AN ABSTRACT OF THE THESIS OF

Abdulmagid M. Alsheikh for the degree of Master of Science in Botany and Plant Pathology presented on June 8, 1981

Title: Taxonomy of Desert Truffles, the Genera Phaeangium and Tirmania

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Dr. James M. Trappe

Mycorrhizal fungi are important in food production of arid lands. The desert truffles not only form a symbiotic association with range plants but also form fruiting bodies which are both prized as food and nutritious. The taxonomy and ecology of two genera of desert truffles are treated in this thesis.

The genus Phaeangium containing the sole species P. lefebvrei Pat., occurs from Algeria East to the Arabian Penninsula. It has been variously interpreted by past authors. Most placed it in the genus Picoa, which is characterized by a verrucose ectal excipulum and smooth spores. P. lefebvrei, however, proves to have minutely ornamented spores when fully mature, a feature overlooked in the past (most collections represented in herbaria are immature, and the spore ornamentation has not developed). In addition, it has a tomentum of surface-granulated hyphae. P. lefebvrei is redescribed and placed in the family Pyronemataceae (Pezizales). It is novel in being commonly

scratched out of the soil and eaten by birds, which probably thereby disperse the spores. It is likely a mycorrhizal fungus with annual Helianthemum spp.

The genus Tirmania contains two species, T. nivea (Desf. ex Fr.) Trappe and T. pinoyi (Maire) Mal., which both occur from Morocco East to Iraq and the Arabian Penninsula. The genus is characterized by smooth sporocarps, asci which turn green to blue in Melzer's reagent, and double-walled spores with a smooth outer layer and a minutely reticulate-roughened inner layer. The two species are much alike, but T. nivea has ellipsoid spores and T. pinoyi has globose spores. Tirmania is placed in the family Pezizaceae (Pezizales). Both species produce large sporocarps that are collected and marketed as food. Their spores appear to be dispersed by abrasion of exposed, dried-in situ sporocarps by wind-blown sand. They are demonstrated mycorrhiza formers with annual Helianthemum spp.

Taxonomy of Desert Truffles:

the Genera *Phaeangium* and *Tirmania*

by

Abdulmagid M. Alsheikh

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Head of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

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Typed by Janell Meehan for Abdulmagid M. Alsheikh

TO MY GRANDMOTHER

I dedicate this thesis to my grandmother, Latifah Jasem AlMureikhi, who gave me strong, continuous encouragement and patience from my early school years on; and to my parents, brothers and sisters.

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Finally, a word of appreciation for the Scholarship Committee at the Kuwait Institute for Scientific Research, which provided me with the financial support to pursue my graduate studies.

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CHAPTER 1

INTRODUCTION

It may seem unbelievable that deserts can produce an item of food as luxurious as truffles, but ancient accounts of Jews and Moslems suggest that desert truffles were the manna of the Israelites (Rayss, 1959). Bedouins have collected truffles for unknown generations for food and as a cure for some eye diseases.

The desert truffles of North Africa and West Asia (Phaeangium, Terfezia, and Tirmania spp.) are associated with certain vascular plants, with which they form a special type of mycorrhiza. Many possible host species, both annuals and perennials, have been suggested for desert truffles on the basis of field observations. As of now, however, only two annuals, Helianthemum ledifolium and H. salicifolium, have been experimentally confirmed as mycorrhizal hosts of desert truffles (Awameh, et al., 1979). Fruiting of the truffles follows 3 to 4 months of favorable fall and winter rainfall, the same conditions that the host plants must have to flourish. A single host annual can produce at most one truffle, and often many host plants appear to contribute jointly to production of one truffle (Awameh and Alsheikh, 1979a). This

contrasts to the truffles of southern Europe, many of which can be produced annually in association with a single oak tree over many decades.

The geology of the deserts of the Arabian Penninsula has been studied extensively and intensively, with oil providing the impetus. Studies of the ecosystems and their plants has lagged behind. This is especially true of the fungi. Several vascular plant floras of the region have been published, but none has been devoted to the fungi. The few reports available on the fungi are scattered in the scientific literature, and most of these are of specimens sent to the mycologist authors by adventurous travellers or colonial officials.

Most mycological study of the Arabian Penninsula has focused on the botany, ecology, physiology, and utilization of desert truffles. They are of great economic importance in the countries where they occur and offer the potential for important food production in deserts. Unfortunately, desert truffle crops vary widely in abundance from year to year, with complete crop failures in many years. The dream of large, dependable, annual truffle harvests will become a reality only through intensified research. The rising problem of food shortage in arid regions poses the challenge of utilizing vast, open desert regions to produce this food of high protein, mineral and vitamin content.

An initial need in desert truffle research is taxonomic revision and clarification. The early taxonomic work was mostly by French mycologists, who dealt with species collected in the French colonies of

North Africa. Most species now known to occur over most of the Arab countries were originally described from Morocco, Algeria, and Tunisia. Additional species were described from western Asia, only later to be found in North Africa as well. The scientific names of these taxa often reflect their origin, e.g. the generic name Terfezia was derived from the Arabic term for truffles, "terfes" or "terfas". Names of French collectors or even colonial officers are also commemorated: the genus Tirmania was named for Governor-General Tirman of Algeria.

The classification and botanical nomenclature of desert truffles has undergone many changes over the last century. This resulted in part because many taxa were first described from dried, immature specimens. As more collections and more developmental stages have become available for critical study, it has become possible to emend species descriptions for greater accuracy and to re-evaluate relationships between species, genera, and families. The chapters that follow in this thesis represent a beginning at this task with the genera Phaeangium and Tirmania. Future work is planned by the author for the large genus Terfezia, which has never been monographed.

The relationships of genera of hypogeous Ascomycetes to each other and to epigeous taxa has long been controversial. The order Tuberales, based essentially on the hypogeous habit with no regard to other characters, was recently discarded as artificial by Trappe (1979). He related the various genera of hypogeous taxa to epigeous families and genera in the Pezizales (excepting Carbomyces and Elaphomyces, each of which was retained in a monotypic family and order). He placed the

genus Tirmania, treated later in this thesis, in the family Pezizaceae. He did not accept the genus Phaeangium, but, as a result of the work reported in this thesis, Phaeangium can be resurrected and assigned to the family Pyronemataceae (Pezizales).

Such new approaches to relationships between fungal taxa, together with more critical study and more complete description of taxa than has been done in the past, will pave the way to better understanding of desert fungi. It will increase the precision of research on their ecology and physiology, because different organisms will not be confused with each other. These improvements in knowledge are vital to rational development of methods for cultivating desert truffles.

The deserts of the Arabian Penninsula are barely explored for fungi. As testified by the truffles already known to occur there, deserts can be good habitats for specially adapted fungi. As mycological exploration of deserts intensifies, more will be revealed about the importance of fungi to desert ecosystems. Such knowledge can be used to increase the productivity of deserts for food. Tirmania and Terfezia spp. are demonstrated mycorrhiza formers with plants valuable for grazing (Awameh et al., 1979). Other mycorrhizal fungi are sure to be important in crop and range productivity in arid lands, especially the Endogonaceae (Trappe, 1981). Such fungi can make a big difference in productivity of crops in saline soils (Hirrel and Gerdemann, 1980), a particularly important consideration in desert agriculture. Pathogens

of food plants in desert regions are sure to become important as agriculture expands. The rising problem of food shortage in arid zones poses the challenge of utilizing these vast, open regions to produce highly nutritious food. Knowledge of the fungi is vital for meeting this challenge.

CHAPTER 2

Taxonomy of *Phaeangium lefebvrei*, a Desert Truffle Eaten by Birds

by

Abdulmagid M. Alsheikh

Oregon State University, Department of Botany and Plant Pathology

Corvallis, Oregon 97331

and

James M. Trappe

United States Department of Agriculture, Forest Service

Pacific Northwest Forest and Range Experiment Station

Forestry Sciences Laboratory

Corvallis, Oregon 97331

ABSTRACT

The desert truffle genus Phaeangium Patouillard, synonymized with Picoa by R. Maire, is resurrected. Phaeangium has ornamented spores at maturity and a tomentose peridium, whereas Picoa has smooth spores and no tomentum. Phaeangium and its single species, P. lefebvrei are redescribed and placed in the family Pyronemataceae, tribe Mycolachneeae. In 1978 the senior author collected quantities of a small truffle in several desert habitats in Kuwait. We determined it to be Phaeangium lefebvrei Pat. (Picoa lefebvrei (Pat.) Maire). These collections provided excellent material to redescribe this species and to reexamine its hitherto disputed generic assignment.

