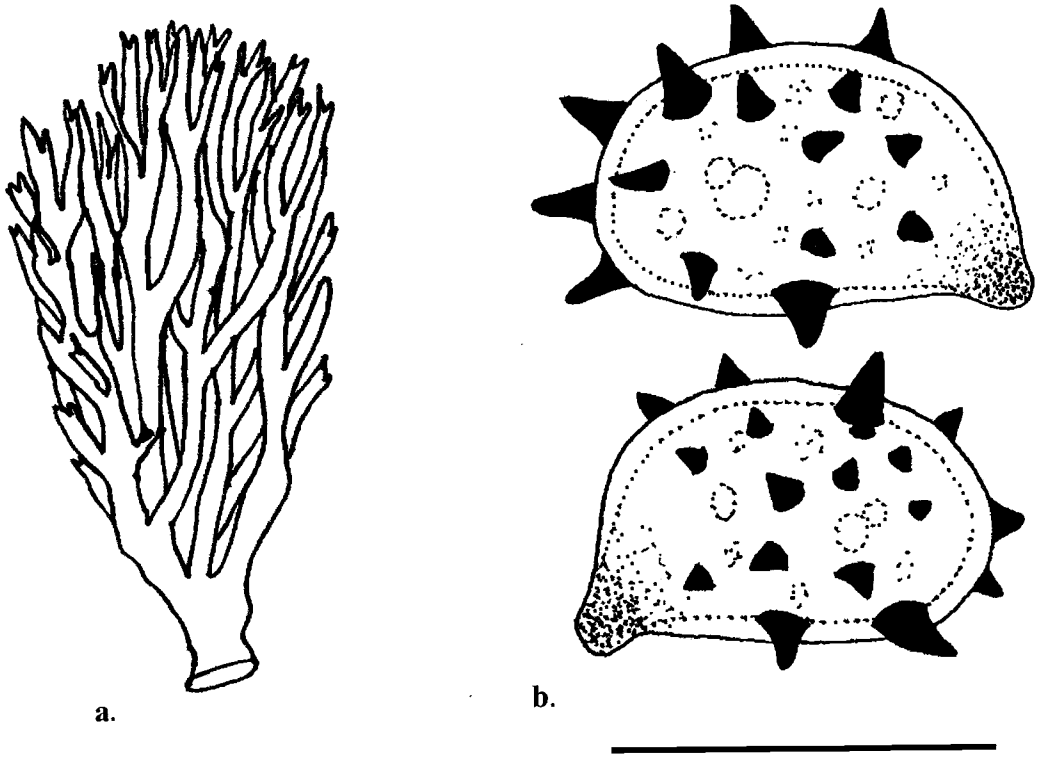


Figure 6.32. *Phaeoclavulina ochracea* (Bres.) Giachini, *sp. prov.*: (a) basidioma (× 2); (b) spores (bar = 5 µm).

in *R. ochracea* var. *sicco-olivacea* seems to be an environmental variation of *P. ochracea*.

Lazo (1972) described *Ramaria flaccida* var. *chilensis* as producing 'ochraceous yellow to brownish', profusely branched basidiomata, common to central Chile. According to Petersen (1981) this is a synonym of *P. ochracea* because of the similar morphological features, and also because they share the same distribution. The same is true for *Ramaria intricatissima*, which was considered a synonym of *P. ochracea* by Giachini (chapter 2) because they share the same macro and micro morphological features.

Phaeoclavulina ochraceo-virens* (Jungh.) Giachini, *sp. prov. Fig. 6.33

≡*Clavaria ochraceo-virens* Jungh., Linnaea 5:407. 1830.

≡*Ramaria ochraceovirens* (Jungh.) Donk var. *ochraceovirens*, Bibliotheca Mycologica 21:112. 1933.

=*Clavaria abietina* Pers. f. *abietina*, *nom. illeg.*, Mycologia Europeae 1:164. 1822 (*non Clavaria abietina* Fr., Systema Mycologicum 1:469. 1821).

≡*Merisma abietina* (Pers.) Spreng., Systema Vegetabilium 4:495. 1827.

≡*Clavariella abietina* (Pers.) P. Karst., Revue Mycologique 3:21. 1880.

≡*Ramaria abietina* (Pers.) Quél., Flore Mycologique de la France, p. 467. 1888.

=*Clavaria abietina* var. *virens* Gillet, Tableaux Analytiques des Hyménomycètes de France, p. 183. 1884.

=*Clavaria abietina* subsp. *cyanescens* (H. Post) Romell, *in* Krok and Almquist, Svensk Flora för Skolor, 2 ed. 1911 (not located, *fide* Corner, Annals of Botany Memoir 1:611. 1950).

=*Clavaria virescens* Gramberg, Jahrgang 5(2/3):57. 1921.

≡*Ramaria virescens* Gramberg, *in* Michael, Führer für Pilzfreunde 3:320. 1927.

=*Clavaria cyanescens* S. Lundell, *in* Krok and Almquist, *Svensk Flora för Skolor*, 5 ed., 2:286. 1932 (not located, *fide* Corner, Annals of Botany Memoir 1: 611. 1950).

=*Ramaria ochrochlora* Furrer-Ziogas & Schild, *in* Schild, Fungorum Rariorum Icones Coloratae 5:17. 1971.

=*Ramaria ochraceovirens* var. *parvispora* K.S. Thind, Khurana & S.C. Kaushal, Kavaka 11:33. 1982.

Macroscopic characters: **Basidiomata** 1.5-4.5 cm tall, in some cases up to 8 × 5 cm, compact, ramarioid, repeatedly branched (Figure 6.33). **Branches** 1-2 mm thick below, slender, crowded, erect, irregularly branched, polychotomous then dichotomous, forked or cristate near apices, blunt, pale yellow, pale orange or olive-orange, green or olive-green when bruised or weathered; nodes often slightly flattened or spreading; axils mostly U-shaped; apices acute, green or olive-green when bruised or weathered. Data on **hymenium** configuration not recorded. **Stipe** 5-15 × 3-8 mm, coriaceous when fresh, brittle on drying, white tomentose at the base. Data on **context** not recorded. **Odor** faintly earthy. **Taste** slightly bitter to sour. **Spore print color** not recorded.

Microscopic characters: All tissues of thin- to slightly thick-walled, cyanophilic **hyphae** 3-9 µm wide, up to 12 µm wide in some places; the wider hyphae mainly parallel and sparingly branched, the narrower with frequent lateral interweaving and often surrounding the wider hyphae, often swollen at the clamps and occasionally with a short clavate branch; clamp connections present; gleoplerous hyphae not seen. **Basidia** 42-62 × 5-7.5 µm, clavate, mostly with 4 sterigmata 4-8 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 6-12 × (3-) 4-4.5 (-5.5) µm, orange or cinnamon in mass, ellipsoid to lacrimoid; ornamentation of cyanophilic, fine to rough warts (Figure 6.33); data on apiculus not recorded.

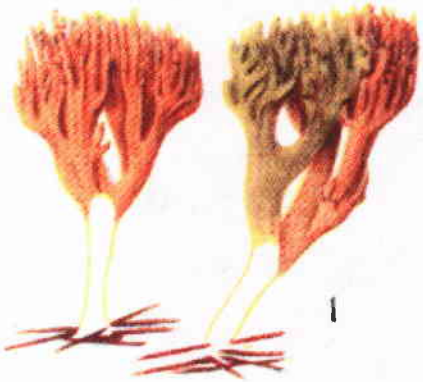
Habit, habitat and distribution: Terrestrial, caespitose from a floccose white mycelium with rhizomorphs, in humus or needle litter in Canada (Petersen 1981), Europe (Corner 1950, Karsten 1880, Persoon 1822, Sprengel 1827), India (Thind *et*

al. 1982), and the USA (Coker 1923). In the USA observed under *Pseudotsuga menziesii* (Mirb.) Franco.

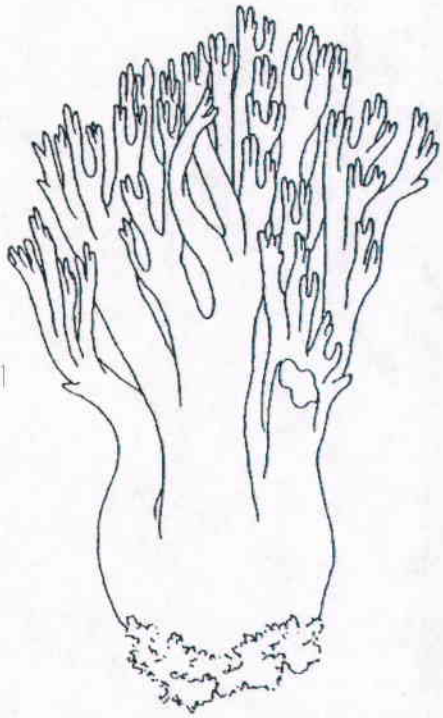
Type (holotype): No location, no date, herb. Junghuhn no. 69 (L – as *Clavaria ochraceo-virens*). The loan of the type was not granted.

Collections examined: **SWITZERLAND:** Brienz, Chin-Vos, Chel Chapella, Eugadin, 16 June 1969, *A. Knapp*, in Herb. Schild 18 (ZT – as *Ramaria ochrochlora*; Location unknown, 1969, *E. Schild* (TENN 34569 – **holotype** – 36817, 36020 – as *Ramaria ochrochlora*).

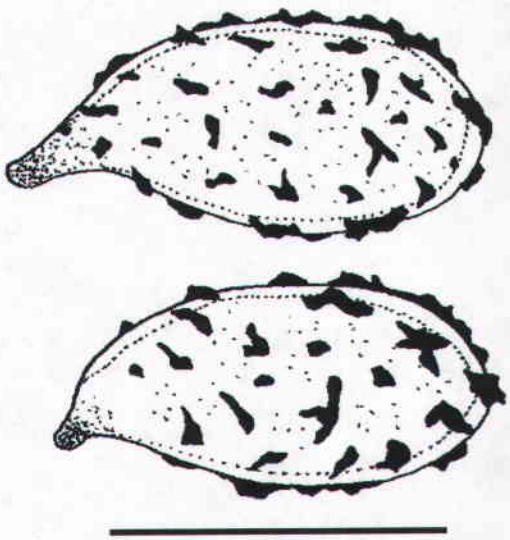
Discussion: This description was also based on notes from Donk (1933), Karsten (1880), Michael (1927), Persoon (1822), Sprengel (1827), and Thind *et al.* (1982). As mentioned by Corner (1950), rephrasing Donk (1933), "it is regrettable that this unfamiliar, though descriptive name must be revived for the common fungus which has been widely known as *Clavaria abietina*." As emphasized by Corner (1950), *C. abietina* Fr. must undoubtedly be *Clavaria invalii* Cotton & Wakef., though *C. abietina* Pers., which supplied the specific epithet, is *Clavaria ochraceo-virens* (≡*P. ochraceo-virens*). He further adds that Fries persistently intended a non-virescent *Clavaria* for *C. abietina*, as shown by his 'forma *personii*' (Fries 1874). However, there can be no doubt that *C. invalii* and the virescent '*C. abietina*' were generally confused until Cotton and Wakefield (1919) described *C. invalii*. Today the species is known to indicate the non-virescent species of conifer woods with echinulate spores. *Ramaria abietina* (Pers.) Quél. is based on *Clavaria abietina sensu* Pers., not Fr., and thus, the epithet '*abietina*' cannot be used for *C. abietina* Fr. Today the species is known to indicate the non-virescent species of conifer woods with verrucose spores.



a.



b.



c.

Figure 6.33. *Phaeoclavulina ochraceo-virens* (Jungh.) Giachini, *sp. prov.*: (a, b) basidiomata (× 1, × 0.5, respectively); (c) spores (bar = 10 µm). Drawings of basidiomata modified from Corner (1950) and Petersen (1981), with permission.

Phaeoclavulina pancaribbea* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.34

≡*Ramaria pancaribbea* R.H. Petersen f. *pancaribbea*, Bibliotheca Mycologica 79:88. 1981.

=*Ramaria pancaribbea* f. *caerulea* R.H. Petersen, Bibliotheca Mycologica 79:90. 1981.

Macroscopic characters: **Basidiomata** up to 8 × 5 cm, ramarioid, repeatedly branched. **Branches** ascending, branching polychotomous, brown below, paler olive above, especially when young, then finally concolorous; axils rounded; tips rounded to acute, paler than branches, often with blue or blue-green tones. **Hymenium** amphigenous, rarely with decurrent sterile areas, smooth. **Stipe** up to 40 × 6 mm, grooved, with a basal mat and white rhizomorphs, white to cream colored where protected, dark brown where exposed, occasionally with blue tones, everywhere slowly bruising brick red, turning to red-brown, with such colors persisting when dry. Data on **context** not recorded. **Odor** mild, musty to sweet. **Taste** bitter and astringent. **Spore print** yellow-brown.

Microscopic characters: **Branch context** of thin-walled, smooth, parallel hyphae 2.5-11 µm wide; clamp connections present, ampulliform clamps common and up to 8 µm; gleoplerous hyphae not observed. **Basidia** 45-60 × 8-10 µm, clavate, with (2-) 3-4 stout sterigmata persistent after spore discharge; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 8-12 × 6-8.5 µm, yellow-brown in mass, obovoid; ornamentation of cyanophilic, forked or lobed, stout, blunt or truncate warts and longitudinal ridges up to 2.5 µm tall (Figure 6.34); apiculus prominent, up to 2 µm long.

Habit, habitat and distribution: Gregarious or rarely caespitose. On soil in Costa Rica (Petersen 1981), French Guiana (Petersen 1981), and southeastern USA (Petersen 1981).

Collections examined: **FRENCH GUIANA. CAYENNE**: May-June, *Richard 13* (FH). **UNITED STATES. NORTH CAROLINA:** Macon Co., Coweeta Hydrol. Lab.,

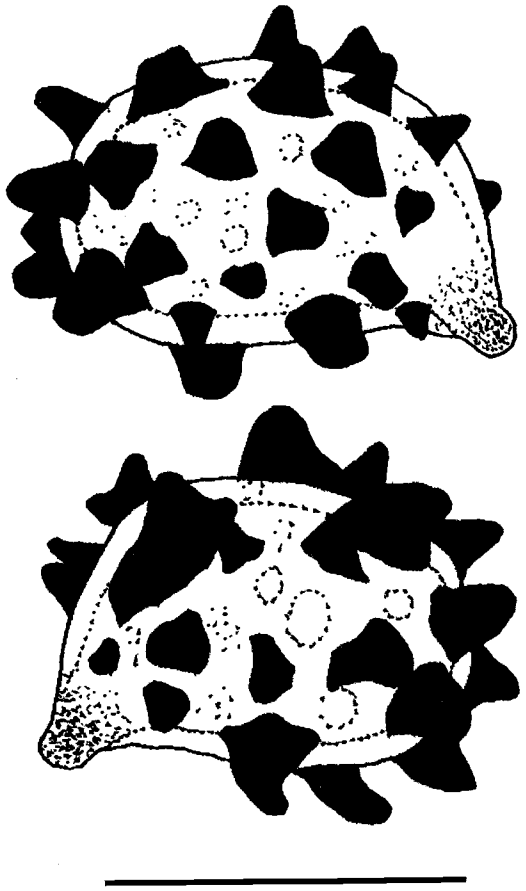


Figure 6.34. Spores (bar = 10 μm) of *Phaeoclavulina pancaribbea* (R.H. Petersen) Giachini, *sp. prov.* Drawings modified from Petersen (1981), with permission.

29 July 1967 (TENN 32686 – as f. *caerulea*), and 10 August 1971 (TENN 36113 – as f. *caerulea*). **TENNESSEE:** Blount Co., Great Smoky Mountains Nat. Park, Cades Cove, 20 July 1966, *R.H. Petersen* (TENN 31836 – as *Ramaria pancaribbea* – **holotype**), 31 August 1963 (TENN 26033), 3 August 1964 (TENN 26305), and 26 August 1966 (TENN 31844, 31879); Blount Co., Great Smoky Mountains Nat. Park, Sugar Cove, 27 July 1967 (TENN 32644 – as f. *caerulea*).

Discussion: This species has been mistaken with *P. guyanensis* and *P. zippelii* in the past. Basidiomata of *P. pancaribbea* are similar but stouter and shorter than those of *P. gigantea*, giving them a stockier appearance. Additionally, no blue tips are seen in the description of *P. gigantea* or its synonyms. Two varieties that fall under the epithet '*pancaribbea*' were proposed in the past: forma *caerulea* (Petersen 1981), and variety *zealandica* (Petersen 1988). The former is described as typical for forma *pancaribbea* but with obvious blue-green tones on apices and/or stipe surfaces. However, in the description of *Ramaria pancaribbea* var. *zealandica*, Petersen (1988) revealed that the species did not have any tones of blue or green on branch tips but that *R. pancaribbea* actually did. Giachini (chapter 2), after analyzing the types for both species proposed to synonymize *R. pancaribbea* f. *pancaribbea* and *R. pancaribbea* f. *caerulea* and raise *R. pancaribbea* var. *zealandica* to species rank (≡*P. zealandica*).

Phaeoclavulina quercus-ilicis* (Schild) Giachini, *sp. prov. Fig. 6.35

≡*Ramaria quercus-ilicis* Schild, Zeitschrift für Mykologie 64:53. 1998.

Macroscopic characters: **Basidiomata** 3-5.5 × 1-2.8 cm, ramarioid, repeatedly branched (Figure 6.35). **Branch** 2-3 mm thick, erect, dichotomously to polychotomously ramified, branches cylindrical to subcylindrical, more or less divergent to parallel, surface rugulose, pale yellow when young, becoming pale orange to orange with age, and then orange vinaceous; apices 2-3 ramified, concolorous with the branches, not changing color when bruised. **Hymenium**

amphigenous, rugulose. **Stipe** 15-30 mm long, more or less equal, often incurved, partially hollow, delicate, the base off-white, pale orange upward, then orange brunnescent. **Context** off-white then creamy white, not changing when exposed or bruised. **Odor** slightly earthy. **Taste** more or less earthy, somewhat bitter. **Spore print color** not recorded.

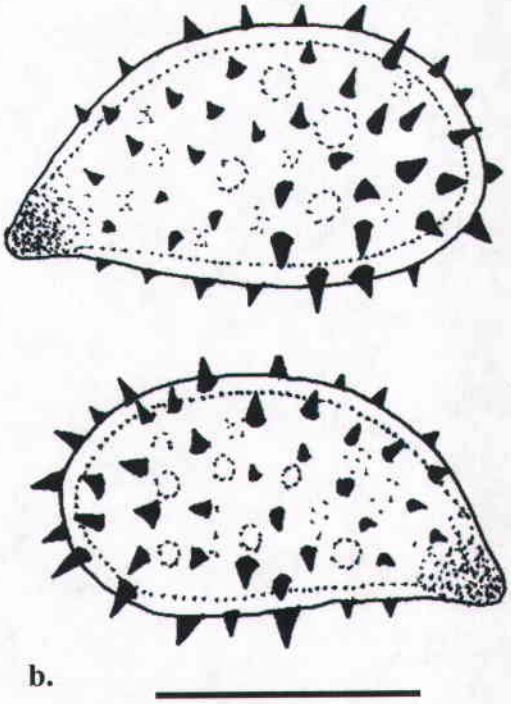
Microscopic characters: **Stipitipellis** of more or less parallel hyphae with branch connections, 1.5-6.5 µm wide, ampulliform swelling up to 9 µm. **Context** hyphae 1.5-6.5 (-12) µm wide; clamp connections present; gleoplerous hyphae rare, cyanophilic, 2.5 µm wide. Rhizomorphs long, parallel to irregular, 1.5-4 µm wide, often with septa and ampulliform swellings up to 5-8 µm; clamp connections present. **Basidia** 25-37 × 6-7 µm, clavate, with 4 sterigmata 4-5.5 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 5-9.5 × 2.5-5.5 µm, orange in mass, obovoid to lacrimoid; ornamentation of cyanophilic spines (Figure 6.35); apiculus 0.5-1 µm long.

Habit, habitat and distribution: Under *Quercus ilex*, on the edge of a forest in Treviso, Veneto, Italy (Schild 1998).

Collections examined: **ITALY. VENETO:** Villa di Villa, Comune Cordignano, about 20 km from Pordenone, 23 October 1993, *E. Schild 2024* (ZT – as *Ramaria quercus-ilicis* – **holotype**).

Discussion: Even though the basidiomata and the form of the spores resemble those of *P. flaccida* and *P. roellinii*, *P. quercus-ilicis* exhibits color and habitat quite distinct from the previous two. Microscopically these three species are certainly close and difficult to separate solely from herbaria material. *Phaeoclavulina roellinii* has significant quantities of stellate crystal aggregates in the rhizomorphs, a phenomenon not seen in *P. quercus-ilicis*.

a.



b.

Figure 6.35. *Phaeoclavulina quercus-ilicis* (Schild) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 5 µm). Photo and spores modified from Schild (1998), with permission.

Phaeoclavulina roellinii* (Schild) Giachini, *sp. prov. Fig. 6.36

≡*Ramaria roellinii* Schild, Schweizerische Zeitschrift für Pilzkunde 56:97. 1978.

Macroscopic characters: **Basidiomata** 1.2-3.5 × 0.7-2.4 cm, ramarioid. **Branches** up to 2 mm thick, sparsely to repeatedly branched up to 4 ranks, pale orange when young; tips acute to rounded, paler than branches. **Hymenium** amphigenous. **Stipe** 4-8 × 0.6-2 mm (*fide* Petersen 1981), pale orange, subtended by a tangle of delicate, white rhizomorphic strands. Data on **context** not recorded. **Odor** mildly fresh and slightly penetrating. **Taste** distinctly bitter and astringent. **Spore print color** not recorded.

Microscopic characters: **Context** of thin- to slightly thick-walled, hyaline hyphae 2-10 µm wide; clamp connections present; stellate crystals present. Rhizomorphic strands of thin-walled, parallel, pyriform hyphae 2-3.5 µm wide; clamp connections present, ampulliform clamps occasional; stellate crystals abundant, minute. **Basidia** 25-35 × 6-9.5 µm, clavate, with (3-) 4 straight sterigmata up to 6.5 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 6.5-8 × 3.5-4.5 µm, ellipsoid to lacrimoid; ornamentation of cyanophilic, acute (>1 µm tall) and blunt spines ≤1 µm tall (Figure 6.36); apiculus small, inconspicuous, eccentric.

Habit, habitat and distribution: With mosses and lichens in Europe (Petersen 1981, Schild 1978) – Germany, Italy, Switzerland, and the northeastern USA (Petersen 1981).

Collections examined: **ITALY.** Trento, 20 September 1972 (TENN 36804). **SWITZERLAND:** Brienz, 9 September 1972 (TENN 36833). **GENEVA:** Vallon de l'Allondon, above Malval, no date, *O. Rollin 1076* (ZT – as *Ramaria roellinii* – **holotype**).

Discussion: This species is easily confused with *P. flaccida* from which it differs in its smaller size, sparing branch pattern, and smaller spores. According to Petersen (1981) the reduced stature of the basidiomata may be caused because it cohabits with mosses and lichens.

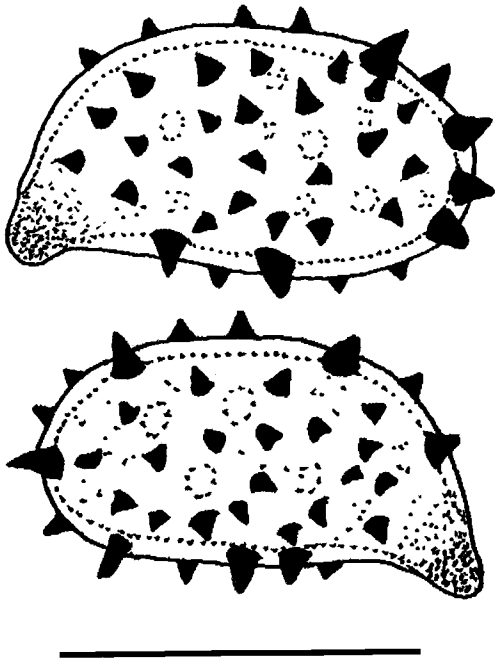


Figure 6.36. Spores (bar = 5 μm) of *Phaeoclavulina roellinii* (Schild) Giachini, *sp. prov.* Spore drawings modified from Petersen (1981), with permission.

