

# Chapter 2

## Nomenclatural History and Genealogies of Desert Truffles

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### 2.1 Introduction

The term “desert truffle” is neither a phylogenetic nor a taxonomic term, and as those fungi have played an important role in the life of the native people of deserts, they have had from ancient times—and still do—a common knowledge of truffles (see Chap. 15 by Shavit as well as other chapters in this volume). We are unaware of any definition of a truffle, especially above the species rank, for which desert habitat was used as a taxonomic character.

To discuss the phylogenetic history and the genealogies of desert truffles, we first need to define what fungi are considered to be desert truffles. Although this whole book focuses on these fungi, and generally those who study them understand what they are, it is not easy to state an operative definition. First we confront the problem of how to define a truffle. A wide definition considers all fungi with hypogeous or partly hypogeous, macroscopic sporocarps as truffles. Using a narrow definition, we could consider only hypogeous ascomycetes as truffles once belonging to the order Tuberales (Læsøe and Hansen 2007). Sometimes in everyday or commercial contexts only fungi belonging to the genus *Tuber* are considered as truffles.

Second, we must face the definition of a desert, or at least the question of the common features of deserts. Truffles are diverse, especially when defined sensu

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## 2.2 Taxonomy and Nomenclature

### 2.2.1 *Terfezia: The Most Speciated Desert Truffle Genus*

#### 2.2.1.1 The Pre-molecular Era

The genus *Terfezia* (Tul. & Tul.) Tul. & Tul. (Ascomycotina) was raised by Tulasne and Tulasne (1851) from the rank of subsection within the genus *Choiromyces* they had described earlier (Tulasne and Tulasne 1845). They included three species in *Choiromyces* subsection *Terfezia*: *C. leonis* Tul. & C. Tul., *C. leptodermus* Tul. & C. Tul., and *C. olbiensis* Tul. & C. Tul., which they had described in 1844. In 1851 the Tulasne brothers added two more species: *T. berberidiodora* Tul. & C. Tul. and *T. oligosperma* Tul. & C. Tul., both of which were later transferred to other genera. Nevertheless, Moris (1829) was the first to describe a *Terfezia* species (as *Tuber arenarium* Moris) from Sardinia, later recombined as *Terfezia arenaria* (Moris) Trappe. Zobel (1854) erected a new genus, *Tulasneinia*, to accommodate *T. leonis* and *T. olbiensis*.

Late in the nineteenth century colonial officers and botanists exploring Asia and Africa sent truffle specimens bought in local markets or collected in the field to mycologists in Europe, where most species were described and named (Chatin 1891a, b, c, d, e, 1892a, b, c, 1893, 1894a, b, 1895a, b, c, 1896a, b, 1897; Maire 1907; Patouillard 1894a, b, 1899). Many names have proven to be synonyms of earlier described species (Alsheikh 1994). Malençon (1973) described *T. eremita* Malençon from Mauritania and discussed some ecological aspects of *Terfezia* species in North Africa.

The information on early history, taxonomy, ecology, and chemical composition of desert truffles from North Africa, southwest Asia, and southern Europe was summarized in Chatin's (1892a) book "La Truffe" (recent information is summed up in the various chapters of this volume).

Meanwhile, other newly described *Terfezia* species from around the world have been transferred to other genera when data permitted or remain of uncertain status pending further investigation. From Italy Mattiolo (1887) described *Choiromyces terfezioides* Mattir., which Fischer (1897) transferred to *Terfezia* and then to a new genus, *Mattirolomyces* (Fischer 1938). Trappe (1971) subsequently reduced *Mattirolomyces* to a subgenus in *Terfezia* (see below). Ellis (1887) reported *T. leonis* from southern Louisiana; Harkness (1899) later determined this to be a new species, which he named *T. spinosa* Harkn. Spegazzini (1887) described *Tuber argentinum* var. *pampeanum* Speg. from Argentina, but it was found to be synonymous with *Terfezia longii* Gilkey (1947), described from New Mexico. Hennings (1897) described *T. pfeilii* Henn. from southwest Africa, and Heim (1934) described *T. decaryi* R. Heim from Madagascar. Marasas and Trappe (1973) described *T. austroafricana* Trappe & Marasas from southwest Africa and noted that Pole-Evans' (1918) *T. clavervyi* Chatin from the Kalahari Desert was *T. pfeilii*. From Japan, Imai (1933) described *T. gigantea* S. Imai, later also found in the USA

(Gilkey 1947, 1954; Trappe and Sundberg 1977), while Boedijn (1939) described *T. indica* Boedijn from Sumatra as the first collection from Southeast Asia.

