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Chapter 12

Biogeography and Ecology of Tulasnellaceae

Franz Oberwinkler, Darío Cruz, and Juan Pablo Suárez

12.1 Introduction

Schröter (1888) introduced the name *Tulasnella* in honour of the French physicians, botanists and mycologists Charles and Louis René Tulasne for heterobasidiomycetous fungi with unique meiosporangial morphology. The placement in the Heterobasidiomycetes was accepted by Rogers (1933), and later also by Donk (1972). In Talbot's conspectus of basidiomycetes genera (Talbot 1973), the genus represented an order, the Tulasnellales, in the Holobasidiomycetidae, a view not accepted by Bandoni and Oberwinkler (1982). In molecular phylogenetic studies, Tulasnellaceae were included in Cantharellales (Hibbett and Thorn 2001), a position that was confirmed by following studies, e.g. Hibbett et al. (2007, 2014).

12.2 Systematics and Taxonomy

Most tulasnelloid fungi produce basidiomata on wood, predominantly on the underside of fallen logs and twigs. Reports on these collections are mostly published in local floras, mycofloristic listings, or partial monographic treatments.

F. Oberwinkler (✉)

Institut für Evolution und Ökologie, Universität Tübingen, Auf der Morgenstelle 1, 72076 Tübingen, Germany

e-mail: franz.oberwinkler@uni-tuebingen.de

D. Cruz • J.P. Suárez

Museum of Biological Collections, Section of Basic and Applied Biology, Department of Natural Sciences, Universidad Técnica Particular de Loja, San Cayetano Alto s/n C.P., 11 01 608 Loja, Ecuador

Unfortunately, the ecological relevance of *Tulasnella* fruiting on variously decayed wood or on bark of trees is not understood. It would appear plausible to assume that *Tulasnella* species are involved in wood decay, and that they may function in anamorphic stages as mycobionts in close by habitats. Therefore it seemed imperative to include in this overview of tulasnelloid mycobionts also reports on basidiomata.

Though some well developed *Tulasnella* species can be recognized in the field by the experienced mycologist with some certainty, correct identification of the genus was only possible microscopically in pre-molecular times. Most tulasnelloid fungi were sampled by collectors interested in corticiaceous fungi. Reports on these collections are mostly published in local floras, mycofloristic listings, or partial monographic treatments. Some of these publications are used to document biogeographical patterns on continental scales (Table 12.1). Because of considerable taxonomic difficulties and inaccuracies in traditional microscopic identification of *Tulasnella* morphospecies, they cannot be used for an attempt to disentangle their distribution areas. However, molecular data may help to overcome this bottleneck.

In several *Tulasnella* species the hymenial surface has a rosy to faintly violaceous tint (Fig. 12.1). Basidiomata consist of a few basal hyphae with or without clamps. Normally a simple but rarely considerably thickened hymenium is developed. Subhymenial structures may be lacking, and consequently single generative hyphae produce meiosporangia. Such growth forms or developmental stages cannot be detected in the field. These are only detected microscopically by chance, growing on the surface of other fungi, especially their hymenia. The growth can be intrahymenial, e.g. in *T. inclusa* (*Gloeotulasnella i.*, Christiansen 1959), or, rather exotically, parasitising on amoebae (*T. zoocytica*, Drechsler 1969).

The anamorphic stage of *Tulasnella* has been named *Epulorhiza* (Moore 1987), and it has been often used in mycorrhiza studies. Since the concept “One fungus = one name” was implemented at the International Botanical Congress XVIII, Melbourne, July 2011 (McNeill and Turland 2011; McNeil et al. 2012), the name *Epulorhiza* became synonymous. Nevertheless, articles dealing with *Epulorhiza* are included in our review, even when it appears uncertain in several cases, whether or not *Tulasnella* is involved. For the reason of taxonomic clarity in the following text, a short comment on the *Ceratobasidium-Rhizoctonia* complex is included here. In various treatments, the formal taxonomy of the so-called “form genus *Rhizoctonia*” has been dealt with (e.g. González Garcia et al. 2006; Yang and Li 2012). As pointed out by Oberwinkler et al. (2013), the name *Ceratobasidium* can only be applied for *Ceratobasidium calosporum* and the genera *Koleroga*, *Oncobasidium*, *Uthatabasidium*, and *Ypsilonidium* have to be put under synonymy of *Rhizoctonia*. The latter one has priority over *Thanatephorus*. Unfortunately, these taxonomic re-arrangements were widely ignored in a recent paper by González et al. (2016).

Micromorphological characteristics of *Tulasnella* species include unique basidia with strongly swollen sterigmata (Fig. 12.1), also called epibasidia, which is a misleading term. After meiosis in the basidium, haploid nuclei and the basidial cytoplasm migrate through the sterigmata into the terminally developing basidiospores. In the basal position, the sterigmata become secondarily septate. Apically

Table 12.1 Compilation of perfect stages of Tulasnellaceae species, arranged according to Fig. 12.2

Regions		Europe					Asia		Af	America			Pac	Aus
Subdivisions		N	W	C	E	S	te	tr		N	C	S		
Species	Spores													
<i>T. eichleriana</i>	Globose–elliptical	•	•	•	•	•	•				•			•
<i>T. violea</i>		•	•	•			•					•		
<i>T. zoocytia</i>										•	•			
<i>T. cystidiophora</i>		•	•	•										
<i>T. pacifica</i>														•
<i>T. bourdotii</i>			•	•										
<i>T. subglobispora</i>		•		•										
<i>T. hyalina</i>			•	•										
<i>Pseudotulasnella guatemalensis</i>											•			
<i>T. guttulata</i>														
<i>T. traumatica</i>			•								•			
<i>T. conidiata</i>			•								•			
<i>T. valentini</i>	Oblong–elliptical			•										
<i>Stilbotulasnella conidiophora</i>														•
<i>T. albidia</i>		•	•	•	•	•								
<i>T. pinicola</i>			•	•							•			
<i>T. thelephorea</i>		•	•	•	•	•								
<i>T. asymmetrica</i>														•
<i>T. pruinosa</i>		•	•	•		•								
<i>T. dissitispora</i>	Phaseoli-form-subcylindrical		•											
<i>T. tomaculum</i>		•	•	•	•	•					•	•		
<i>T. andina</i>												•		
<i>T. irregularis</i>														•
<i>T. fuscoviolacea</i>				•	•	•								
<i>T. rubropallens</i>			•	•		•								•
<i>T. griseorubella</i>		•		•										
<i>T. bifrons</i>			•								•			
<i>T. robusta</i>												•		
<i>T. cruciata</i>				•										•
<i>T. kirschneri</i>							•							
<i>T. pallidocrema</i>		•												
<i>T. balearica</i>	Sigmoid					•								
<i>T. deliquescens</i>		•		•										
<i>T. quasiflorens</i>		•												
<i>T. curvispora</i>	Allantoid			•										
<i>T. permacra</i>			•											
<i>T. allantospora</i>		•	•	•							•		•	•
<i>T. danica</i>			•	•							•			
<i>T. saveloides</i>		•	•		•									
<i>T. aggregata</i>											•			
<i>T. anguifera</i>	Spiral		•											
<i>T. interrogans</i>			•	•										
<i>T. falcifera</i>			•											
<i>T. helicospira</i>			•	•								•		
<i>T. calospora</i>	Fusiform-subfusi-form		•	•	•	•				•	•		•	•
<i>T. eremophila</i>										•				
<i>T. kongoensis</i>										•				
<i>T. brinkmannii</i>				•										
<i>T. pallida</i>		•	•	•	•	•								
<i>T. echinospora</i>		•	•				•							

• records arranged geographically. C central, E east, N north, S south, te temperate, tr tropical, W west. Literature: **Europe:** Bresadola (1903), Bourdot and Galzin (1927), Pearson (1928), Strid (1975), Torkelsen (1977), Hjortstam (1978), Wojewoda (1978, 1983, 1986), Hauerslev (1989), Roberts (1992, 1993a, b, 1994a, b, 1996, 1999, 2003), Dueñas (1996, 2001, 2005), Van de Put and Antonissen (1996), Roberts and Piątek (2004), Ordynets (2012), Kunttu et al. (2015), Polemis et al. (2016). **Asia:** Doğan and Kurt (2016). **Africa:** Crous et al. (2015). **North America:** Rogers (1933), Olive (1946). **Central America:** Roberts (2006). **South America:** Martin (1939), Lopez (1987), Greslebin and Rajchenberg (2001), Cruz et al. (2011, 2014, 2016), Nouhra et al. (2013). **Pacific area:** Olive (1957), Bandoni and Oberwinkler (1982). **Australia:** Warcup and Talbot (1967, 1971, 1980). Orig