Phaeoclavulina sikkimia **(S.S. Rattan & Khurana) Giachini,** ***sp. prov.*** Fig. 6.37

≡*Ramaria sikkimia* S.S. Rattan & Khurana, Bibliotheca Mycologica 66:18. 1978.

Macroscopic characters: **Basidiomata** up to 17 × 5.5 cm, ramarioid, repeatedly branched (Figure 6.37). **Branches** polychotomous below, dichotomous above, parallel, brown; internodes long, slender, up to 4 mm long; axils rounded; apices acute, prolonged, off-white, yellow, orange to brown. **Hymenium** amphigenous, except at axils, occasionally slightly decurrent. **Stipe** up to 30 × 15 mm, discrete, white and pruinose below, bruising brown. **Context** paler than the surface of the basidioma. **Odor** not distinct. **Taste** slightly bitter. **Spore print color** not recorded.

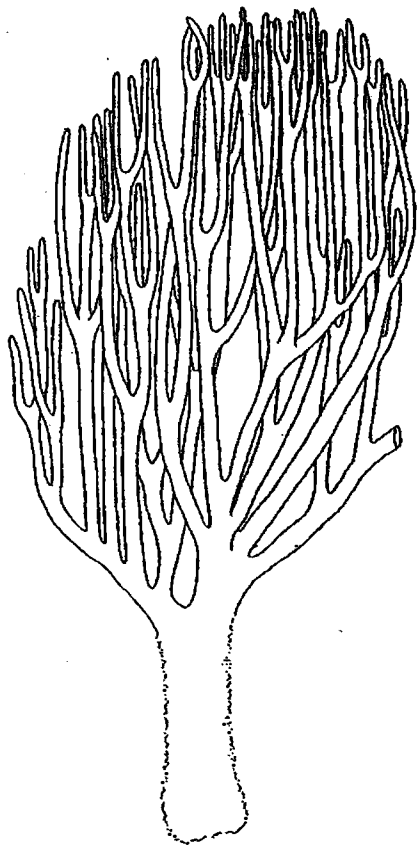
Microscopic characters: **Branch context** of thin-walled, parallel, smooth, inflated hyphae 2.5-13.5 µm wide, with common ampulliform swellings; clamp connections present; gleoplerous hyphae simple, uncommon, cyanophilic, up to 2 µm wide. **Basidia** 60-70 × 7.5-9 µm, clavate, pale yellow, with (2-) 3 (-4) sterigmata up to 7 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 6.5-9 × 4.5-6 µm, dark golden yellow in mass, obovoid to lacrimoid; ornamentation of indistinct, cyanophilic warts up to 2 µm tall (Figure 6.37); apiculus up to 1.5 µm long, obconical, gradual.

Habit, habitat and distribution: Solitary to gregarious, on forest litter in the Himalayan Mountains of India (Rattan and Khurana 1978).

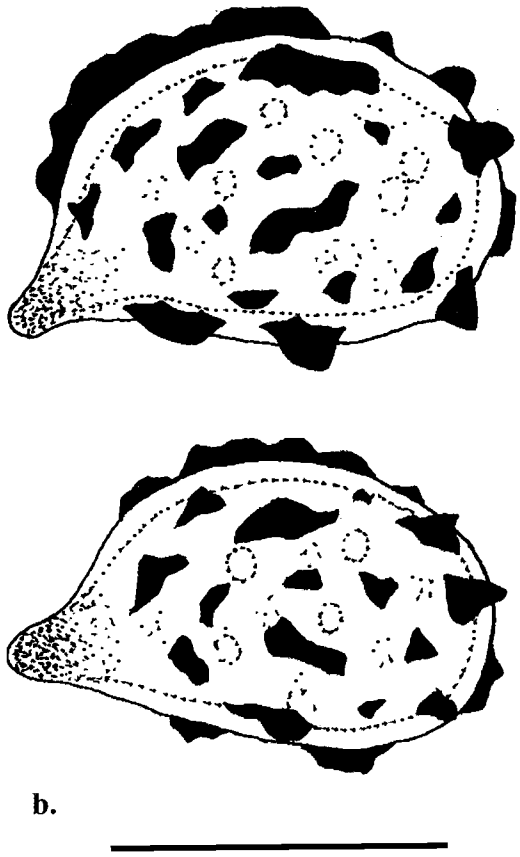
Type (holotype): **INDIA:** West Bengal, Darjeeling, Manebhangjung, 31 August 1964, *S.S. Rattan 223* (PAN – as *Ramaria sikkimia*).

Discussion: The herbarium PAN was contacted for loan of the type for this species but no answer was obtained. Therefore, this description was based on notes from Petersen (1981) and Rattan and Khurana (1978).

Although Singh (1977) and Rattan and Khurana (1978) considered *P. sikkimia* to be most closely related to *Ramaria guyanensis* (≡*P. guyanensis*) and *R. zippelii* (≡*P. zippelii*), both of these latter species are predominantly 2 sterigmatic



a.



b.

Figure 6.37. *Phaeoclavulina sikkimia* (S.S. Rattan & Khurana) Giachini, *sp. prov.*: (a) basidioma (× 1); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

and are, according to Petersen (1981), not close to *P. sikkimia*. The spores of *P. sikkimia* resemble those of *P. guyanensis, P. pancaribbea*, and *P. echinovirens*. In fact, the only major differences between *P. echinovirens* and *P. sikkimia* are the color of the tips of the basidiomata, orange-yellow in *P. echinovirens* and off-white, yellow, orange to brown in *P. sikkimia*, and the size of the spores, which are larger for the former.

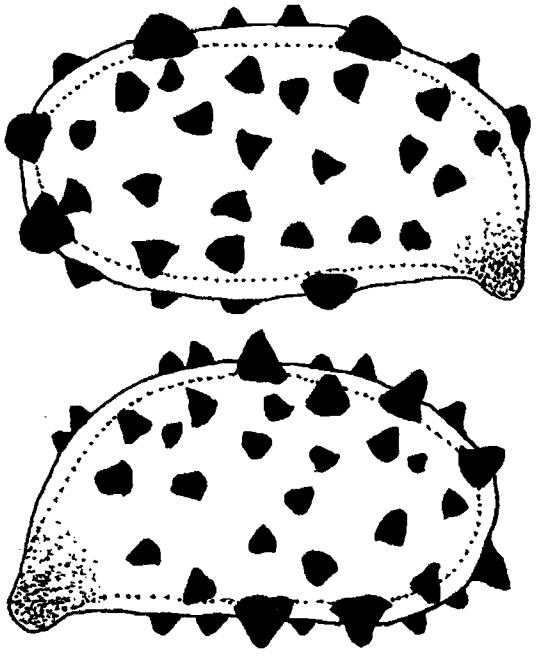
Phaeoclavulina tropicalis* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.38

≡*Ramaria tropicalis* R.H. Petersen, Bibliotheca Mycologica 79:173. 1981.

Macroscopic characters: **Basidiomata** up to 16 × 3.5 cm, ramarioid, repeatedly branched (Figure 6.38). **Branches** up to 8 cm long, ascending, branching dichotomously, branches cylindrical, becoming grooved on drying, upward more yellow to pale orange, pale brown elsewhere; axils rounded to narrowly rounded; apices up to 3 mm long, rounded-acute, golden yellow to orange. **Hymenium** amphigenous. **Stipe** up to 80 × 12 mm, distinct, tomentose, sordid white to pale violet-gray, surface and context brown on handling; stipe base expanding slightly at substrate level, subtended by a dense tangle of white, fragile rhizomorphs. Data on **context**, **odor**, **taste,** and **spore print color** not recorded.

Microscopic characters: **Branch context** of two types: (a) medullary tissue of thin- to slightly thick-walled, generally parallel and loosely arranged hyphae, hyaline singly, pale orange in mass, 4-13 µm wide; clamp connections present, ampulliform clamps rare, and (b) cortical tissue of thin-walled, agglutinated, narrow hyphae. **Basidia** 40-55 × 7-8 µm, hyaline singly, pale orange in mass, with 4 sterigmata. Hymenial **cystidia** absent. **Spores** 9.5-11.5 × 4.5-6 µm, ellipsoid to lacrimoid; ornamentation of discrete, blunt to acute, cyanophilic spines up to 1.5 µm tall; spore aberrations common, usually of length up to 17 µm and width to a

a.



b.

Figure 6.38. *Phaeoclavulina tropicalis* (R.H. Petersen) Giachini, *sp. prov.*: (a) basidioma (× 0.8); (b) spores (bar = 5 μm). Drawings modified from Petersen (1981), with permission.

maximum of 4.5 µm, these usually much less highly ornamented than normal (Figure 6.38); apiculus eccentric.

Habit, habitat and distribution: Ivory Coast and Liberia, Africa (Petersen 1981).

Collections examined: **COTE D'IVOIR.** Font du terre, 17 November 1974, *G. Gilles 44* (PC). **LIBERIA:** Nengbe, 9 April ?, *Harley 551* (NY – as *Ramaria tropicalis* – **holotype**).

Discussion: The notes indicate that the pale coloration of the stipe changes when bruised or handled. This species is close to *P. pancaribbea*, from which it separates by the basidioma color and spore ornamentation. *Phaeoclavulina tropicalis* has pale orange to pale brown basidiomata with golden yellow to orange tips and the spores are echinulate. *Phaeoclavulina pancaribbea* has brown-olive basidiomata, blue to green tips, and scattered warts on the spore surface.

Phaeoclavulina vinaceipes* (Schild) Giachini, *sp. prov. Fig. 6.39

≡*Ramaria vinaceipes* Schild, Zeitschrift für Mykologie 56(1):131. 1990.

Macroscopic characters: **Basidiomata** 6-11 × 8 cm, upright, ramarioid, more or less repeatedly branched (Figure 6.39). **Branches** 2-8 mm thick below, irregularly round, smooth to weakly rugulose, dichotomously to trichotomously branched upward, brightly yellow, with older branches more orange or yellow-brown; branch axils nearly in U-shape, only rarely acute, usually crenate; apices usually composed of two thin, lash-like branchlets, concolorous with the branches or a little brighter. Data on **hymenium** configuration not recorded. **Stipe** 20-30 × 4-7 mm thick below, 7-10 mm above, subcylindrical, sometimes with two or more individuals growing together, base sulcate or crenate, sometimes slightly bulbous, with white rhizomorphs that grow into the woody substrate; white, upward orange, usually bruising magenta to violet-brown or pink-red, although the reaction is not always seen, especially in older specimens. **Context** sordid white, sometimes yellow in upper branches under the hymenium, drying up orange or creamy white, sometimes

soon bruising violet when exposed or handled, generally flexible or flexible fragile. **Odor** earthy. **Taste** earthy to slightly bitter. **Spore print color** not recorded.

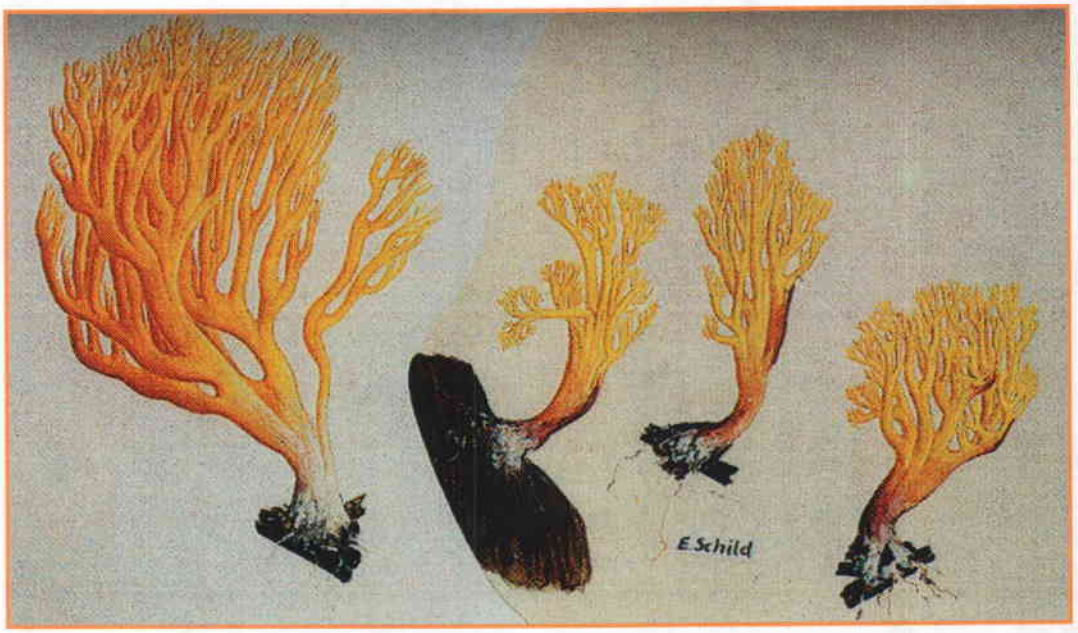
Microscopic characters: **Branch context** of regularly parallel, smooth, pale olive-green hyphae (1.5-) 2.5-11.5 µm wide near the subhymenium; clamp connections present. **Stipe context** of irregular hyphae (1.5-) 2-8 (-11.5) µm wide; clamp connections present and with ampulliform swellings, otherwise equal as in the branch context. **Subhymenial trama** of irregular, more or less parallel, smooth, hyaline to pale yellow hyphae 1.5-3.5 µm wide. Rhizomorphs 1.5-3.5 µm wide, with cloud-like accumulations of gray-green crystal aggregates of diverse forms, individually measuring 2-8 µm long, frequently with ampulliform swellings up to 11.5 µm; clamp connections present and usually pale gray-green. **Basidia** 28-35 × 4.5-5.5 µm, clavate, orange-green to olive-green, with (2-3-) 4 sterigmata 2-5 µm long; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 4.5-9.5 × 2.5-4.5 µm, pale olive-orange to olive-green in mass, ellipsoid; ornamentation of strongly cyanophilic spines between 0.1 and 1 µm tall (Figure 6.39); apiculus usually 0.5-1 µm long, acyanophilic or only weakly cyanophilic.

Habit, habitat and distribution: On wood. Known only from Germany (Schild 1990).

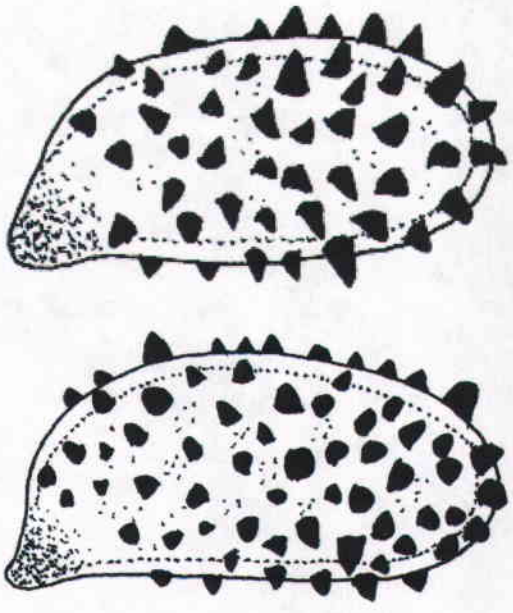
Collections examined: **GERMANY:** Wasenweilerwald, 3 September 1976, *S. Elsner and D. Knoch 1056* (M – as *Ramaria vinaceipes* – **holotype**).

Discussion: The olive-orange to olive-green spore mass and the small echinulate spores bear a remarkable resemblance to *P. flaccida*. *Phaeoclavulina vinaceipes* is also similar to *P. ochracea*. However, *P. ochracea* is never brightly yellow as are some specimens of *P. vinaceipes*, but rather orange and somewhat paler. In addition, the spores of *P. ochracea* are considerably smaller than those of *P. vinaceipes*.

The complicated crystalline material often adhering to the rhizomorphs is also observed in *P. glauco-aromatica* and *P. roellinii*. *Phaeoclavulina vinaceipes* differs from *P. roellinii* by having larger basidiomata and spores, and from *P. glauco-aromatica* by having smaller spores and a distinctly different distribution.



a.



b.

Figure 6.39. *Phaeoclavulina vinaceipes* (Schild) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 5 μm). Photo and spores modified from Schild (1990), with permission.

Phaeoclavulina zealandica* (R.H. Petersen) Giachini, *sp. prov. Fig. 6.40

≡*Ramaria pancaribbea* var. *zealandica* R.H. Petersen, Department of Scientific and Industrial Research Bulletin 263:1988.

Macroscopic characters: **Basidiomata** up to 9 × 5 cm, ramarioid, repeatedly branched, erect, all parts bruising dark brown to black-brown. Major **branches** 2-4, ascending, cylindrical to slightly flattened, polychotomous below, dichotomous above, brown to dark brown; internode length diminishing gradually and irregularly distally; axils narrowly rounded; apices around 2 mm thick, rounded-digitate to slightly inflated, pale yellow or off-white when young, pale brown when mature but not golden yellow, dark yellow or orange. **Hymenium** unilateral, the fertile areas smooth, watery in appearance, the sterile areas decurrent from the axils, appearing scurfy, ferruginous from the spores. **Stipe** 5-20 × 3-6 mm, usually flattened, fibrous to fibrous-fleshy, abruptly rounded and minutely hispid at the base, off-white but not white. Data on **context** not recorded. **Odor** weakly spicy and aromatic. **Taste** weak to slightly bitter. **Spore print** ferruginous.

Microscopic characters: **Branch context** of thick-walled, generally parallel, hyaline hyphae 2.5-10 μm wide; clamp connections present. **Basidia** 50-75 × 5-10 μm, clavate, with 4 sterigmata persistent after spore discharge; clamp connections present at base. Hymenial **cystidia** absent. **Spores** 8-11 × 6.5-8 μm, ferruginous in mass, subglobose to lacrimoid; ornamentation of cyanophilic blunt warts and longitudinal ridges up to 3 μm tall (Figure 6.40); apiculus wide, gradual.

Habit, habitat and distribution: In *Podocarpus* spp. in New Zealand (Petersen 1988).

Collections examined: **NEW ZEALAND**: Fox Glacier, Westland Nat. Park, Road to Gillespie's Beach, 9 May 1982, *R.H. Petersen 43383* (PDD 43383 – as *Ramaria pancaribbea* var. *zealandica* – **holotype**; isotype at TENN).

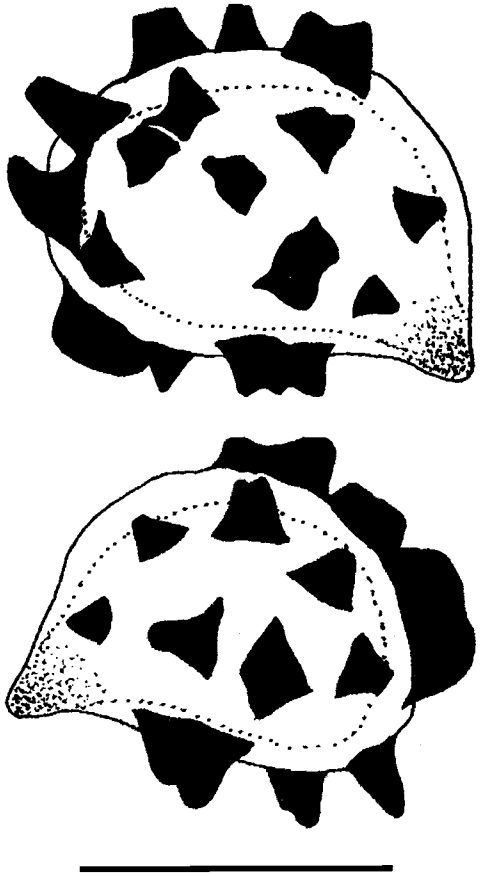


Figure 6.40. Spores (bar = 10 μm) of *Phaeoclavulina zealandica* (R.H. Petersen) Giachini, *sp. prov.* Spore drawings modified from Petersen (1981), with permission.

Discussion: The species is similar, and indeed a variety of *P. pancaribbea* according to Petersen (1988). They have similar basidioma stature and color, similar basidia with 4 sterigmata, similar spore ornamentation of longitudinal ridges rather than only warts, but distinct bruising reactions. However, spores of *P. pancaribbea* are slightly larger than those of *P. zealandica*, and the distribution for the two species is quite distinct. After examining the types for *P. pancaribbea* and *P. zealandica* Giachini (chapter 2) considered them to be distinct.

Phaeoclavulina zippelii* (Lév.) Giachini, *sp. prov. Fig. 6.41

≡*Clavaria zippelii* Lév., Annales des Sciences Naturelles Botanique 3(2):215. 1844.

≡*Phaeoclavulina zippelii* (Lév.) Overeem, Bulletin du Jardin Botanique de Buitenzorg 3(5):276. 1923.

≡*Ramaria zippelii* (Lév.) Corner f. *zippelii*, Annals of Botany Memoir 1:632. 1950.

=*Merisma guadelupense* Lév., Annales des Sciences Naturelles Botanique 3(5):157. 1846.

≡*Pterula guadelupensis* (Lév.) Sacc., Sylloge Fungorum Omnium Hucusque Cognitorum 6:742. 1888.

≡*Lachnocladium guadelupense* (Lév.) Pat., Journal de Botanique 3:3. 1889.

≡*Dendrocladium guadelupense* (Lév.) Lloyd, Mycological Notes 60:870. 1919.

=*Clavaria nigrescens* Fr., Nova Acta Regiae Societatis Scientiarum Upsaliensis 3:116. 1854.

=*Clavaria thwaitesii* Berk. & Broome, Journal of the Linnean Society of London. Botany 14:75. 1875.

=*Lachnocladium hookeri* Berk., *in* Berkeley and Broome, Journal of the Linnean Society of London. Botany 14:75. 1875.

=*Lachnocladium englerianum* Henn., Die Natürlichen Pflanzenfamilien, 1 ed., p. 138. 1897b.

=*Clavaria aeruginosa* Pat., Bulletin de la Société Mycologique de France 14:189. 1898.

≡*Ramaria zippellii* var. *aeruginosa* (Pat.) R.H. Petersen, Bibliotheca Mycologica 79:96. 1981.

=*Lachnocladium albidum* Pat., Bulletin de la Société Mycologique de France 14:188. 1898.

≡*Ramaria albida* (Pat.) Corner, Annals of Botany Memoir 1:554. 1950.

=*Clavaria phaeocladia* Pat., Bulletin de la Société Mycologique de France 14:189. 1898.

=*Lachnocladium neglectum* Massee, ?, (not located, *fide* Corner, Annals of Botany Memoir 1:633. 1950).

Macroscopic characters: **Basidiomata** up to 13 × 4 cm, ramarioid, repeatedly branched (Figure 6.41). **Branches** 4-6 mm wide below, 1.5-2 mm above, cylindrical, crowded, polychotomous at first (3-8 teeth), becoming 2-3-chotomous toward the tips, outer branches often curved ascending, uppersides of the branches and axils more or less sterile, subtomentose, pale yellow to pale orange, then pale brown, dusted with cinnamon spores, all parts soon bruising orange vinaceous or vinaceous brown; axils rounded, internodes diminishing gradually, rather long below; tips quite prolonged with age (up to 15 mm long), slightly incurved, rounded or rather bluntly tapered, abruptly white, creamy yellow, or pale blue-green (*fide* Petersen 1981). **Hymenium** often unilateral, with sterile upper or inner branch surfaces paler than fertile surfaces. **Stipe** 10-50 × 10 mm, distinct, cylindrical, rather long and slender, thickened upward, deeply rooted, white tomentose below, soon bruising pale brown-lavender or violet on exposure or handling. **Context** tough, fibrous, white, immediately bruising lavender-brown when cut or exposed. **Odor** strong, of *Ganoderma* (paracresol). **Taste** bitter. **Spore print** ferruginous.