Fischer (1897, 1938), Bataille (1921), and Mattiolo (1922) provided keys for the known species in Africa, Asia, and Europe. Gilkey (1947) provided a key for the North American species. Ceruti (1960) presented Latin descriptions and watercolor paintings of most North African and European *Terfezia* species. Alsheikh (1994) monographed *Terfezia* worldwide with keys and descriptions. Note, however, that these treatments preceded phylogenetic analytical techniques, so many include species now placed in other genera.

Fischer (1897) first proposed family status for the Terfeziaceae and included it in the Tuberales. Trappe (1971) emended the family concept and later transferred it to the order Pezizales after abandoning the polyphyletic order Tuberales (Trappe 1979).

#### **2.2.1.2 Molecular Phylogenetic Revisions: Decreasing *Terfezia* Species Richness, Increasing Genetic and Morphological Uniformity**

Trappe was correct considering Tuberales as polyphyletic (see the comprehensive review by Læsøe and Hansen 2007), but some decisions regarding desert truffles have been falsified by later molecular phylogenetic analyses (see below in detail). The “Terfeziaceae” was not supported by molecular phylogenetic analyses; the species are considered as belonging to Pezizaceae (Læsøe and Hansen 2007), but “Terfeziaceae” is still sporadically used as a fungal family. The molecular taxonomic revisions have increased the geographic uniformity of the genus *Terfezia*, only species from the Mediterranean region and the Middle East being proven to belong to the *Terfezia* s.str. Generic assignments of species thought to represent *Terfezia* in North America (Kovács et al. 2008, 2011a), South Africa (Ferdman et al. 2005; Trappe et al. 2010a, b), and Australia (Trappe et al. 2010a, b) had to be revised. Also, the very first molecular phylogenetic analyses (see below) revealed the genus *Mattirolomyces* to be distinct from *Terfezia*. The molecular taxonomic revisions also revealed an intraspecific diversity of *Terfezia* species and diverse species complexes (Díez et al. 2002; Aviram et al. 2004; Ferdman et al. 2009; Sbissi et al. 2011; Kovács et al. 2011b; and see Chap. 3 by Bordallo and Rodríguez).

#### **2.2.2 *Mattirolomyces*: An Expanding Genus Containing Desert Truffles**

*Mattirolomyces* is not a typical desert truffle genus. Our recent revisions of *Terfezia* species and truffles collected in widely separated desert regions have revealed that *Mattirolomyces* is more diverse geographically and taxonomically than thought before, so we present a short history of the genus here. Mattiolo originally described *Choiromyces terfezioides* from Piemonte, Northern Italy (Mattiolo 1887).

Fischer (1938) concluded that the species represented a distinct genus, which he named *Mattirolomyces* for “the Mattirol fungus” with the sole species *M. terfezioides* (Mattir.) E. Fisch. Besides its most frequent habitat of mixed *Robinia pseudoacacia* forests on sandy soils in the Danube-Tiscia interfluvies, it occurs in other habitats such as farm and urban environments, but not deserts or semiarid areas.

Trappe (1971) moved *Mattirolomyces* into *Terfezia* and changed its rank to a subgenus. Later molecular phylogenetic analyses proved *Mattirolomyces* to be a distinct genus (Percudani et al. 1999; Díez et al. 2002; Hansen et al. 2001; Læsøe and Hansen 2007) within the Pezizaceae. Healy (2003) described a second *Mattirolomyces* species, *M. tiffanyae* Healy, from a non-desert habitat in Iowa, but molecular phylogenetic analysis showed it does not belong to *Mattirolomyces* but represents a new genus (*Temperantia*) within Pezizaceae (Kovács et al. 2011a). True desert truffles first appeared in *Mattirolomyces* when hypogeous ascomycetes of the Australian Outback and the Kalahari were revised by use of molecular phylogenetic methods (Trappe et al. 2010a, b). *Mattirolomyces mulpu* Kovács, Trappe & Claridge was described as a new species and *M. austroafricanus* (Marasas & Trappe) Kovács, Trappe & Claridge as a new combination when the generic position of *Terfezia austroafricana* was corrected by phylogenetic analysis. The taxon richness of the genus increased by two more species when North American *Terfezia* species were analyzed (Kovács et al. 2011a). Although *M. mexicanus* Kovács, Trappe & Alsheikh probably has an arid location and *M. spinosus* (Harkn.) Kovács, Trappe & Alsheikh does not, the habitat collection data for either are inadequate, so they cannot be confirmed as desert truffles. *Mattirolomyces* had been a monotypic taxon for decades. Now it includes five species, and we are aware of one more (Kovács et al. unpublished data) from four continents (or five, if we consider the Beijing urban collection of *M. terfezioides* as well) and both Northern and Southern Hemispheres. Considering the habitats of the species, *Mattirolomyces* represents the widest geographic and climatic range of truffle genera that include desert truffles.