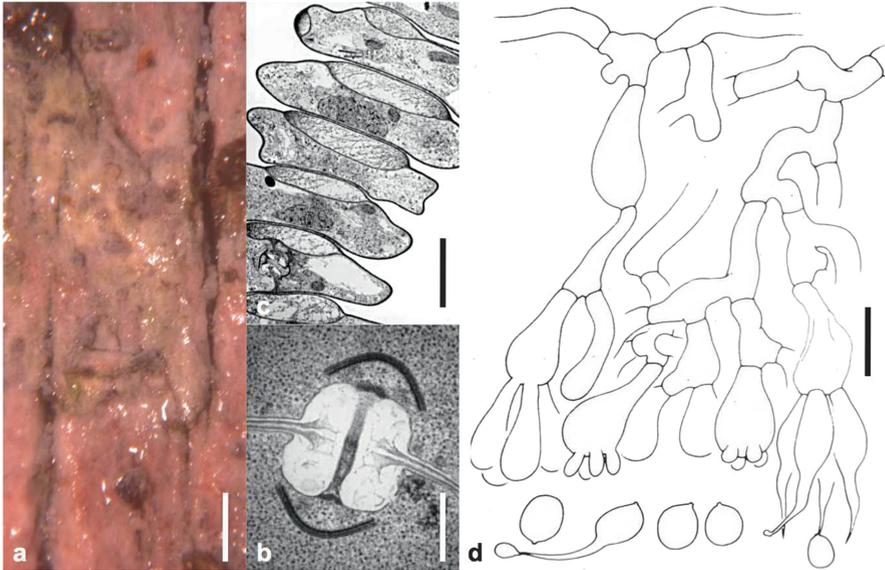


Fig. 12.1 *Tulasnella violacea* (a, d) and *Tulasnella* spp. (b, c): (a) hymenial surface, bar 5 mm; (b) dolipore with continuous parenthesomes, bar 0.1 µm; (c) spirally growing hypha with cell wall extensions (arrows), bar 2 µm; (d) section through basidiome with basidia and basidiospores, one forming a secondary spore, bar 5 µm. From Oberwinkler (2012)

partly septate basidia have been reported for *Pseudotulasnella guatemalensis* (Lowy 1964). Basidiospores germinate by hyphae or secondary ballistospores. Dolipores with continuous parenthesomes are a constant ultrastructural feature in *Tulasnella* (Fig. 12.1). However, parenthesomes could not be found in dolipores of *Stilbotulasnella conidiophora* (Bandoni and Oberwinkler 1982). Other apparently unique ultrastructural features include cell wall expansions filled with amorphous matrix (Fig. 12.1). It is unknown whether this character is representative in all or most of *Tulasnella* species. Morphological and ultrastructural characters were indicative of a separate systematic position in former heterobasidiomycetous fungi, but precise phylogenetic position of *Tulasnella* within Basidiomycota remained unsettled.

There is a set of micromorphological characters in *Tulasnella* species, which appear to be applicable for circumscribing taxa. However, even in the case of very accurate microscopic work, there remains much uncertainty about the variability of structural features. This explains at least partly why reliable species identification is difficult and quite often questionable. This situation became strikingly evident, when molecular analyses showed that morphospecies were often not verifiable or included cryptic taxa (Taylor and McCormick 2008; Cruz et al. 2014). Whether the finding of Linde et al. (2013) in Australian orchid mycorrhizae, that an eight-locus analysis is broadly congruent with the solely ITS based result, can be generalized, remains questionable. For taxonomic details and nomenclature of *Tulasnella*

species we refer to Cruz et al. (2014, 2016). Table 12.1 provides an overview about the basic morphological features and distribution of Tulasnellaceae morphospecies.

12.3 Phylogenetic Position of *Tulasnella*

A sequence database for the identification of ectomycorrhizal basidiomycetes included also *Tulasnella* (Bruns et al. 1998). Tulasnelloid orchid associates clustered with good support within the cantharelloid clade. In an attempt to identify single pelotons of *Dactylorhiza majalis* using single-strand conformation polymorphism and mitochondrial ribosomal large subunit DNA sequences, Kristiansen et al. (2001) found two taxa, *Tulasnella*, and a second one, distantly related to *Laccaria*. As sister of the *Tulasnella* cluster, *Sebacina* sp. was found, and both together appeared in a neighbour position to cantharelloid fungi. An expanded taxon set of basidiomycetes was used by Bidartondo et al. (2003) to resolve the phylogenetic placement of *Aneura* (*Cryptothallus*) associated fungi (see Sect. 12.5.1). They were phylogenetically well supported with *T. asymmetrica* as a sister taxon and *T. obscura* and *T. calospora* in the same clade. Similar results were obtained by Kottke et al. (2003), focusing on the mycobiont of *Aneura pinguis*, and Weiß et al. (2004) in an approach covering most of heterobasidiomycetous genera sequenced at that time. Resupinate homobasidiomycetes were analyzed molecularly by Binder et al. (2005), again fitting *Tulasnella* species to the cantharelloid clade but without substantial support. The results of Moncalvo et al. (2006) in analyzing the cantharelloid clade were also ambiguous concerning *Tulasnella* in nuc-rDNA and RPB2 together with mtSSU genes. Shimura et al. (2009) sequenced the Japanese *Cypripedium macranthos* mycobiont and found a weakly supported sister relationship to *Cantharellus* spp. and related taxa, including *Sistotrema* sp., in a very limited sampling. In a comprehensive analysis of publicly available sequences of Ceratobasidiaceae s.l. and related taxa, Veldre et al. (2013) included also some anamorphic tulasnelloid strains and *T. cystidiophora*. Both groups clustered in a sister relationship and were positioned in the Cantharellales. Also in the review on Agaricomycetes of Hibbett et al. (2014), the Tulasnellaceae are included in the Cantharellales.

12.4 The Presumable Age of *Tulasnella* and Evolution of Plant Associations

Taylor and Berbee (2006) dated Basidiomycota between 1489 and 452 Mya, the huge timespan resulting from the uncertainty in determining the age of the ascomycetous fossil *Paleopyrenomycites*. A maximum age of the evolutionary root in Marchantiophyta is calculated for 450 Mya by Clarke et al. (2011), 520–470 Mya

by Cooper et al. (2012), and 475 Mya by Sun et al. (2014). In a detailed time scale, Cooper et al. (2012) mark a divergence time of 100–50 Mya for *Aneura pinguis* and *A. mirabilis*. It may be concluded that *Tulasnella* mycobionts share the same age of their liverwort photobionts. The second calibration approach of Taylor and Berbee (2006) was used by Garnica et al. (2016) to determine divergence times in Sebaciales and other taxa of Basidiomycota. For Cantharellales they found 317–128 Mya with an average of 203 Mya. With some caution, a similar age interval may be adopted for Tulasnellaceae. Orchids originated approximately 100–80 Mya before present (Givnish et al. 2015), thus indicating a similar age of their mycobionts, including *Tulasnella*.

Yukawa et al. (2009) summarized the occurrence of ORM mycobionts in major clades of the Orchidaceae. Tulasnellaceae were reported from Apostasioideae, Vanillinae, Cyrtopodioideae, Disinae, Orchidinae, Goodyerinae, Prasophyllinae, Diuridinae, Caladeniinae, Neottieae, Dendrobiinae, Malaxideae, Calypsoeae, Pleurothallidinae, and Cymbidiinae.

12.5 Biotrophic Associations of *Tulasnella*

12.5.1 *Tulasnella* Associated with Liverworts

Liverwort mycobionts were examined in the course of an extensive study of biodiversity in a tropical cloud forest in South Ecuador (Kottke et al. 2003). *Aneura pinguis* was associated with *Tulasnella* species related to *T. asymmetrica* (Fig. 12.2), while Jungermanniales (*Lophozia* spp. and *Calypogeia muelleriana*) involved sebacinoïd mycobionts. The same sequence group of *T. asymmetrica* (AY152406) was recovered in a study on the enigmatic hepatic *Aneura mirabilis* (as *Cryptothallus mirabilis*, Wickett and Goffinet 2008) mycobionts in Europe by Bidartondo et al. (2003). *Aneura mirabilis* is a mycoheterotrophic liverwort and specialized as an epiparasite on *Tulasnella* species that form ectomycorrhizae with surrounding trees like *Alnus glutinosa*, *Betula pubescens*, *Pinus pinaster*, *P. muricata* or *Salix aurita* and *S. cinerea* (Bidartondo et al. 2003). In a geographically strongly expanded study on liverwort-fungal symbioses, Bidartondo and Duckett (2010) reported Aneuraceae-associated *Tulasnella* from Europe, North and South America, East Asia and New Zealand.