This truffle fruits from January to April in North Africa and the Middle East during years of adequate rainfall. In Kuwait it is confined to gypsiferous and calcareous, gravelly deserts, where it is scratched out and eaten by several species of migrating birds.

Phaeangium was erected as a monotypic genus by Patouillard (1894) to accomodate a new truffle species from Tunisia, P. lefebvrei. The type collection was characterized by Patouillard as having a smooth, villose, brown surface; a milk-white, homogenous gleba with no suggestion of veins; and stipitate asci containing 2-8 ovoid, smooth, hyaline spores. Patouillard felt that this taxon did not fit in the genera Picoa or Leucangium, which have verrucose sporocarps and round or mucronate spores, nor in Tirmania, which has pale colored, glabrous sporocarps and glebae with pockets of asci separated by sterile veins.

In 1901, Hennings described a new truffle from Algeria as "Terfezia ? schweinfurthii," characterized as having at maturity a light brown, subgranulose surface; a white, even gleba; and stipitate asci containing 4-8 globose spores that in youth are hyaline and smooth but by maturity are light yellow to light brown and granulose. He noted that the spores he examined were possibly mostly immature and deviated from "the type" (of Terfezia?), but he suggested a relationship to Terfezia leptoderma Tul.

Maire (1906) examined the type of T. schweinfurthii and compared it to Patouillard's description and illustrations of Phaeangium lefebvrei. He noted that the spores of T. schweinfurthii are ellipsoid and constantly smooth rather than globose and "rugose" as described by Hennings (Maire ascribed the "rugose" appearance to the character of the spore cytoplasm, although Hennings (1901) had actually used the term "granulose"). Having concluded that the specimens of T. schweinfurthii closely matched Patouillard's description and illustrations of

Phaeangium lefebvrei, Maire synonymized the two species.

Maire (1906) then disputed Patouillard's description of the sporocarp surface as smooth, because the Hennings specimens were minutely verrucose; and of the gleba as homogeneous, because the Hennings material had sterile veins in the gleba. He noted that Picoa juniperi Vitt. and P. carthusiana Tul. & Tul. have occasional hyphae emerging from the sporocarp surface. On the basis of these observations, he could see no reason for erection of the genus Phaeangium and recombined the species as Picoa lefebvrei (Pat.) Maire.

Some mycologists subsequently accepted Maire's conclusions (Mattirolo, 1914; Fischer, 1938; Trappe, 1971, 1975, 1979). Others continued to recognize the genus Phaeangium (Fischer, 1908; Massee, 1909; Bataille, 1931). In no case, however, have these decisions been based on further critical study of the types or a broad representation of additional collections. Therefore, we reexamined the types of both Phaeangium lefebvrei and Terfezia schweinfurthii plus as many other collections as could be located.

METHODS

Hand sections were mounted in 5% KOH, Melzer's reagent, and cotton blue-lactophenol. Fresh specimens were killed and fixed in FAA, embedded in paraffin, microtomed, and stained in safranin-fast green. Selected dried specimens were rehydrated in water and similarly treated to obtain thin sections.

RESULTS

PHAEANGIUM Patouillard, J. Bot. 8:155-156, 1894. Non Saccardo, Syll. Fung. 16:764, 1902.

≡*Angiophaeum* Saccardo nom. illeg., Syll. Fung. 14:29, 1899.

Sporocarps hypogeous, brown, verrucose, thinly to unevenly tomentose, lacking a basal tuft of hyphae. *Gleba* solid, with fertile pockets separated by sterile veins, lacking a sterile base. *Asci* obovoid to ellipsoid or subglobose, 8-spored at maturity, nonamyloid. *Spores* hyaline, smooth in youth but by maturity minutely ornamented.

Type Species. - *P. lefbvrei* Pat.

Entymology. - Greek, *phaeo* - ("dark") + *angion* ("vessel"). Patouillard did not indicate his reasons for coining this name.

Discussion. - Saccardo (1889) erected subgen. *Phaeangium* within the genus *Cenangium* but later (1902) elevated it to generic rank. He (1899) meanwhile proposed the name *Angiophaeum* to replace *Phaeangium* Pat. Because *Phaeangium* as a generic name has priority over Saccardo's use of that name, it stands as valid for the desert truffle. So far as we can determine, Saccardo never published the combination *Angiophaeum lefebvrei*.

PHAEANGIUM LEFEBVREI Patouillard, J. Bot. 8:155-156, 1894.

(Figs. 1 -5, Plate 1, and Figs. 1-4, Plate 2)

=Terfezia schweinfurthii Hennings, Hedwigia 40, Beibl. 4:100, 1901.

=Picoa lefebvrei (Patouillard) Maire, Ann. Mycol. 4:332, 1906.

Sporocarps gregarious in groups of 4-5 or occasionally as many as 12, 5-25 mm x 5-30 mm, subglobose to irregular, light to dark brown, nearly smooth to covered with minute, rounded to angular verrucae, thinly to erratically densely brown-tomentose. Gleba solid, in youth evenly white, at maturity with near white to faintly yellowish brown, rounded fertile pockets separated by white, sterile but otherwise undifferentiated veins. Odor and taste faint (but so far recorded only for relatively immature specimens).

Spores broadly ellipsoid to globose, 23-28(-30) x 23-26 µm (when immature, swelling up to 50 µm in KOH mounts), hyaline, containing a large, single guttule, in youth thin-walled and smooth, by maturity the walls 2-3 µm thick and ornamented with scattered to crowded, hyaline papillae 0.2-0.5 x 0.2-0.5 µm. Spore walls and papillae cyanophilic, light yellow to light olive in Melzer's reagent. Asci (2)-8 spored, ellipsoid to subglobose or obovoid, 54-90(-100) x (40-)50-70 µm, short-stipitate, hyaline, with walls < 0.5 µm thick, pale yellow in Melzer's reagent, autolysing at maturity.

Ectal excipulum 35-195 µm thick, including verrucae 75-125 µm tall, of ellipsoid to globose or subpolygonal cells 10-35 µm in diam, the cell walls yellow to brown and 0.5-3(-6) µm thick; hyphae of tomentum arising from surface cells, cylindric, 7-13 µm in diam, smooth or with surface granules, hyaline to light brown. Ental excipulum 100-150 µm thick, abruptly differentiated from the ectal excipulum as interwoven, cylindrical, hyaline hyphae 3-12 µm in diam, the walls up to 1 µm thick, occasional cells subglobose to globose. Glebal hyphae hyaline, 8-23 µm in diam, the walls ± 0.5 µm thick.

Distribution and Season.--Algeria East to Kuwait in deserts, January to April but predominantly March.

Etymology.--Honoring Commander Lefebvre of Gabes, Tunisia, who dispatched the type collection to Patouillard.

Collections examined.--TYPE: Tunisia, entre Ras el Oued ex el Hamdon, leg. Lefebvre, 1894 (F, isotype TO). OTHER COLLECTIONS: Algeria--Biskra, am Wege zum Col Sfa, leg. G. Schweinfurth, 26 Mar. 1901 (TO, type of Terfezia schweinfurthii); pr. Biskra, in der Wuste, 21 Mar. 1901 (S, paratype of T. schweinfurthii (S); Laghouat, 3, Jan. 1910 (PC); Hauts-Plateux a Chellala, leg. R. Maire, Mar. 1922 (M) and Maire #8385, Mar. 1924 (BPI). Tunisia--Gafsa, Mar. 1898, Patouillard (F); Patouillard, no other data (M, OSC, PC). Libya--Ain Scersciara, leg. R. Pampanini, 20 Mar. 1913 (PRM); Wadi Msaaba, leg. R. Pampanini, 22 Mar. 1913 (TO, OSC). Iraq--western desert, Al Jezira, leg. Hussein Al-Ani, 15 April 1965 (K). Kuwait--Alsalmi, leg. Abdulmagid Alsheikh, 28 Feb. 1978, Trappe 5369 (OSC and Kuwait Inst. Sci. Res.).