### 2.3 How Many Lineages Are Out There? Phylogenies of Desert Truffles Worldwide

The first molecular phylogenetic study mentioning desert truffles was by O'Donnell et al. (1997), a landmark paper on phylogeny of truffles and morels. Partial sequences of the small (18S, SSU) and large (28S, LSU) subunits of the nuclear ribosomal RNA gene (nrDNA) were analyzed. The paper reveals the misplacement of several taxa, shows the traditional concept of Tuberales to be wrong, and proposes that the hypogeous life-form has evolved several times within Pezizales. *Redellomyces donkii* (Malençon) Trappe, Castellano & Malajczuk was included in the analyses, but it is still unclear if *Redellomyces westralensis* (G.W. Beaton & Malajczuk) Trappe, Castellano & Malajczuk should be considered a desert truffle

(see below and Chap. 14 by Claridge et al.). The phylogenetic position of *Picoa* is suggested by O'Donnell et al. (1997): "Preliminary 28S rDNA sequence data from the type species of *Picoa*, *P. juniperi* Vittad. (O'Donnell et al. unpublished data), suggests that it is more closely related to *Otidea* (Pers.) Bonord. than the taxa sampled in this study." The comprehensive review by Læsøe and Hansen (2007) also cited this unpublished information. O'Donnell et al. (1997) were the first to support Trappe's (1979) hypothesis that transitions from epigeous to hypogeous life-forms happened independently within the Pezizales, and those characters are homoplastic.

In 1999 two papers included desert truffles in the phylogenetic analyses. The first desert truffle sequence was analyzed and published in Percudani et al. (1999) and also used by Norman and Egger (1999). Percudani et al. (1999) sequenced the nrDNA SSU of nine hypogeous fungi and the ITS of three of them. The nine species included *Terfezia arenaria* and *Mattirolomyces terfezioides* (as *Terfezia terfezioides*), but only SSU sequences were obtained from those two taxa. They extended their dataset with sequences published by O'Donnell et al. (1997). In these analyses both *M. terfezioides* and *T. arenaria* grouped unambiguously in the Pezizaceae. The result "strongly supports the emendation of Pezizaceae to include the hypogeous genera *Pachyphloeus* and *Terfezia*" (Percudani et al. 1999). *Terfezia arenaria* and *M. terfezioides* had distant positions in the phylogeny, and it was the first molecular analysis supporting the distinct nature of *Mattirolomyces* after its emendation into *Terfezia*. Epigeous taxa were underrepresented and only a few taxa of Pezizaceae were included in the analyses. *Terfezia arenaria* was a sister species of *Cazia flexiascus* Trappe, and their clade got a 92 % ML bootstrap support. The authors discussed in detail the phylogenetic resolution power of the nrDNA SSU sequences and considered the gene as "capable of resolving phylogenetic relationships." Norman and Egger (1999) used the same two SSU sequences, but their study considerably expanded the taxon sampling from Pezizaceae, especially from *Peziza*. Although they analyzed SSU, ITS, and LSU sequences, these two taxa were represented only in the SSU dataset. In the analyses *T. arenaria* also grouped with *Cazia* with high reliability but low bootstrap value. *Mattirolomyces terfezioides* branched into a distant lineage of the phylogeny and grouped with the *Peziza vesiculosa* group with moderate support. Norman and Egger (1999) strengthened the hypothesis that hypogeous life-forms had originated several times within the Pezizales. They also emphasized the problems of the concept of Pezizaceae and the distinct nature of the genus *Mattirolomyces*, stating that "*Terfezia* is paraphyletic, and that morphological similarities between *T. arenaria* and *T. terfezioides* are a result of convergence" (Norman and Egger 1999). The genus *Terfezia* was polyphyletic instead of paraphyletic in their analyses (Norman and Egger 1999).