Microscopic characters: **Branch context** of thin-walled, strictly parallel hyphae 2.5-8 µm wide, agglutinated when dry, pale yellow in mass; clamp connections present; gleoplerous hyphae occasional, not limited by septa. Other **hyphae** thin or slightly thick-walled, walls smooth, occasionally with short, clavate, slightly inflated, thin-walled branches up to 30 × 10 µm, with frequent H-connections; clamp connections present. **Basidia** 40-50 × 7-9 µm, subclavate to clavate, with 1-2 stout, conical, divergent sterigmata up to 10 µm long. Hymenial **cystidia** absent. **Spores** 10-15.5 × 6-10 (-11) µm, orange to dark orange in mass, ellipsoid to lacrimoid; ornamentation of strongly cyanophilic, acute, usually straight, hyaline spines 1-3.5 (-4) µm tall (Figure 6.41); apiculus pronounced.

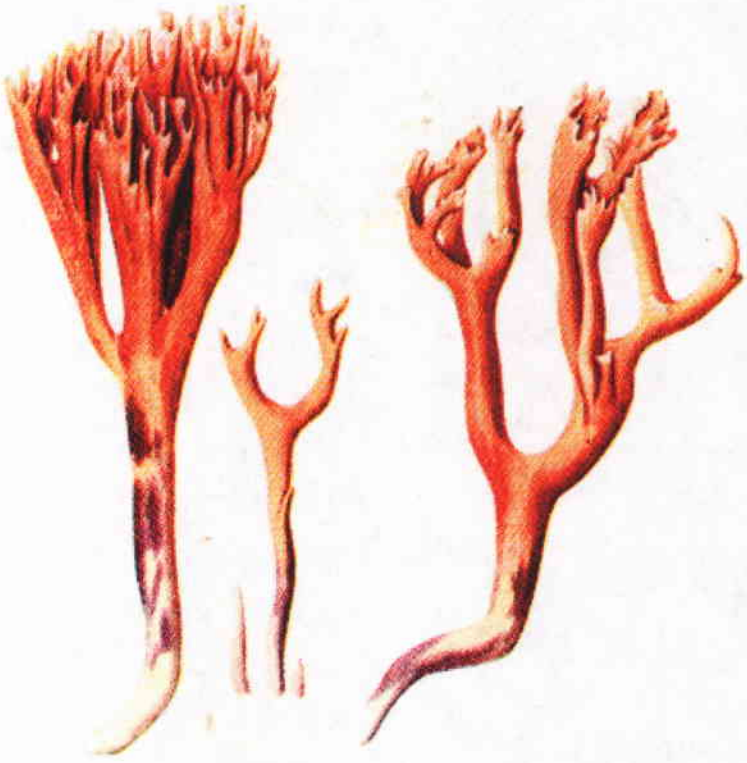
Habit, habitat and distribution: Solitary to gregarious, on the ground in forests of Australia, Borneo (Coker 1923, Corner 1950, 1970), Brazil (Corner 1970), Colombia (Petersen 1981), Cuba (Coker 1923, Petersen 1981), French Guiana (Petersen 1981), Hawaii (http://www.mycena.sfsu.edu/), India (Corner 1950), Japan (Corner 1970, Imai 1941), Java (Corner 1950, Overeem 1923, Petersen 1981), Malaysia (Corner 1950, Petersen 1981), New Caledonia (Corner 1950), Papua New Guinea (Corner 1950, Petersen 1981), Peru (Corner 1970, Petersen 1981), Philippines (Petersen 1981, Teodoro 1937), Russia (Corner 1970, Parmasto 1965), Sri Lanka (Corner 1950, Petch 1925, Petersen 1981), and the USA – Maryland, North Carolina, and Washington DC (Coker 1923, Corner 1970, Petersen 1981).

Collections examined: **AUSTRALIA. NEW SOUTH WALES**: Duck Creek Road, 22 km WNW of Bulahdelah, 32° 21' S, 151° 58' E, 140 m alt., 22 April 1990, *H. Lepp 369* (CANB 643441 – as *Ramaria* sp.). **COLOMBIA. CAUCA**: El Tambo, 27 October 1937, *K. von Sneidern* (S). **FRENCH GUIANA. CAYENNE:** 1836, ex. Herb. Montagne (PC – as *Clavaria tubulosa*). **INDONESIA. SUMATRA:** Padangse Benedenlanden, September 1913, *Jacobsen and van Heurn* (TENN 36033). **JAVA**: No location, no date, *Clautrian* (FH – as *Clavaria phaeocladia* – **neotype**). **PAPUA NEW GUINEA. PAPUA**: Kanosia, 2 July 1935, *C.E. Carr 11201* (NY).

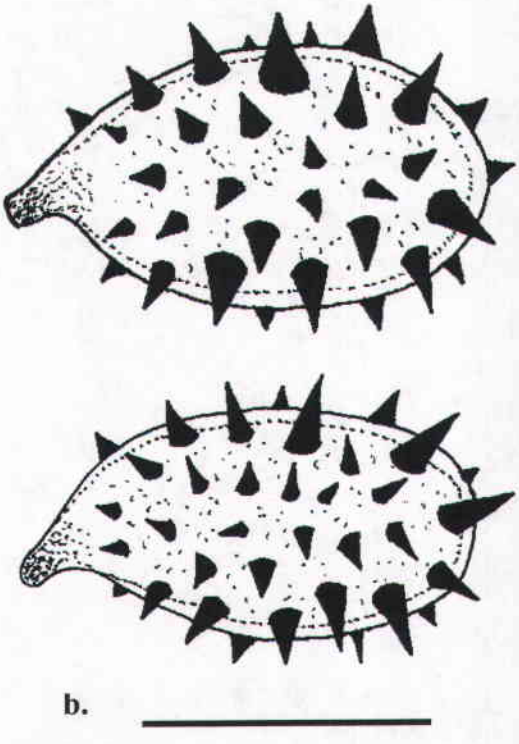
PERU. DEPTO. LORETO: Gamitanacocha, Rio Mazán, 7 February 1935, *J.M. Schunke 179* (NY).

Discussion: Characters of fresh specimen were described from notes by Berkeley and Broome (1875), Berkeley and Curtis (1869), Corner (1950), Lloyd (1919), Patouillard (1898), Peck (1902), Petersen (1981), and Saccardo (1888, 1912). *Ramaria zippelii* is similar to *R. grandis* (Corner 1950). Corner (1950) further adds: "indeed, *Ramaria grandis* may be identical, because the only difference that I can detect in its description is a richer brown color." Later Corner (1970) considered *R. grandis* a synonym of *R. zippelii*. *Ramaria grandis* (≡*R. cyanocephala*), originally described from Maryland, was considered a 'luxurious' form of *R. zippelii* described from the Pacific tropics (Petersen 1976b). As explained under *P. cyanocephala*, the two species are separated on the basis of basidiomata stature (larger in *P. cyanocephala*) and color of the tips (white for *P. zippelii* and blue or greenish blue for *P. cyanocephala*), as well on molecular data (Giachini, chapter 2).

A significant feature of *P. zippelii* and *P. cyanocephala* is the pantropical distribution also observed for various other *Phaeoclavulina* spp. Based on this and other examples it is now clear that the southern Appalachian Mountains may represent the northernmost refugium of a tropical flora and, as such, offer an area where the circumboreal fungal flora at high elevations is interfaced with a tropical element at low elevations (Petersen 1976b).



a.



b.

Figure 6.41. *Phaeoclavulina zippellii* (Lév.) Giachini, *sp. prov.*: (a) basidiomata (× 1); (b) spores (bar = 10 µm). Photo modified from Corner (1950).

DISCUSSION

Reexamination of generic types within *Gomphus sensu lato* revealed an inadequacy of characters to differentiate taxa. This led to the use of molecular techniques to delineate new boundaries within *Gomphus sensu lato* and related genera within the Gomphales (Giachini, chapter 2). The data not only revealed the non-monophyletic status of *Gomphus sensu lato* but also delineated intergeneric and interspecific boundaries within the family Gomphaceae. Based on those results, species of *Gomphus sensu lato* were segregated into *Gomphus sensu stricto*, *Gloeocantharellus, Phaeoclavulina,* and *Turbinellus*.

Phaeoclavulina currently encompasses pileate species formerly in *Gomphus sensu lato* and ramarioid species previously residing in *Ramaria* subgenus *Echinoramaria*. *Phaeoclavulina* spp. are predominantly lignicolous and long assumed to be saprotrophic, although several species are also terrestrial. There is no empirical evidence, however, for the substrate affinity of *Phaeoclavulina* spp., so further study is necessary to identify their habitat.

Phaeoclavulina spp. particularly resemble the genus *Ramaria*. The main differences observed with *Ramaria* are: (a) the echinulate, verrucose, subreticulate or reticulate spores of *Phaeoclavulina* compared to the smooth or ridged spores of *Ramaria*, and (b) the generally lignicolous habit of *Phaeoclavulina* compared to the mycorrhizal status of most species of *Ramaria*.

Phaeoclavulina differs from *Gloeocantharellus* and *Gomphus sensu stricto* primarily on macroscopic features. *Phaeoclavulina* has ramarioid, unipileate or merismatoid basidiomata, while *Gloeocantharellus* and *Gomphus* have merismatoid basidiomata with funnel- or fan-shaped pilei. Microscopically *Phaeoclavulina* spp. have echinulate, verrucose, subreticulate or reticulate spores while most *Gloeocantharellus* and *Gomphus* species, except for *G. echinosporus*, have verrucose spores. Furthermore, many species of *Phaeoclavulina* are both lignicolous and terrestrial, while those of *Gloeocantharellus* and *Gomphus* seems to be exclusively terrestrial.

Species of *Phaeoclavulina* differ from those in *Turbinellus* both on macro as well as micro morphological features. *Turbinellus* basidiomata are pale yellow to cream colored, pale brown, yellow-orange to red, and most have funnel-shaped, scaly pilei. The scaliness varies among species but is always visible to the naked eye. *Phaeoclavulina*, on the other hand, produces glabrous to subtomentose basidiomata that do not have the combination shape-color as seen in *Turbinellus*. Microscopically they are also quite distinct. Species of *Turbinellus* lack clamp connections, whereas those of *Phaeoclavulina* possess them. The spores of *Turbinellus* are verrucose while those of *Phaeoclavulina* can be echinulate, verrucose, subreticulate or reticulate.

A noteworthy characteristic of many *Phaeoclavulina* species is their cosmopolitan distribution. *Phaeoclavulina* species fruit literally everywhere. As verified in individual species descriptions, species occur in the tropics, subtropics, as well as temperate habitats. They are, however, more abundant in the tropics and subtropics. In addition, a few species have a pantropical distribution, with a refugium in the Appalachian Mountains of the USA. Perhaps one of the main reasons for this great success on dispersion and establishment relies on their nutritional mode. Because many species have both terrestrial and lignicolous substrate affinity, it tremendously widens their opportunity for successful establishment in places of limited resources.

This significant but yet poorly studied genus, observed in many forest ecosystems throughout the world needs further attention for a worldwide circumscription. The lineage represented by *Phaeoclavulina* is an important link between club-like and resupinate fungi, and further studies are necessary to unveil its evolutionary relationships with other members of the Gomphales. Further studies, focusing on ecological and evolutionary aspects, are necessary to better understand the placement and role of *Phaeoclavulina* species among other gomphoid/ramarioid fungi.

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CHAPTER 7

Phylogenetic Relationships of the Gomphales based on nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA combined Sequences

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ABSTRACT

Phylogenetic relationship among Geastrales, Gomphales, Hysterangiales, and Phallales was estimated via nuclear large subunit ribosomal DNA (nuc-25S-rDNA), mitochondrial small subunit ribosomal DNA (mit-12S-rDNA), and mitochondrial *atp*6 DNA (mit-*atp*6-DNA) combined sequences. Eighty-one taxa comprising 19 genera and 58 species were investigated, including members of the families Clathraceae, Gautieriaceae, Geastraceae, Gomphaceae, Hysterangiaceae, Phallaceae, Protophallaceae, and Sphaerobolaceae. Although some nodes deep in the tree could not be fully resolved, some well-supported lineages were recovered, and the interrelationships among *Gloeocantharellus, Gomphus, Phaeoclavulina*, and *Turbinellus*, and the placement of *Ramaria* are better understood. Both *Gomphus sensu lato* and *Ramaria sensu lato* comprise paraphyletic lineages within the Gomphaceae. It is also clear how the subgenera of *Ramaria* are distributed and how each subgenus is related to other members in the Gomphales. Within *Gomphus sensu lato*, genera are separated based on the presence/absence of clamps, spore ornamentation (echinulate, verrucose, subreticulate or reticulate), and basidioma morphology (fan-shaped, funnel-shaped or ramarioid). *Gautieria*, a sequestrate genus in the family Gautieriaceae was recovered as monophyletic nested with members of *Ramaria* subgenus *Ramaria*. This agrees with previous observations showing common traits shared by these two ectomycorrhizal fungi, such as the presence of fungal mats in the soil. *Clavariadelphus* was recovered as sister group to *Beenakia, Kavinia,* and *Lentaria*. The results reaffirm the relationships existent between the Geastrales, Gomphales, Hysterangiales, and the Phallales, suggesting extensive convergence in basidioma morphology among members of these groups. A more extensive sampling, focusing on other loci (protein-coding genes have been shown to be phylogenetically informative) may be useful to answer some of the questions regarding the evolutionary relationships among these groups of organisms.

INTRODUCTION

The gomphoid fungi occupy a unique and important position in the phylogeny of higher Basidiomycetes (Bruns *et al.* 1998, Hibbett and Thorn 2001, Pine *et al.* 1999). They are a prominent component of most terrestrial ecosystems and perform a variety of ecological roles as saprophytes and mutualists. The fungi in this group are also characterized by a wide range of basidioma morphologies from stalked ramarioid/clavarioid to cantharelloid-gomphoid, club, resupinate odontoid, to sequestrate. In addition, gomphoid fungi have historically shown to be evolutionarily close related to fungi in the orders Geastrales, Hysterangiales, and Phallales (Colgan *et al.* 1997, Hibbett *et al.* 1997, Humpert *et al.* 2001, Pine *et al.* 1999).

The taxonomy of these higher basidiomycetes has traditionally relied upon morphological characters known to be subject to parallel evolution and phenotypic plasticity (Moncalvo *et al.* 2000). As a result, many modern genera and families are artificial, and mycologists still disagree about taxonomic limits and identity of natural groups in the orders Geastrales, Gomphales, Hysterangiales, and Phallales.

Earlier workers (Eriksson 1954, Heim 1954, Maire 1902, 1914) recognized the relatedness of diverse morphologies within the Gomphales from microscopic and macrochemical characters, including cyanophilic spore ornamentation, chiastic basidia, hyphal construction, and positive hymenial reaction to ferric sulfate (Donk 1961, 1964, Eriksson 1954, Petersen 1971a, Villegas *et al.* 1999). Donk (1961, 1964) proposed the family Gomphaceae to include the resupinate odontoid genera *Kavinia* and *Ramaricium*, the stalked clavarioid-ramarioid genera *Lentaria* and *Ramaria*, the stalked hydnoid genus *Beenakia,* the stipitate agaricoid genus *Gloeocantharellus*, and the pileate genera *Chloroneuron* and *Gomphus*. Corner (1970) later proposed Ramariaceae to include *Delentaria, Kavinia, Lentaria,* and *Ramaria.* He excluded the pileate genera because there were no intermediate species linking the gomphoid and ramarioid morphologies. Petersen (1971a) suggested a gomphoid ancestral morphology for the group and later revised Donk's

and Corner's familial classifications to include *Beenakia, Gomphus, Kavinia, Ramaricium, Ramariopsis,* and *Ramaria* (Petersen 1973, 1988).

Morphological and more recently molecular data (mitochondrial and nuclear rDNA) have been used to infer inter- and intra-specific relationships among genera in this group of fungi. According to Pine *et al.* (1999), Villegas *et al.* 1999, Humpert *et al.* 2001, and more recently Giachini (chapter 2), the order Gomphales includes the genera *Beenakia, Clavariadelphus, Gautieria, Gloeocantharellus, Gomphus, Kavinia, Lentaria, Phaeoclavulina, Ramaria, Ramaricium*, and *Turbinellus*. These authors also showed the Gomphales to be a sister group of the Hysterangiales, represented by the families Hysterangiaceae (*sensu* E. Fisch.) and Protophallaceae (*sensu* Zeller). The Hysterangiales, in turn, are a sister group to the Phallales, represented by the families Clathraceae (*sensu* Chevall.) and Phallaceae (*sensu* Corda). These are a sister group to the Geastrales, represented here by the Geastraceae (*sensu* Corda) and Sphaerobolaceae (*sensu* J. Schröt.).

Villegas *et al.* (1999), using morphological traits, proposed the order Gomphales to be monophyletic and delimited by the presence of mycelial cords or rhizomorphs. It included the families Beenakiaceae (*Beenakia, Kavinia,* and *Ramaricium*), Gomphaceae (*Gomphus* and *Gloeocantharellus*), Lentariaceae (*Lentaria*), and Ramariaceae (*Ramaria*). According to Singer (1949), Heim (1954), Heineman (1958), Donk (1964), and recently Giachini (chapter 2), *Clavariadelphus* is a member of the Gomphales. The results of Villegas *et al.* (1999), however, disagree with the premises that *Clavariadelphus, Gomphus,* and *Ramaria* are members of the same order. According to those authors *Clavariadelphus* is not grouped within but rather a sister group to the Gomphales.

Pine *et al.* (1999) and Humpert *et al.* (2001), on the other hand, using sequences of both mitochondrial (mit-12S-rDNA) and nuclear (nuc-25S-rDNA) loci, showed that a gomphoid-phalloid clade including *Clavariadelphus, Geastrum, Gloeocantharellus, Gomphus* (monophyletic), *Lentaria, Ramaria* (paraphyletic), *Pseudocolus,* and *Sphaerobolus* was recovered in all analysis performed. Pine *et al.* (1999) showed that *Gomphus sensu lato* represented a terminal monophyletic group

in the gomphoid-phalloid clade (although just two taxa were sampled), having *Ramaria* as sister group (see figures 1 through 3 in Pine *et al.* 1999). Based on morphological as well as molecular characters, Giachini (chapter 2) revisited the generic concepts in the family Gomphaceae and recombined the species of *Gomphus sensu lato* into *Gloeocantharellus*, *Gomphus sensu stricto*, and the resurrected genera *Phaeoclavulina* and *Turbinellus*.

Cantharelloid/gomphoid and clavarioid fungi have historically been prominent in hypotheses about the origin of fleshy basidiomycetes (Corner 1966, Corner 1972, Harrison 1971, Heim 1954, Jülich 1981, Miller and Watling 1987, Petersen 1971a, Singer 1947, 1986). Their fruiting forms can be arranged in a transformation series, from club at one end, cantharelloid/gomphoid intermediately, and agaricoid at the other extreme. Corner (1972) proposed the "*Clavaria* theory" of basidiomycete evolution in which cantharelloid and clavarioid fungi were to be regarded as ancestral, and from which all other Homobasidiomycetes have been derived. He suggested that simple club (e.g. *Clavaria*) morphology with smooth hymenium originated intermediate cantharelloid species (e.g. *Cantharellus, Craterellus*), and from those cantharelloid species derived the wrinkled or folded hymenium species of gomphoid fungi (e.g. *Gomphus, Turbinellus*). Other authors agree that there must have been transformations among ramarioid, cantharelloid, and agaricoid forms, but propose the opposite polarity, suggesting that lineages containing cantharelloid, ramarioid, and club like fungi have been derived from agaricoid ancestors (Arpin and Fiasson 1971, Fiasson *et al.* 1970, Petersen 1971a, Singer 1986).

In this paper we analyze phylogenetic relationships among major evolutionary lineages of gomphoid fungi using combined sequence data from nuclear (nuc-25S-rDNA) and mitochondrial-encoded ribosomal and non-ribosomal RNA genes (mit-12S-rDNA, mit-*atp*6-DNA). Taxonomic sampling for this study has been focused on the order Gomphales *sensu* Jülich (1981). Major questions tested in this study were: 1) is *Gomphus sensu lato* monophyletic? 2) Are genera within *Gomphus sensu lato* monophyletic? 3) Are the Gomphales, Hysterangiales,

Phallales, and Geastrales closely related? 4) How is the evolution of basidiomata morphology, presence/absence of clamp connections, and substrate affinity within the order Gomphales? Our results provide molecular support for many well-defined groups within the Gomphales and also help to resolve phylogenetic relationships of some controversial taxa, ultimately reinforcing the long-suggested evolutionary relationships of the Geastrales, Gomphales, Hysterangiales and Phallales.

MATERIAL AND METHODS

Taxonomic sampling

Holotypes and representative specimens of the Gomphales were examined and sampled when available. Specimens were obtained from the following herbaria: BPI, BR, DSH, FH, K, MICH, NYS, O, OSA, OSC, PERTH, PDD, SFSU, SUC, TENN, Trappe, UC, and UPS (http://www.nybg.org/bsci/ih/ih.html). In addition to herbaria dried specimens, fresh specimens collected mainly in the Pacific northwestern USA (PNW) were also included. When possible, at least two collections of each species were sampled. This sampling included 19 genera in a total of 81 taxa comprising 58 species of the Geastrales, Gomphales, Hysterangiales, and Phallales. Species selected for phylogenetic analysis are listed in table 7.1, along with taxonomic classification according to Giachini (chapter 2) and Humpert *et al.* (2001), as well as GenBank accession numbers of the three genes sequenced. Three species, *Bondarzewia* sp, *Cortinarius iodes*, and *Russula* sp. were included in the analysis as outgroup for rooting purposes.

Identification of species and nomenclature used in this study were based on the use of holotype and paratype specimens, taxonomic keys and species descriptions (Corner 1950, 1966, 1969, 1970, Giachini, chapter 2, Marr and Stuntz 1973, Petersen 1971b, 1981, 1988, Roberts 1999, Schild 1998), the grouping of

non-type specimens with type material, and the sampling of multiple unique collections of the same morphological species whenever possible. All specimens are maintained as vouchers and are available from the respective herbaria (Table 7.1).

DNA extraction

Genomic DNA was extracted from holotype and representative collections by a CTAB extraction method following protocols described by Gardes and Bruns (1993) with subsequent purification with a glassmilk kit (BIO 101, Carlsbad, CA, USA). Two hundred μL of 2 × CTAB lysis buffer (100 mM Tris-HCL – pH 8.0, 1.4 M NaCl, 20 mM EDTA, 2% Hexadecyltrimethylamonium bromide – CTAB, and 0.2% β-mercaptoethanol added just prior to using) was added to 1.5 mL centrifuge Eppendorf tubes (USA Scientific, Ocala, FL, USA) containing 3 to 5 g of fresh or dried tissue. The tissue was then macerated with a Ryobi cordless drill and reusable (Kontes) pellet pestles (Fisher Scientific, Pittsburgh, PA, USA) previously autoclaved. After maceration, another 400 μL of CTAB was added to the emulsion. The buffer-suspended samples were frozen and thawed five times by passing the tubes between a dry-ice-ethanol bath and a 65 C heat bath. After the final thaw, the tissue was incubated at 65 C for 1 hr. One volume of chloroform was added to each sample and mixed by briefly vortexing. The samples were then centrifuged at 12000 rpm for 15 min at room temperature. The aqueous phase was removed from each tube and transferred to a new centrifuge tube. If the aqueous phase looked turbid, the chloroform treatment was repeated. A 5 μL glass milk solution (following the manufacturer's protocol) was added to each sample. The tubes were incubated in a turning hybridization oven for a minimum of 30 min at ambient temperature. The solution was then spun for 30 sec and the supernatant was carefully removed. Three washes with an ethanol solution were employed to

Table 7.1. Taxa included in the phylogenetic analyses of the Gomphales.