Discussion.--Patouillard (1894) and Trappe (1971, 1975, 1979) examined specimens that we now know to be immature and consequently regarded the spores as smooth. The spore ornamentation is most evident on the specimens examined by Hennings (1901), who described the spores as "levi vel granuloso, an maturis?" Maire (1906) either examined immature specimens sent to him by Hennings or overlooked the spore ornamentation. In any event, this character precludes inclusion of P. lefebvrei in Picoa. Moreover, Picoa sensu stricto is not tomentose. Trappe (1979) included "pubescence" in his description of Picoa to accomodate P. lefebvrei.

Trappe's (1979) synoptic key to the genera of hypogeous Ascomycotina can be amended by designating Phaeangium as genus no. 32 to appropriate choices within each couplet. No. 21 (Picoa) should be deleted from couplet 1-7-c (pubescent surface). Immature Phaeangium specimens will separate from Picoa at that couplet, and mature specimens will additionally separate in couplet 5-3, with the smooth spores of Picoa listed only in 5-3-a and the warty spores of Phaeangium only in 5-3-c. The only other desert hypogeous Ascomycete that has a verrucose surface and smooth spores is Picoa juniperi Vitt. Its peridium, however, is brownish black to black and is not tomentose in contrast to P. lefebvrei, which has a light brown to brown, tomentose peridium.

The tomentose ectal excipulum and warty spores remove Phaeangium from the family Balsamiaceae, (Trappe, 1979), where P. lefebvrei was an anomaly. It does fit most comfortably in the tribe Mycolachneeae of the

Pyronemataceae (Pezizales) as emended by Korf (1972). It closely resembles the genus Stephensia in most respects, and until we discovered the warty ornamentation on spores of very mature specimens, we have considered Stephensia as a possible generic home for the species. It appears closely related to the epigeous genus Trichophaea, to which it keys in Korf's (1972) synoptic key to the genera of Pezizales.

ECOLOGY

Distribution, Season, and Habitat.--P. lefebvrei has been noticed by mycologists only infrequently. Most collections have been provided to mycologists by travelers or colonial officials early in the century, and the region in which it occurs is rarely visited by mycologists. To our knowledge it is not sold in Arab markets as are the larger desert truffles (Terfezia and Tirmania spp.). Nonetheless, at least in Kuwait, it can be very common, as reported by Dickson (1955) and observed by the senior author in 1978. It fruits hypogeously but near the soil surface. As the sporocarps expand, they raise a mound of soil which tends to crack radially as it dries. Although the sporocarps are small, their tendency to fruit in clusters of 4-5 or more can result in a fairly obvious mound.

Patouillard (1894) found his first specimens included in a collection of Terfezia boudieri Chat. from Tunisia. The senior author collected his specimens in Feb. 1978 in the habitat of and about a month earlier than the season for other desert truffles. Bedouins told him that where P. lefebvrei occurs, Tirmania spp. will fruit nearby.

Data on the habitat of P. lefebvrei are available only for the senior author's collections in southwestern Kuwait (Alshagaya and Alsalmi) and in far western Kuwait near the border with Saudi Arabia (along the Alatraf highway). The collection sites are all on the Dibdibah formation, a gypsiferous to calcareous gravelly desert,

generally with several cm of loamy sand over a gravelly hardpan. Meteorological data for Kuwait and soil temperature for a representative Dibdibah site for Oct. to April, 1977-78 are presented in Table 1.

Table 1. Mean monthly soil and air temperatures, rainfall, and relative humidity, 1977-78, as recorded by Kuwait International Airport weather station.

Month	Temperature °C			Rainfall mm	Relative humidity
	Air	Soil			
		5 cm	10 cm		
Oct.	25.5	27.0	27.7	56.6	49.5
Nov.	18.6	18.5	19.2	02.2	55.0
Dec.	15.7	15.2	16.1	44.8	67.5
Jan.	13.4	12.8	13.5	44.0	65.0
Feb.	15.9	16.3	17.0	03.1	56.5
Mar.	19.7	20.4	20.9	29.3	48.5
Apr.	25.7	26.9	27.2	00.6	30.5
				Total 180.6	

Haloxylon salicornicum (Moq.) Boiss. is the only perennial shrub common on the Dibdibah formation. Mounds of wind-deposited sand accumulate around the base of this shrub. Otherwise, the desert floor is bare during the summer until after the fall rains begin in Oct.-Nov. Then seeds of annuals germinate and, if rainfall is adequate, a relatively

dense cover can develop (primarily Arnebia, Astragalus and Plantago spp., Helianthemum ledifolium (L.) Mill, H. salicifolium (L.) Mill), and Schismus barbatus (L.) Thell.). Haloxylon (Chenopodiaceae) is likely to be nonmycorrhizal, and Arnebia, Astragalus, Plantago, and Schismus are in families likely to be vesicular-arbuscular mycorrhizal in desert habitats (Trappe, 1981). This leaves the Helianthemum spp. as the probable mycorrhizal hosts of P. lefebvrei, as they are demonstrated to be for Terfezia and Tirmania spp. (Awameh and Alsheikh, 1979; Awameh et al., 1979).

Mattirolo (1914) found a perithecial hyperparasite on two collections of P. lefebvrei from Tunisia. He identified it as Melanospora zobelii (Corda) Fuckel. Udagawa and Cain (1969) concluded, however, that this species has been misinterpreted since it was originally described. We did not find these specimens in Mattirolo's herbarium at Torino, so for the present the identity of the parasite remains in question.

Feeding by Birds.--P. lefebvrei is detected and picked out of the ground by migrating birds in winter and early spring (Dickson, 1955). Some of the specimens collected by the senior author have distinct peck holes (Fig. 1, Plate 1). He observed 11 bird taxa engaged in this activity (identifications by use of Bruun and Singer, 1972; Heinzel et al., 1977; Meinertzhagen, 1954): Alaemon alaudipes alaudipes (hoopoe lark), A. a. doriae (bifasciated lark), Ammomanes cincturus (bar-tailed desert lark), A. deserti (desert lark), Cursorius cursor (cream-colored courser),

Eremophila bilopha (Temminck's horned lark), E. alpestris (shore lark), Galerida cristata (crested lark), G. thecklae (Theckla's lark), Prunella atrogularis (black-throated accentor), and Upupa epops (hoopoe).

To our knowledge, this is the first report of birds actively seeking and scratching out a fungus for food. Sutherland and Crawford (1979) observed Canada jays (Perisoreus canadensis) feeding on a large, yellow plasmodium of a slime mold, and Bailey (1904) reports that Canada jays and other birds feed on "toadstools". The junior author has observed California quail (Lophortyx californica) pecking caps of Suillus spp. and has lost specimens of Rhizopogon spp. being dried in the sun to marauding Oregon jays (Perisoreus obscurus). Pecking on mushrooms may be in search of insect larvae. These activities by birds seem opportunistic, in comparison with the searching for P. lefebvrei by birds in the Kuwaiti desert. The relative lack of food in the desert perhaps leads to intensified use by birds of what is available at any given time. In any event, it seems possible that birds disperse spores of P. lefebvrei as do mammals for hypogeous fungi in temperate forests (Maser et al., 1978).

ETHNOBOTANY

Various local arabic names are applied to P. lefebvrei by Bedouins, so we may infer that they have long known of it. A general, common term for desert truffles is "fuga", derived from the verb "fagah", literally to explode or expand suddenly. The Bedouins are mystified by the rapid appearance of the truffles, because they never see any seeds. Dickson (1955) records two Bedouin names for P. lefebvrei: "bird's fuga" (or, more properly, "fuga altoyoor"), and "haberi". Bedouins contacted by the senior author also used the term "hohbar". These last two terms literally translate as "a small piece of fine, boneless meat".

P. lefebvrei does not have a distinctive taste, and to our knowledge it is not marketed as are the Terfezia and Tirmania spp. It is, however, collected and eaten raw by Bedouin children as they find it. It is also used by Bedouins as bait for traps when hunters want to live-trap birds.