Hansen and her colleagues (Hansen et al. 2001) published a comprehensive phylogenetic study with a massive taxon sampling of Pezizaceae with a special emphasis on *Peziza*. They focused on phylogenetic relations and reevaluation of morphological characters used in the systematics of the group. In the detailed introduction and overview of the genera they discussed general features of the

taxa and previous molecular phylogenetic results on *Terfezia* and *Tirmania*. They amplified and sequenced a segment containing the D1–D2 loop region of the nrDNA LSU gene. The choice of this segment strongly influenced later studies of desert truffles aiming to analyze a well-established reliable dataset. *Tirmania pinoyi* and *T. nivea* but no *Terfezia* species were involved in their sophisticated phylogenetic analyses. *Tirmania* grouped into “group VI” similarly to *Cazia*; *Cazia flexiascus* was a sister group of *Terfezia arenaria* in previous studies (see above). Hansen et al. (2001) considered *Terfezia arenaria* also belonging to “group VI,” along with various other hypogeous taxa. They discuss the excipular structure of stereothecia of *Cazia*, *Terfezia*, and *Tirmania*. Based on Norman and Egger’s (1996) results, Hansen et al. (2001) considered *Mattirolomyces terfezioides* to be “supported within, or as a sister lineage to, group IV based on nSSU sequences.”

Díez et al. (2002) presented the first molecular phylogenetic examination of intrageneric relations of desert truffles. The nrDNA ITS of 38 specimens of two *Tirmania* and four *Terfezia* spp. plus *Mattirolomyces terfezioides* were studied by use of RFLP; in all, 18 species were sequenced. They also confirmed the separation of *Mattirolomyces terfezioides* from *Terfezia* species. They concluded, “Phylogenetic analyses indicated a close genetic relationship between *Tirmania* and *Terfezia*. They may have arisen from a single evolutionary lineage of pezizalean fungi that developed the hypogeous habit as an adaptation to heat and drought in Mediterranean ecosystems.” However, as noted by Læsøe and Hansen (2007), the limited taxon sampling from Pezizaceae makes both the relationship of the two taxa and the evolutionary hypothesis a bit uncertain. Díez et al. (2002) could not satisfactorily align two *Peziza* ITS sequences, so they excluded those from the analyses; they interpreted this as proof for the monophyly of the *Terfezia/Tirmania* clade. The most important findings of the study concerned host relations and edaphic preferences of *Terfezia* spp. and the prediction of intraspecific genetic variations of *Terfezia* species.

Hansen et al. (2005) revisited their earlier phylogenetic analysis of *Peziza* and the Pezizaceae (Hansen et al. 2001). The new dataset contained 69 species of the Pezizales, and in addition to the nrDNA LSU segment, RNA polymerase II (RPB2) and the  $\beta$ -tubulin gene sequences were sequenced and involved in the analyses. Besides the two *Tirmania* species that were studied previously, three *Terfezia* species (*T. arenaria*, *T. boudieri*, *T. claveryi*) were also included. However, none of the three *Terfezia* spp. were represented by all three loci: from *T. arenaria* only the  $\beta$ -tubulin were analyzed, from *T. boudieri* Chatin the nrDNA LSU and the  $\beta$ -tubulin, and from *T. claveryi* the nrDNA LSU and RPB2 sequences. Fourteen “fine-scale lineages” of the Pezizaceae were identified during the sophisticated phylogenetic analyses of the dataset, and the topology was identical with the previous LSU nrDNA-based results. Nevertheless, the relative branching orders and the relations of the lineages could not be completely resolved. Both *Terfezia* and *Tirmania* nested into the *Peziza depressa-Ruhlandiella* lineage, which gained strong support in the combined analyses of the three loci. *Terfezia* showed close relationship with *Peziza* spp. Their phylogenetic analyses of the Pezizales showed no novelty about the desert truffles (only one *Terfezia* sequence was included in the



dataset). Hansen et al. (2005) hypothesized that “the *P. depressa-Ruhlandiella* lineage could be a mycorrhizal lineage.” Comparing the three loci they found RPB2 as “the most informative single gene region based on resolution and clade support.” However, the LSU sequences were almost as useful and much easier to amplify. This plus the reliable, massive dataset published for the Pezizaceae (Hansen et al. 2001, 2005) and the Pezizales (Hansen and Pfister 2006) made the LSU D1–D2 region a useful locus to study generic positions of desert truffles.

Two new genera, *Kalaharituber* and *Eremiomyces*, were erected when *Terfezia pfeilii* Henn. and *Choiromyces echinulatus* Trappe & Marasas were subjected to molecular taxonomic analysis (Ferdman et al. 2005). The D1–D2 LSU and ITS regions were amplified and analyzed together with sequences of *Terfezia*, *Tirmania*, *Mattirolomyces*, *Tuber*, and *Choiromyces* species, so the sampling focused on hypogeous taxa related to the original generic positions of the species. In spite of the narrow taxon sampling of the lineages, the relative branching order of the lineages unambiguously showed the wrong generic assignation of the two species. *Eremiomyces echinulatus* (Trappe & Marasas) Trappe & Kagan-Zur was distant from *Choiromyces* s. str. and grouped into *Pezizaceae* instead of *Tuberaceae*. *Kalaharituber pfeilii* (Henn.) Trappe & Kagan-Zur separated from *Terfezia* species, but its branching did not reveal any information about its family position, although it was closer to *Pezizaceae* than to *Tuberaceae*. However, the molecular results and the morphological features convinced the authors to erect new genera, and later analyses (Læsøe and Hansen 2007) confirmed that the lineages were distinct even when more representatives of the *Pezizaceae* and *Pezizales* were involved in the phylogenetic datasets.