Thallose European and Andean species of Aneuraceae (Metzgeriales) host *Tulasnella* mycobionts of high diversity especially in the European samples (Nebel et al. 2004; Pressel et al. 2010; Preußing et al. 2010). These interactions were considered by Krause et al. (2011) as a model of early evolved symbiotic associations. It is most likely that specific *Tulasnella* species occur together with the hosts throughout their distribution range.

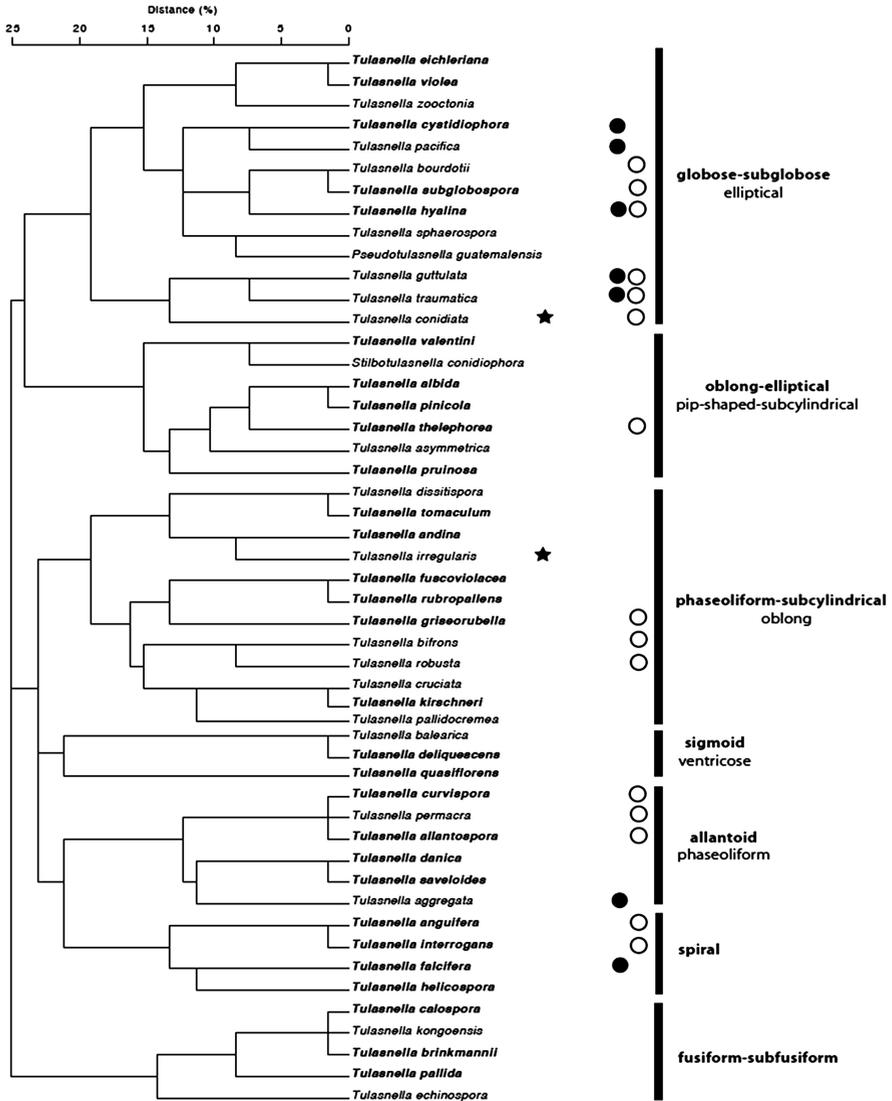


Fig. 12.2 Dendrogram of Tulasnellaceae species inferred by Jaccard analysis of all available structures from 48 taxa, including the new species *Tulasnella andina* and *T. kirchneri*. Names of species presented in detail by Cruz et al. (2016) are written in bold. Seven groups are defined, based on basidiospore morphology. Other characters are indicated by symbols: clamp connections (unfilled circles), cystidia (filled circles), chlamydospores (filled stars). From Cruz et al. (2016)

12.5.2 *Ectomycorrhiza (EcM)*

The ectomycorrhizal lifestyle in fungi, including *Tulasnella*, and dealing with diversity, distribution and evolution, was reviewed by Tedersoo et al. (2010). In a study on ectomycorrhizal liaisons between forest orchids and trees in the Bavarian northern Frankenalb, Bidartondo et al. (2004) mention *Tulasnella* and tulasnelloid fungi as “lineages that contain some ectomycorrhizal strains”, however, without further explanation.

In a wet Tasmanian sclerophyll forest, Tedersoo et al. (2008a) report several unidentified *Tulasnella* species associated with *Eucalyptus regnans* (Myrtaceae), *Nothofagus cunninghamii* (Nothofagaceae), and *Pomaderris apetala* (Rhamnaceae). The authors mention that *Tulasnella* is commonly observed in Tasmania but seldom recorded in the Northern Hemisphere as EcM mycobionts. This comment appears hardly probable for the real ECM occurrence of *Tulasnella*, but matches literature information at present. Nevertheless, when studying the community composition of *Picea abies* and *Betula pendula* seedlings in three Estonian old-growth forests, Tedersoo et al. (2008b) found that “ordination analyses suggested that decay type determined the composition of EcM fungal community in dead wood”. In fact, in this study, *Tulasnella* EcMs were verified for the first time in the Northern Hemisphere besides the experimental synthesis study of Bidartondo et al. (2003).

12.5.3 *Tulasnella Orchid Mycorrhiza (OM)*

In seed germination experiments of orchids, Bernard (1899, 1909) and Burgeff (1909, 1932, 1936) detected the importance of fungal mycobionts during the early developmental stages. At that time, identification of the mycobionts was impossible. In addition, Burgeff (1932) treated the biology of symbiosis in tropical orchids extensively. After a review of OMs by Rasmussen (2002), Dearnaley (2007) updated new publications in this field. The trophic relationships in orchid mycorrhizae, including Tulasnellaceae, and their implications for conservation were summarized by Rasmussen and Rasmussen (2007). In a review on mutualistic, root-inhabiting fungi of orchids, Kottke and Suárez (2009) compiled also reports of tulasnelloid mycobionts, some of them associated with epiphytic tropical orchids. The complex of requirements of germination and seedling establishment in orchids, including tulasnelloid mycobionts, were comprehensively treated by Rasmussen et al. (2015). Suárez and Kottke (2016) summarized their overview on ORMs in tropical mountain forests in Ecuador that main fungal partners, including *Tulasnella*, correspond to findings in other biomes. Partial genome sequences of two *Tulasnella* mycobionts, originating from Australian *Chiloglottis* and *Drakaea* orchid species, may allow to obtain insight in evolutionary trends of tulasnelloid OM (Ruibal et al. 2013).

12.6 Biogeography of *Tulasnella*

12.6.1 Europe

Europe has the most abundant records of *Tulasnella* as fruit-bodies and in molecular identification events from plant roots (Fig. 12.3). Hadley (1970) reported no specificity of *Tulasnella calospora* in symbioses tests with European orchids, *Coeloglossum viride*, *Dactylorhiza purpurella*, *Goodyera repens* and the tropical *Cymbidium canaliculatum*, *Epidendrum radicans*, *Laeliocattleya* cv., *Spathoglottis plicata*, and considered it as a potential universal orchid symbiont. Dijk et al. (1997) stated that “*Epulorhiza repens* has been isolated from a vast amount of terrestrial orchids, and is considered a ubiquitous orchid endophyte”. *Tulasnella* was the predominant mycobiont in 59 root samples of seven European and North American *Cypripedium* species (Shefferson et al. 2005). In addition, mycorrhizal specificity of 90 populations of 15 *Cypripedium* taxa across Europe, Asia, and North America was quantified by Shefferson et al. (2007). The orchids were associated almost exclusively with Tulasnellaceae mycobionts.