ACKNOWLEDGEMENT

Darr M. Duff produced thin-sectioned and stained microslides which were invaluable for study of the anatomy of P. lefebvrei. The ink drawings are by Wendy Mader. The studies were supported in part by the Kuwait Institute for Scientific Research as a fellowship to Alsheikh, and National Science Foundation Grant GB-27378 to Trappe. We thank the Directors of these herbaria for generously providing access to specimens: Lloyd Herbarium, National Fungus Collections, Beltsville (BPI); Farlow Herbarium, Harvard University, Cambridge (F); Botanische Staatssammlung, Munich (M); Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris (PC); Mykologicke Oddeleni Prirod Muzea Narodniho Muzea v Praze, Prague (PRM); Naturhistoriska Riksmuseet, Stockholm (S); and Istituto Botanico dell'Universita, Torino (TO).

Plate 1

Figs. 1-5. Phaeangium lefebvrei. 1. Ascocarps, one with a bird's peck (PK) and the verrucae. 2. Gleba, showing sterile veins, and the labyrinthine fertile pockets. 3. Tissue in cross section, showing fertile tissue and spores (S), sterile vein (V), X52. 4. Tissue in cross section under low magnification, showing internal venation (V), fertile tissues, peridium (ectal excipulum) and verrucae, X33. 5. Tissue in cross section, verruca (Vr), peridium (2-layered), (P) and gleba (G), X131.

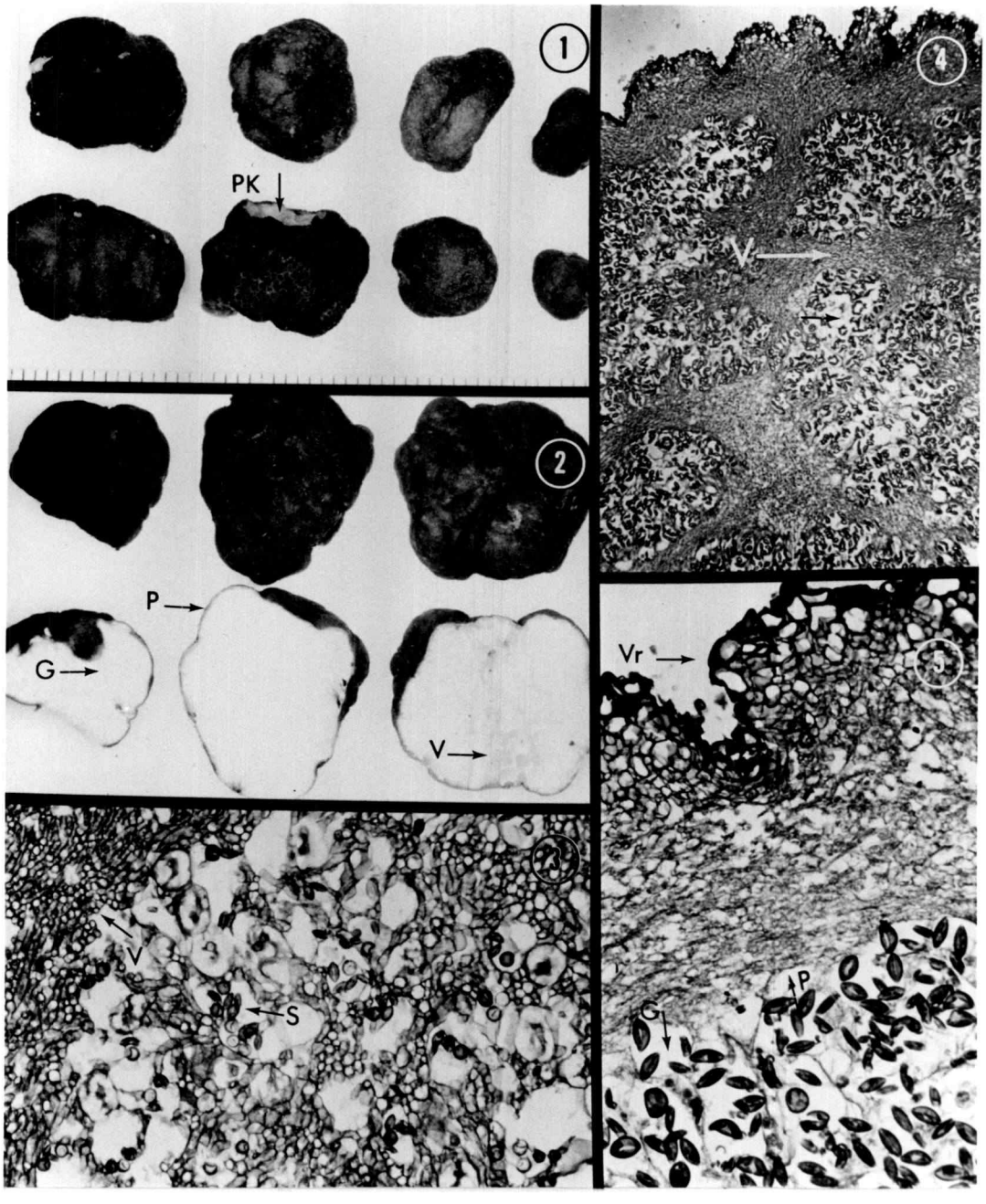
1
PK
2
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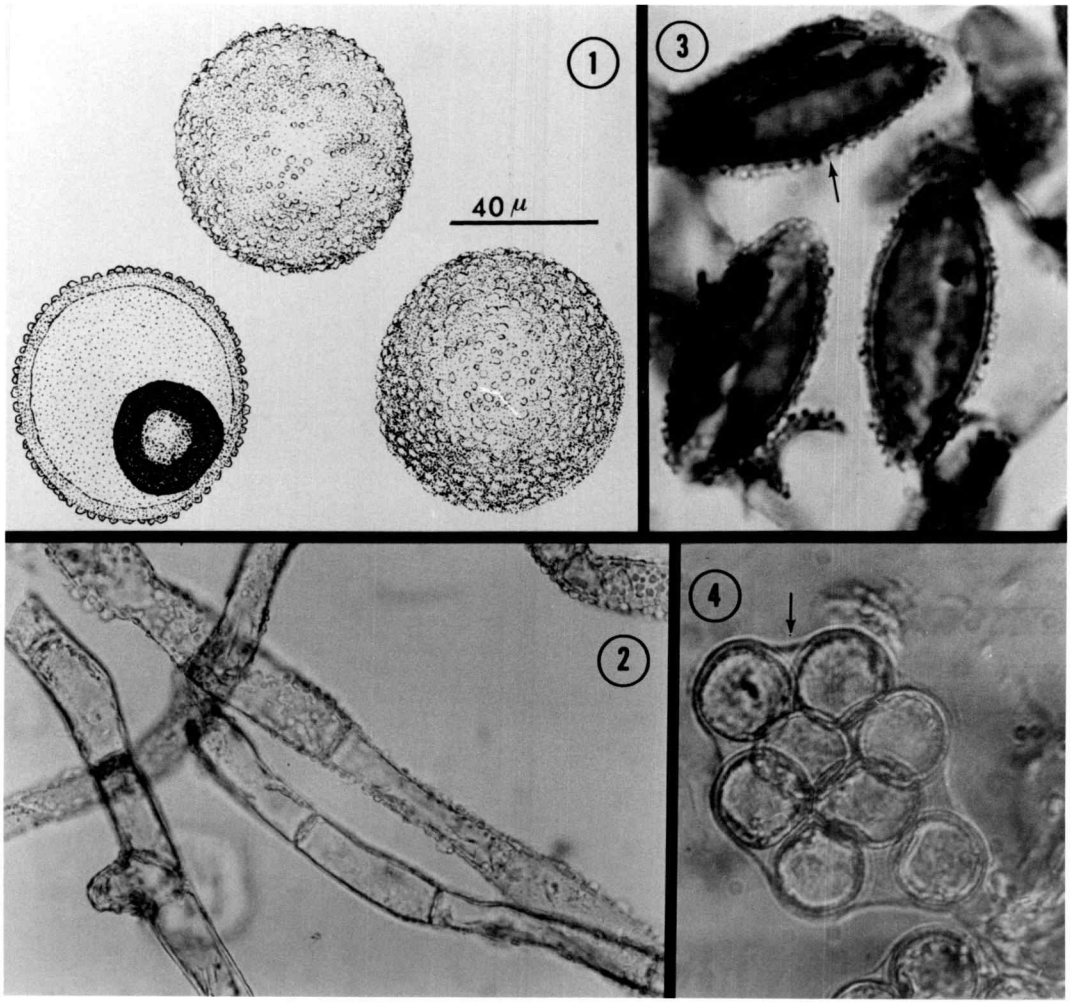
Plate 2

Figs. 1-4. Phaeangium lefebvrei. 1. Ornamented spores with guttule. 2. Peridial branched, septate tomenta, X523. 3. Spore walls with ornamentation, X1307. 4. 8-spored ascus, X1307.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CHAPTER 3

DESERT TRUFFLES: THE GENUS *TIRMANIA*

ABDULMAGID M. ALSHEIKH

Oregon State University, Department of Botany and Plant Pathology, Corvallis, Oregon 97331, U.S.A.

and

JAMES M. TRAPPE

United States Department of Agriculture, Forest Service
Pacific Northwest Forest and Range Experiment Station
Forestry Sciences Laboratory, Corvallis, Oregon 97331, U.S.A.