Læsøe and Hansen (2007) published a comprehensive paper on the former *Tuberales* genera now assigned to the *Pezizales*. The LSU sequences of almost 200 species, 55 hypogeous and 139 epigeous, were analyzed. Several truffle genera containing desert truffles were involved in the phylogenetic analyses: *Terfezia*, *Tirmania*, *Mattirolomyces*, *Kalaharituber*, and *Eremiomyces*. Inclusion of the latter two, both new genera, confirmed their inclusion in the *Pezizaceae*: *Kalaharituber* formed a lineage with *Iodowynnea*, whereas the position of *Eremiomyces* was ambiguous within the family. The others generally nested into the same lineages as in previous analyses of the LSU sequences. Their detailed presentation of the different truffle genera includes *Picoa* and *Carbomyces*. Concerning the phylogenetic position of *Picoa*, Læsøe and Hansen (2007) cite O'Donnell et al. (1997) as close to *Otidea*. *Carbomyces* was also mentioned as receiving ongoing molecular taxonomic study by K. Hansen.

Kovács et al. (2008) removed the Japanese/North American *Terfezia gigantea* S. Imai from both *Terfezia* and the *Pezizaceae* on the basis of molecular phylogenetic results and morphology. Although SSU, ITS, and LSU sequences were gained, only the SSU phylogeny of representatives of five families of the *Pezizales* was presented. They erected the new genus *Imaia* with its single species, *I. gigantea* (S. Imai) Trappe & Kovács. It is not a desert truffle, but results of the revision together with previous molecular phylogenetic results of *Mattirolomyces terfezioides* and *Kalaharituber pfeilii* showed that the genus *Terfezia* sensu lato