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp*6-rDNA
Beenakia fricta Maas Geest.	2083	K	AY574693	AY574766	AY574833
Clathrus cibarius (Tul.) E. Fisch.	107652	OSC	AY574641	AY574715	AY574783
Clavariadelphus ligula (Schaeff.) Donk	67068	OSC	AY574650	AY574723	AY574793
C. occidentalis Methven	37018	OSC	AY574648	AY574721	AY574791
C. truncatus Donk	67280	OSC	AY574649	AY574722	AY574792
Gallacea Scleroderma (Cooke) Lloyd	59621	OSC	AY574645	AY574719	AY574787
Gautieria monticola Harkn.	65121	OSC	AY574651	AY574724	AY574794
G. parksiana Zeller & C.W. Dodge	58907	OSC	AY574652	AY574725	AY574795
Geastrum saccatum Fr.	23765	Trappe	AY574646	AY574720	AY574788
Gloeocantharellus dingleyae (Segedin) Giachini	30179*	PDD	AY574668	AY574741	–
G. novae-zelandiae (Segedin) Giachini	44960*	PDD	AY574666	AY574739	AY574809
G. pallidus (Yasuda) Giachini	54917*	BPI	AY574673	AY574746	AY574815
G. papuanus Giachini, Bougher, Castellano & Trappe	06707114*	PERTH	AY574667	AY574740	AY574810
G. purpurascens (Hesler) Singer	12793	TENN	AY574683	AY574756	AY574823
G. purpurascens (Hesler) Singer	14265*	TENN	AY574684	AY574757	AY574824
Gomphus brunneus (Heinem.) Corner	034190-46	BR	AY574680	AY574753	AY574821
G. clavatus (Pers.) Gray	97616	OSC	AY574664	AY574737	AY574807
G. clavatus (Pers.) Gray	s.n.	UPS	AY574665	AY574738	AY574808
Hysterangium coriaceum R. Hesse	64939	OSC	AY574686	AY574759	AY574826
H. crassum (Tul. & C. Tul.) E. Fisch.	110447	OSC	AY574687	AY574760	AY574827
H. occidentalis Harkn.	47048	OSC	AY574685	AY574758	AY574825
Kavinia alboviridis (Morgan) Gilb. & Budington	102140	O	AY574692	AY574765	AY574832
K. himantia (Schwein.) J. Erikss.	102156	O	AY574691	AY574764	AY574831
Lentaria pinicola (Burt) R.H. Petersen	M89**	SUC	AY574688	AY574761	AY574828
Lentaria pinicola (Burt) R.H. Petersen	M46	SUC	AY574689	AY574762	AY574829
Lentaria pinicola (Burt) R.H. Petersen	M560	SUC	AY574690	AY574763	AY574830
Mutinus elegans (Mont.) E. Fisch.	107657	OSC	AY574643	AY574717	AY574785
Phaeoclavulina africana (R.H. Petersen) Giachini	39621*	TENN	AY574653	AY574726	AY574796
P. cokeri (R.H. Petersen) Giachini	36030*	TENN	AY574701	AY574774	AY574843
P. curta (Fr.) Giachini	8711	OSC	AY574713	–	AY574858

Table 7.1. Taxa included in the phylogenetic analyses of the Gomphales (*cont.*).

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp6*-rDNA
P. cyanocephala (Lév.) Giachini	37827	TENN	AY574710	AY574779	AY574854
P. eumorpha (P. Karst.) Giachini	36218	TENN	AY574712	AY574781	AY574856
P. eumorpha (P. Karst.) Giachini	37842	TENN	–	AY574782	AY574857
P. gigantea (Pat.) Giachini	109*	FH	AY574703	AY574776	AY574845
P. grandis (Corner) Giachini	073158-06*	BR	AY574678	AY574751	AY574820
P. guadelupensis (Pat.) Giachini	120*	FH	AY574682	AY574755	–
P. guyanensis (Pat.) Giachini	84*	FH	AY574706	–	AY574848
P. insignis (Pat.) Giachini	104*	FH	AY574704	–	AY574846
P. longicaulis (Pat.) Giachini	33826	TENN	AY574700	AY574773	AY574842
P. ochraceo-virens (Jungh.) Giachini	23475	OSC	AY574714	–	AY574859
P. pancaribbea (R.H. Petersen) Giachini	31836*	TENN	AY574707	–	AY574849
P. subclaviformis (Berk.) Giachini	073159-07*	BR	AY574679	AY574752	–
P. viridis (Pat.) Giachini	97708	OSC	AY574675	AY574748	AY574817
P. viridis (Pat.) Giachini	1853	FH	AY574676	AY574749	AY574818
P. viridis (Pat.) Giachini	4302	PERTH	AY574677	AY574750	AY574819
Phallus impudicus L.	107655	OSC	AY574642	AY574716	AY574784
Protubera nothofagi Castellano & Beever	59699	OSC	AY574644	AY574718	AY574786
Pseudocolus fusiformis (E. Fisch.) Lloyd	96-033	DSH	AF518641	AF026666	–
Ramaria apiculata (Fr.) Donk	23549	OSC	AY574695	AY574768	AY574836
R. apiculata var. *brunnea* R.H. Petersen	53935	TENN	AY574696	AY574769	AY574837
R. araiospora var. *araiospora* Marr & D.E. Stuntz	M739*	SUC	AF213068	AF213141	AY574838
R. araiospora var. *araiospora* Marr & D.E. Stuntz	M556	SUC	AY574697	AY574770	AY574839
R. botrytis var. *botrytis* (Pers.) Ricken	M457	SUC	AY574698	AY574771	AY574840
R. botrytis var. *botrytis* (Pers.) Ricken	M740	SUC	AY574699	AY574772	AY574841
R. circinans (Peck) Marr & D.E. Stuntz	s.n.	NYS	AY574702	AY574775	AY574844
R. circinans var. *anceps* Marr & D.E. Stuntz	M615*	SUC	AY574711	AY574780	AY574855
R. gelatiniaurantia var. *violeitingens* Marr & D.E. Stuntz	M830	SUC	AY574708	AY574777	AY574851
R. rainieriensis Marr & D.E. Stuntz	M231	SUC	AF213115	AF213135	AY574834
R. rainieriensis Marr & D.E. Stuntz	M431	SUC	AY574694	AY574767	AY574835
R. rubribrunnescens Marr & D.E. Stuntz	M844*	SUC	AF213098	AF213142	AY574852

Table 7.1. Taxa included in the phylogenetic analyses of the Gomphales (*cont.*).

Taxa[a]	Collection[b]	Herbarium[c]	GenBank accession numbers		
			nuc-25S-rDNA	mit-18S-rDNA	mit-*atp*6-rDNA
R. stuntzii Marr	M214	SUC	AF213102	AF213134	AY574850
R. suecica (Fr.) Donk	s.n.	BPI	AY574705	–	AY574847
R. vinosimaculans Marr & D.E. Stuntz	23287	OSC	AY574709	AY574778	AY574853
Sphaerobolus stellatus Tode	96-015	DSH	AF393077	AF026662	AY574789
S. stellatus Tode	SS28	–	AY574647	AY488024	AY574790
Turbinellus flabellatus (Berk.) Giachini	191†	FH	AY574674	AY574747	AY574816
T. flabellatus (Berk.) Giachini	1770*	K	AY574681	AY574754	AY574822
T. floccosus (Schwein.) Earle	MY-1839	OSA	AY574654	AY574727	AY574797
T. floccosus (Schwein.) Earle	MY-1840	OSA	AY574655	AY574728	AY574798
T. floccosus (Schwein.) Earle	69167	OSC	AY574656	AY574729	AY574799
T. floccosus (Schwein.) Earle	33233	TENN	AY574657	AY574730	AY574800
T. floccosus (Schwein.) Earle	21238†	SFSU	AY574658	AY574731	AY574801
T. floccosus (Schwein.) Earle	33295†	TENN	AY574659	AY574732	AY574802
T. floccosus (Schwein.) Earle	5588†	MICH	AY574660	AY574733	AY574803
T. floccosus (Schwein.) Earle	10721†	MICH	AY574661	AY574734	AY574804
T. floccosus (Schwein.) Earle	759902†	UC	AY574662	AY574735	AY574805
T. floccosus (Schwein.) Earle	924302†	UC	AY574663	AY574736	AY574806
T. fujisanensis (S. Imai) Giachini	MY-1841	OSA	AY574670	AY574743	AY574812
T. fujisanensis (S. Imai) Giachini	MY-1842*	OSA	AY574669	AY574742	AY574811
T. kauffmanii (A.H. Sm.) Giachini	10069*	MICH	AY574671	AY574744	AY574813
T. kauffmanii (A.H. Sm.) Giachini	97590	OSC	AY574672	AY574745	AY574814
Outgroup					
Bondarzewia berkeleyi (Fr.) Bondartsev & Singer	93-190	DSH	SARn	U27026	–
Cortinarius iodes Berk. & M.A. Curtis	JM96/23	–	AF042613	AF026675	AF388826
Russula sp.	s.n.	–	U11926	U27074	AF002148

[a] Epithets according to Giachini (2004a), Humpert *et al.* (2001), Marr and Stuntz (1973), and Petersen (1981, 1988).
[b] * Indicates holotype specimens; ** indicates paratype specimens; s.n. indicates no number; † indicates type for older name (see Giachini 2004a for details).

[c] Herbarium for source of collections: BPI = U.S. National Fungal Collections – Beltsville; BR = Herbarium of the National Botanical Garden of Belgium – Meise; DSH = Personal collection of Dr. David S. Hibbett, Biology Department, Clark University – Worcester; FH = Farlow Herbarium of Cryptogamic Botany – Cambridge; K = Royal Botanic Gardens Herbarium – Kew; MICH = University of Michigan Fungus Collection – Ann Arbor; NYS = Herbarium of the New York State Museum – Albany; O = Herbarium of the Botanical Museum of Oslo – Oslo; OSA = Osaka Museum of Natural History – Osaka; OSC = Oregon State University Herbarium – Corvallis; PDD = New Zealand Plant Diseases Division Herbarium – Auckland; PERTH = CSIRO Forestry and Forest Products Herbarium – Perth; SFSU = Harry D. Thiers Herbarium at San Francisco State University – San Francisco; SUC = State University of New York Herbarium – Oneonta; TENN = University of Tennessee Herbarium – Knoxville; Trappe = Personal collection of Dr. James M. Trappe, Department of Forest Science, Oregon State University – Corvallis; UC = University of California Herbarium – Berkeley; UPS = Herbarium of the Uppsala Botanical Museum of Uppsala University – Uppsala.

remove extra and undesirable pieces of dirt and particulate substances. Following the final steps, the pellet was air dried for 30 min under hood flow before resuspension in 25-30 µL sterile-distilled water or TE. Some taxa proved to be extremely difficult to yield workable DNA fragments, particularly old specimens and/or those with dark pigments, and protocols were modified to reduce the concentrations of those pigments following the procedures described by Pine *et al.* (1999), in an attempt to yield enough DNA for amplification of the target regions.

Amplification of the nuc-25S-rDNA

Approximately 650 bp (base pairs) of the large subunit of the nuclear ribosomal DNA (nuc-25S-rDNA) were amplified via polymerase chain reaction (PCR) using different primer-pair combinations. LROR (5'-ACC CGC TGA ACT TAA GC-3') and LR3 (5'-CCG TGT TTC AAG ACG GG-3') were initially employed (Vilgalys and Hester 1990, White *et al.* 1990). For those specimens that could not be amplified with the described primer-pair (mainly aged specimens, which tend to have degraded DNA), an extra pair of primers, RAM 1 (5'-CGY GAC TGA CTT CAA RCG-3') and RAM 3 (5'-GCG AAC AAG TAC CGT GAG-3') (Humpert *et al.* 2001) was used in addition to the previously listed set (Figure 7.1, table 7.2). This approach reduced the size of the template DNA to be amplified and increased the yield of DNA amplification. PCR reactions were performed in 50 µL reaction mixtures containing ddH_2O, 1 µL of DNA template, 4 µL of each 10 µM primer, 5 µL of *Taq* 10x buffer, 5 µL of 2.5 mM dNTP mix, 3 µL of 25 mM $MgCl_2$, and 0.5 µL of 5U/µL *Taq* polymerase. PCR reaction parameters were performed as follows: 94 C (3 min), [94 C (1 min), 51 C (30 sec), 72 C (1 min)] x 29 times, [94 C (1 min), 51 C (30 sec), 72 C (1 min) + 5 sec/cycle] x 4 times, 72 C (5 min), and 4 C (30 min) on a Programmable Thermal Controller (PTC)-100 thermal cycler (MJ Research, Inc., Waltham, MA, USA).

Figure 7.1. Primer diagrams of the genetic regions examined in the study.

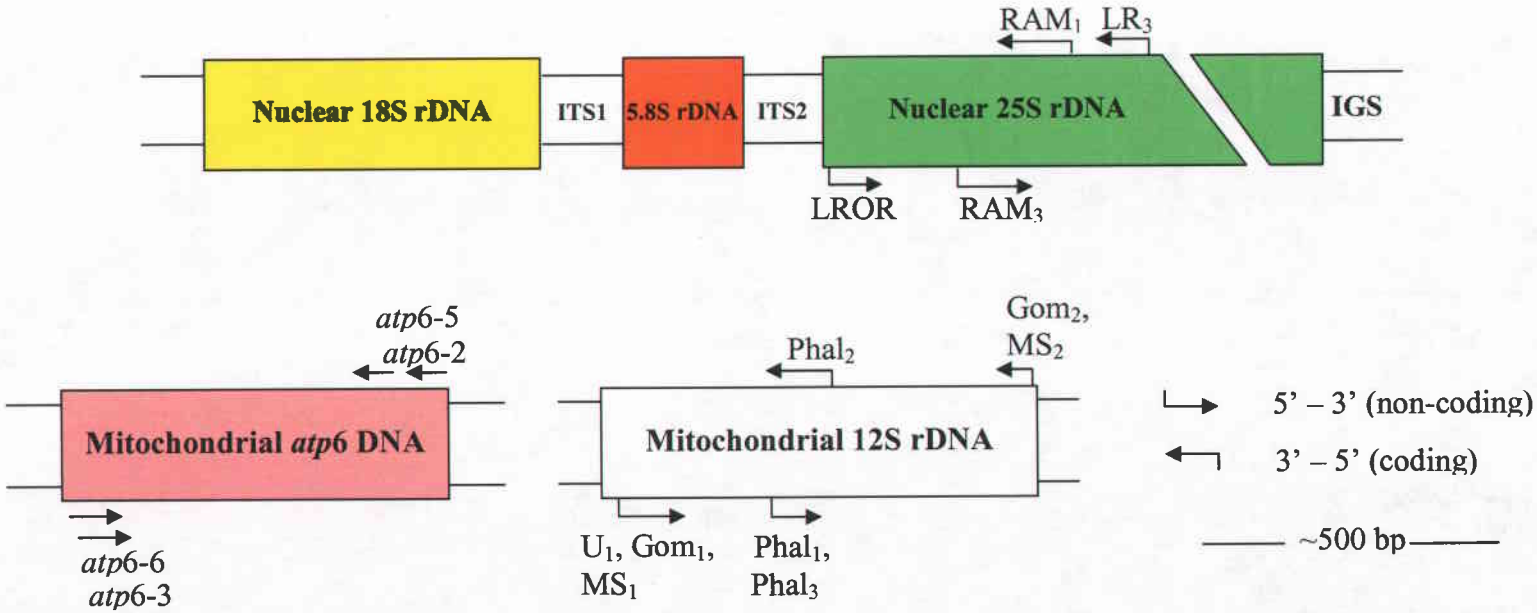

Table 7.2. List of primers employed in the study.

Primer	Sequence	Tm	Author
*atp*6-2	5'-TAA TTC TAN WGC ATC TTT AAT RTA-3'	44	Kretzer and Bruns (1999)
*atp*6-3	5'-TCT CCT TTA GAA CAA TTT GA-3'	50	Kretzer and Bruns (1999)
*atp*6-5	5'-ATY GCTTTA GAA AGT TYM TTT GC-3'	56	Giachini (Chapter 2)
*atp*6-6	5'-GGD ATR AAR WAW GAR AAR AAR TG-3'	55	Giachini (Chapter 2)
Gom1	5'-AYG ARA TMT CCC AAG TAG AG-3'	62	Giachini (Chapter 2)
Gom2	5'-TAC TYA CAA GGC GGA ATG G-3'	65	Giachini (Chapter 2)
LROR	5'-ACC CGC TGA ACT TAA GC-3'	54	White *et al.* 1990
LR3	5'-CCG TGT TTC AAG ACG GG-3'	60	White *et al.* 1990
MS1	5'-CAG CAG TCA AGA ATA TTA GTC AAT G-3'	63	White *et al.* 1990
MS2	5'-GCG GAT TAT CGA ATT AAA TAA C-3'	53	White *et al.* 1990
Phal1	5'-CCA KAA GAC TCG GTA AKG-3'	45	Giachini (Chapter 2)
Phal2	5'-TTA CCG AGT CTT CTG GCA C-3'	67	Giachini (Chapter 2)
Phal3	5'-AGA CTC GGT AAK GCC ARA G-3'	65	Giachini (Chapter 2)
RAM1	5'-CGY GAC TGA CTT CAA RCG-3'	60	Humpert *et al.* (2001)
RAM3	5'-GCG AAC AAG TAC CGT GAG-3'	57	Humpert *et al.* (2001)
U1	5'- TAA TTT TGG TGC CGA TTG AAC G-3'	57	T.D. Bruns web page

Amplification of the mit-12S-rDNA

Approximately 600 bp of the mit-12S-rDNA were amplified using PCR reactions. Several primer sets had to be employed for the amplification of the mit-12S-rDNA due to the constant unsuccessful amplifications observed for some of the collections. A few extra primers had to be designed to allow for DNA amplification. Primers employed in the amplification of the mit-12S-rDNA template included Gom1 (5'-AYG ARA TMT CCC AAG TAG AG-3') (Giachini, chapter 2), Gom2 (5'-TAC TYA CAA GGC GGA ATG G-3') (Giachini, chapter 2), MS1 (5'-CAG CAG TCA AGA ATA TTA GTC AAT G-3') (White *et al.* 1990), MS2 (5'-GCG GAT TAT CGA ATT AAA TAA C-3') (White *et al.* 1990), Phal1 (5'-CCA KAA GAC TCG GTA AKG-3') (Giachini, chapter 2), Phal2 (5'-TTA CCG AGT CTT CTG GCA C-3') (Giachini 2004a), Phal3 (5'-AGA CTC GGT AAK GCC ARA G-3') (Giachini, chapter 2), and U1 (5'- TAA TTT TGG TGC CGA TTG AAC G-3') (http://plantbio.berkeley.edu/~bruns/primers.html). Primers were coupled as exemplified in figure 7.1 and table 7.2 to generate the highest amplification yields. PCR reactions and parameters were as for the nuc-25S-rDNA.

Amplification of the mit-*atp*6-DNA

Approximately 700 bp of the *atp*6 region were amplified using primarily the primer-pair *atp*6-2 (5'-TAA TTC TAN WGC ATC TTT AAT RTA-3') and *atp*6-3 (5'-TCT CCT TTA GAA CAA TTT GA-3') (Kretzer and Bruns 1999). Primers *atp*6-5 (5'-ATY GCTTTA GAA AGT TYM TTT GC-3') and *atp*6-6 (5'-GGD ATR AAR WAW GAR AAR AAR TG-3') (Giachini, chapter 2) were designed to amplify those samples that did not amplify when using *atp*6-2 and *atp*6-3 (Figure 7.1, table 7.2). Other primers designed by Kretzer and Bruns (1999) were also employed but without success. PCR reactions were prepared under the same

conditions specified for the nuc-25S-rDNA, and the reactions performed as follows: 94 C (1 min), [94 C (35 sec), 40 C (55 sec), 72 C (1 min)] x 4 times, [94 C (35 sec), 48 C (55 sec), +24 C (1 C/4 sec), 72 C (1 min + 4 sec/cycle)] x 25 times, 72 C (10 min), and 20 C (10 min).

DNA sequencing

Amplified DNA was detected via gel electrophoresis (1-2%), visualized with ethidium bromide under transiluminator, and quantified with a low DNA mass ladder (Gibco-BRL, Life Technologies, Gaithersburg, MD, USA). Positive PCR products were then purified with either one of the following kits: Glassmilk kit (BIO 101, Carlsbad, CA, USA), QIAquick PCR purification kit (QIAGEN, Inc., Valencia, CA, USA), or Exosap-IT kit (Amersham Biosciences UK Limited, Little Chalfont Buckinghamshire, England), following the manufacturer's protocol. Yield was determined in agarose gels (1-2%), except for Exosap-IT kit, which dispenses this extra step. Nucleotide sequences were determined by the cyclic reaction termination method. Sequencing reactions and the processing of reaction products were performed following instructions for the ABI PRISM™ (PE Applied Biosystems, Foster City, CA, USA) and Amersham™ Dye Terminator Cycle Sequencing Core Kits (Amersham Biosciences UK Limited, Little Chalfont Buckinghamshire, England). Internal primers were applied whenever possible. Electrophoresis and data collection were performed on an ABI Model 373A automated DNA Sequencer (Perkin-Elmer Corporation, Wellesley, MA, USA). Sequencing Analysis (version 2.1.2) and Sequence Navigator (version 1.0.3) were used for processing the raw data.

Sequence alignment and phylogenetic analyses

Sequence contigs were assembled and manually edited with SeqEd version 1.0.3 (Applied Biosystems, Inc., Foster City, CA, USA). Alignment was done by visual examination in PAUP* version 4.0b10 (Swofford 2002) with a color font. Sequences immediately adjacent to the priming sites of the sequencing primers and some hypervariable regions were of low quality in some of the sequences, and therefore excluded from the analysis. Within the areas included in the active data set, most single-basepair alignment gaps and ambiguous insertions/deletions (indels) were treated as missing data. Phylogenetic analyses were performed on the combined dataset of the three loci mentioned above using 2 methods: maximum parsimony (MP) and Bayesian posterior probability (Metropolis-Coupled Markov Chain Monte Carlo, or MCMCMC, or MC^3).

Maximum parsimony analysis were conducted in PAUP* 4.0b10 (Swofford 2002). Uninformative characters plus non-alignable areas of the dataset were removed to reduce noise and to increase the reliability of the results. Most parsimonious trees (MPTs) were recovered using the heuristic search option (TBR and MULPARS on) with 10000 replicates of random sequence addition. Support for individual branches was tested with bootstrap analysis (1000 replicates) under the parsimony criterion with full sequence addition (TBR and MULPARS on). All MPTs recovered were subsequently compared to each other under the maximum likelihood criterion (Kishino-Hasegawa 1989). Significant topological differences under the maximum parsimony criterion and the combinability of the data were estimated via the Shimodaira and Hasegawa (1999) likelihood test ($p \leq 0.05$).

A second analysis was run with Mr. Bayes version 3.0 (Huelsenbeck and Ronquist 2002) under the posterior probability theorem (MC^3) with 3000000 chains. We applied independent models for each partition using general time reversible (GTR) and gamma (δ) distribution.

Alternative phylogenetic hypotheses reflecting different classifications and species relationships were constructed in MacClade version 3.03 (Maddison and

Maddison 1992) and PAUP* 4.0b10 (Swofford 2002). These trees were used as constraint starting topologies in maximum parsimony analyses in the heuristic search option (100 random sequence additions, TBR, and MULPARS off). Most parsimonious trees recovered with and without constraints were compared by the Kishino-Hasegawa (K-H) test implementing the likelihood model described above (Table 7.3). Character state reconstruction for substrate affinity, basidiomata morphology, and presence/absence of clamp connections were performed in Mr. Bayes (MC^3) (Huelsenbeck and Ronquist 2002); equal weights for all character state transformations were assumed.

Character mapping

The character states at ancestral nodes are normally not known and thus constitute parameters to be estimated. The objective is to derive statements and values that can be used to suggest that one value at a node is more or less likely than some other (Pagel 1994, 1999). In order to estimate these values, we first need to denote a model of character evolution. For this study, GTR (likelihood) was found to best fit to our data. Adopting GTR in the computer-based program Multi-state (Pagel 1994 - http://www.ams.rdg.ac.uk/zoology/pagel/mppubs.html), we calculated trait evolution for characters representing substrate affinity, presence/absence of clamp connections, and basidiomata morphology for the node/clade denoting the order Gomphales.