ABSTRACT

The genus Tirmania and its two species, T. nivea and T. pinoyi, are redescribed. They are distinct from other desert truffles in having asci that become blue to green in Melzer's reagent and hyaline, double-walled spores with a smooth, outer wall and minutely reticulate-roughened inner wall. Both species form mycorrhizae with annual Helianthemum spp. and are known only from gypsiferous, saline, or gypsiferous-saline, gravelly deserts in North Africa and West Asia. They have been prized from ancient times as a nutritious, seasonal food. If cultivation methods can be developed for insuring dependable annual yields of desert truffles, many deserts used now only for spring grazing could produce significant amounts of additional food.

The genus Tirmania was erected by Chatin (1891, 1892) to accomodate North African desert truffles with smooth, ellipsoid spores. Such truffles, earlier described by Desfontaines and validated by Fries (1823), were clearly distinct from the better known desert truffle of the genus Terfezia, which had ornamented, globose spores. Trappe (1971) further discovered that the asci of Tirmania spp. became blue in Melzer's reagent, whereas those of Terfezia spp. did not. He emended the description of Tirmania to include a species with minutely roughened, globose spores and amyloid asci. The species was first described by Maire (1906) as Terfezia pinoyi but subsequently transferred to Tirmania by Malencon (1973). This paper is intended to redescribe the genus Tirmania, and to discuss some of its taxonomic and ecological aspects.

Several other Tirmania taxa have been described on the basis of modest morphological differences, but our studies of herbarium specimens and many fresh specimens reveal that all fall within the limits of variation of the two species described below. This variation is related both to developmental stages and to weather conditions during sporocarp development or at time of collection.

METHODS

Anatomy of fresh and rehydrated specimens was observed microscopically with mounts in 5% KOH, Melzer's reagent, and cotton blue-lactic acid. Paraffin embedded and microtomed sections stained with safranin-fast green were also examined.

RESULTS

TIRMANIA Chatin, Bull. Soc. Bot. France 38:61-62. 1891.

Type species: T. africana Chatin (= T. nivea (Desf. ex Fr.) Trappe).

Ascocarps hypogeous to partially emergent, irregularly globose to lobed or turbinate, the base furrowed and with profuse, attached mycelia that usually break off unless sporocarps are excavated with great care. Peridium yellowish white to light pinkish brown or brown, glabrous, uneven, often cracked at maturity to expose the gleba. Gleba solid, of white to light yellow or pink fertile pockets separated by narrow, white to pale yellow, sterile veins. Spores globose to ellipsoid, hyaline, smooth or minutely roughened. Asci (4-)8-spored at maturity, subglobose to pyriform or broadly clavate, pale bluish green to strongly blue in Melzer's reagent.

Etymology: In honor of M. Tirman, the governor-general of Algeria, who sent the type collection to Chatin.

Discussion: Trappe (1979) transferred Tirmania from the Terfeziaceae to the Pezizaceae in view of its blue to green reaction in Melzer's reagent. It is known only from North Africa and West Asia (Al-Delaimy, 1970, 1977; Awameh and Alsheikh, 1979a, 1979b; Binyamini, 1980; Chatin, 1890, 1891, 1892; Hennings, 1895; Malencon, 1973; Moustafa, 1975; Patouillard, 1894; Rayss, 1959).

KEY TO TIRMANIA SPP.

Spores subglobose to broadly ellipsoid----------1. T. nivea

Spores globose----------2. T. pinoyi

1. TIRMANIA NIVEA (Desf. ex Fries) Trappe, Trans. Brit. Mycol. Soc. 57:88. 1971. (Figs. 1-3, Plate 3)

Tuber niveum Desfontaines ex Fries, Syst. Mycol. 2:292, 1823. (non sensu Krombholz, Nat. Abbild. Beschreib. Schwamme 8:17. 1843. =Choiromyces venosus Fr.).

Terfezia ovalispora Patouillard in Dybowski, nom. nud. Le Nat. 1890.

Tirmania africana Chatin, Bull. Soc. Bot. France 38:61-62. 1891.

T. cambonii Chatin, La Truffe, p. 81. 1892.

T. ovalispora (Patouillard in Dybowski) Patouillard comb. illeg., Cat. Raisonne Plant. Cellul. Tunisie, p. 95. 1892.

T. ovalispora var. tellieri Patouillard, Bull. Soc. Mycol. France 15:59. 1899.

Terfezia africana (Chatin) Maire, Bull. Soc. Hist. Nat. Afrique 7:294. 1916.

Illustrations: Awameh and Alsheikh (1979b, Figs. 1 and 2),Ceruti (1960, pl. 37), Chatin (1892, pl. 11 and 12), Fischer (1897, fig. 223), Fischer (1938, fig. 19), Patouillard (1892b, pl. 1).

Ascocarps hypogeous to partially emergent, subglobose to turbinate, (6-15)(-20) x 6-12 cm, often lobed, furrowed, or with irregular depressions, the base narrowed and with copious attached

mycelium that often breaks off unless sporocarps are excavated with care. Excipulum 0.5-1.5 mm thick, glabrous, unpolished, often cracked to expose the gleba, yellowish white to pale pinkish brown, often olivaceous to orange brown where exposed, when dried yellowish brown to orange brown. Gleba solid, fleshy, with white to near white or pale pink sterile veins radiating from the sporocarp base and branching to enclose labyrinthine, ivory to light yellow pockets of fertile tissue, the pockets elongated and up to 5 x 4 mm broad near the sporocarp base, grading to ± isodiametric and 1-2 mm in diam near the upper surface of the sporocarp, when dried light to dark brown. Odor and taste pleasant, yeasty or of freshly baked bread.

Spores broadly ellipsoid to subglobose, 14-18 x 10-14 µm, when immature inflating to much larger size in KOH, hyaline, the walls 1.0-1.5 µm thick and 2-layered: outer layer 0.2-0.4 µm thick, smooth when fully rehydrated; inner layer ± 1 µm thick, smooth to minutely reticulate-roughened, the ridges inconspicuous in KOH but more evident in Melzer's reagent or cotton blue, in which the ridges stain deeply and appear to protrude into the outer wall layer; spores with a single large guttule and, at maturity, a de Bary bubble in Melzer's solution or after warming in cotton blue but in KOH only after several hours immersion.

Asci (4-)8-spored at maturity, ellipsoid to pyriform, broadly clavate or clavate, or infrequently reniform or subglobose, 37-91 x 35-55 µm, mostly longer than broad, with a short, simple to obscurely croziered stem 7-12 µm broad; walls 1-1.5 µm thick, hyaline, faintly to strongly diffuse bluish green to blue in Melzer's reagent, the color gradually fading.

Ectal excipulum 35-90 µm thick, of interwoven hyphae 5-14 µm in diam at septa with scattered cells somewhat inflated, the walls hyaline to light yellow and ± 1 µm thick, the cells readily collapsing to form an amorphous outer covering on the sporocarp. Ental excipulum differentiated as a layer 35-90 µm thick, of periclinally interwoven hyphae 12-28 µm in diam at septa, the cells mostly inflated to 25-45 µm, hyaline, thin walled, grading to the gleba of interwoven hyphae 8-20 µm in diam at septa with isodiametric to cylindric, mostly inflated cells.

Etymology: Latin, "nivea" ("snowy white"), in reference to the color of the gleba and young peridium.