The mycobiont septal structure of native terrestrial French *Dactylorhiza majalis* (Strullu and Gourret 1974) and Italian *D. maculata*, *D. sambucina*, and *Platanthera bifolia* (Filipello Marchisio et al. 1985) was studied with the transmission electron microscope. They authors found dolipores with continuous parentheses, suggesting *Sebacina* and/or *Tulasnella* mycobionts, which were finally identified by Andersen (1990) as *T. deliquescens* and *T. calospora*, respectively. A remarkable experimental approach was carried out by Smreciu and Currah (1989), who studied symbiotic and asymbiotic germination of seeds of north temperate terrestrial orchids in Europe and

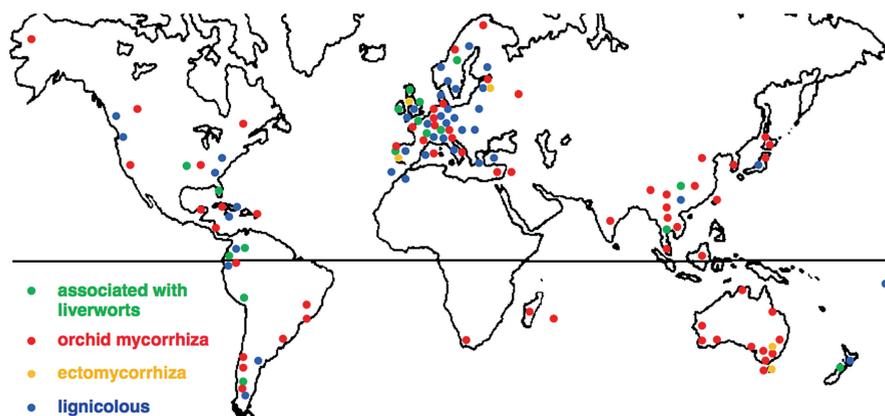


Fig. 12.3 Sampling localities for *Tulasnella* spp., extracted from literature. Tulasnelloid associates with liverworts are marked with *green dots*. Orchid mycorrhizae (*red dots*) summarize isolates of *Tulasnella* from orchid roots and molecularly identified samples. Tulasnelloid ectomycorrhizae are marked with *yellow dots*. Lignicolous (*blue dots*) means that basidiomata were collected on wood

North America. The European species included *Dactylorhiza maculata*, *D. sambucina*, *Epipactis palustris*, *E. purpurata*, *Gymnadenia conopsea*, *G. odoratissima*, *Neottia nidus-avis*, *Nigritella nigra*, and *Orchis morio*. It appears that mycobionts of these mostly widespread orchids were predominantly tulasnelloid fungi, except in *N. nidus-avis* and *E. purpurata*. Rasmussen and Rasmussen (1991) tried to identify experimentally the environmental conditions for germination and seedling development in *D. majalis* together with *T. calospora*. A stimulating effect of *Tulasnella* (*Epulorhiza repens*) and *Rhizoctonia* (*Ceratorrhiza* sp.) on the growth of Dutch *Dactylorhiza* spp. and *Orchis morio* was reported by Dijk and Eck (1995). Single-strand conformation polymorphism and mitochondrial ribosomal large subunit DNA sequences were used by Kristiansen et al. (2001) to identify *T. deliquescens* and *Laccaria* sp. as *D. majalis* mycobionts from single pelotons. Various fungal strains, isolated from non orchid sources were used to test symbiotic germination of British *D. fuchsii* (Salman et al. 2001). Besides *Ceratobasidium cornigerum*, also *T. helicospora* stimulated germination of the orchid seeds and promoted seedling growth. From a wetland of Bavaria, Bidartondo et al. (2004) reported *Tulasnella* as a mycobiont of *D. majalis*. Unidentified *Tulasnella* OM symbionts were found in *D. baltica*, *E. atrorubens*, and *O. militaris* in Estonian mine tailing hills and pristine sites (Shefferson et al. 2008). Most likely the seed germination experiments of the boreal-alpine *D. lapponica*, collected from the Solendet Nature Reserve in Central Norway, were enhanced by tulasnelloid mycobionts (Øien et al. 2008). In analyzing the mycobionts of five *Dactylorhiza* species in Belgium, Jacquemyn et al. (2012) concluded that orchid rarity is related to mycorrhizal specificity and fungal distribution. In an extensive study of 114 sampled individuals from one to three populations of 14 species of *Dactylorhiza* in Belgium, France, Italy, Portugal, Sweden and the United Kingdom, Jacquemyn et al. (2016b) suggested that habitat-driven variation occurs in mycorrhizal communities in which *Tulasnella* plays an essential role.

Tulasnelloid mycobionts of *Epipactis palustris* were reported from Northeast Bavarian wetlands (Bidartondo et al. 2004). Multiple independent colonization events of former lignite mining areas in Eastern Germany by *E. palustris* were documented by Esfeld et al. (2008) and observed in different rockgarden areas of Tuebingen Botanical Garden by the first author between 1975 and 1995 (unpubl). In a comparative study of *E. helleborine*, *E. neerlandica*, and *E. palustris* in Belgium, *Tulasnella* was only retrieved from the latter photobiont (Jacquemyn et al. 2016a). In ten North American and European *Goodyera* species, *Tulasnella* was only found in *G. pubescens* and *G. repens* in the USA (McCormick et al. 2004; Shefferson et al. 2010). In their study on carbon and nitrogen exchange in *Goodyera repens*, Liebel et al. (2015) found *Tulasnella* and *Ceratobasidium* as the most frequent mycobionts of the orchid species.

Fungi from the roots of the common terrestrial orchid *Gymnadenia conopsea* included typical ORMs of the Tulasnellaceae and Ceratobasidiaceae as well as several ectomycorrhizal taxa of the Pezizales (Stark et al. 2009). In this orchid, Těšitelová et al. (2013) found evidence that polyploidization can be associated with a shift in their tulasnelloid mycorrhizal symbionts. Among a variety of ascomycetous and

basidiomycetous associates of *Himantoglossum adriaticum*, Tulasnellaceae were identified in two protected areas of Central Italy (Pecoraro et al. 2013).

Liparis loeselii and *Hammarbya paludosa* are wetland specialists associated with tulasnelloid mycobionts in Hungary (Illyés 2011). In situ and in vitro germination of *L. loeselii* were studied by Illyés et al. (2005). They found *Tulasnella* (*Epulorhiza*) and *Ceratobasidium* (*Rhizoctonia*) as mycorrhizal partners. Broader samplings with *Dactylorhiza incarnata*, *Epipactis palustris*, *Gymnadenia conopsea*, *Ophrys oestriifera*, *Op. sphegodes*, and *Orchis militaris*, *Or. palustris*, and *Or. purpurea* indicated *Tulasnella* associations to prefer wetter habitats (Illyés et al. 2009), or to tolerate a wide spectrum of water availability (Illyés et al. 2010). Here, the question arises, what constrains the distribution of orchid populations (McCormick and Jacquemyn 2014), a question that should better be modified into what constrains the distribution of orchid-mycobiont associations. Recently Jacquemyn et al. (2015b) reported Tulasnellaceae in the roots and the soil of the green *Neottia ovata* (*Listera ovata*) in eastern Belgium. It is noteworthy to mention that tulasnelloid mycobionts have not been found in the achlorophyllous *N. nidus-avis* (e.g. Selosse et al. 2002).

The mycorrhizal fungal diversity of *Orchis militaris*, including tulasnelloid associates, detected in some Hungarian habitats, is considered to be essential for the wide ecological range of the orchid species (Ouanphanivanh et al. 2007). In a multidisciplinary approach of the simultaneously investigated mediterranean *Orchis simia*, *O. anthropophora*, and their hybrid *O. × bergonii*, Schatz et al. (2010) compared leaf growth, seed viability, emitted scent, and mycorrhizal species and their rate of infection. The mycobionts were unidentified *Tulasnella* species. Five *Orchis* species, *O. anthropophora*, *O. mascula*, *O. militaris*, *O. purpurea*, and *O. simia*, sampled from the Netherlands to Italy by Jacquemyn et al. (2010), contained a majority of *Tulasnella* mycobionts. In three closely related and hybridizing species, *O. anthropophora*, *O. militaris*, and *O. purpurea*, the influence of mycorrhizal associations on reproductive isolation of the orchids appeared to be of minor importance (Jacquemyn et al. (2011a). Girlanda et al. (2011) reported *Tulasnella calospora* mycobionts in the mediterranean meadow orchids *Ophrys fuciflora*, *Anacamptis laxiflora*, *O. purpurea*, and *Serapias vomeracea*. In a comprehensive survey of 16 European and Mediterranean *Orchis* species, Jacquemyn et al. (2011b) found dominating *Tulasnella* OMs from the Netherlands, Belgium, France, Portugal, Italy, Cyprus, and Israel. For the persistence and rarity of *A. morio* and *Dactylorhiza fuchsii* in Belgian habitats, Bailarote et al. (2012) suggested that fungal diversity with dominating *Tulasnella* are not necessarily related. Studies conducted in the Gargano National Park in southern Italy by Jacquemyn et al. (2014, 2015a) comprised *Anacamptis pyramidalis*, *A. (Orchis) morio*, *A. papilionacea*, *Neotinea maculata*, *N. ustulata*, *Orchis anthropophora*, *O. italica*, *O. pauciflora*, *O. provincialis*, *O. quadripunctata*, *Ophrys apulica*, *Op. biscutella*, *Op. bombyliflora*, *Op. sphegodes*, *Op. sicula*, *Op. tenthredinifera*, *Serapias bergonii*, *S. cordigera*, *S. lingua*, and *S. vomeracea*. The mycobionts of coexisting orchid species had distinct mycorrhizal communities and were predominantly recruited by *Tulasnella* and *Rhizoctonia* ("Ceratobasidiaceae"). A broad