Table 7.3. Kishino-Hasegawa likelihood test results.

Topology[a]	Trees[b]	-*ln* likelihood	*p*[c]
Unconstrained	3	20283.09185	Better
Monophyletic *Gomphus sensu lato*	2	20592.30503–20597.07762	<0.0001*
Monophyletic *Phaeo+Gloeo+Gom*	1	20630.80136	<0.0001*
Monophyletic *Phaeo+Gloeo+Turb*	8	20608.04892–20623.80385	<0.0001*
Monophyletic *Phaeo+Gom+Turb*	10	20595.90882–20614.11428	<0.0001*
Monophyletic *Phaeo+Gloeo*	1	20550.19484	<0.0001*
Monophyletic *Phaeo+Gom*	1	20612.56469	<0.0001*
Monophyletic *Phaeo+Turb*	3	20648.44839–20657.53649	<0.0001*
Monophyletic *Gloeo+Gom+Turb*	2	20549.91723–20554.45501	<0.0001*
Monophyletic *Gloeo+Gom*	1	20571.14433	<0.0001*
Monophyletic *Gloeo+Turb*	7	20534.76597–20553.41940	<0.0001*
Monophyletic *Gom+Turb*	1	20578.88126	<0.0001*

[a] *Gloeo* = *Gloeocantharellus*; *Gom* = *Gomphus*; *Phaeo* = *Phaeoclavulina*; *Turb* = *Turbinellus*.

[b] The best -*ln* likelihood tree from the maximum parsimony analyses.

[c] Probability of getting a more extreme *t*-value under the null hypothesis of no difference between the two trees (two-tailed test); * statistically significant at $p<0.05$.

RESULTS

Sequence alignment and nucleotide sequence variation

An alignment of 84 taxa over 2000 positions long was obtained. After removal of the 5' and 3' positions (incomplete for several taxa), 2063 positions remained in the final analyses. Alignment over a broad taxonomic sampling was not attainable for a few hypervariable, indel-rich regions, and those were removed from the analyses. However, subsets of related taxa aligned well within those divergent domains, suggesting that they had phylogenetic information at lower taxonomic levels. A few remaining single-gap regions occurring in only one or few sequences were removed before sequence analyses due to the possibility that they represented sequencing errors. In contrast, several gap regions with short indels were recorded as phylogenetically informative. In all, 314 positions corresponding to regions with problematic alignments were removed, and 120 indel positions were recorded. Of the 2063 characters included in the analyses, 758 were constant, 328 variable characters were parsimony-uninformative, and 685 were parsimony-informative. The final alignment is available in the web as a NEXUS file (SN1858).

Phylogenetic trees

The analyses of the three combined loci after removing ambiguous and constant characters yielded three MPTs of 4967 steps (Figure 7.2). For those trees, the CI was 0.287, the RI 0.566, and the RC 0.163. Figure 7.3 depicts the consensus tree obtained for the taxa studied. For this tree, Bayesian posterior probability values (MC^3) are presented above branches and bootstrap values greater than 50 are presented below branches. The results obtained support the monophyletic status

and illustrate a close evolutionary relationship among the orders Geastrales, Gomphales, Hysterangiales and Phallales, corroborating results previously obtained by Hibbett *et al.* 1997, Humpert *et al.* 2001, and Pine *et al.* 1999. These results are also in agreement with the findings of Giachini (chapter 2) on the paraphyletic status of *Gomphus sensu lato*. They also show the monophyletic status of *Gloeocantharellus, Gomphus*, *Phaeoclavulina*, and *Turbinellus*. Furthermore, the phylogenetic analyses corroborate previous results on the paraphyletic status of *Clavariadelphus, Kavinia*, and *Ramaria*, and the monophyletic status of *Gautieria*, *Lentaria*, and *Ramaria* subgenus *Ramaria* (Humpert *et al.* 2001). Within the Hysterangiales the results show a monophyletic *Hysterangium*. In the Geastrales they support a monophyletic *Sphaerobolus* (Figure 7.2). In summary, the results suggest a monophyletic status for all genera within Geastrales, Hysterangiales, and Phallales, although more data is necessary before any final conclusion is made.

Geastrales, Hysterangiales, and Phallales

The results of the three combined loci supported previous hypothesis of a Geastrales-Hysterangiales-Phallales relationship to the Gomphales (Colgan *et al.* 1997, Hibbett *et al.* 1997, Humpert *et al.* 2001). Both Bayesian MC^3 and bootstrap values indicated a consistent and confident resolution for the evolutionary placement of Geastrales, Hysterangiales, and Phallales in relation to the Gomphales. Three genera were sampled for the Hysterangiales: *Gallacea, Hysterangium*, and *Protubera*, which suggested the Hysterangiales to be a sister group of the Gomphales (Figure 7.2). *Hysterangium* was recovered as monophyletic, but a larger sampling in this genus is required before any final conclusion on its monophyletic status. Four genera of the Phallales were sampled: *Clathrus, Mutinus, Phallus*, and *Pseudocolus*. Results showed this order to be a sister group to the Hysterangiales (Figure 7.2). The Geastrales, represented in this study by *Geastrum* (earth-star fungus) and *Sphaerobolus* (cannon-ball fungus),

were recovered as a basal, more primitive sister lineage (Figure 7.2). The placement of earth-star and cannon-ball fungi as ancestral lineage for the Gomphales-Hysterangiales-Phallales have not been discussed in the literature before, and beyond the basic hymenomycete features shared by these taxa, there are no further morphological characters identified to support this evolutionary relationship. Further sampling of representatives of the Geastrales might aid on understanding this evolutionary placement.

Character mapping

Characters for substrate affinity, presence/absence of clamp connections, and basidioma morphology are shown in figure 7.2. Evolution of substrate affinity indicates an ambiguous (lignicolous or terricolous) substrate affinity as ancestral for the Gomphales with one derivation of the strictly terricolous condition for *Clavariadelphus* and the clade containing *Gloeocantharellus, Gomphus, Ramaria* subgenera *Laeticolora* and *Ramaria, Turbinellus,* and the sequestrate genus *Gautieria* (Figure 7.2). Evolution of basidioma macromorphology suggests that the ramarioid morphology is ancestral for the Gomphales with multiple derivations of diverse basidiomata morphologies, i.e., club, gomphoid, odontoid, resupinate, and sequestrate (Figure 7.2). The presence or absence of clamp connections was also mapped and shows that there were multiple gains and losses of this feature throughout the evolutionary history of the Gomphales (Figure 7.2). The results inferred an ancestral clamped condition with multiple losses of clamps occurring in some species of *Beenakia, Gloeocantharellus*, *Kavinia,* and *Ramaria* subgenera *Laeticolora* and *Ramaria*, and for all species of *Gautieria.*

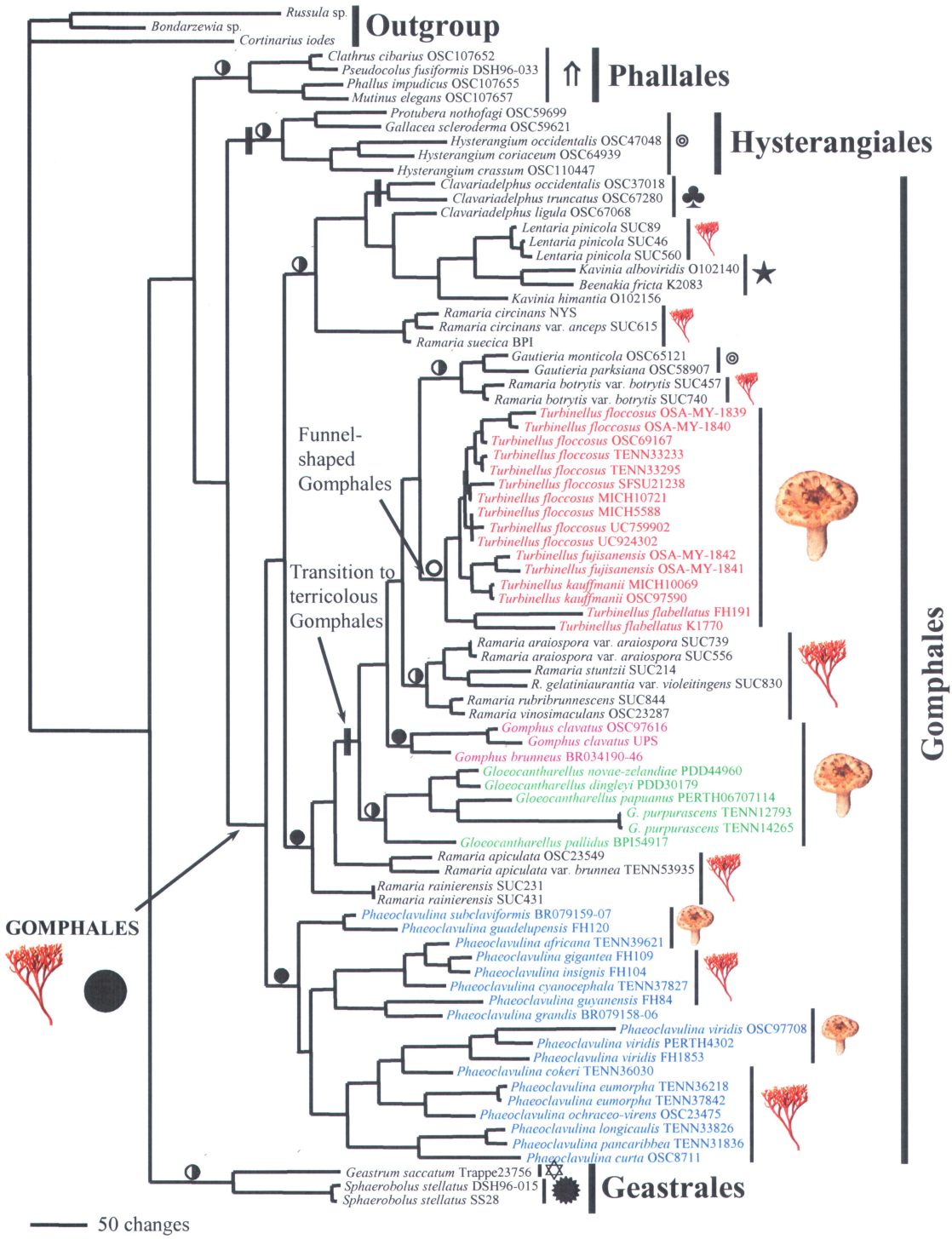

Figure 7.2. Cladogram of 1 of 3 most parsimonious (MP) trees recovered from phylogenetic analyses of the nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA combined sequences. Tree length = 4967; CI=0.287, RI=0.566, RC=0.163. Basidiomata morphology: = ramarioid; = club; = cantharelloid-gomphoid; = stink horn; = sequestrate; = earth-star; = cannon ball; = odontoid/resupinate. Transition to a terricolous substrate affinity is indicated by the symbol . Clamp connections are indicated with the following symbols: = clamp connection present; = clamp connections absent; = clamp connections present in some species while absent in others.

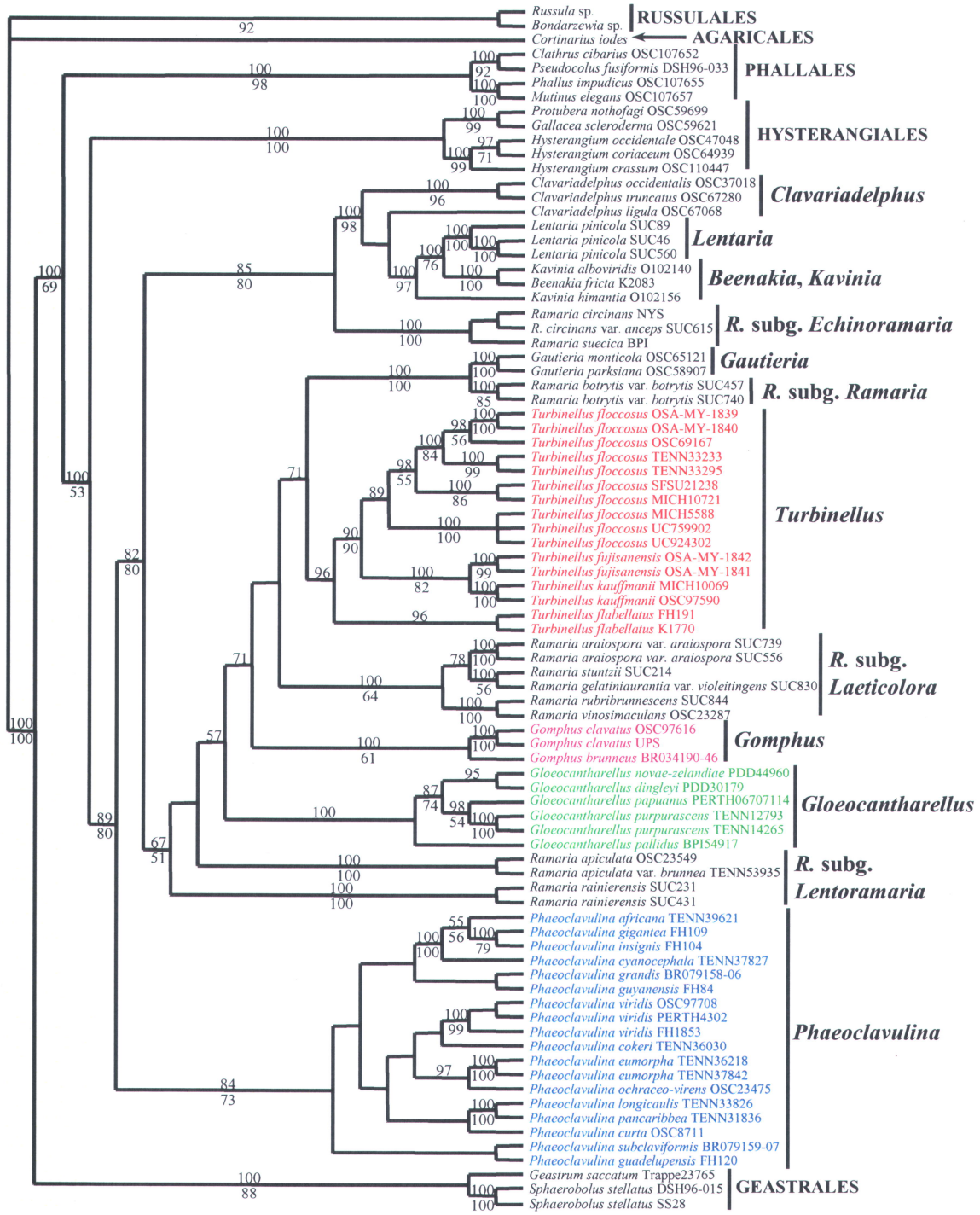

Figure 7.3. Strict consensus cladogram of 3 equally parsimonious (MP) trees of 4967 steps based on nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA combined sequences. MC^3 and Bootstrap values above 50% are indicated above and below respective internode, respectively. CI=0.287, RI=0.566, RC=0.163.

Kishino-Hasegawa and Shimodaira-Hasegawa tests

The results of the Kishino-Hasegawa (1989) and Shimodaira-Hasegawa (1999) tests are presented in table 7.3 and figure 7.4, respectively. Hypotheses for the Kishino-Hasegawa test were as follow: (i) *Gomphus sensu lato* constrained to monophyly; and (ii) monophyly of combination sets involving at least two of the genera *Gloeocantharellus, Gomphus*, *Phaeoclavulina* and *Turbinellus* on all possible fashions.

The Shimodaira-Hasegawa test was employed to test the combinability of the three loci sampled. With the exception of mit-12S-rDNA, the results indicate that the three datasets were combinable at $p \leq 0.05$. Since the results for the mit-12S-rDNA locus were marginal for some combination sets, we decided to combine the three loci for further analyses.

DISCUSSION

Combinability of the datasets

Although independent analyses of the three data sets produced somewhat different resolutions regarding a few weakly supported terminal nodes, the overall topological reconstructions obtained for each of the three independent loci was very similar. The Shimodaira-Hasegawa (1999) test for data combinability showed that the nuc-25S-rDNA and mit-*atp*6-DNA are statistically combinable at p=0.111-0.574 (Figure 7.4). mit-12S-rDNA, on the other hand, seems to be the most divergent locus. According to the Shimodaira-Hasegawa (1999) test, mit-12S-rDNA is not statistically combinable with either nuc-25S-rDNA ($p<0.0001$) or mit-*atp*6-DNA ($p<0.0001$). When forcing the data from mit-12S-rDNA into the topology of the best parsimonious tree obtained with the nuc-25S-rDNA data, the

results obtained indicate that they are combinable (p=0.001-0.751) (Figure 7.4). The divergence observed for the mit-12S-rDNA locus maybe due to the faster or slower rate of evolution suspected for this genomic region when compared to the nuc-25S-rDNA and mit-*atp*6-DNA regions. The presence of large indels observed throughout the mit-12S-rDNA locus indicates that this genomic region provides a different resolution than the nuc-25S-rDNA or mit-*atp*6-DNA.

Support for a Geastrales-Gomphales-Hysterangiales-Phallales relationship

The three independent loci examined support a close phylogenetic relationship among the Geastrales, Gomphales, Hysterangiales, and the Phallales (Figures 7.2 and 7.3). Relationships among stinkhorns, earth-stars, the cannon-ball fungus, ramarioid-clavarioid, and cantharelloid-gomphoid fungi have only recently been proposed in the literature (Hibbett *et al.* 1997, Humpert *et al.* 2001, Pine *et al.* 1999). Evolutionary relationships for the fungi belonging to some of those groups have been proposed in the past, and for some, i.e. the Gomphales, there is an extensive literature review on the topic, mostly done upon the study of morphological characters (Corner 1966, 1969, Donk 1964, Giachini *et al* 2001, Maire 1902, 1914, Petersen 1968, 1971a). As for the relationships among Geastrales, Gomphales, Hysterangiales, and Phallales identified by Pine *et al.* (1999) and corroborated by Humpert *et al.* (2001) and observed here, there are no morphological synapomorphies yet identified that unite the distinct clades. Some authors have suggested parenthosomal perforations (Pellegrini and Patrignani 1994) while others have suggested spindle orientation (Pine *et al.* 1999) to be the uniting features for those taxa. However, these characters have proven to be uninformative due to their homoplastic status.

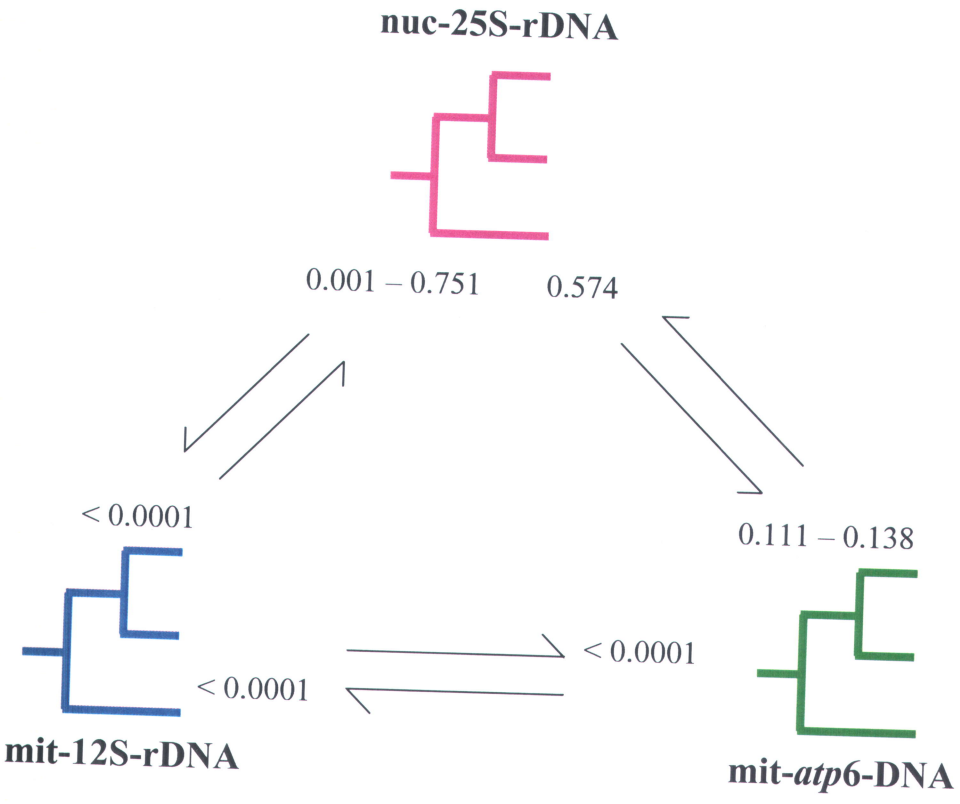

Figure 7.4. Shimodaira-Hasegawa compatibility test.

Rejection of a monophyletic Gomphus sensu lato

Phylogenetic analyses of the combined nuc-25S-rDNA, mit-12S-rDNA, and mit-*atp*6-DNA rejected the monophyletic condition for *Gomphus sensu lato* (Table 7.3). The results indicate *Gloeocantharellus, Gomphus*, *Phaeoclavulina*, and *Turbinellus* as monophyletic genera (Table 7.3, figure 7.2). *Gautieria* and *Ramaria* nested within *Gomphus sensu lato*, whereas *Beenakia, Clavariadelphus, Kavinia,* and *Lentaria* were recovered as a sister group to it. Clades represented by the above mentioned taxa received high likelihood (Bayesian posterior probability – MC^3) and bootstrap support (Figure 7.3). The Kishino-Hasegawa test indicated significantly worse trees when *Gomphus sensu lato* or combinations of taxa within *Gomphus sensu lato* were constrained to the monophyletic condition (Table 7.3), indicating that a confident resolution of the phylogeny of the Gomphales was obtained after the combination of more than one locus. This suggests that a combination of fast evolving (mit-12S) and protein coding (*atp*6) genes provided a consistent resolution for the placement and evolutionary history of this group.

Evolution of substrate affinity

The analyses indicated an ambiguous ancestral condition for substrate affinity for the Gomphales [*L*(*m, Gomphales terricolous* = 26.13), *L*(*m, Gomphales lignicolous* = 27.74) – χ^2 >0.05] (Figure 7.2). The most basal lineage of the Gomphales is composed of the lignicolous/terricolous species of *Phaeoclavulina* (Figure 7.2). *Phaeoclavulina* species possess monomitic hyphae and grow on needle, twig litter, rotten wood, or soil (Humpert *et al.* 2001, Marr and Stuntz 1973, Petersen 1981).

Strictly terricolous substrate affinity for the Gomphales is derived at the terminal node containing *Clavariadelphus* and at the internal node comprising *Gloeocantharellus, Gomphus, Ramaria* subgenus *Laeticolora, Turbinellus,*

Ramaria subgenus *Ramaria*, and the sequestrate genus *Gautieria* (Figure 7.2). The mycorrhizae of *Gomphus clavatus* (Agerer *et al.* 1998), *Turbinellus floccosus* (Masui 1926, 1927), and 4 terricolous *Ramaria* subgenus *Laeticolora* (Agerer *et al.* 1996abcd) species have been described, and it is assumed that more if not most terricolous species of the Gomphales are mycorrhizal. Importantly, related taxa including *Gautieria* and *Hysterangium* are known mycorrhizal associates (Castellano 1998, Griffiths *et al.* 1991, Miller and Miller 1988), but the mycorrhizal status of most lignicolous/terricolous species of the Gomphales is still unknown.