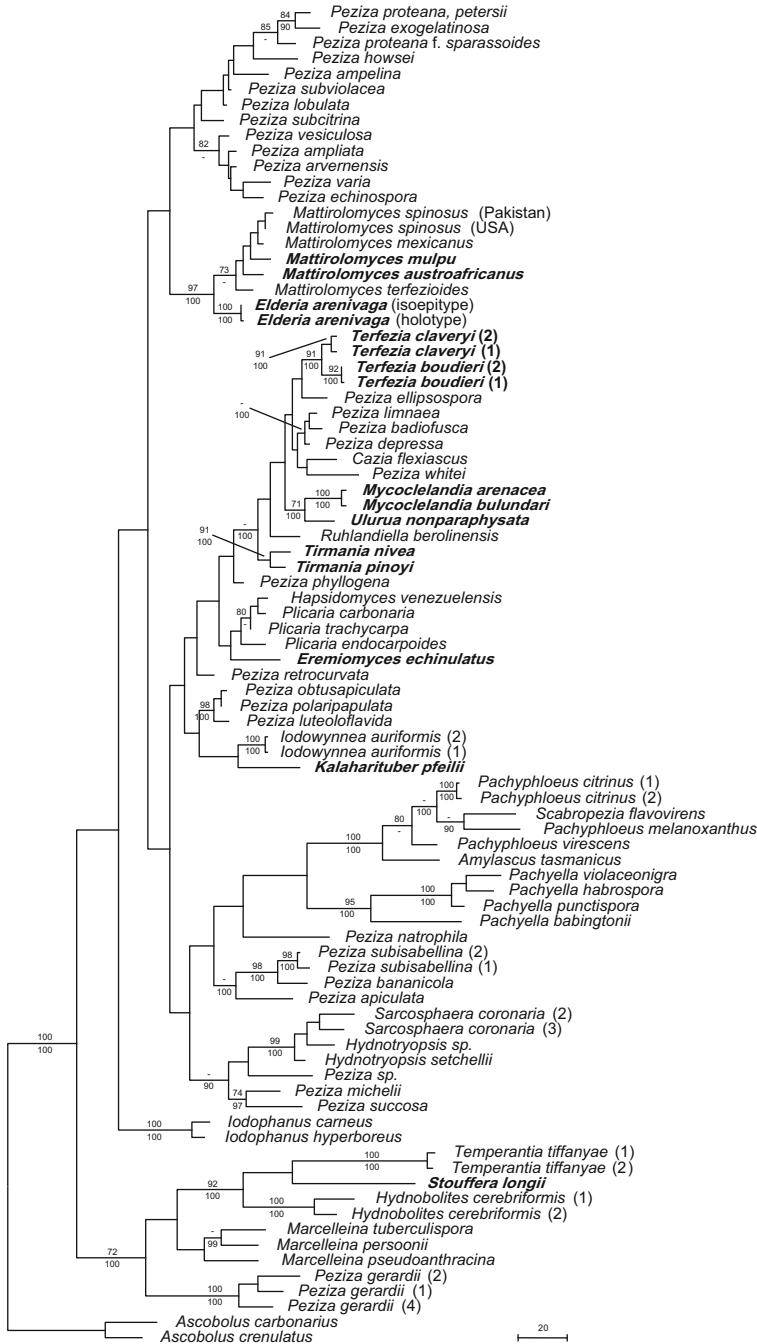


contained numerous, well-known desert truffles, was not monophyletic, and needed revision.

Sbissi et al. (2010) presented phylogenetic results on *Picoa juniperi* Vittad. and *P. lefebvrei* (Pat.) Maire. In addition to a morphological comparison of the two species, they sequenced the ITS and LSU region of 12 specimens, as the sequencing of one LSU failed, two *P. lefebvrei* and nine *P. juniperi* specimens were involved in the final phylogenetic analyses of the LSU and ITS dataset, including sequences from public databases. They stated: “Ribosomal DNA analyses have enabled the genus *Picoa* to be assigned to the Pyronemataceae and to confirm that *Picoa* is closely related to *Geopora* (Tedersoo et al. 2010).” Although the phylogenetic trees presented show only the topology and the supports of the branches/clades, it was clear that *Geopora* is a closer relative of *Picoa* than *Otidea* was. However, the unpublished results of O’Donnell et al. (1997) that *Picoa* is related to *Otidea* were true, considering the taxon sampling in their analysis.

In comparative taxonomy of the desert truffles of the Australian Outback and the Kalahari, six Australian and three Kalahari taxa were analyzed and redescribed: eight of the nine belonged to the Pezizaceae (Trappe et al. 2010a, b). The SSU, ITS, and LSU segments were amplified and sequenced when possible and the partial LSU sequences (see above) used to analyze the phylogenetic position of the taxa within the Pezizaceae. *Mycoclelandia* [represented by *M. arenacea* (Trappe) Trappe & G.W. Beaton and *M. bulundari* (G.W. Beaton) Trappe & G.W. Beaton)] and *Ulurua nonparaphysata* Trappe, Claridge & Kovács (a new genus and species described in the paper) nested into the *P. depressa-Ruhlandiella* lineage sensu (Hansen et al. 2005). *Elderia arenivaga* (Cooke & Massee) McLennan formed a well-supported clade with *Mattirolomyces*, and both branched with the *Peziza* s. str. lineage. It was the first paper evidencing that *Mattirolomyces* is not monotypic. Two desert truffles were found to belong to the genus: *M. mulpu* described as a new species from Australia while *M. austroafricanus* was published as a new combination for *Terfezia austroafricana*. The other desert truffle taxa, which have been analyzed in previous phylogenetic works, branched at the same position as previously on the phylogram of the family. Based on the phylogenetic analyses presented, if only the so-called fine-scale lineages sensu Hansen et al. (2005) of the family are considered, four desert truffle lineages appeared in the phylogeny of the Pezizaceae. The paper deals with *Redellomyces westraliensis* belonging to the Tuberaceae—but the authors emphasized the species “was found in a swale along a streambank.”

When American *Terfezia* species and *Mattirolomyces tiffanyae*, now *Temperantia tiffanyae* (Healy) K. Hansen, Healy & Kovács., were revised (Kovács et al. 2011a), the SSU, ITS, and LSU sequences were obtained, but only the phylogeny calculated from the LSU sequence dataset was presented (Fig. 2.2). All desert truffle taxa mentioned above were involved in the phylogenetic analyses, and their branching was as in previous analyses (see above). Species and collections previously considered as *Terfezia* (*T. spinosa*, “*T. mexicana*,” *T. longii*) were assigned to different genera. *Mattirolomyces spinosus* and *M. mexicanus* expanded the genus *Mattirolomyces*, the former being represented by one collection that