spectrum of mycobionts, including *Tulasnella*, were found to be associated with *O. tridentata* in Central Italy by Pecoraro et al. (2012). The temporal variation in mycorrhizal diversity of *A. morio* from North Italian meadows was analysed by Ercole et al. (2014). The fungi, manually isolated from pelotons, were common *Tulasnella* in autumn and winter, the pezizacean clade very frequent in spring, and *Ceratobasidium* more frequent in summer. In 16 Mediterranean orchid species of the genera *Anacamptis*, *Ophrys*, *Orchis*, and *Serapias*, Pellegrino et al. (2014) found 18 operational taxonomic units (OTUs) of *Tulasnella* and “Ceratobasidiaceae”. Mycobiont analyses of the mediterranean *Op. bertolonii* revealed *Tulasnella* as the dominant fungal partner (Pecoraro et al. 2015). The fine-scale spatial distribution of OM fungi, including *Tulasnella*, in soils of host-rich mediterranean grasslands of northern Italy was screened by Voyron et al. (2016) and found to be extremely sporadic. The spatially tight dependency of tulasnelloid associates of orchids was clearly documented in populations of *A. morio*, *Gymnadenia conopsea*, and *O. mascula* in Southern Belgium (Waud et al. 2016a). Also in Belgium, the majority of mycobionts of *O. mascula* and *O. purpurea* appeared to be *Tulasnella* (Waud et al. 2016b).

Bidartondo et al. (2004) reported *Tulasnella* as mycobiont of *Platanthera chlorantha* from the Bavarian Frankenalb. In a study on the evolution of endemic Azorean orchids, also ORMs were analyzed, and *T. calospora* and *Tulasnella* spp. were found in *Platanthera* species (Bateman et al. 2014). Kohout et al. (2013) studied the fungal communities associated with *Pseudorchis albida* in the Šumava National Park, Czech Republic. The mycobionts of the orchid were four unnamed *Tulasnella* strains. In protocorms of *P. albida*, also from this country, and in *Serapias parviflora* from Sardinia, *Tulasnella* spp. were detected by Stöckel et al. (2014). Protocorms of the mediterranean orchid *Serapias vomeracea* were colonized by *Tulasnella calospora* in an experimental study of Balestrini et al. (2014).

12.6.2 Temperate Asia

Whole rDNA analyses of roots and leaves of *Bletilla ochracea* from a mountain near Guiyang in Guizhou Province, China, provided a high number of fungal OTUs, dominated by ascomycetes (Tao et al. 2008). In addition, also *Epulorhiza* sp. could be identified. Eom (2012) isolated *T. calospora*, *T. irregularis*, and *Tulasnella* sp. from terrestrial Korean *Bletilla striata*, *Calanthe discolor*, *Cymbidium goeringii*, and *Pogonia minor*. Eom (2015) identified *T. calospora* and *Tulasnella* sp. in *Cephalanthera falcata*, *C. longibracteata*, *Platanthera chlorantha*, and *P. mandarinorum* in Korea. Jiang et al. (2011) isolated *Tulasnella* spp. from *Changnienia amoena*, an orchid distributed in various provinces of Central China.

Lee and You (2000) identified *Tulasnella repens* in the native Korean *Cymbidium goeringii*. Korean species of *Cymbidium* were successfully inoculated with *Tulasnella repens* by Lee et al. (2001). In a comparative study, Ogura-Tsujita et al. (2012) tried to find a correlation in mycobiont's association in *Cymbidium* during

the evolution of autotrophy to mycoheterotrophy. *Tulasnella* dominated in the autotrophic *C. dayanum*, were less frequent in mixotrophic *C. goeringii* and *C. lancifolium* and absent in mycoheterotrophic *C. macrorhizon* and *C. aberrans*. In five Korean terrestrial orchids, *C. goeringii*, *Spiranthes sinensis*, *Calanthe discolor*, *Bletilla striata*, and *Pogonia minor*, Youm et al. (2012) identified *Tulasnella calospora*, *T. irregularis*, *T. sp.*, and *Sebacina vermifera*.

The mycobiont of the threatened orchid *Cypripedium macranthos* var. *rebunense*, from Rebun Island northwest of Hokkaido was identified as *Tulasnella* (Shimura et al. 2009). Mycobionts of six endangered slipper orchid species from Southwestern China, *Paphiopedilum micranthum*, *P. armeniacum*, *P. dianthum*, *Cypripedium flavum*, *C. guttatum*, and *C. tibeticum*, were identified as *Tulasnella* spp. by Yuan et al. (2010). Hayakawa et al. (1999) isolated *Tulasnella deliquescens* from naturally occurring protocorms, seedlings, and adult Japanese *Dactylorhiza aristata*. Most of the OM fungi in *Dendrobium fimbriatum* and *D. officinale* from Guangxi were identified as members of the Tulasnellaceae by Xing et al. (2013). Tan et al. (2014) used their *Tulasnella* isolates of *D. officinale* from Yunnan to carry out seed germination experiments. They found different interactive capacities in two fungal strains.

As mycobionts of *Epipactis thunbergii*, Eom and Kim (2013) identified i. a. *T. calospora* and *Tulasnella* sp. *E. thunbergii* and *Habenaria radiata* were colonized by the ecologically adapted, associated with various mycobionts in manmade wetlands in the Hiroshima Prefecture, Japan (Cowden and Shefferson 2013). While a diverse suite of fungal symbionts was found in *H. radiata*, *E. palustris* was nearly exclusively inhabited by *Tulasnella* spp. Based on the morphology and cultures of isolates with anastomoses, Uetaka et al. (1999) identified *Epulorhiza repens* in the Japanese terrestrial orchids *Gymnadenia camtschatica*, *Platanthera tipuloides* and *Pogonia japonica*. In nine species of the genus *Holcoglossum* from Yunnan and Guangxi, *T. calospora* and the anamorphic tulasnelloid *Epulorhiza* were found (Tan et al. 2012). From different populations of *Liparis japonica* in Northeast China, Ding et al. (2014) identified fungi of the *T. calospora* species group. In situ and in vitro specificity between mycobionts and *Spiranthes sinensis* var. *amoena* was analyzed by Masuhara and Katsuya (1994). The germination was mainly induced by *Tulasnella* (as *Rhizoctonia repens*).

12.6.3 Subtropical and Tropical Asia

Apostasioideae are considered the basal group of the Orchidaceae (Chase et al. 2003). Five studied *Apostasia* species had *Botryobasidium* and *Ceratobasidium* mycobionts, and the related *Neuwiedia veratrifolia* was associated with *Ceratobasidium* and *Tulasnella* (Yukawa et al. 2009). Most of the mycobiont isolates of *Neuwiedia veratrifolia*, collected in Borneo, could be assigned to *Tulasnella* by Kristiansen et al. (2004).