Distribution, Habitat and Season: Morocco east to Iraq and the Arabian Peninsula in deserts, January to June but mostly February to April. Chatin (1892) and Mattirolo (1922) report an October collection of T. nivea from Algeria and Libya, respectively. In our experience and in Malencon's (1973) judgement, T. nivea always fruits in the spring. The dates of the October collections may be erroneous, or perhaps spring fructifications dried in situ and were collected the following October.

Collections Examined: Neotype--TUNISIA: M'Zab, leg. J. Dybowski, March 1890 (type of Terfezia ovalispora Pat. nom. nud.; PC, isotype TO). Other Collections--MOROCCO: Hammada de la Daoura, NE of l'Oued Draa, leg. Reymond, 16 April 1952, Malencon 2354 (OSC, RAB). ALGERIA: Figuig region, leg. Foley, April 1913, Exsiccatum R. Maire Mycotheca Boreali-Africana 194, T. ovalispora (BERN, NY, OSC); near Djanissat, herb. C.-J. Pitard, 13 April 1913 (PC); Oued Rirgh, R. Heim (PC); Biskra, herb. Chatin, April 1892 (PC); (no locality on packet), herb. Chatin, 2 June 1890 (PC); Marche de Batna, leg. L. Riousset, April 1965,

Trappe 4555 (OSC); no locality cited, herb. Chatin, 2 June 1890 (PC), Feb. 1892 (TO, as T. cambonii) and undated (S, as T. africana and TO, as T. cambonii). TUNISIA: M'Zab, herb. Chatin, 16 Jan. 1891 (PC); Hadjeb-el-Aioun, leg. Patouillard, Mar. 1891 (NY, TO); Medenine, leg. Lefebvre, Mar. 1894 (FH, OSC, TO); Gafsa, leg. Tellier, Mar. 1898, herb. Patouillard (FH, type of T. ovalispora var. tellieri); Sidi, near Bir-Mekides (Gafsa), herb. Patouillard, April 1898 (TO); Gabes, leg. Lefebvre, Mar. 1894 (FH); no locality cited, Patouillard, 2 packets (NY, OSC); no locality cited, herb. Bresadola (UPS); no locality cited, herb. Patouillard (S). LIBYA: Ghudamis, leg. Trotter, 1914 (TO); Oasis Ghudamis (PRM704237); Mizdah, Gebel-Garvan, 13 Jan. 1925 (TO); Shahhat (Cyrene), Ghemines, leg. Zanon, Oct. 1919 (TO); Tripolitania, no locality cited, leg. Destree, April 1896 (OSC, TO); ISRAEL: Negev, Mifthakhim, leg. N. Tadmor, 2 Mar. 1956 (K); Negev, no locality cited, leg. R. Kenneth, de Vries 85 (CBS, OSC); no locality cited (OSC, K). SAUDI ARABIA: Jiddah, H.S.B. Philby, 1935 (K, OSC). IRAQ: no locality cited, leg. Ibrahim Al-Sohaily, 1976, Trappe 4555 (OSC). KUWAIT: leg. Dickson, 23 Mar. 1935 (K); Al-Salmi, leg. A. Alsheikh, Feb. 1978, Trappe 5273 (OSC and Kuwait Inst. Sci. Res.).

Discussion: The nomenclatural history of this species is confused, in that both Chatin and Patouillard received collections at about the same time but from different sources, examined each other's materials, rushed into print in several different outlets each with a flurry of nomina nuda and concurrent descriptions, and thereafter disputed priority of their respective names (T. ovalispora Pat. and T. africana Chat.). Mattirolo (1922) partially outlines these events. The precise

dates of valid publication of their names is now difficult, perhaps impossible, to determine. However, the point becomes moot with designation of Tuber niveum Desf. ex Fr. as the name with priority (Trappe 1971).

The Flora Atlantica herbarium of Desfontaines at Paris contains a few specimens of fungi, but a thorough search by J. Trappe and R. Heim revealed no specimens of T. niveum. Other Desfontaines collections are at the University of Firenze, but again a search for T. niveum by Trappe proved fruitless. Therefore, as a neotype for T. niveum we designate Patouillard's type collection of Tirmania ovalispora at PC with an isotype at TO. This material is well matured and shows all the distinctive characters of the species.

The types of Chatin's T. africana and T. cambonii could not be located. Chatin's herbarium is lost (R. Heim, personal communication), but he did share specimens, which he identified, with a number of mycologists. Our examination of these materials confirmed in all cases the synonymy of both Chatin's species with T. ovalispora. Hennings (1895) records T. nivea (as T. africana) from Egypt, near Alexandria. This is the only report from the Nile drainage. The collection cannot be located, and was probably destroyed along with the other Hennings collections in Berlin during World War II.

2. TIRMANIA PINOYI (Maire) Malencon, Persoonia 7:277. 1973. (Figs. 1-4, Plate 4)

T. patouillardii Pinoy nom. nud., Bull. Soc. Mycol. France 22:LXXVII. 1906.

Terfezia pinoyi Maire, Ann. Mycol. 4:332. 1906.

Illustrations: Ceruti (1960, pl 53), Maire (1907, fig. 1), Malencon (1973, fig. 4), Mattirolo (1922, fig. 27), Trappe (1979, fig. 10).

Ascocarps hypogeous to partially emergent, irregularly globose to turbinate, 4-9 x 3.7 cm, often lobed or with irregular depressions, the base furrowed and with copious attached mycelium. Excipulum up to 1.5 mm thick, glabrous, unpolished, white to light yellowish brown, developing olivaceous patches with age or where exposed, when dried yellowish brown to orange brown. Gleba solid, fleshy, with narrow, white to near white or pale pink sterile veins radiating from the sporocarp base and branching to enclose labyrinthine, white pockets of fertile tissue, the pockets up to 10 x 4 mm near the sporocarp base, grading to ± isodiametric and 1-2 mm in diam near the upper surface of the sporocarp, with Melzer's reagent glebal veins orange and fertile pockets bluish green, when dried yellowish brown to dark brown. Odor and taste pleasant, ± fruity or yeasty or of freshly baked bread.

Spores globose, 15-20 µm in diam (diameters at right angles sometimes varying by up to 1 µm), hyaline, ± 1.5 µm thick and 2-layered: outer layer 0.2-0.5 µm thick, smooth when fully rehydrated; inner layer 1 µm thick, minutely reticulate, the ridges inconspicuous in KOH but more

evident in Melzer's reagent or cotton blue, in which the ridges stain deeply and appear to protrude into the outer wall layer; spores with a single, large guttule and, at maturity, a de Bary bubble in Melzer's solution or after warming in cotton blue but in KOH only after several hours immersion.

Asci (4-)8 spored at maturity, ellipsoid to pyriform or broadly clavate or infrequently reniform or subglobose, 51-110 x 38-63 µm, mostly longer than broad, with a short, simple to obscurely croziered stem 14-27 x 8-17 µm; walls ± 1 µm thick, hyaline, faintly diffuse green to blue in Melzer's reagent, the color gradually fading.

Ectal excipulum 50-150 µm thick, of appressed, interwoven hyphae (3-)5-10(-15) µm in diam at septa, occasional cells inflated (up to 35 µm), the walls hyaline to light yellow and ± 1 µm thick, the cells readily collapsing to form an amorphous, outer covering on the sporocarps. Ental excipulum differentiated as periclinally interwoven hyphae 5-12 µm in diam at septa, the cells mostly inflated to 8-25 µm, the walls hyaline and < 0.5 µm thick. Gleba not differentiated from the ental excipulum.

Etymology: in honor of Maire's friend and collaborator, E. Pinoy.

Distribution, Habitat, and Season: Morocco east to Iraq and the Arabian Penninsula in deserts, February to April.