**Fig. 2.2** One of 375 most parsimonious phylogenetic trees inferred from a dataset of partial LSU sequences showing positions desert truffle genera within the Pezizaceae. *Ascobolus crenulatus* served as outgroup. Desert truffles are shown in **boldface**. Parsimony bootstrap (PB) values are shown *above* the branches, while the Bayesian posterior probabilities (PP) are *below*. Bootstrap

might have been collected in an Arizona desert (see Trappe et al. Chap. 8, this volume). *Stouffera* was described as a new genus for *T. longii*. *Stouffera longii* (Gilkey) Kovács & Trappe represented a distinct lineage at a basal branch of the Pezizaceae forming a clade with *Hydnobolites* and *Temperantia tiffanyae* (Fig. 2.2). However, as all those taxa represented quite long branches, this group might result from long-branch attraction. The desert truffle genus *Terfezia* disappeared from the American truffle mycota (Kovács et al. 2011a).

Sbissi et al (2011) presented the intraspecies variability of *Terfezia boudieri* from southern Tunisian locations based on RFLP analyses of the ITS region of 163 samples. Thirty ITS were sequenced and analyzed; the phylogram showed only topology. Apparently *T. boudieri* has considerable intraspecific variation. A high intraspecific and intrasporocarpic ITS variability was detected when Spanish *Terfezia* collections were studied (Kovács et al. 2011b). Kovács et al. (2011b) described a new *Terfezia* species and suggested that probably the lineages of the *T. olbiensis* species complex represent several morphospecies described previously but considered as synonyms. These two papers (Sbissi et al 2011; Kovács et al. 2011b) focus more on intrageneric, intraspecific variations and intrageneric species relations of desert truffles and not the phylogenetic position of desert truffles in higher taxonomic groups. Intraspecies/intrahyphal genetic variation was reported from *T. boudieri* as well (Aviram et al. 2004; Ferdman et al. 2009).

When the first report of *Picoa lefebvrei* from Iran was published (Ammarellou et al. 2011), both ITS and LSU regions were sequenced from an Iranian (*P. lefebvrei*) and a Spanish sample (*P. juniperi*), and the partial LSU sequences were analyzed together with species from Pyronemataceae gained from public databases. Although the phylogenetic tree published shows no information about distances, its broad taxon sampling of the family enables more precise interpretation of the phylogenetic position of *Picoa*. The genus nested into the *Geopora-Tricharina* clade of the family and showed a close relationship to *Geopora*.

*Carbomyces* represents an enigmatic desert truffle genus (see Trappe et al. Chap. 8, this volume), and the first molecular phylogenetic results about these truffles were published only recently (Moreno et al. 2012). They did not mention that they are first to do so, but no phylogenetic information about *Carbomyces* had been published before. Moreno et al. (2012) obtained ITS and LSU sequences only from *C. emergens* Gilkey. When the LSU sequence was analyzed together with others from the family Pezizaceae, *C. emergens* formed a clade with the *Kalaharituber-Iodowynnea* lineage but with low support. Moreno et al. (2012) write that their results are “in accordance with data obtained by Karen Hansen (pers. comm.).” The LSU analyses confirmed by BLAST of the ITS sequences “linked *C. emergens* to *Terfezia* and *Kalaharituber* (84 % and 83 % identity in 68 % and 65 % coverage, respectively).” It shows the ambiguous branching of *Carbomyces* in accordance with the blast result of the LSU sequence. *Carbomyces* is similarly distant from all Pezizaceae represented in the

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**Fig. 2.2** (continued) values below 70 % and PP below 95 % are not shown (modified from Kovács et al. 2011a; with kind permission of Mycologia)

analyses. As the family position of *Carbomyces* position is not completely clear, it is important to analyze a broader taxon sampling of Pezizales.

Hansen et al. (2013) published a comprehensive multilocus phylogeny of the Pyronemataceae with analyses of different life history traits and ancestral states. Although no *Picoa* species was included in the analyses, the taxa overlap with the aforementioned studies (Sbissi et al. 2010; Ammarellou et al. 2011) enabling one to assume that *Picoa* belongs to the *Scutellinia-Trichophaea* lineage, and together with that group, most probably to the *Geopora-Tricharina*-“*Pustularia*” clade. Thus, biological evolutionary aspects of fungi have been explored through phylogenetic analyses in which lineages with desert truffles were represented.

Basidiomycetes have been overrepresented in diversity studies of ectomycorrhizal fungi before the advent of molecular diversity screening methods. Tedersoo et al. (2006) revealed that several lineages of the Pezizales contain EM fungi, identified by use of ITS and LSU sequences. Although the EM sampling area did not represent deserts or even semiarid regions, the results revealed ectomycorrhizal strategy in *Terfezia-Peziza depressa* clade of Pezizaceae and the *Geopora-Tricharina* lineage of Pyronemataceae where the desert truffles *Terfezia* (s.str.), *Tirmannia*, and *Picoa* belong, respectively.