Evolution of clamp connections

The presence of clamp connections is ancestral in the Gomphales with multiple losses of the clamped condition [$L(m,$ *clamped Gomphales* $= 37.88)$, $L(m,$ *unclamped Gomphales* $= 42.42) - \chi^2 < 0.001$] (Figure 7.2). This finding is consistent with Corner's (1966) hypothesis of clamp connection evolution in the Gomphales, suggesting that there are varying degrees of clamp possession in the species he studied and assuming that the 'clampless' state was a derivative of the clamped state with intermediate degrees of clamp production. Humpert *et al.* (2001) showed species of *Ramaria* subgenus *Lentoramaria* lacking clamp connections to be more basal in an evolutionary study of the Gomphales and Phallales. Marr and Stuntz (1973) identify *Ramaria*-species pairs linked to and differing from other *Ramaria*-species pairs primarily in the possession of clamp connections. Production of clamp connections is variable for species of *Beenakia*, *Kavinia*, and *Ramaria* subgenera *Laeticolora* and *Ramaria*. Invariable presence of clamp connections is only observed in species of *Clavariadelphus*, *Gomphus*, *Lentaria*, and *Phaeoclavulina*. Absence of clamp connections is the rule for *Gautieria* and *Turbinellus*. Presence of clamp connections is also variable within members of the Geastrales, Hysterangiales and Phallales (Figure 7.2).

Polarity of basidioma morphology

The results of this study showed ramarioid morphology as ancestral for the Gomphales, with multiple derivations of distinct basidiomata morphologies, i.e., club, odontoid, gomphoid, resupinate, and sequestrate [*L(m, ramarioid Gomphales* = 47.56), *L(m, gomphoid Gomphales* = 52.52) – χ^2 <0.001] (Figure 7.2). The molecular analyses carried out in this study support the results suggested by Humpert *et al.* (2001) in their study on the molecular phylogenetics of *Ramaria*. Petersen (1971a) hypothesized the resupinate-odontoid genera *Kavinia* and *Ramaricium* to be derived from *Ramaria* subgenus *Lentoramaria*. Our results are consistent with the hypothesis that *Beenakia, Kavinia*, and *Lentaria* are derived within the club-like and terricolous genus *Clavariadelphus*.

The *Clavariadelphus-Gomphus sensu lato* evolutionary relationship was first elaborated by Corner (1966) while discussing the probable relationship of *Clavariadelphus* and *Cantharellus*. Petersen (1971a) agrees with Corner's theory that the truncate or turbinate growth form found in *Clavariadelphus* is similar to that observed in *Gomphus* subgenus *Gomphus*, which included *G. guadelupensis* and *G. viridis*, now in *Phaeoclavulina* (Giachini, chapter 2). As stated by Petersen (1968), the spores most heavily ornamented in both genera are those of *Gomphus guadelupensis* (≡*P. guadelupensis*) and *G. viridis* (≡*P. viridis*). Both of these species have caespitose basidiomata with fan-shaped pilei. The pileus surface is undifferentiated, with generally erect, sometimes fascicled, narrow hyphal tips, a condition also observed in most truncate basidiomata of *Clavariadelphus* (Petersen 1971a, Wells and Kempton 1968). Another character that links *Clavariadelphus, Gomphus,* and *Ramaria* is the inflated (ampulliform), thick-walled clamp connections. In addition, non-inflated clamp connections observed in certain species of *Ramaria* are quite similar to those seen in *Clavariadelphus*.

These shared characteristics are strong evidence of the links between *Clavariadelphus, Gomphus,* and *Ramaria*. For many years, the characters mentioned above were the only clues to a missing gap between *Gomphus*,

Clavariadelphus, the various subgenera of *Ramaria*, and others. The relationship could not be drawn very specifically until recently, since the intermediates were recognized to be probably extinct, for the most part (Petersen 1971a). Nevertheless, Petersen (1971a) and others (Eriksson 1954, Heim 1954, Maire 1902) discussed the similarities observed among these genera, specifically for species like *Gomphus clavatus, Ramaria fennica,* and *R. testaceoviridis* (among others), which share a violaceous coloration on young basidiomata that can be lost with age or from spore deposit. Another example was *G. guadelupensis* (≡*P. guadelupensis*) and the so-called *Ramaria grandis-R. longicaulis* complex (≡*C. cyanocephala* and *P. guyanensis*, respectively), which "share rich brown coloration, rusty spore color, very coarse spore ornamentation, and agglutinated basidia" (Petersen 1971a).

Evolution of sequestrate fungi from epigeous Gomphales

Gautieria is a sequestrate fungal genus long known to belong to the Gautieriaceae in the Gautieriales (Zeller and Dodge 1918). As shown by Humpert *et al.* (2001) and corroborated here, *Gautieria* is closely related to *Ramaria*, more specifically a sister group to *Ramaria* subgenus *Ramaria*, and therefore is part of the order Gomphales (Figure 7.2).

As discussed by Fischer (1933) and Cunningham (1942), *Gautieria* is regarded as coralloid/ramarioid with tramal plates growing outward from a central sterile base, resulting in the formation of pockets or locules. Alternatively, the development of *Gautieria* has also been described as forate by other authors with formation of the branches occurring from inward growth of exterior tissue (Dring 1973, Fitzpatrick 1913, Miller and Miller 1988). The striate or ribbed spores of *Gautieria* have once indicated a close evolutionary relationship with the Boletales (Smith 1973). Because the Gautieriales possess true hymenium with one side of the basidia exposed to an open air space and the other side bound by the trama, *Gautieria* has also been suggested to evolve from a hymenomycete (Dring 1973),

more specifically from a ramarioid ancestor (Humpert *et al.* 2001). This finding is consistent with those of Bruns *et al.* (1998), who showed that *Gautieria* was closely related to *Gomphus, Kavinia,* and *Ramaria*. It is also consistent with the findings of Agerer (1999) who documented that the Gomphales, Geastrales, and Gautieriales all share unique ampulate rhizomorphic morphology. According to that author they share the ramarioid, and not the boletoid type. In addition, species of *Gautieria* and *Ramaria* subgenus *Ramaria* share similar striate spores. The only difference between the spores of *Gautieria* and those of *Ramaria* subgenus *Ramaria* is the statismosporic versus ballistosporic condition (Humpert *et al.* 2001). Other cases are known where epigeous and sequestrate taxa differ in the trait of spore symmetry, but retain other overall characteristics (Bruns *et al.* 1992, Hibbett *et al.* 1997, Lebel 1998, Mueller and Pine 1994, Thiers 1984, Thiers and Trappe 1969).

Conclusion

Results from this study corroborate previous results rejecting the monophyly of *Gomphus sensu lato* (Giachini chapter 2). Furthermore, they support the monophyletic conditions for *Gloeocantharellus, Gomphus*, *Phaeoclavulina*, and *Turbinellus* (Figure 7.2). They also reinforce previous observations by Humpert *et al.* (2001) on the ramarioid ancestral condition for the Gomphales, and the independent derivations of club, gomphoid, odontoid, resupinate, and sequestrate morphologies. The coralloid-ramarioid morphology however, is not indicative of a natural monophyletic group. This condition was rather gained and lost several times during the course of evolution. These data also suggest an ambiguous character state condition for substrate affinity in the Gomphales.

Fungi in the Geastrales-Gomphales-Hysterangiales-Phallales have been known for years to have important ecological roles (symbionts, decomposers, etc.). With this study, important information has been added for the clarification of the evolutionary history of the Gomphales. However, further studies are required to

fully unveil the morphological characters that unite these fungi. Comparative studies on the anatomy and biochemistry of these taxa might expose unique morphological features that unite the lineage.

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CHAPTER 8

Relationships of Gomphoid Fungi to Coarse Woody Debris and Stand Age in mixed Conifer Forests in the Pacific Northwestern USA

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ABSTRACT

The relationship of fungal species *Gomphus clavatus* and *Turbinellus floccosus* to stand age, volume and decay class of coarse woody debris (CWD) was assessed from 56 stands in 6 physiographic provinces of the Pacific northwestern USA. The results indicate that total volume of CWD but not stand age was related to the probability of occurrence of basidiocarps of *G. clavatus*: the larger the volume of CWD, the higher the likelihood of occurrence of that species. Both stand age and volume of CWD in late stages of decomposition (CWD_{4+5}) were directly associated with the probability of occurrence of basidiocarps of *T. floccosus*. The results indicate that habitat requirements varied between species, and that potential habitats for the maintenance of these species should be composed of old-growth legacies rather than simply old-growth forests.

INTRODUCTION

Recent years have witnessed an unprecedented increase in the information regarding species composition of ectomycorrhizal (ECM) communities. Much has been learned about the mycorrhizal symbiosis and its importance to tree nutrition and carbon balance. Awareness had also increased that soil microorganisms, in particular fungi, can significantly influence aboveground organism dynamics and ecosystem processes as a whole (Copley 2000, Horton and Bruns 2001, Read 1998, Taylor 2002, van der Heijden *et al.* 1998). Others have shown the effects of particular biotic and abiotic factors, such as precipitation, temperature, soil composition, stand age, coarse woody debris, etc; on the occurrence and frequency of mycorrhizal fungi (Lu *et al.* 1999, Matsuda and Hijii 1998, O'Dell *et al.* 1999, Smith *et al.* 2002, Sverdrup-Thygeson and Lindenmayer 2003, Trappe *in press*).

Although much research has been conducted over the years to determine the ecosystematic role of certain fungi and the factors regulating fungal biodiversity, little information is available on the basic biology or habitat requirements of many species. Following the 1994 Northwest Forest Plan (NWFP), special concern has been devoted to conserving biodiversity and species viability in the Pacific northwestern USA by maintaining appropriate habitats. The document listed 180 species of fungi of concern in the range of the northern spotted owl (*Strix occidentalis caurina*) (U.S.D.A. and U.S.D.I. 1994ab). Among those are *Gomphus bonarii* (*Turbinellus floccosus*), *Gomphus clavatus, Gomphus floccosus* (*Turbinellus floccosus*), and *Gomphus kauffmanii* (*Turbinellus kauffmanii*). Although suggested to be linked to late-stage forests of the Pacific northwest (U.S.D.A. and U.S.D.I. 1994ab), no empirical evidence was available to determine the extent and factors regulating the distribution of these species in the conifer-dominated forests of that region.

Among the factors considered crucial for the maintenance of viable populations of fungi is the volume and stage of decomposition of coarse woody debris (CWD). CWD is an important component of forest ecosystems, reducing

erosion, affecting soil development, serving as storage units of nutrients and water, providing major source of energy and nutrients, serving as seedbeds for plants, providing shelter for small animals, and as a major habitat for decomposers and heterotrophs (Franklin *et al.* 1987, Harmon 2001, Harmon *et al.* 1986, Maser *et al.* 1988, McCombe and Lindenmayer 1999). Smith *et al.* (2002) showed a positive effect of CWD in late stages of decomposition on the occurrence of the ectomycorrhizal fungus *Pilloderma fallax* in both old growth and young stands of Douglas fir (*Pseudotsuga menziesii*) in the West Cascades of Oregon.

This study focused on identifying to what extent do stand-age, and volume and decay class of CWD explain the presence and distribution of *Gomphus clavatus* (Pers.) Gray, *Turbinellus floccosus* (Schwein.) Earle, and *T. kauffmanii* (A.H. Sm.) Giachini in forests of northern California, western Oregon, and western Washington.

Study Species

Gomphus clavatus is an epigeous basidiomycete in many conifer forests of the northern hemisphere and is easily identified by its combination of orangish brown to overall creamy violet to dark violet basidiocarps, verrucose spores, and presence of clamp connections. *Gomphus clavatus* is inferred to form ectomycorrhizae with species of *Abies* (Pantidou 1980) and *Picea* (Agerer *et al.* 1998), but probably also with other plant species.

Turbinellus floccosus is an epigeous basidiomycete in conifer forests of the northern hemisphere and is identified by the combination of orange red to scarlet basidiocarps, scaly pileus, absence of clamp connections, and verrucose spores. It has been suggested to form ectomycorrhizae with conifers. Masui (1926) was the first to document the close association of *Cantharellus floccosus* (*T. floccosus*) and the roots of *Abies firma* Siebold and Zucc. in Japan. He also concluded that other species of *Abies*, such as *A. maryiana* (Miyabe & R.R. Kudo) Miyabe & R.R. Kudo

and *A. sachalinensis* (F. Schmidt) Mast., had similar associations with that fungus in natural conditions. Masui (1927) also confirmed the association of *T. floccosus* and *Pinus densiflora* Siebold and Zucc. *Turbinellus floccosus* has also been suggested to be mycorrhizal with *Abies alba* Mill. (Khokhryakov 1956), *Abies nephrolepsis* (Trautr.) Maxim. (Bulakh 1978), *Abies religiosa* (H.B.K.) Schltr. and Cham. (Valdés-Ramirez 1972), *Pseudotsuga menziesii* (Mirb.) Franco (Trappe 1960), and *Tsuga heterophylla* (Raf.) Sarg. (Trappe 1960, Kropp and Trappe 1982). Guzmán and Villarreal (1985) also suggest it to be mycorrhizal with species of *Abies* and *Pinus*.

Turbinellus kauffmanii is only known from eastern and western North America. It is characterized by basidiocarp pilei with central, large, recurved scales, which grade to dot-like toward the margin. These scales can be washed away in older specimens to expose the smooth to fibrillose surface of the pileus. Although producing large and conspicuous basidiocarps, *T. kauffmanii* is uncommon in North America. Its microscopic features include large spores and absence of clamp connections. Its mycorrhizal status and substrate affinity have not been studied. Since both *T. floccosus* and *T. kauffmanii* occupy similar habitats, the latter likely also forms ectomycorrhizae with the same conifer species identified for *T. floccosus*.

Study Region

The study was conducted in temperate forests of 6 of the 12 physiographic provinces delineated by the NWFP in northern California, western Oregon, and western Washington (Figure 8.1). The areas included in this study are administered by either the National Park Service or the U.S. Forest Service.

Dominant tree species vary between stands by elevation and physiographic province. *Pseudotsuga menziesii* is dominant for the Cascades and Willamette Valley. *Picea sitchensis* and *P. menziesii* are co-dominants for the Coast Range

physiographic provinces. *Acer*, *Vaccinium*, and fern species compose the understory of most stands visisted (Table 8.1).

MATERIAL AND METHODS

Sampling design

The design was a 2^2 factorial with stand age (years) and volume of CWD (m^3 m^{-2}) as explanatory variables. Fifty-six stands were selected: 7 in the California Coast Range, 4 in the Oregon Coast Range, 5 in Oregon's Willamette Valley, 9 in Washington's western Cascades (near Mt. Rainier National Park), 26 in the western Oregon Cascades, and 5 in the eastern Oregon Cascades (Figure 8.1, table 8.1). A three-hectare plot was surveyed in each selected stand once each during fall of 1999, 2000, and 2001, for basidiocarps of *G. clavatus, T. floccosus*, and *T. kauffmanii*. The presence/absence of each species was recorded along with data on the habitat characteristics of each stand.

Stand selection and description

Stands of conifer forests were randomly selected according to proximity to a road system. Stand conditions varied from region to region and by landscape orientation. Elevation ranged from 3 to 1600 meters. In the Coast Range physiographic provinces, which according to the NWFP encompass shoreline plus Coast Range Mountains, stands were mostly at lower elevations than in the Cascades or Willamette Valley (Table 8.1). Mean elevation of stands was 110 meters for the Coast Range, 850 meters for the Cascades, and 460 meters for the Willamette Valley provinces.

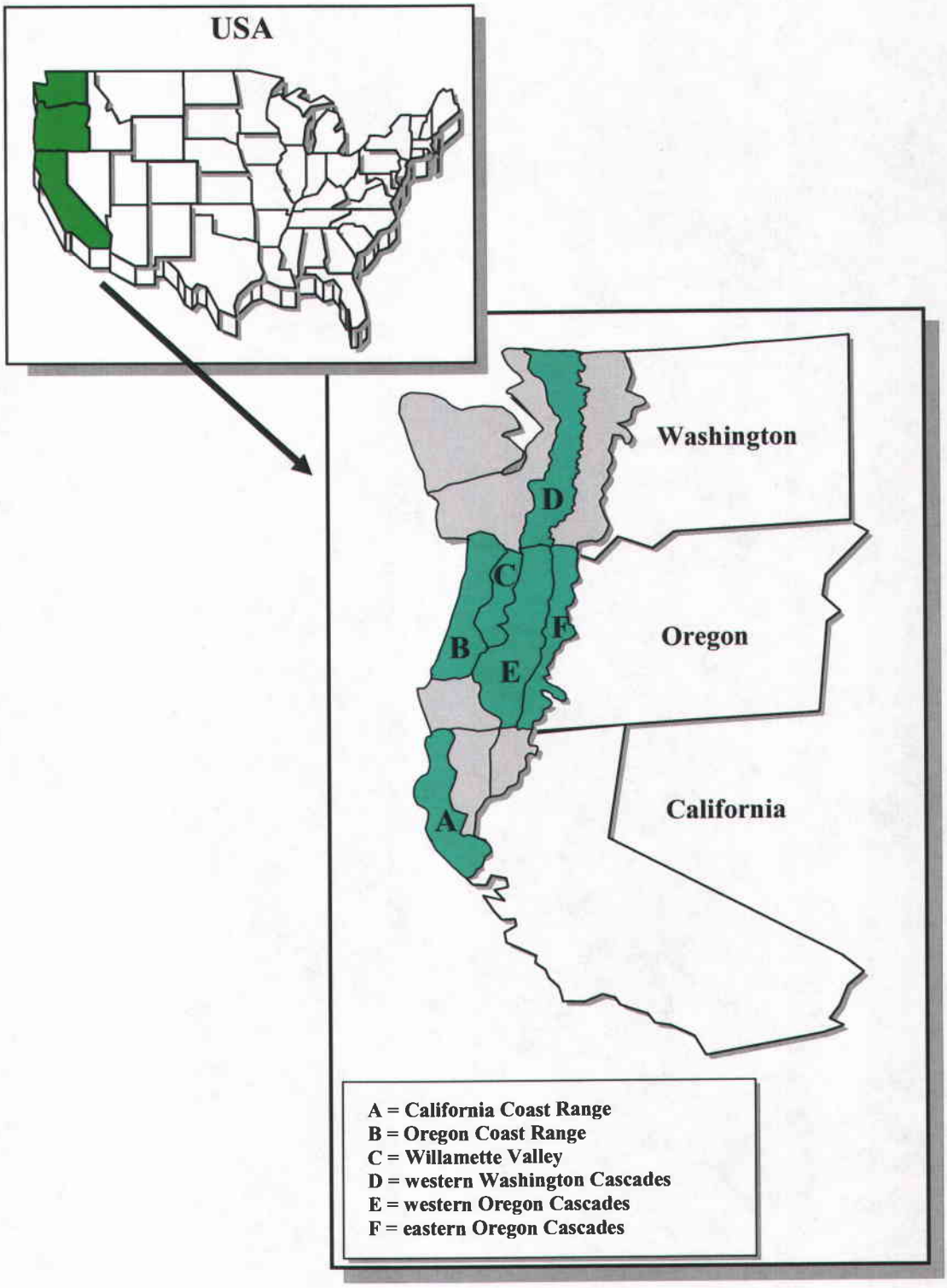

Figure 8.1. Physiographic provinces visited during the course of the study.

Table 8.1. Physiographic provinces, stand location, and main plant species recorded in the study of distribution of *Gomphus clavatus* and *Turbinellus floccosus* in the Pacific Northwest of the USA.

Physiographic provinces[‡]	County/State	Site	Latitude	Longitude	Altitude (meters)	GC[£]	TF[†]	Vegetation*
A	Del Norte/CA Coast	Lake Earl St. Wildlife	N 41° 46.128'	W 124° 14.281'	3	+	+	2, 12, 17, 22, 23, 27, 29, 34, 35, 42, 44
A	Mendocino/CA Coast	Jackson St. For.	N 39° 24.916'	W 123° 45.995'	3	+	+	11, 17, 18, 23, 27, 28, 29, 30, 37, 40, 43, 44
A	Mendocino/CA Coast	Jackson St. For.	N 39° 24.170'	W 123° 43.186'	120	+		11, 17, 18, 27, 28, 29, 37, 43, 44
A	Mendocino/CA Coast	Jackson St. For.	N 39° 20.889'	W 123° 34.814'	180		+	10, 18, 27, 28, 29, 37, 43
A	Mendocino/CA Coast	Jackson St. For.	N 39° 20.936'	W 123° 32.647'	240		+	17, 18, 20, 27, 28, 29, 37, 44
A	Mendocino/CA Coast	Jackson St. For.	N 39° 22.734'	W 123° 48.876'	20		+	2, 12, 17, 18, 22, 25, 27, 29, 37, 40, 42, 43
A	Mendocino/CA Coast	Jughandle St. Reserve	N 39° 19.792'	W 123° 44.530'	63	+	+	2, 17, 18, 27, 30, 37, 42, 44
B	Lane/OR Coast	Siuslaw Nat.. For.	N 44° 16.063'	W 124° 06.109'	80			5, 8, 17, 22, 27, 29, 35, 40, 43, 44
B	Lane/OR Coast	Siuslaw Nat. For.	N 44° 16.064'	W 124° 07.109'	80			5, 8, 11, 22, 27, 29, 35, 40, 43, 44
B	Lane/OR Coast	Siuslaw Nat. For.	N 44° 09.652'	W 124° 06.784'	3			1, 11, 17, 22, 23, 27, 28, 43, 44
B	Lincoln/OR Coast	Siuslaw Nat. For.	N 44° 17.382'	W 124° 06.368'	395			8, 17, 27, 35, 40, 43, 44
C	Benton/OR Coast	Siuslaw Nat. For.	N 44° 32.189'	W 123° 32.781'	1390			4, 28, 29, 34, 35, 40
C	Benton/OR Coast	McDonald St. For.	N 44° 39.758'	W 123° 15.118'	149		+	5, 8, 27, 28, 29, 36, 38, 43
C	Benton/OR Coast	McDonald St. For.	N 44° 38.555'	W 123° 16.377'	243			5, 8, 27, 28, 43
C	Benton/OR Coast	McDonald St. For.	N 44° 38.173'	W 123° 17.579'	257			8, 27, 28, 36
C	Benton/OR Coast	McDonald St. For.	N 44° 38.555'	W 123° 16.377'	243			5, 7, 8, 27, 28, 39, 40
D	Lewis/WA Cascades	Gif. Pinchot Nat. For.	N 46° 42.419'	W 122° 14.749'	165	+		5, 28, 40
D	Lewis/WA Cascades	Gif. Pinchot Nat. For.	N 46° 41.705'	W 122° 14.092'	180	+		5, 28, 40
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 56.542'	W 121° 54.924'	300	+		1, 13, 19, 27, 28, 35, 39, 40, 43, 44
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 45.251'	W 121° 48.342'	300	+	+	1, 17, 27, 28, 30, 39, 40, 43
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 55.997'	W 121° 54.375'	360	+	+	1, 28, 40, 43
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 46.050'	W 121° 52.575'	390		+	1, 11, 13, 19, 27, 28, 35, 40, 43
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 44.508'	W 121° 53.277'	390		+	1, 12, 40
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 45.043'	W 121° 33.744'	360		+	1, 5, 12, 28, 29, 39, 40, 43

Table 8.1. Physiographic provinces, stand location, and main plant species recorded in the study of distribution of *Gomphus clavatus* and *Turbinellus floccosus* in the Pacific Northwest of the USA (*cont.*).