The mycobiont of the “Chinese King Medicine Orchid”, *Anoectochilus roxburghii*, was identified as *Epulorhiza* sp. and was successfully used in co-culture experiments to improve the growth of the host plant (Li et al. 2012). Dan et al. (2012) found that eight of 42 OM fungal strains tested including three *Epulorhiza* spp. enhanced the growth of the host plantlets. The endophyte promoting the growth and contents of kinsenosides and flavonoids of *A. formosanus* was identified as *Epulorhiza* sp. by Zhang et al. (2013). Likewise, in seven localities of Taiwan, Jiang et al. (2015) isolated mycobionts of this medicinally used orchid. No increase in orchid seed germination was found when *Tulasnella* strains were applied that clustered in clade III of their study. Mycobionts of the Chinese medicinal orchid *Dendrobium officinale* were identified as *Epulorhiza* sp. and inoculation of the fungus resulted in promoted seedling growth (Jin et al. 2009). For symbiotic seed germination of *D. draconis* and *Grammatophyllum speciosum*, native orchids of Thailand, the anamorph of *Tulasnella calospora* proved to be most effective to stimulate protocorm development (Nontachaiyapoom et al. 2011). In contrast, Salifah et al. (2011) found that seed germination rates in this orchid were best when co-cultured with *Fusarium* sp. Five *Tulasnella* isolates of four *Dendrobium* species from Chiang Rai Province of Thailand showed different promoting effects on seed germination (Swangmaneecharern et al. 2012). The in situ seed baiting of the epiphytic *D. aphyllum* from the Xishuangbanna tropical Botanical Garden in South Yunnan, studied by Zi et al. (2014), revealed *Tulasnella* spp. as mycobionts. In contrast, Agustini et al. (2016) isolated *Rhizoctonia*-like fungi from *D. lancifolium* var. *papuanum* and *Calanthe triplicata* from Papua, which was considered of “*Ceratobasidium*” relationship. Khamchatra et al. (2016a) isolated *T. violea* and *Epulorhiza repens* from the Thai epiphytic *D. friedricksianum*. Under in vitro culture conditions, Wang et al. (2016) found promoted *D. catenatum* seedling growth from Hainan with dual inoculation of *Epulorhiza* and *Enterobacter* or *Herbaspirillum* bacteria.

Commercially grown Thai species and hybrids of *Cymbidium*, *Dendrobium*, and *Paphiopedilum* were used by Nontachaiyapoom et al. (2010) for isolation of mycobionts. They identified *Tulasnella* anamorphs. *Tulasnella* spp., isolated from wild and horticulturally grown *Cymbidium* spp. in SW-China, were used to test growth differences in co-cultures with *C. hybridum*, an important pot ornamental orchid (Zhao et al. 2014a). In addition, deep sequencing-based comparative transcriptional profiles of these photo- and mycobionts were carried out (Zhao et al. 2014b). The positive experiments were indicative for application in *Cymbidium*'s commercial cultivation. Mycobionts of *C. faberi*, *C. goeringii*, and *C. goeringii* var. *longibracteatum*, also from SW-China, included *Tulasnella* spp. (Huang and Zhang 2015). Yu et al. (2015) isolated and identified endophytes, and *Tulasnella* ORMs from roots of *C. goeringii* and *C. faberi*.

The germination and development of the terrestrial *Arundina chinensis*, *Spathoglottis pubescens*, and *Spiranthes hongkongensis* from various locations of Hong Kong were found to be strongly stimulated by *Epulorhiza* isolates (Shan et al. 2002). Isolated *E. repens* from the Thai terrestrial *S. plicata* enhanced seed germination in vitro considerably (Athipunyakom et al. 2004a). From this orchid species

of Papua, Sufaati et al. (2012) reported *Tulasnella* mycobionts. In a study on mycorrhizal associations and root morphology of 31 terrestrial and epiphytic orchids species of the Western Ghats, southern India, also *S. spicata* was included (Sathiyadash et al. 2012). Regarding the mycobionts, there is only the single remark that the orchids “had moniliform structures resembling those of *Tulasnella calospora* (*Epulorhiza repens*) in the cortical and root hair cells”.

In the endangered epiphytic Thai slipper orchid *Paphiopedilum villosum*, *Tulasnella* sp. could be identified as mycobiont (Khamchatra et al. 2016b). A highly compatible *Epulorhiza* strain was used to demonstrate promotion of seed germination and protocorm development in *Papilionanthe teres* from Xishuangbanna, South China (Zhou and Gao 2016). In seed germination and seedling development of the Thai terrestrial orchid *Pecteilis susanna*, the incubation of *Tulasnella* enhanced growth considerably (Chutima et al. 2011). Isolates from the tropical orchids *Arachnis* sp., *Arundina graminifolia*, *Dendrobium crumenatum*, *Diplocaulobium enosmum*, *Oncidium* hybr., *Vanda* hybr., and *Spathoglottis plicata* in Singapore comprised both *Sebacina* and *Tulasnella* mycobionts (Ma et al. 2003). Mycobionts isolated from pelotons of *Calanthe rubens*, *Ca. rosea*, *Cymbidium sinense*, *Cy. tracyanum*, *Goodyera procera*, *Ludisia discolor*, *Paphiopedilum concolor*, *P. exul*, *P. godefroyae*, *P. niveum* and *P. villosum* were identified as *Epulorhiza calendulina*, *E. repens*, and *Tulasnella* sp. among multiple mycobionts (Athipunyakom et al. 2004b). Suryantini et al. (2015) reported on *Epulorhiza* and *Tulasnella* spp. associated with epiphytic *Ca. vestita* and *Bulbophyllum beccarii* from West Kalimantan. Seed germination of the epiphytic, therapeutically valuable orchid *Coelogyne nervosa*, endemic to south India, was higher when inoculated with *Epulorhiza* sp. (Sathiyadash et al. 2014).

12.6.4 North America

Rhizoctonia anaticula was described by Currah (in Currah et al. 1987), based on five isolates of native Alberta orchids, and later transferred into the tulasnelloid anamorphic genus *Epulorhiza* (Currah et al. 1990). The same mycobiont was also isolated from *Calypso bulbosa* and *Platanthera obtusata* sampled in various locations of Alberta (Currah and Sherburne 1992; Currah et al. 1988). The TEM micrographs indicate tulasnelloid fungi (Currah and Sherburne 1992). Smreciu and Currah (1989) recovered potentially high percentage of tulasnelloid mycobionts in symbiotic and asymbiotic germination of seeds of north temperate terrestrial orchids *Amerorchis rotundifolia*, *Ca. bulbosa*, *Coeloglossum viride*, *Corallorhiza maculata*, *Co. trifida*, *Cypripedium calceolus*, *Goodyera repens*, *Platanthera hyperborea*, *P. obtusata*, and *P. orbiculata*, four of them also occurring in Europe. So far, it remains unsettled what *Ceratobasidium cereale*, a mycobiont of *G. repens*, is (Peterson and Currah 1990). In germination experiments of *P. hyperborea* seeds, mycobionts of uncertain taxonomic position, like *Rhizoctonia cerealis* or *Ceratohiza goodyerae-repentis*, were used (Richardson et al. 1992).

The orchid–mycobiont association was studied in detail in *Goodyera repens*, a terrestrial orchid of the eastern United States (McCormick et al. 2006). It was found that protocorms and adult orchids were able to switch with closely related *Tulasnella* fungi. In germination tests of seeds of *Goodyera discolor*, *Liparis liliifolia* and *Tipularia discolor*, McCormick et al. (2012) used fungal strains isolated from adult orchids and found that *Tulasnella* was involved in all cases.

Shefferson et al. (2005) detected *Tulasnella* spp. in root samples of *Cypripedium californicum*, *C. fasciculatum* and *C. montanum* in California; *C. candidum* and *C. parviflorum* in Illinois and Kentucky, *C. guttatum* in Alaska. Whitridge and Southworth (2005) reported Tulasnellaceae associated with *Cypripedium fasciculatum*, and with *Piperia* sp. One of the rarest North American terrestrial orchids, *Piperia yadonii*, showed non-specific ORMs, including Tulasnellaceae (Pandey et al. 2013). In *Encyclia tampensis* of South Florida, Zettler et al. (2013), reported *T. irregularis* as mycobiont and essential fungal partner during seed germination. The symbiotic germination of *Spiranthes lacera*, with a naturally occurring endophyte, *Ceratorhiza* cf. *goodyerae-repentis*, and with *Epulorhiza repens* was tested by Zelmer and Currah (1997). The orchid occurs in the eastern, northern and central parts of North America. The symbiotic germination of *S. brevibras* showed *Epulorhiza* mycobionts, and the reintroduction of the endangered orchid, native to Florida, was discussed by Stewart et al. (2003).