In a literature review plus meta-analyses, Tedersoo et al. (2010) discussed the possible ectomycorrhizal lifestyle and biogeography of fungal phylogenetic lineages. EcM were identified in the “/geopora” lineage and “/terfezia-peziza depressa” lineages. Based on missing EcM hosts in desert habitats, Tedersoo et al. (2010) doubted the (ecto)mycorrhizal strategy of *Carbomyces*, *Eremiomyces*, and *Kalaharituber*; the endomycorrhizal interactions of the latter were proven previously (Kagan-Zur et al. 1999 and see Chap. 5 by Roth-Bejerano et al.). They also discussed another desert truffle lineage: “*Mattirolomyces* and an Australian desert truffle *Elderia* are probably nested within *Peziza* s. str., a clade with no known EcM species.” Kovács et al. (2003, 2007, 2011c) have questioned the mycorrhizal strategy of *M. terfezioides* as a result of their studies on that species.

Healy et al. (2013) presented a surprising discovery of widespread presence of mitotic spore mats within EcM Pezizales. The ITS and LSU regions were used for phylogenetic analyses of datasets containing several desert truffle taxa as well. The sampling areas of the mats were not arid regions. No desert truffle was conspecific with mitosporic spore mat samples, but the “/terfezia-peziza depressa” lineage contained several examples. In the “News and views” part of the same issue of the journal, Tedersoo et al. (2013) presented interesting results on “endophytic” (i.e., mostly only sequences gained from plant tissues) and “endolichenic” lifestyle within Pyronemataceae. No *Picoa* sequences were included, but these results reveal the diversity of distribution and lifestyle of pezizalean taxa.

## 2.4 Considerations for Future Research

What can all these results show? Trappe and Claridge (2005) hypothesized that the extraordinary richness of hypogeous fungal taxa in drought-prone Australia is due in part to the selection pressure imposed by dry weather. Wet weather that initiates sporocarp formation is often interrupted by warm, drying weather there. Epigeous fungi often desiccate before maturing spores, whereas fungi protected from desiccation belowground have a better chance to complete their life cycle. Claridge et al. (Chap. 14 in this volume) detail the dependence of desert truffles on rainfall events. An important question is how complicated might be the adaptation of truffles to the extreme biotic conditions of deserts. One cannot consider this question independently from the evolution of hypogeous ascomata. Several phylogenetic studies on Pezizales presented above discussed the problem of the evolution of truffles and hypothesized that the hypogeous nature of fruiting bodies might be under the control of a not very complex genetic toolbox, and that is why hypogeous fungi could appear in several phylogenetic lineages. And the desert truffles spread through these lineages. Considering the fine-scale lineages of Pezizaceae sensu Hansen et al. (2005), adaptation of truffles to desert environments has evolved in at least four lineages (Fig. 2.2). This is a very conservative estimate, as we do not consider the potential within-lineage appearance of this adaptation, and we regard the clade formed by the long branches of the *Carbomyces-Kalaharituber-Iodowynnea* as one lineage. Besides these adaptations in Pezizaceae, at least one desert truffle lineage evolved in Pyronemataceae where *Picoa* resides. Based on this multiple adaptation we might hypothesize that, similarly to the evolution of the hypogeous fruiting body, adaptation of truffles to desert environments might not have a very complicated genetic background.

The advent of the next generation sequencing technique has enabled the fast and cost-effective sequencing of complete genomes of filamentous fungi. Several comparative genomic analyses revealed genomic and functional diversities in biological strategies such as wood decaying (Eastwood et al. 2011; Floudas et al. 2012) or ectomycorrhiza forming (Martin et al. 2010). *Terfezia boudieri* is on the list of fungi whose genome has recently been sequenced as planned (Plett and Martin 2011) but is still being annotated (Sitrit et al. personal communication). The 1,000 fungal genome initiative (Grigoriev et al. 2011) aims to sequence at least two genomes from each family of fungi; as we write this chapter, *T. boudieri* is the sole desert truffle whose complete genome has been sequenced. We agree with a conclusion of Sterflinger et al. (2012) in their review of fungi of hot and cold deserts: “Due to their enormous stress tolerance, desert fungi could also be a promising source for new biotechnological and medical adaptations. ...” Comparative genomics may reveal the key components of how desert truffles evolved the adaptation to their extreme environments.

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