Physiographic provinces[‡]	County/State	Site	Latitude	Longitude	Altitude (meters)	GC[£]	TF[†]	Vegetation*
D	Pierce/WA Cascades	Mt. Rainier Nat. Park	N 46° 44.517'	W 121° 33.483'	375	+	+	1, 5, 12, 17, 28, 29, 39, 40
E	Douglas/OR Cascades	Umpqua Nat. For.	N 43° 12.727'	W 122° 08.160'	1594		+	2, 16, 26
E	Douglas/OR Cascades	Umpqua Nat. For.	N 43° 13.702'	W 122° 34.877'	1350			5, 17, 28, 40, 43
E	Klamath/OR Cascades	Deschutes Nat. For.	N 43° 34.418'	W 121° 58.476'	1348			3, 14, 28, 30, 40
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 39.144'	W 122° 01.741'	1348		+	1, 2, 16, 21, 28, 30, 40
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 50.469'	W 122° 41.389'	540			5, 12, 17, 27, 28, 30, 35, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 42. 991'	W 122° 21.577'	903			5, 12, 17, 27, 28, 30, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 38.106'	W 122° 10.026'	936			5, 7, 12, 17, 27, 28, 30
E	Lane/OR Cascades	Willamette Nat. For.	N 44° 12.216'	W 122° 02.486'	1080	+		5, 12, 19, 28, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 52.821'	W 122° 05.231'	900	+		5, 16, 27, 28, 30, 33, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 53.094'	W 122° 05.489'	960			5, 27, 28, 31, 30, 33, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 54.620'	W 122° 04.274'	900			12, 15, 27, 28, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 58.724'	W 122° 05.972'	900	+		5, 12, 27, 28, 29, 33, 39, 40
E	Lane/OR Cascades	Willamette Nat. For.	N 43° 59.124'	W 122° 10.392'	900	+	+	12, 17, 27, 28, 29, 30, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 44° 07.529'	W 122° 02.486'	990	+		12, 17, 28, 30, 39, 40, 43
E	Lane/OR Cascades	Willamette Nat. For.	N 44° 10.221'	W 122° 04.197'	1035			5, 7, 28, 39, 40
E	Lane/OR Cascades	Willamette Nat. For.	N 44° 07.821'	W 122° 17.354'	1140		+	2, 5, 12, 16, 17, 28, 30, 38, 39, 40, 44
E	Lane/OR Cascades	Willamette Nat. For.	N 44° 16.386'	W 122° 07.117'	945		+	3, 5, 7, 9, 17, 27, 28
E	Linn/OR Cascades	Willamette Nat. For.	N 44° 20.859'	W 122° 15.617'	1200		+	2, 4, 20, 28, 29, 33, 34, 39, 40, 43
E	Linn/OR Cascades	Willamette Nat. For.	N 44° 20.978'	W 122° 14.556'	992		+	2, 4, 5, 28, 29, 30, 39, 40, 43
E	Linn/OR Cascades	Willamette Nat. For.	N 44° 39.759'	W 121° 53.443'	1200	+	+	5, 7, 12, 15, 17, 28, 30, 38, 39, 40, 43
E	Linn/OR Cascades	Willamette Nat. For.	N 44° 20.284'	W 122° 15.412'	990			5, 12, 16, 27, 28, 29, 30, 32, 33, 36, 39, 40
E	Linn/OR Cascades	Willamette Nat. For.	N 43° 32.128'	W 122° 26.871'	900		+	5, 7, 8, 12, 27, 28, 29, 40
E	Marion/OR Cascades	Willamette Nat. For.	N 44° 45.748'	W 122° 05.397'	803		+	5, 7, 12, 14, 17, 27, 28, 30, 38, 39, 40, 43

Table 8.1. Physiographic provinces, stand location, and main plant species recorded in the study of distribution of *Gomphus clavatus* and *Turbinellus floccosus* in the Pacific Northwest of the USA (*cont.*).

Physiographic provinces‡	County/State	Site	Latitude	Longitude	Altitude (meters)	GC£	TF†	Vegetation*
E	Marion/OR Cascades	Willamette Nat. For.	N 44° 45.748'	W 122° 05.397'	803			5, 12, 14, 17, 27, 28, 30, 39, 40
E	Marion/OR Cascades	Willamette Nat. For.	N 44° 44.423'	W 122° 03.240'	900	+	+	1, 5, 11, 12, 28, 29, 30, 39, 40
E	Marion/OR Cascades	Willamette Nat. For.	N 44° 41.302'	W 122° 00.630'	589			5, 7, 8, 12, 17, 27, 28, 29, 30, 38, 40
F	Clackamas/OR Cascades	Mt. Hood Nat. For.	N 45° 09.376'	W 121° 44.282'	1184		+	3, 24, 28, 30, 40, 41, 43
F	Clackamas/OR Cascades	Mt. Hood Nat. For.	N 45° 06.638'	W 121° 46.454'	1014		+	3, 24, 28, 30, 38, 40, 41, 43
F	Clackamas/OR Cascades	Mt. Hood Nat. For.	N 45° 18.707'	W 122° 04.978'	949	+	+	3, 12, 27, 28, 30, 39, 40, 41, 43
F	Clackamas/OR Cascades	Mt. Hood Nat. For.	N 45° 15.244'	W 121° 55.536'	717		+	1, 6, 9, 17, 19, 27, 28, 30, 39, 43
F	Hood River/OR Cascades	Mt. Hood Nat. For.	N 45° 11.701'	W 121° 41.354'	1184		+	12, 28, 30, 40

‡ A = California Coast Range, B = Oregon Coast Range, C = Willamette Valley, D = western Washington Cascades, E = western Oregon Cascades, F = eastern Oregon Cascades; £ = *Gomphus clavatus*; † = *Turbinellus floccosus*, + = present; *Vegetation recorded in this study listed by species (Alaback *et al.* 1994, Randal *et al.* 1994):

1 = *Abies amabilis* (Douglas) J. Forbes - Pacific silver fir
2 = *Abies grandis* (Douglas:D. Don) Lindl. - grand fir
3 = *Abies lasiocarpa* (W. Hook.) Nutt. - subalpine fir
4 = *Abies procera* Rehder - noble fir
5 = *Acer circinatum* Pursh - vine maple
6 = *Acer douglasii* Hook. - rocky mountain maple
7 = *Acer macrophyllum* Pursh - bigleaf maple
8 = *Alnus rubra* Bong. - red alder
9 = *Alnus sinuata* (Regel) Rydb. - sitka alder
10 = *Arbutus menziesii* Pursh - madrone
11 = *Athyrium filix-femina* (L.) Roth - lady fern
12 = *Berberis nervosa* Pursh - Oregon grape
13 = *Blechnum spicant* (L.) Roth - deer fern
14 = *Castanopsis chrysophylla* (Douglas) DC. - chinquapin
15 = *Ceanothus velutinus* Douglas - snowbrush
16 = *Chimaphila umbellata* (L.) Nutt. - prince's pine
17 = *Gaultheria shallon* Pursh - salal
18 = *Lithocarpus densiflora* (H. Hook. and Arn.) Rehder - tanoak
19 = *Oplopanax horridum* (Sm.) Mig. - devil's club
20 = *Oxalis oregana* Nutt. - Oregon oxalis
21 = *Picea engelmanii* (Parry) Engelm. - Engelmann spruce
22 = *Picea sitchensis* (Bong.) Carrière - sitka spruce
23 = *Pinus contorta* var. *contorta* (Douglas) Loudon - lodgepole pine
24 = *Pinus monticola* (Douglas) D. Don - Western white pine

Table 8.1. Physiographic provinces, stand location, and main plant species recorded in the study of distribution of *Gomphus clavatus* and *Turbinellus floccosus* in the Pacific Northwest of the USA (*cont.*).

‡ A = California Coast Range, B = Oregon Coast Range, C = Willamette Valley, D = western Washington Cascades, E = western Oregon Cascades, F = eastern Oregon Cascades; £ = *Gomphus clavatus*; † = *Turbinellus floccosus*, + = present; *Vegetation recorded in this study listed by species (Alaback *et al.* 1994, Randal *et al.* 1994):

25 = *Pinus muricata* D. Don - bishop pine
26 = *Pinus ponderosa* (Douglas) G. Lawson and C. Lawson - ponderosa pine
27 = *Polystichum munitum* (Kaulf.) Presley - sword fern
28 = *Pseudotsuga menziesii* (Mirb.) Franco - Douglas-fir
29 = *Pteridium aquilinum* (L.) Kuhn - braken fern
30 = *Rhododendron macrophyllum* G. Don - Pacific rhododendron
31 = *Ribes sanguineum* Pursh - red-flowering currant
32 = *Rubus acaulis* Michx. - dwarf nagoonberry
33 = *Rubus lasiococcus* Gray - dwarf bramble
34 = *Rubus parviflorus* Nutt. - thimbleberry
35 = *Rubus spectabilis* Pursh - salmonberry
36 = *Rubus ursinus* Cham. & Schltdl. - Pacific blackberry
37 = *Sequoia sempervirens* (D. Don) Endl. - giant sequoia
38 = *Taxus brevifolia* Nutt. - Pacific yew
39 = *Thuja plicata* (Donn) D. Don - Western-red-cedar
40 = *Tsuga heterophylla* (Raf.) Sarg. - Western hemlock
41 = *Tsuga mertensiana* (Bong.) Carrière - mountain hemlock
42 = *Umbellularia californica* (H. Hook. and Arn.) Nutt. - California bay
43 = *Vaccinium parvifolium* Sm. - red huckleberry
44 = *Vaccinum ovatum* Pursh - evergreen huckleberry

In general stands were multi-storied, mostly closed canopy, but mostly with occasional gaps. At high elevations, such as in the Mt. Hood National Forest, overstories were co-dominated by *Picea* and *Abies*, whereas *Pseudotsuga* and *Tsuga* predominated at lower elevations. In the Coast Range provinces *Picea, Pinus,* and *Pseudotsuga* were the main overstory components.

Mid-stories, when present, were composed of *Lithocarpus densiflora-Umbellularia californica* in the California Coast Range and *Taxus brevifolia-Castanopsis chrysophylla* in the Oregon Cascades. *Acer circinatum*, *A. macrophyllum*, and *Rhododendron macrophyllum* occurred in all provinces but were most common in Oregon.

The understory was mostly composed of small shrubs such as *Berberis nervosa*, *Gaultheria shallon*, *Polystichum munitum*, *Ribes* spp., *Rubus* spp., and *Vaccinum* spp. Significant numbers of pines were present only in the Coast Range physiographic provinces. Numerous mosses and liverworts were found, particularly in moist sites (see table 8.1 for a complete list of vascular plant species found in each stand).

Seral stages

Seral stages, or the series of relatively transitory plant communities that develop during ecological succession from bare ground to the climax stage were determined by studying the stand structure and age of the predominant cohort (U.S.D.A. and U.S.D.I. 1994a). Stand age, determined by an increment boring, ranged from 30 to 500 years for the predominant cohort of trees. If the bole radius of a sampled tree was greater than the 45 cm length of the increment borer, the age was extrapolated from the rings at the pith end of the core. Seral stage was used to categorize stands in the field but age was ultimately used as a continuous rather than categorical explanatory variable. This approach allowed for a better understanding of the effects of age of the trees on the probability of finding the

species of interest. Tree age was also needed for classifying stands into seral groups or stages.

According to the standards published in the NWFP (U.S.D.A. and U.S.D.I. 1994b), the oldest stands of "early seral stage" visited in this study were about 130 years old. They were predominantly dominated by even-aged *P. menziesii* and *T. heterophylla* in the Cascades, and *Abies grandis*, *Picea sitchensis*, and *T. heterophylla* in the Coast Range physiographic provinces (Table 8.1). The youngest "late seral" stands were about 180 years old (Table 8.2). No stands older than 150 years were seen in the Coast Range provinces. Predominant cohorts were *P. menziesii* and *T. heterophylla*, and a mixed species mid-story.

The youngest stand visited was 30 years old and composed of even-aged 30 feet tall *P. menziesii*, with moderate to no understory vegetation. The oldest was around 500 years old and primarily composed of *P. menziesii* (80%) and *T. heterophylla* (18%), with occasional representatives of *Thuja plicata.* In general these stands were moist, mossy, with medium to high volumes of CWD.

Volume of coarse woody debris (CWD)

A line intercept sampling design (van Wagner 1968, Harmon and Sexton 1996) was employed to estimate the volume of CWD per unit area, measured in cubic meters of CWD per square meter of forest floor (m^3 m^{-2}). A 200 meter transect was established in each stand. Each piece of CWD, both above and below ground, crossed by the transect line was recorded by decay class and diameter. Transects were always set as a cross with four 50 meter lines. The formula used to calculate the volume of CWD per unit area (V) is:

$$V = \pi^2 \Sigma (d^2/8L) \qquad (a);$$

Table 8.2. Physiographic provinces, stand age, and volume of CWD in mixed conifer forests in California, Oregon, and Washington (USA).

Physiographic Province*	County/State	*G. clavatus*	*T. floccosus*	Stand age (years)	Volume of CWD (m^3 ha^{-1})		
					CWD_{1+2+3}	CWD_{4+5}	CWD_{Total}
A	Del Norte/CA Coast	+	+	70	140	109	249
A	Mendocino/CA Coast		+	52	240	100	340
A	Mendocino/CA Coast	+		150	170	90	260
A	Mendocino/CA Coast		+	150	210	18	228
A	Mendocino/CA Coast	+	+	120	24	8	32
A	Mendocino/CA Coast	+	+	150	180	114	294
A	Mendocino/CA Coast		+	100	85	9	94
B	Lane/OR Coast			70	15	108	123
B	Lane/OR Coast			60	52	35	87
B	Lane/OR Coast			120	52	160	212
B	Lincoln/OR Coast			70	335	46	381
C	Benton/OR Coast			200	140	55	195
C	Benton/OR Coast			60	74	60	134
C	Benton/OR Coast			50	100	41	141
C	Benton/OR Coast			60	26	44	70
C	Benton/OR Coast		+	200	423	45	468
D	Lewis/WA Cascades	+		200	236	75	311
D	Lewis/WA Cascades	+		50	562	290	852
D	Pierce/WA Cascades		+	250	431	642	1073
D	Pierce/WA Cascades	+		400	1250	390	1640
D	Pierce/WA Cascades		+	500	384	186	570
D	Pierce/WA Cascades	+	+	150	186	300	486
D	Pierce/WA Cascades	+	+	180	258	139	397
D	Pierce/WA Cascades		+	250	88	122	210
D	Pierce/WA Cascades	+	+	300	485	283	768
E	Douglas/OR Cascades			400	258	87	345
E	Douglas/OR Cascades		+	200	115	62	177
E	Klamath/OR Cascades			250	114	430	544
E	Lane/OR Cascades		+	400	470	180	650
E	Lane/OR Cascades			200	61	37	98
E	Lane/OR Cascades			400	190	350	540
E	Lane/OR Cascades			30	303	86	389
E	Lane/OR Cascades		+	130	75	132	207
E	Lane/OR Cascades		+	300	327	72	399
E	Lane/OR Cascades			100	173	97	270
E	Lane/OR Cascades	+		250	277	247	524
E	Lane/OR Cascades			150	36	47	83
E	Lane/OR Cascades	+		200	236	338	574
E	Lane/OR Cascades	+		200	145	176	321
E	Lane/OR Cascades	+		400	242	557	799

Table 8.2. Physiographic provinces, stand age, and volume of CWD in mixed conifer forests in California, Oregon, and Washington (USA) (*cont.*).

Physiographic Province*	County/State	*G. clavatus*	*T. floccosus*	Stand age (years)	Volume of CWD (m^3 ha^{-1})		
					CWD_{1+2+3}	CWD_{4+5}	CWD_{Total}
E	Lane/OR Cascades			50	635	164	799
E	Lane/OR Cascades	+	+	200	107	450	557
E	Linn/OR Cascades	+	+	300	584	366	950
E	Linn/OR Cascades		+	150	440	320	760
E	Linn/OR Cascades		+	120	87	149	236
E	Linn/OR Cascades			35	302	51	353
E	Linn/OR Cascades		+	250	196	220	416
E	Marion/OR Cascades		+	400	266	86	352
E	Marion/OR Cascades			31	114	66	180
E	Marion/OR Cascades	+	+	500	352	219	571
E	Marion/OR Cascades			180	198	186	384
F	Clackamas/OR Cascades	+	+	100	59	165	224
F	Clackamas/OR Cascades		+	110	240	450	690
F	Clackamas/OR Cascades		+	200	60	59	119
F	Clackamas/OR Cascades		+	400	140	290	430
F	Hood River/OR Cascades		+	400	190	220	410

* A = California Coast Range, B = Oregon Coast Range, C = Willamette Valley, D = western Washington Cascades, E = western Oregon Cascades, F = eastern Oregon Cascades.

where d is the diameter (m) of each CWD piece intersected by the transect and L is the transect length (m).

Coarse woody debris (CWD) classification

Coarse woody debris (pieces ≥10 cm in diameter) were classified according to the system proposed by Fogel *et al.* (1973). This system rates CWD by its level of decay on a scale of 1 to 5. Class 1 is any fresh fallen wood that still has twigs and bark intact. Class 2 has mostly intact bark, but all twigs and fine limbs are gone. Class 3 woody debris has loosened bark, sapwood is softening, but the heartwood is sound or not yet permeated by roots. In fallen trees the round shape of the logs is still evident. In class 4 the bark is mostly gone, the sapwood is punky, cross-sectioned the shape of the material is oval rather than round, and roots are invading the heartwood. According to Sollins (1982), branch stubs can be pulled off from class 4 CWD but not from class 3 CWD. And finally class 5, which has punky heartwood and sapwood, is cubically rotted and overall permeated by roots. Only traces of the original shape of the CWD are observed in this stage of decomposition.

For statistical analysis CWD was grouped into categories: one containing the data for CWD classes 1+2+3 (early stage of decomposition – CWD_{1+2+3}), a second one containing the data for CWD classes 4+5 (late stage of decomposition – CWD_{4+5}), and a third containing the data for the total volume of CWD regardless of decay class (CWD_{Total}).

Statistical analyses

No data transformation was required for the explanatory variables used in the logistic regression model. Logistic regression was employed because it provides

the probability for any given event, and from the probability it is possible to obtain the odds ratio for the likelihood of that event, given a set of explanatory variables (Allison 1999). The odds ratio demonstrates how much more likely an event is expected to be under a given scenario versus another, and it is expressed either in absolute or integral infinite values. Odds ratios for a continuous variable give the change in the log odds for an increase of one unit in the specified explanatory factor.

If any of the fungal species examined were recorded from a stand at any given time during data collection, then that stand was scored as 'positive or present' for that species. Logistic regression is generally used to analyze probabilities of an event, in other words, occurrences of that event, and is robust to null data points (Allison 1999), e.g. if a species is found just once at a site then it does not matter whether it is seen again or not during future survey iterations.

Because age was recorded in years, ranging from 30 to 500, and volume of CWD was recorded in cubic meters per square meter of area, ranging from 0.001 to 0.064, an adjustment was required to standardize the data into more or less equal magnitudes for accurate performance of the logistic regression model. Therefore, all CWD data were calculated on a hectare (ha) basis, instead of a squared meter (m^2) basis, to equate numerically with the data for age.

All statistical analyses were performed in SAS (2001). For all multiple analyses the best (most parsimonious) model was selected via the AIC method (Sakamoto *et al.* 1986). For all analyses, I tested for biologically relevant interactions between explanatory variables and those statistically significant at 95% ($p<0.05$) were included in the final model.

RESULTS

Species distribution

No *T. kauffmanii* was found in any stand visited. *Turbinellus kauffmanii* has been regarded as one of the more rare species of gomphoid fungi in the PNW (U.S.D.A. and U.S.D.I. 1994ab). Even though it produces large basidiocarps, few are often found even when weather conditions seem favorable. For this study, *T. kauffmanii* was seen only 4 times, always in the surroundings but never inside the boundaries of a sampled stand, and only in western Oregon (1 basidiocarp), and western Washington (3 basidiocarps) Cascades.

In addition, no specimens of *G. clavatus* or *T. floccosus* were observed in stands located in the Oregon Coast Range.

Probability/odds for the occurrence of basidiocarps of Gomphus clavatus

Gomphus clavatus was present in 33% (18/56) of the stands: 67% (6/9) in the western Washington Cascades, 56% (4/7) in the California Coast Range, 27% (7/26) in the western Oregon Cascades, and 20% (1/5) in the eastern Oregon Cascades. *Gomphus clavatus* was never recorded from the Willamette Valley or the Oregon Coast physiographic provinces (Table 8.3).

Only the total volume of CWD was statistically significant (p=0.0315) in predicting the occurrence of *G. clavatus* in any given stand (Table 8.4). Age and volume of CWD in early (CWD_{1+2+3}) or late (CWD_{4+5}) stages of decomposition were not statistically significant. Therefore, the final most parsimonious model for predicting the probability of presence of *G. clavatus* was:

$$\text{Logit}(\mu) = \beta_0 + \beta_1.\text{CWD}_{\text{Total}} \qquad (b);$$

Probability/odds for the occurrence of basidiocarps of Turbinellus floccosus

Turbinellus floccosus was present in 52% (29/56) of the stands: 100% (6/6) in the eastern Oregon Cascades, 86% (6/7) in the California Coast Range, 67% (6/9) in the western Washington Cascades, 43% (11/26) in the western Oregon Cascades, 20% (1/5) in the Willamette Valley, and was not recorded from any stand in the Oregon Coast Range physiographic province (Table 8.3).

Age of the stands (p=0.008), CWD_{4+5} (p=0.04), and the interaction term of age and CWD_{4+5} (p=0.03) were statistically significant to predict the occurrence of *T. floccosus* (Table 8.4). Neither CWD_{1+2+3} nor the total volume of CWD ($\text{CWD}_{\text{Total}}$) were statistically significant in predicting the occurrence of *T. floccosus*. The probability of occurrence is expressed on a scale of 0 to 1 and may be interpreted as the "percent chance of" finding *T. floccosus* on a specific site given the stand's age and the volume of CWD, in this case CWD_{4+5}.

The final most parsimonious model for predicting the probability of the presence of *T. floccosus* was as follow:

$$\text{Logit}(\mu) = \beta_0 + \beta_1.\text{Age} + \beta_2.\text{CWD}_{4+5} - \beta_3.\text{Age}*\text{CWD}_{4+5} \qquad (c);$$

Correlation

The correlation between the two variables (age and CWD_{4+5}) involved in the model to predict the occurrence of *T. floccosus* was 0.16 (p=0.0021), indicating that they are not statistically correlated (Table 8.5). In other words, the effect of one explanatory variable in predicting the occurrence of *T. floccosus* is not directly

correlated to the effect of the other. No correlation was observed between age and any of the CWD variables considered.

Volume of coarse woody debris (CWD)

Mean volumes of CWD differed among sites and physiographic provinces: 210 m^3 ha^{-1} (32-340 m^3 ha^{-1}) in the California Coast Range, 200 m^3 ha^{-1} in both the Oregon Coast Range (87-381 m^3 ha^{-1}) and the Willamette Valley (70-468 m^3 ha^{-1}) provinces, 440 m^3 ha^{-1} (83-950 m^3 ha^{-1}) in the western Oregon Cascades, 370 m^3 ha^{-1} (119-690 m^3 ha^{-1}) in the eastern Oregon Cascades, and 700 m^3 ha^{-1} (210-1640 m^3 ha^{-1}) in the western Washington Cascades.

The stand with the lowest volume of CWD recorded in this study (32 m^3 ha^{-1}) was in the California Coast Range. The stand with the highest volume (1640 m^3 ha^{-1}) was 400-years-old in the western Washington Cascades at Mt. Rainier National Park. That particular stand had never been logged or managed, which explains its high volume of CWD. High volumes of CWD are common in the PNW (Harmon 2001), especially in unlogged stands, or areas of major natural disturbance (Agee and Huff 1987, Spies *et al.* 1988). Trappe (*in press*) recorded volumes of CWD up to 3477 m^3 ha^{-1} for mixed conifer forests in the PNW.

Relationships of CWD to the occurrence of basidiocarps of **Gomphus clavatus**

Only the total volume of CWD (CWD_{Total}) was statistically significant in predicting the occurrence of *G. clavatus* for the stands visited in this study.

The probability of occurrence of *G. clavatus* increases proportionally to the increase of volume of CWD_{Total} independently of stand age (Figure 8.2). The probability of occurrence of *G. clavatus* for stands with low volumes of CWD_{Total}

(30 m^3 ha^{-1}) is only about 14%, whereas it reaches 92% in stands with volumes near 1650 m^3 ha^{-1} (Figure 8.2).