Collections Examined: Type--ALGERIA: Sidi-Khalifa, pres le Kreider, Hauts Plateaux Oranais, 18 April 1906 (TO). Other Collections--MOROCCO: Bou-Bernous, au marche de Ksar-es-Souk, G. Malencon 2352, Mar. 1939 (OSC, RAB). ALGERIA: Hauts-Plateux a Chellala, leg. Alquer, 20 Mar. 1913, Exsiccatum R. Maire Mycotheca

Boreali-Africana 146 (BERN, BPI, K, M, OSC, TO); El Aridia, ded. Boudier, April 1906, herb. Patouillard (FH); Ain Sefra, ex Boudier, 1906 (TO, as Terfezia boudieri); Sud Oranais, herb. Patouillard (TO); Berri-Abbes, J. Nicot, Mar. 1955 (PC). LIBYA: Cirenaica, Zavia Micheli, leg. Festa, 1922 (OSC, TO). SYRIA: in desert, leg. S. V. Tyan, 14 Feb. 1973, Trappe 3616 (OSC). IRAQ: Baghdad, May 1888, ex herb. Sydow (S, as Terfezia hafizii); Baghdad, 1888, ex herb. Rehm (S, as Terfezia leonis); Abu Ghraib near Baghdad, 1964 (M); Jebah, NE of Rawah (K); Zbaidi, NE of Rawah (K); in desert (no locality cited), leg. H. Y. Al-Ani, 20 Mar. 1969, Trappe 1839 (OSC); purchased in market (no locality cited). Y. Al-Doory, Trappe #2117 (OSC). KUWAIT: Comm. R. W. G. Dennis, Feb. 1972, Trappe 3187 (OSC); purchased in Al-Ahmadi market by H. Macksad, Mar. 1972, Trappe 3194 (OSC); in desert, leg. M. Nasser, Feb. 1972, Trappe 3496 (K, OSC); in desert, leg. A. F. Moustafa, Trappe 3647 (OSC); Al-Salmi, 120 km SW of Kuwait City, leg. A. Alsheikh, Feb. 1978, Trappe 5272, and 7 Mar. 1978, Trappe 5370 (both in OSC and Kuwait Inst. Sci. Res.).

Discussion: T. pinoyi strikingly resembles T. nivea in most characters other than spore shape and size. The reticulum on the inner spore wall is more easily detected in T. pinoyi than in T. nivea. That, plus the globose spores of T. pinoyi, led to its retention in Terfezia until the green to blue reaction of its asci to Melzer's reagent was discovered. The reaction is generally weak in T. pinoyi, and is often undetectable in young specimens.

ECOLOGY OF TIRMANIA

Tirmania nivea and T. pinoyi have been demonstrated to form a unique type of mycorrhizae with desert annuals in the family Cistaceae, Helianthemum ledifolium (L.) Mill and H. salicifolium (L.) Mill (Awameh and Alsheikh, 1979a; Awameh, et al., 1979). Binyamini (1980) reported H. sessiliflorum as an associate of T. nivea, and the perennial H. lippii (L.) Dum. has also been observed as a potential host (Dickson, 1955; Rayss, 1959). Other annual and perennial associates include Plantago and Artemesia spp. (Awameh and Alsheikh, unpublished data; Binyamini, 1980), but these commonly occur with Helianthemum spp. in desert habitats. Whether or not they form mycorrhizae with Tirmania spp. remains unknown.

The habitat and ecology of Tirmania spp. have been studied in detail only in Kuwait (Awameh and Alsheikh, 1979a). There Tirmania spp. occur along with Terfezia spp. in gravelly gypsiferous, gypsiferous-saline, or saline deserts as described by Halwagy and Halwagy (1974a). Sporocarp production is correlated with amount and seasonal distribution of rainfall: a minimum of 180 mm, well distributed from October or November through March, produces a rich development of annuals, including Helianthemum spp. This, in turn permits mycorrhiza formation by Tirmania with vigorous hosts, a requisite for good sporocarp formation. Late rainfall delays germination and growth of the annuals. Their subsequent development is retarded by low winter temperatures, and young shoots can be killed by frost (Halwagy and Halwagy, 1974b). In late February, the annuals mature and shed seed. At this time Tirmania begins to fruit if the

weather has permitted development of healthy hosts and if there has been no spring drought.

Sporocarps of Tirmania form in the soil at depths of 1-6 cm (mostly 1-4 cm) among roots of Helianthemum spp. (Awameh and Alsheikh, 1979a). As the sporocarps enlarge, they raise a mound of soil that cracks radially as it dries. Because Tirmania spp. are quite large, the mound is usually prominent. Wind blows the soil from the mound to expose the upper part of the sporocarps. At this time the ectal excipulum collapses to form a dense, amorphous hide on the sporocarp surface.

Mammals are important in dispersal of spores of hypogeous fungi in north temperate forests (Maser, et al., 1978), and birds appear to be involved with spore dispersal of the small desert truffle, Phaeangium lefebvrei Pat. (Alsheikh and Trappe, unpublished data). No animals have been observed to feed on Tirmania spp. (although stomach contents of animals native to Tirmania habitats need to be examined during the fruiting season to be sure of this point). Spores are dispersed by physical means, however. After sporocarps are uncovered by wind erosion they dry in situ. Abrasion by wind-blown sand subsequently wears them away, and spores and sporocarp fragments are disseminated by the wind. Awameh and Alsheikh (1979b) found that spore germination of both T. nivea and T. pinoyi was faster for spores from sporocarps dried intact for 30 days in the desert sun than for spores from fresh sporocarps. Their data suggest that these species are well adapted to in situ drying and subsequent wind dissemination.

UTILIZATION AND ETHNOBOTANY OF *TIRMANIA* SPP.

Both *Tirmania* spp. are edible and have long been prized for culinary use in Arab countries. During their relatively short fruiting season in years of abundance, they are marketed at prices comparable to those of meat, and, indeed, served instead of meat. In years of scarcity, they command even higher prices. In some areas of the Arabian Gulf region, royal families claim the truffle crop during seasons of abundance and have truffle lands patrolled until most of the crop is harvested. Only then can others collect. Bedouins in Kuwait told the senior author that they use *Tirmania* spp. in treatment of some ophthalmic diseases. Rayss (1959) suggests that *Tirmania* spp. may have been the manna of the Israelites.

Analyses of *Tirmania* sporocarps (also termed "zbaidy" or "zobidy") indicate contents of several minerals and vitamins; 17 amino acids, including nine essentials; and relatively high protein contents (Al-Delaimy, 1977; Al-Delaimy and Ali, 1970; Chatin, 1892b; El-Gendy and Alami, 1976). Only Chatin (1892) identified the *Tirmania* spp. that were analysed, and his methods were primitive by todays' standards. The nutritional value of both species needs critical reexamination.

Al-Delaimy and Ali (1970) also studied the conditions for optimum storage of fresh *Tirmania* spp. and the microorganisms associated with spoilage.

Tirmania and Terfezia spp. have considerable economic value in the countries where they occur and provide a much desired source of food. Unfortunately, crops vary markedly from year to year because of variations in weather. Development of cultivation methods, e.g. through irrigation with well water in droughty years, could provide an important step in productive use of arid lands. The Kuwait Institute for Scientific Research currently has a research program on cultivation of desert truffles. Both spores and cultured mycelium have been used successfully as mycorrhizal inoculum on Helianthemum spp. (Awameh, et al., 1979).

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Plate 3

Figs. 1-2. Tirmania nivea. Tissues in cross section. 1. Peridium (ectal excipulum) and ental excipulum. 2. Gleba, showing fertile tissue and a sterile vein (A11X33). Fig. 3. Double-walled spore.