In an integrated approach to *Rhizoctonia* taxonomy, Mordue et al. (1989) succeeded in taxonomically separating orchid isolates, i.e. tulasnelloid mycobionts from other *Rhizoctonia*-like fungi. A key and notes for the genera of fungi, mycorrhizal with orchids, and a new species in the genus *Epulorhiza*, was provided by Currah and Zelmer (1992). *Ceratorhiza pernecatena* and *Epulorhiza calendulina* were described as mycorrhizal fungi of terrestrial orchids in the Canadian prairies by Zelmer and Currah (1995), tulasnelloid mycobionts at least in one case. *Epulorhiza inquilina* was proposed for the mycobiont of the mature orchids *Platanthera clavellata*, *P. cristata* and *P. integrilabia* in Canada (Currah et al. 1997). For the propagation of the auto-pollinated terrestrial *P. clavellata* in the southern Appalachians, *Epulorhiza* spp. strains were applied in vitro by Zettler and Hofer (1998). In *P. praeclara* of midwestern prairies, *Epulorhiza* and *Ceratorhiza* were found and used in symbiotic seed germination and coinoculations by Sharma et al. (2003a, b). Also in the endangered Hawaiian endemic *Platanthera leucophaea*, *Epulorhiza* was found as mycobiont (Zettler et al. 2005).

Seeds of the endangered epiphytic orchid *Epidendrum nocturnum* from Florida were germinated in vitro with *Epulorhiza repens* (Massey and Zettler 2007; Zettler et al. 2007). Mycorrhized seedlings could successfully be reintroduced in the Florida Panther National Wildlife Refuge. Symbiotic seed germinations of three semi-aquatic orchids, *Habenaria macroceratitis*, *H. quiqueseta*, and *H. repens* from Florida had *Epulorhiza* mycobionts (Stewart and Zettler 2002). Later, in *H. macroceratitis*, Stewart and Kane (2006) isolated six *Epulorhiza* strains. *Epulorhiza* sp. was present in seed germination of *H. repens* in situ beyond its range in southern North America (Keel et al. 2011).

12.6.5 Central and South America

Unfortunately, in their study on basidiomycetous endophytes from the roots of epiphytic orchids in La Selva, Costa Rica, Richardson et al. (1993) use the generic names *Moniliopsis* and *Ceratorhiza* for the isolates. Though it is most likely that *Tulasnella* is included in these fungi, verification is impossible. Otero et al. (2002) isolated *Rhizoctonia*-like fungi inclusive of *Tulasnella* from orchids in Puerto Rico. They included the epiphytic species *Campylocentrum fasciola*, *C. filiforme*, *Ionopsis satyrioides*, *I. utricularioides*, *Psychilis monensis*, *Tolumnia variegata*, and the terrestrial *Erythrodes plantaginea*, *Oeceoclades maculata*, and *Oncidium altissimum*. In Brazil, *Epulorhiza epiphytica* was isolated from mycorrhizal roots of epiphytic orchids and described as a new tulasnelloid anamorph by Pereira et al. (2003), and additional ORMs from neotropical orchids were characterized morphologically and molecularly by Pereira et al. (2005b), and for Laeliinae by Almeida et al. (2007).

Kottke et al. (2008) used sequence data of *Tulasnella* and other mycobionts to interpret fungal networks between diverse photobionts, including epiphytic orchids and Aneuraceae. Mosquera-Espinosa et al. (2010) studied 12 fungal isolates of eight Colombian orchids and reported *Ceratobasidium* spp. as mycobionts. However, a proper taxonomic identification was not achieved. Mycorrhizal networks with prominent *Tulasnella* OM mycobionts were considered to promote and stabilize the neotropical mountain rain forest (Kottke et al. 2013). Cruz et al. (2014) analyzed the variability of micromorphological features of basidiomata and the genomic polymorphism of *Tulasnella* ORMs in South Ecuadorian orchid species of the genera *Elleanthus*, *Maxillaria*, *Pleurothallis*, *Prostecchia*, and *Stelis*. From five terrestrial orchids of Córdoba, Argentina, *Aa achalensis*, *Cyclopogon elatus*, *Habenaria hexaptera*, *Pelexia bonariensis*, and *Sacoila australis*, Fernández Di Pardo et al. (2015) isolated various mycobionts, including *Epulorhiza*. Suárez and Kottke (2016) summarized main mycobionts, including *Tulasnella*, and their specificities in neotropical orchids of South Ecuadorian rain forests. In an Andean cloud forest of South Ecuador, Suárez et al. (2006) found that diverse tulasnelloid fungi form mycorrhizae with epiphytic *Pleurothallis lilijae*, *Stelis concinna*, *S. hallii*, and *S. superbiens*. A study of Suárez et al. (2016) in Ecuador revealed that *Teagueia* spp. were associated with members of Tulasnellaceae, corresponding to four OTUs. All detected mycobionts had a wide geographical distribution.

Experiments for a symbiotic propagation to reintroduce endangered Mexican terrestrial *Bletia urbana*, *B. campanulata*, and *Dichromanthus aurantiacus* were carried out by Ortega-Larrocea and Rangel-Villafranco (2007), applying anamorphic *Tulasnella* strains. Ovando et al. (2005) isolated and screened endophytic fungi from the roots of the epiphytic orchids *Brassavola nodosa*, *Cattleya skinneri*, and *C. aurantiaca* from Tuzantán, South Mexico. The isolated strains were assigned to 11 fungal genera. Eight strains, used for germination experiments, did not show any promoting effects. However, three strains, including *Epulorhiza*, provided mycorrhizal characteristics in *C. aurantiaca*. A new tulasnelloid anamorph, *Epulorhiza*

amonilioides, lacking monilioid hyphae in pure culture, was isolated from *Brassavola* and *Encyclia* species and described by Almeida et al. (2014) from Bahia, Brazil. When analyzing three sympatric epiphytic Cymbidieae, *Cyrtochilum flexuosum*, *C. myanthum*, and *Maxillaria calantha* from two sites of South Ecuadorian mountain rain forests, Cevallos et al. (2016) concluded that these orchids have site-adjusted OM communities with keystone mycobionts, including *Tulasnella*. In testing seed germination and protocorm development of *Cyrtopodium glutiniferum* from Brazil, Pereira et al. (2015) found promotion by mycorrhizal fungi of the tulasnelloid anamorphs *Epulorhiza* spp. In roots of four *Vanilla* species from Puerto Rico, Costa Rica and Cuba, Porras-Alfaro and Bayman (2007) found mycobionts of *Ceratobasidium*, *Thanatephorus* and *Tulasnella*.

Epulorhiza spp. was isolated from various Brazilian *Epidendrum* species (Pereira 2009, Pereira et al. 2009, 2011a, b, 2014a). From the epiphytic *E. stamfordianum*, *Erycina crista-galli*, and *Stelis quadrifida* from Southeast Chiapas, Mexico, *Ceratorhiza* and *Epulorhiza* mycobionts were reported by Cruz Blasí (2007). Two different *Tulasnella* species were found to be associated with South Ecuadorian *E. rhopalosteles*, an orchid preferably growing on dead trees (Riofrío et al. 2013). Populations of *E. firmum* in Costa Rica had highly diverse and spatially heterogeneous mycobionts, including six *Tulasnella* strains (Kartzinel et al. 2013). The mycobionts of *E. secundum*, a widespread Brazilian orchid, were identified as *Tulasnella* spp. by Pereira et al. (2014a) and as *T. calospora* by Nogueira et al. (2014). In vitro seed germination and protocorm development of Brazilian *Oncidium flexuosum* was studied with mycobionts of *Epulorhiza* and *Ceratorhiza*, earlier isolated from this orchid (Pereira et al. 2005a, c), and Da Silva Coelho et al. (2010) reported regeneration and production of the fungal protoplasts.

Epulorhiza epiphytica was isolated from *Polystachya concreta* and the African *Oeceoclades maculata*, naturalized in the Neotropics, by Pereira et al. (2005b). Nine unnamed morphotypes of fungi, associated with *O. maculata*, were isolated from the understory of Avocado in Brazil by Teixeira et al. (2015).

In the mycorrhizal association of the terrestrial Chilean orchid *Bipinnula fimbriata* also tulasnelloid ORMs were present (Steinfort et al. 2010). Mujica et al. (2016) found that mycorrhizal diversity, including *Tulasnella*, decreased in habitats of *B. fimbriata* and *B. plumosa* with higher N, but increased with P availability in *B. fimbriata*. Morphological and molecular characterization confirmed that Chilean *Chloraea collicensis* and *C. gaviu* mycorrhizal partners belong to *Tulasnella* (Pereira et al. 2014b). In contrast, Atala et al. (2015) reported mycobionts with possible *Thanatephorus* teleomorphs from the critically endangered Chilean *C. cuneata*. However, the data presented cannot exclude tulasnelloid associates. In a study by Herrera et al. (2016), in six *Chloraea* species and *Bipinnula fimbriata* from Chilean Coastal Range and Andes. *Tulasnella* spp. were found as dominating mycobionts. Fracchia et al. (2014) found promoted see germination through tulasnelloid and *Ceratobasidium*-like fungi in *Gavilea australis*, an endangered terrestrial orchid from south Patagonia.