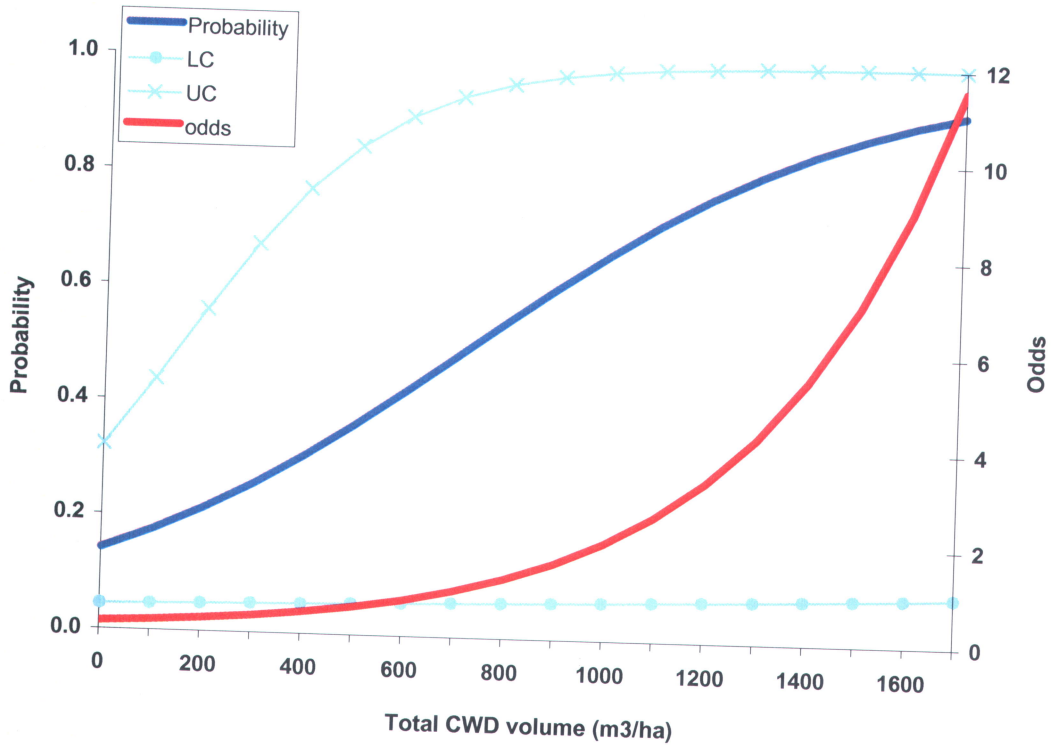

Figure 8.2. Relationship of volume of CWD to the probability and odds of occurrence of basidiocarps of *G. clavatus* in mixed conifer forests in the PNW (LC = lower 95% confidence interval; UC = upper 95% confidence interval for the probability). For data range see tables 8.2 and 8.4.

A similar result is obtained for the odds ratio. The odds ratio for finding *G. clavatus* in stands with large volumes of CWD_{Total} (1640 m^3 ha^{-1}) is about 72 times higher than for stands with low volumes (32 m^3 ha^{-1}) (Figure 8.2).

Table 8.3. Percentage of occurrence of basidiocarps of *Gomphus clavatus* and *Turbinellus floccosus* in mixed conifer forests of six physiographic provinces located in California, Oregon, and Washington (USA).

Physiographic provinces	*Gomphus clavatus* (%)	*Turbinellus floccosus* (%)
California Coast Range	56 (4/7)*	86 (6/7)
Oregon Coast Range	0 (0/4)	0 (0/4)
Willamette Valley	0 (0/5)	20 (1/5)
western WA Cascades	67 (6/9)	67 (6/9)
western OR Cascades	27 (7/26)	43 (11/26)
eastern OR Cascades	20 (1/5)	100 (5/5)

* n/n = number of species-present stands/total number of stands.

Table 8.4. Statistical models for predicting the occurrence of basidiocarps of *Gomphus clavatus* and *Turbinellus floccosus* in mixed conifer forests of six physiographic provinces located in California, Oregon, and Washington (USA).

Gomphus clavatus (Logistic model (n = 56)

Variable	DF	SE	95% CI*		p-value
			LC	UC	
Intercept	1	0.5833	-3.0615	-0.7462	0.002
Volume CWD_{Total}	1	0.0011	0.0004	0.0049	0.0315

Turbinellus floccosus (Logistic model n = 56)

Variable	DF	SE	95% CI		p-value
			LC	UC	
Intercept	1	0.9752	-5.5962	-0.7030	0.0111
Age	1	0.0052	0.0046	0.0254	0.0078
CWD_{4+5}	1	0.0054	0.0054	0.0225	0.0445
Age*CWD_{4+5}	1	0.00003	0.00001	-0.00002	0.0289

* LC = lower 95% confidence interval; UC = upper 95% confidence interval.

Table 8.5. Pearson correlation coefficients (R^2) among explanatory variables.

Variables	Age	CWD_{1+2+3}	CWD_{4+5}	CWD_{Total}
Age	1.0	0.1 (p=0.01)	0.16 (p=0.0021)	0.18 (p=0.0008)
CWD_{1+2+3}	-	1.0	0.14 (p=0.0031)	0.79 (p<0.0001)
CWD_{4+5}	-	-	1.0	0.59 (p<0.0001)
CWD_{Total}	-	-	-	1.0

Habitat characteristics for Gomphus clavatus-*present stands*

Habitat characteristics for stands with populations of *G. clavatus* varied among physiographic provinces. Even though no pattern was detected between plant species and presence of *G. clavatus*, in general it occurred in stands with multi-storied canopies, more than one species of known ectomycorrhizal host, and moss on the forest floor (Table 8.1).

Average age for *G. clavatus*-present stands was 123 years for the California Coast Range (range 70 to 150), 214 years (range 50 to 400) for western Washington Cascades, 293 years (range 200 to 500) for western Oregon Cascades, and 100 years (only one stand) for eastern Oregon Cascades physiographic province (Table 8.2).

***Relationships of stand age and CWD to the occurrence of basidiocarps of* Turbinellus floccosus**

Both age of the stands and volume of CWD_{4+5} were statistically significant in predicting the occurrence of *T. floccosus*. In addition to individual effects of the two explanatory variables the interaction between age and CWD_{4+5} was significant (p=0.03), indicating that the effect of one variable on the likelihood of occurrence of *T. floccosus* varied according to the effect of the other (Table 8.4).

The probability of occurrence of *T. floccosus* increased proportionally to the increase of age of the stands as well as the volume of CWD in late stages of decomposition (Figure 8.3). For younger stands, the higher the volume of CWD_{4+5} the more likely it was to find *T. floccosus*. For older stands, however, the probability of finding *T. floccosus* was about the same of all levels of CWD_{4+5} (Figure 8.3).

The odds ratio gave a similar result to that of the probability, although the values are interpreted in a slightly different way. When older stands (500 years) are

compared to younger stands (30 years) for lower levels of CWD_{4+5} (10 m^3 ha^{-1}), for example, the odds ratio is about 90/0.15. In other words, the odds for the occurrence of *T. floccosus* in older stands with low levels of CWD_{4+5} is about 647 times higher than the odds of occurrence in younger stands with the same or similar volumes of CWD_{4+5} (Figure 8.4). For large volumes of CWD_{4+5} (650 m^3 ha^{-1}), the odds ratio is 748/106, i.e., the chances for the occurrence of *T. floccosus* in older stands are 7 times higher than those of younger stands (Figure 8.4).

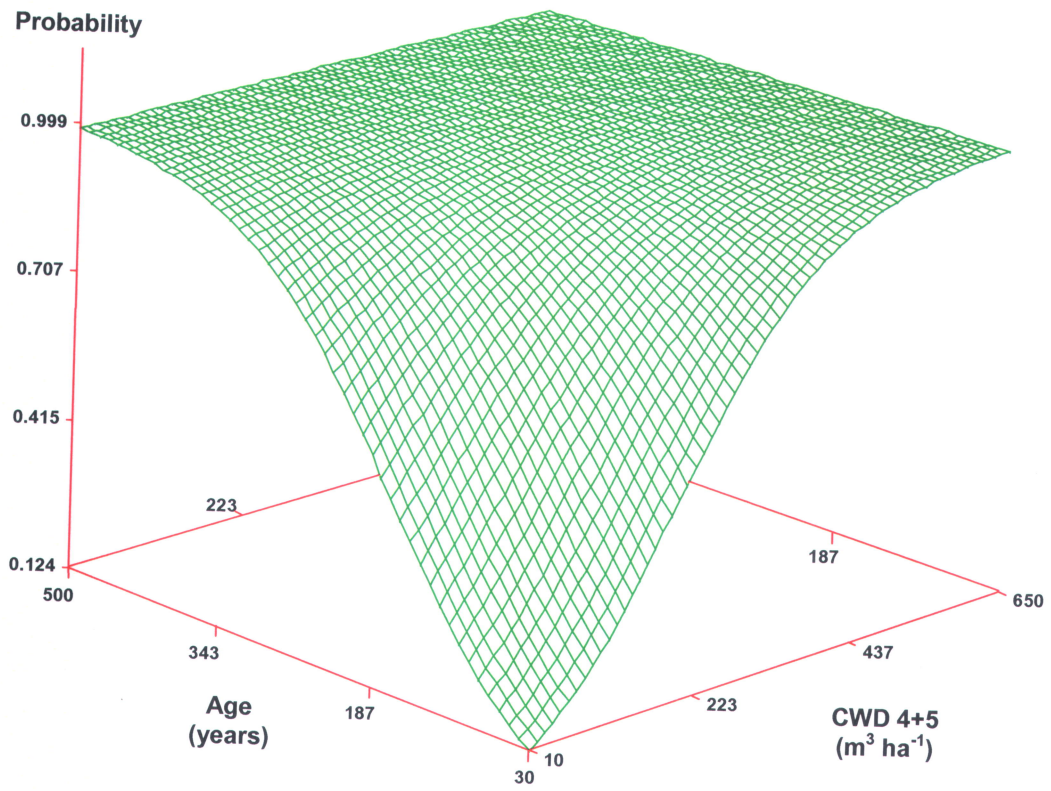

Figure 8.3. Probability of occurrence of basidiocarps of *T. floccosus* as a function of age of the stands (years) and volume of CWD_{4+5} (m^3 ha^{-1}). For data range see tables 8.2 and 8.4.

A similar general conclusion observed for the effect of 'age' is also seen for the effect of CWD_{4+5}. For younger stands (30 years old), the odds for the

occurrence of *T. floccosus* increased proportionally to the increase in volume of CWD_{4+5}. When young stands with small and large volumes of CWD_{4+5} were compared, the chances of finding *T. floccosus* in young stands with 650 m^3 ha^{-1} were 753 times higher than those of young stands with 10 m^3 ha^{-1}, an odds ratio of 106/0.15. For older stands (up to 500 years old), the odds ratio was equally proportional, with a better chance of finding *T. floccosus* in stands with high volumes of CWD_{4+5} than in stands with low volumes (748/90, about 8 times greater).

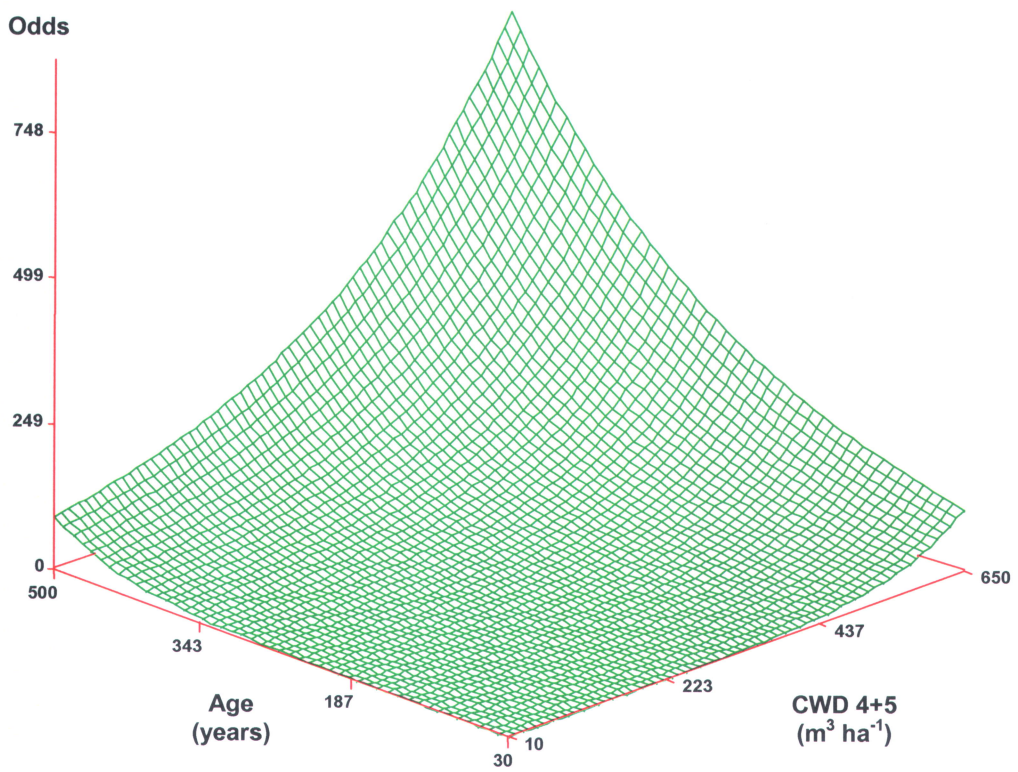

Figure 8.4. Odds for the occurrence of basidiocarps of *T. floccosus* as a function of age of the stand (years) and volume of CWD_{4+5} (m^3 ha^{-1}). For data range see tables 8.2 and 8.4.

In general, these results showed that the odds of finding *T. floccosus* tend to increase proportionally to the increase of both age of the stands and the volume of CWD in late stages of decomposition.

Habitat characteristics for Turbinellus floccosus-*present stands*

Overall characteristics of *T. floccosus*-present stands varied among physiographic provinces (Table 8.1). As for *G. clavatus*, even though no pattern was observed between plant species and the occurrence of *T. floccosus*, the species was always present in stands with at least one species of ectomycorrhizal host, forests with multi-storied canopies, and mossy forest floor.

Average age for *T. floccosus*-present stands was 107 years (range 52 to 150) for the California Coast Range, 200 years (one stand) for the Willamette Valley, 272 years (range 50 to 500) for western Washington Cascades, 269 years (range 120 to 500) for western Oregon Cascades, and 242 years (range 100 to 400) for eastern Oregon Cascades physiographic province (Table 8.2).

DISCUSSION

Stand age and coarse woody debris (CWD)

Stand age was not significant, statistically, in explaining the fruiting patterns for *G. clavatus*. On the other hand, increases in total volume of CWD at the stand level were directly related to increases in the probability for occurrence of *Gomphus clavatus*, independently of age of the cohorts (Figure 8.3). The separation and analysis of CWD into discrete classes (CWD_{1+2+3} and CWD_{4+5}), however, was not statistically significant for predicting the occurrence of the species. The

correlation between the two CWD classes and CWD_{Total} is partially responsible for this result (Table 8.5). Even though the total volume of CWD is directly related to the fruiting of *G. clavatus*, other important variables not considered here, such as soil type, soil moisture, among others, may also be involved in the species' frequency and occurrence. Ultimately, the results indicate that *G. clavatus* is not old-growth dependent, but rather old-growth legacy-dependent species. Old-growth legacy is defined as a set of characteristics that allows for ecosystem sustainability (U.S.D.A. and U.S.D.I. 1994a). Factors related to this condition are presence of diverse strata of forest plant species, age of the cohorts, and presence of large volumes of CWD in all stages of decomposition. In other words, old-growth legacy requires forest processes to be integrated in a manner that they maintain populations rather than isolated individuals (U.S.D.A. and U.S.D.I. 1994ab).

Stand age and CWD_{4+5} were significantly related to the likelihood of occurrence of *T. floccosus* (Table 8.4). Even though age and volume of CWD_{4+5} interacted, *T. floccosus* had a much higher likelihood of occurrence in older than younger stands, independently of the volume of CWD_{4+5} (Figure 8.3). Likewise, stands with large volumes of CWD_{4+5} provided a much higher probability of occurrence of *T. floccosus* than stands with low volumes of CWD_{4+5}, independently of age of the cohorts. This strongly supports the hypothesis (Trappe *in press*, Smith *et al.* 2002) that both stand age and CWD in late stages of decomposition are important for the presence of fungal species associated with the forests in the PNW. Increasing the volume of CWD_{4+5} can account for a significant increase in the probability of finding *T. floccosus* also in younger stands (Figure 8.3). Figure 8.3 indicates that the abundance of CWD_{4+5} is significantly related to the likelihood of occurrence of *T. floccosus* in stands less than 200 years of age. Consistent inputs of new CWD are important for maintaining CWD in all stages of decomposition (Maser *et al.* 1988). These constant inputs not only provide habitat for CWD dependent species but also assure continuity of forest processes essential for the ecosystem sustainability.

Among other factors, coarse woody debris, especially that in well-decayed stages, is a source of moisture through seasonal precipitation variations and thereby help support mycorrhizae during dry spells (Maser *et al.* 1988, Amaranthus *et al.* 1989, Amaranthus *et al.* 1994). Boddy (1983) showed that water could comprise more than half the mass of CWD under some circumstances. In the PNW, the moisture contents of a decaying *P. menziesii* tree bole increases as the decay class increases, and even during the summer it can reach 250% of the dry weight on some class 5 CWD (Maser *et al.* 1988). Trappe and Jumpponen (unpublished data) recorded a 650% moisture content of class 5 CWD during a rainy autumn in an old-growth *P. menziesii* forest in western Oregon. Both diameter and stage of decay affect the ability of CWD to hold moisture, and all size classes of decaying wood act as a moisture store and refugium for tree roots and ectomycorrhizal fungi during dry periods (Stevens 1997). Mycelia of mycorrhizal fungi are common in well-decayed stumps and logs on the forest floor, suggesting that the volume of CWD material per unit of area is directly correlated with the occurrence of certain species of mycorrhizal fungi (M. Trappe *in press*).

Trappe (*in press*) showed that CWD in late stages of decomposition was positively correlated with the presence of *Craterellus tubaeformis* in conifer forests of the PNW. As discussed above, the volume of CWD_{4+5} is directly correlated to the occurrence of *T. floccosus*. Even though *T. floccosus* is a terrestrial species, unlike *C. tubaeformis*, it frequently fruits near or on top of CWD_{4+5}. These logs generally contain abundant hyphae and roots from nearby conifers, notably *T. heterophylla*, suggesting that both take advantage of these water reservoirs during times of draught. The content of water stored in CWD may facilitate the acquisition and storage of nutrients needed for basidiocarp formation during dry, water shortage periods.

The importance of preserving habitat for certain fungal species is well illustrated in figure 8.3. Especially important, in this particular case, is the interaction of stand age and volume of CWD_{4+5}. Figure 8.3 shows that increasing amounts of CWD_{4+5} and older stands positively affect the probability of occurrence

of *T. floccosus*. When large volumes of well-decomposed CWD are available, the effects of a second variable in predicting the occurrence of the fungal species are reduced. The analogy is true for age of the cohorts: the older the trees, the more likely does *T. floccosus* occur independently of volume of CWD_{4+5}. This simply suggests that one variable alone is responsible for most of the total effect observed. However, this conclusion cannot be drawn because of the statistically significant interaction between age and CWD_{4+5} (Table 8.4).

Future implications

Management strategies to provide optimum habitat should include factors such as mature to old-growth stands and an abundance of CWD in all decay classes. Protecting 'legacy' CWD and recruiting a new cohort of class 1 CWD are essential to managing current and future habitats. CWD supply is a continuing cycle, and an ongoing addition of CWD is fundamental to maintain habitat over the long term (Maser *et al.* 1988). Old-growth trees are also related to the maintenance of viable populations of some gomphoid fungi in the conifer forests of the PNW. Additional data need to be gathered, especially for *T. kauffmanii*, to determine if other potential factors are involved in the presence and abundance of these fungal species.

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CHAPTER 9

Conclusions

In this dissertation the holotypes and representative collections of the gomphoid genera related to *Gomphus sensu lato* were examined and several recombinations proposed. Species of *Gomphus sensu lato* were reassigned to *Gomphus sensu stricto*, *Gloeocatharellus, Phaeoclavulina* and *Turbinellus*.

Gomphus sensu stricto is recognized by unipileate to merismatoid basidiomata, depressed, funnel- to fan-shaped pilei, presence of clamp connections, and verrucose spores. It has three described species: *G. brunneus* (Africa), *G. clavatus* (northern hemisphere), and *G. crassipes* (Africa and Spain).

Gloeocantharellus species are characterized by relatively small basidiomata with wrinkled to lamellate hymenia and an abundance of gleoplerous hyphae. The ten described species are distributed primarily in tropical and subtropical regions of Bolivia, Borneo, Brazil, Guam, Hawaii, Malaysia, Papua New Guinea, the Solomon Islands, and Sri Lanka. Some species also occur in Japan, New Zealand, Russia, and the USA.

Turbinellus is the most common and widespread cantharelloid-gomphoid genus in North America and perhaps in the world. Species are in all continents except Australia and Antarctica. It occurs in a variety of forest ecosystems, and some, if not all species are presumed to be ectomycorrhizal with members of the Pinaceae. Among the morphological features important for generic level identification of *Turbinellus* are the scaly, orange-red or brown pilei, the strongly wrinkled and generally pale yellow to yellow-orange hymenia, the absence of clamp connections, and the verrucose, ellipsoid to obovoid spores. Five species are recognized: *T. flabellatus, T. floccosus, T. fujisanensis, T. kauffmanii*, and *T. stereoides*.

The genus *Phaeoclavulina* has 41 species characterized macroscopically by pileate or ramarioid, greenish violaceous, brown, or orange-red basidiomata and wrinkled to smooth hymenia. Microscopic features include monomitic hyphae, presence of clamp connections, and echinulate to verrucose, subreticulate or reticulate spores. The six pileate species are transfers from *Gomphus sensu lato*. These have funnel- to fan-shaped basidiomata and strictly tropical to subtropical distribution. The ramarioid section of *Phaeoclavulina* includes species transferred from *Ramaria* subgenus *Echinoramaria*.

Phylogenetic analyses of the nuclear large subunit ribosomal DNA (nuc-25S-rDNA), mitochondrial small subunit ribosomal DNA (mit-12S-rDNA), and mitochondrial *atp6* DNA (mit-*atp6*-DNA) combined sequences corroborated previous results on the evolutionary relationships among members of the Geastrales, Gomphales, Hysterangiales, and Phallales. Although some nodes deep in the tree could not be fully resolved, some well-supported lineages were recovered, and the interrelationships among *Gloeocantharellus, Gomphus, Phaeoclavulina*, and *Turbinellus*, and the placement of *Ramaria* are better understood. Both *Gomphus sensu lato* and *Ramaria sensu lato* comprise paraphyletic lineages within the Gomphaceae. It is also clear how the subgenera of *Ramaria* are distributed and the relatedness of each of its subgenera to other genera in the Gomphales.

The relationship of *Gomphus clavatus* and *Turbinellus floccosus* to stand age, volume and decay class of coarse woody debris (CWD) was assessed from stands in the Pacific northwestern USA. The results indicate that total volume of CWD but not stand age was related to the probability of occurrence of basidiocarps of *G. clavatus*: the larger the volume of CWD, the higher the likelihood of occurrence of that species. Both stand age and volume of CWD in late stages of decomposition (CWD_{4+5}) were directly associated with the probability of occurrence of basidiocarps of *T. floccosus*. Thus habitat requirements varied between species, and potential habitats for the maintenance of these taxa should contain large amounts of CWD.

This study was intended to shed light on the systematics of *Gomphus sensu lato* and related taxa. It resulted in a new classification and clarified the morphological features important to genus and species level identification. However, much still needs to be done. Perhaps the three main areas of priority would be: a) supply a better sampling for intra-generic classification in *Gloeocantharellus*, b) expand on the study of *Phaeoclavulina*, with emphasis on its substrate requirements, and c) clarify the habitat elements associated with the fruiting patterns of these gomphoid species. Exploration of these topics could potentially reveal features that strongly link the members of Gomphales to the Geastrales, Hysterangiales, and Phallales.

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