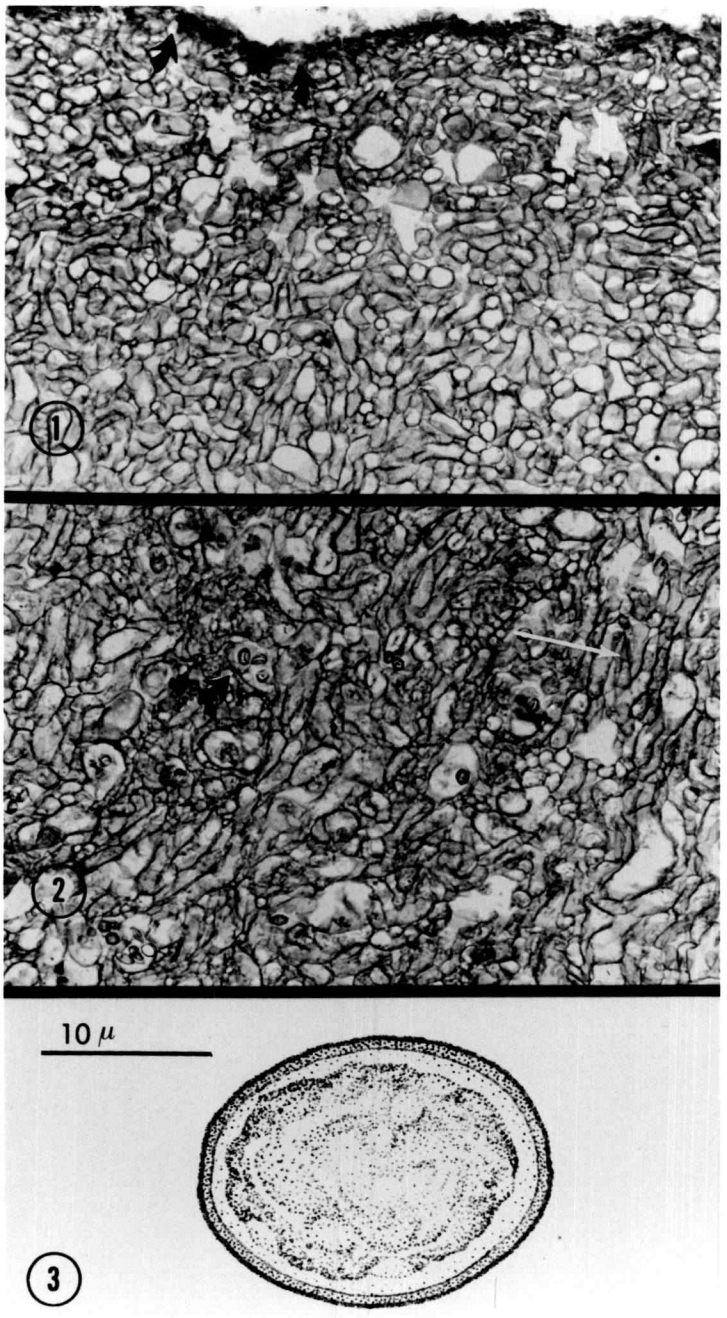
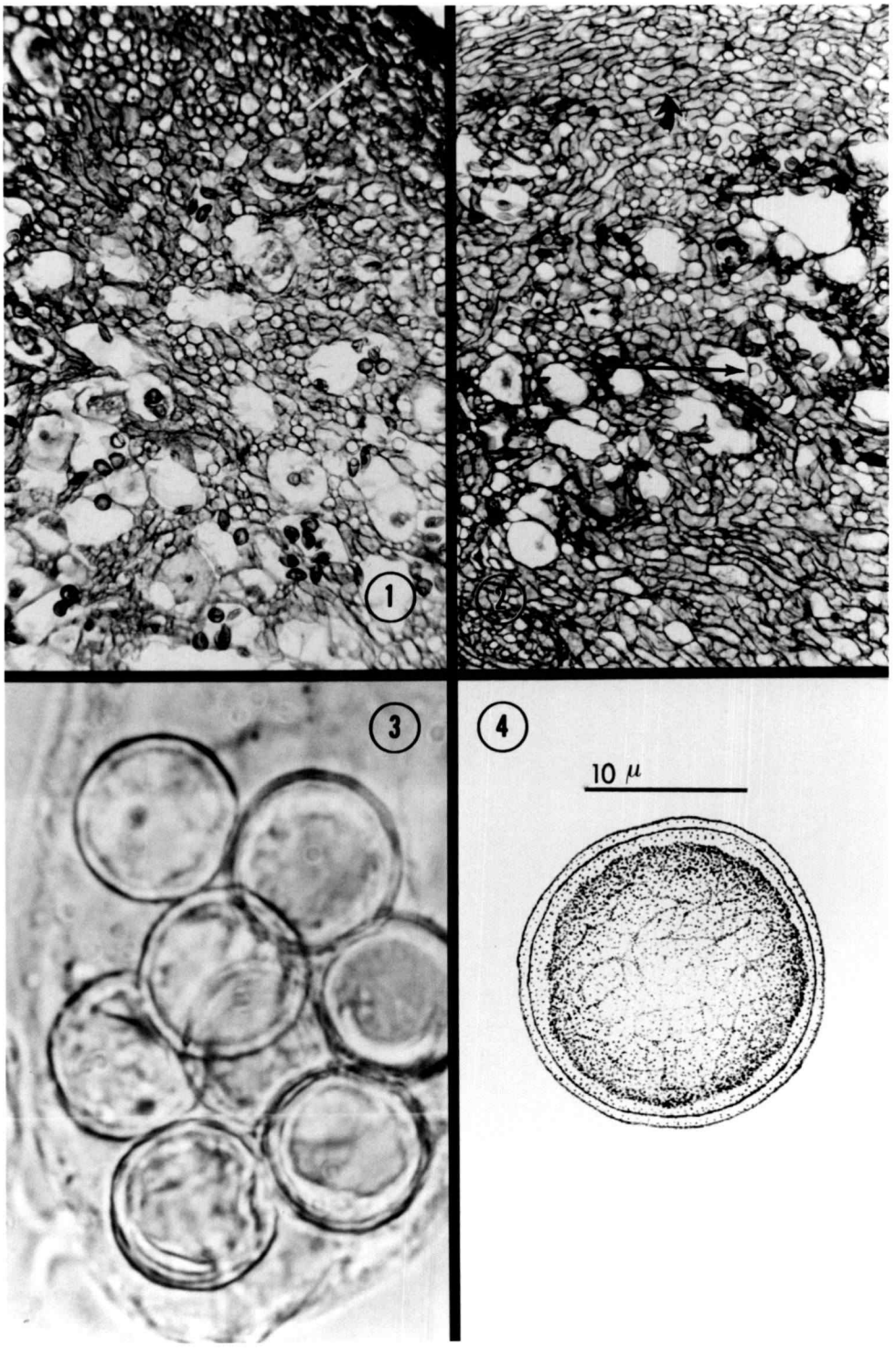

1
2
10 μ
3

Plate 4

Figs. 1-4. Tirmania pinoyi. 1. Tissues in cross section, peridium (ectal excipulum), part of gleba and asci, X131. 2. Gleba, showing fertile tissue and veins, X52. 3. 8-spored ascus, X1307. 4. Spore, with double wall.


1
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CHAPTER 4

CONCLUSIONS

The desert truffle genus Phaeangium has not been accepted by recent authors, who synonymized it with Picoa. Critical study of the type and other available collections, leads to the conclusion that Phaeangium should be retained as a valid genus. It has minutely ornamented spores and an ectal excipular tomentum of large, surface-granulated hyphae, a combination found in no other genus of hypogeous Ascomycetes. The spore ornamentation, evident only on specimens at advanced maturity, was overlooked by earlier workers. Picoa, in contrast, is characterized by smooth spores and an ectal excipulum that lacks a tomentum.

Phaeangium lefebvrei, the only species of the genus, occurs from Morocco East to the Arabian penninsula. Its sporocarps, which rarely exceed 2 cm in diameter, are scratched out of the soil and eaten by migrating birds. This is the first report of birds as potential spore dispersers of a higher fungus.

Tirmania, another genus of desert truffles, has been accepted by most authors since it was originally described in 1891. Considerable confusion existed about its species until recently, however. It is characterized by asci which turn blue to green in Melzer's reagent and by double-walled spores with the outer wall smooth and the inner wall minutely reticulate-roughened. Critical examination of types and other

available collections results in acceptance of two species, T. nivea and T. pinoyi.

T. nivea incorporates several synonyms based on collections with minor differences now recognized as either developmental stages or the influence of weather during sporocarp development. It has ellipsoid spores, in contrast to T. pinoyi which has globose spores. Both species occur from Morocco East to Iraq and the Arabian Penninsula in the same kinds of desert habitats. Macroscopically they are quite similar, with large sporocarps that develop belowground but usually emerge by maturity. The major means of spore dispersal appears to be wind. Sporocarps dry in situ and are then abraided by wind-blown soil.

Tirmania spp. are collected as food and command a good market price. Their abundance varies from year to year, depending on amount and distribution of rainfall from late fall to winter. They are demonstrated mycorrhiza formers with desert annuals in the genus Helianthemum. Enough is now known about their taxonomy and ecology that methods of cultivating them to produce dependable, annual crops seems possible. This has the potential of opening large areas of desert to production of a highly nutritious food crop.

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