12.6.6 Africa

Martos et al. (2012) identified a bipartite network including 73 orchid species and 95 taxonomic units of mycorrhizal fungi across the natural habitats of Reunion Island. 58 tulasnellaceous OTUs were found in 73 orchid species, thus representing the most frequent OM mycobionts. In their study on the evolution of endemic Azorean orchids, Bateman et al. (2014) reported also the mycorrhizal association of *Tulasnella* aff. *Calospora* with *Platanthera algeriensis* in Morocco. Most of the OM fungi of the Itremo region in the Central Highlands of Madagascar were identified as *Tulasnella* (Yokoya et al. 2015). The symbiotic seedling development of the terrestrial *Cynorkis purpurea*, also from the Itremo area, has been tested experimentally by Rafter et al. (2016). Though epiphyte-derived *Sebacina* cultures had the strongest influence, also *Tulasnella* appeared as an advantageous mycobiont. *Disa bracteata* of South Africa was associated with *Tulasnella* spp. in West and South Australia as in its country of origin (Bonnardeaux et al. 2007). In an attempt to elucidate the impact of above- and belowground mutualisms in South African orchid diversification, an irregular pattern of fungal associates, including 35, unspecified *Tulasnella* individuals, were detected (Waterman et al. 2011). The authors concluded that “shifts in fungal partner are important for coexistence but not for speciation” of the host plants.

12.6.7 Australia

When Warcup and Talbot (1967) succeeded to isolate and cultivate OM fungi from terrestrial Australian orchids, and finally obtained perfect states of Rhizoctonias, a new era of experimental mycology and especially of studies in symbiotic systems began. *Tulasnella calospora* was found to be the perfect state of three cultures considered to be *Rhizoctonia repens*. Isolates were obtained from South Australia (*Acianthus exsertus*, *Caladenia reticulata*, *Cymbidium canaliculatum*, *Dendrobium* sp., *Diuris longifolia*, *D. maculata*, and *Thelymitra antennifera*). *Tulasnella asymmetrica* was described as a new species and as mycobiont of *Thelymitra luteocilium* from the Australian Mt. Lofty Range. In a second contribution of the authors (Warcup and Talbot 1971), the description of *Tulasnella asymmetrica* was emended and further orchid hosts were reported from the Mt. Lofty Range: *Thelymitra aristata* (also Cape Jervis), *T. grandiflora*, and *T. pauciflora*. Additional hosts were *Th. epipactoides* (Eyre Peninsula), and *Dendrobium tetragonum* from North Queensland. The basidial stage of the morphotype of *T. allantospora* with clamps was obtained from Mt. Lofty isolates of *Corybas dilatatus*, and basidiocarp samples without clamps were collected on fallen *Eucalyptus* wood in the same locality. The perfect stage of *T. violea* developed from an isolate obtained from *Th. aristata*, collected in Uley, Eyre Peninsula. *Tulasnella cruciata* was introduced as new to science, isolated from the Mt. Lofty Range orchids *Acianthus caudatus* and *Th. pauciflora*, while the strain of *Th. fusco-lutea* originated

from Pomonal, Victoria. In the third joint effort of Warcup and Talbot (1980) to obtain perfect states of OM mycobionts they succeeded with *T. irregularis* sp. nov., isolated from *Dendrobium dicuphum*, sampled near Darwin, Northern Territory. In studying the specificity of ORMs in Australian terrestrial orchids, Warcup (1971) reported that *Th. aristata* is at least associated with three species of *Tulasnella*. In the “Orchids of South Australia” (Bates and Weber 1990), *T. calospora* is listed as mycobiont in orchid species of the genera *Acianthus*, *Diuris*, *Orthoceras*, and *Thelymitra*. For the latter one and *Acianthus*, also *T. cruciata* is mentioned. The symbiotic germination of some Australian terrestrial orchids was analyzed by Warcup (1973) who reported that various isolates of *T. calospora* differed markedly in the efficiency with which they stimulated germination of the *Diuris* and *Thelymitra* photobionts. A close association of this mycobiont with *Diuris* and *Orthoceras* orchids was confirmed by Warcup (1981). The mycorrhizal specificity of *D. fragrantissima* with *Tulasnella* spp. and persistence in a reintroduced population west of Melbourne was studied by Smith et al. (2007, 2010). In *D. magnifica* and *Prasophyllum giganteum*, *T. calospora* was found, and in *Pyrorchis nigricans* isolates *T. danica* were identified (Bonnardeaux et al. 2007).

A narrow group of monophyletic *Tulasnella* symbiont lineages is associated with multiple species of *Chiloglottis* in New South Wales and the Australian Capital Territory (Roche et al. 2010). For *Tulasnella* OM species delimitation in the Australian orchid genera *Chiloglottis*, *Drakaea*, *Paracaleana* and *Arthrochilus*, Linde et al. (2013) used six nuclear loci, two mitochondrial loci, the photo- and mycobiont association and sampling locations in an integrated approach. They found that the *Chiloglottis* isolates belong to one species, and those from *Drakaea* and *Paracaleana* to a sister taxon, a result in accordance with previous ITS analyses. Boddington and Dearnaley (2009) reported a putative mycorrhizal *Tulasnella*-like fungus in the tropical epiphytic *Dendrobium speciosum* of Queensland. In studies of *Drakaea* species in Southwest Australia, Phillips et al. (2011, 2014) found no evidence that *Tulasnella* specificity contributed to the rarity of the orchids.

According to Brundrett (2007), most West Australian orchids studied have highly specific mycorrhizal associations with fungi in the *Rhizoctonia* alliance, most likely including *Tulasnella* spp. The nutrient-acquisition patterns of ORMs, inclusive of *Tulasnella*, appear to explain the diversification in terrestrial orchids in this biodiversity hotspot (Nurfadilah et al. 2013).

Milligan and Williams (1988) obtained 27 tentatively identified *Tulasnella calospora* isolates from *Microtis* spp. at seven sites in the Sydney region. The specificity of associations between *M. parviflora* and *Epulorhiza* spp. was studied by Perkins et al. (1995). The compatibility webs of brief encounters, lasting relationships and alien invasions of West Australian terrestrial orchids were studied by Bonnardeaux et al. (2007), documenting that *M. media*, together with the invasive *Disa bracteata*, had the most ORMs. Mycorrhizal preference apparently promotes habitat invasion of *M. media* in Western Australia (De Long et al. 2013). When studying the effects of endophytic fungi on New Zealand terrestrial *M. unifolia*, *Spiranthes novae-zelandiae*, and *Thelymitra longifolia*, Frericks

(2014) obtained *Tulasnella calospora* isolations and compared them with strains of various geographical origins.

The rare subterranean, achlorophyllous orchid *Rhizanthella gardneri* from western Australia lives in a more than triple association with autotrophic and heterotrophic partners in which, apparently, two *Tulasnella* species are involved (Warcup 1985). In a taxonomic study and an experimental approach to grow *Rhizanthella gardneri* together with *Melaleuca scalena* (Myrtaceae), Bougoure et al. (2009a, b) used as mycobiont an unidentified, so-called “*Ceratobasidium*” with the positive result that 5% of carbon fed to *Melaleuca* as $^{13}\text{CO}_2$ was transferred to *R. gardneri*. Further studies are needed to clarify the taxonomy and whether diverse mycobionts are involved in this association.

12.7 Conclusions

Our literature search for *Tulasnella* on a global scale confirmed that distribution patterns are biased by sampling. Nevertheless, there is unequivocal documentation that *Tulasnella* as a group and certain morphological species have global distribution. Furthermore, it appears obvious that the world-wide distribution of orchids may reflect a similar occurrence of their mycobionts, for which *Tulasnella* species play a crucial role. The same may be true for *Tulasnella* associates of certain liverworts. In addition, lignicolous basidiomata of *Tulasnella* are reported from collecting areas of mycologists, interested in corticioid fungi. Apart from these restrictions, a more adequate interpretation of *Tulasnella*'s biogeography is the distribution pattern of suited habitats which appear to occur in a nearly world-wide range.

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