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REVIEW

Truffle and truffle-like fungi from continental Africa

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Africa is a diverse continent composed of many different terrestrial biomes, from the largest nonpolar desert in the world to equatorial forests and Southern African Fynbos. Biodiversity within the continent is high but much remains to be discovered. Sightings of hypogeous fruiting bodies of mycorrhizal fungi (truffles and truffle-like fungi) have been recorded from the most northern countries of the continent to the most southern countries; they have been widely collected for culinary and medicinal purposes. In this review, we describe the most prominent species of mycorrhizal fungi forming hypogeous fruiting bodies, across six genera. The most ubiquitous of these are the “desert truffle” species and the most common genus of plants with which they associate are those of the genus *Helianthemum*. We also describe the key species of truffle and truffle-like fungi in continental Africa. Where information exists, we describe the ecology, medicinal properties, and ethnomycology of the identified fungi.

Keywords

mycorrhiza; ethnomycology; ecology; hypogeous; diversity

Introduction

Africa is the world's second largest continent with a population exceeding 1.3 billion, representing 17% of the world's population [1]. Africa accounts for 20.4% of the landmass surface of the earth [2] and 8% of the world's forests [3]. Moreover, Africa hosts the largest nonpolar desert in the world, the Sahara. The landmass size and climatic diversity of Africa provide fertile ground for the investigation of many species, especially fungi. However, accurate data about the indigenous use of African fungi have largely been passed between generations only orally [4] and have not been well documented. This is contrasting to the case for other areas of the world, for which historical written documentation regarding fungi is available [5]. Consequently, much historical knowledge of African fungi may have been lost and the diversity of languages in Africa means that such knowledge, where it is recorded in print, is often hard to locate and access by those who are not fluent in the local language [6]. As a consequence, much of the modern-day knowledge about the hypogeous fungi of Africa can be attributed to a small number of studies by international scientists, many of whom are not domiciled within the continent.

There have been relatively few studies on ectomycorrhizal fungi in Africa and even fewer on hypogeous species. However, many of the native tree species do form ectomycorrhizal associations; thus, it is likely that there is diversity of edible hypogeous species. Bâ et al. [7] presented a study of trees in tropical regions of Africa in which ectomycorrhizal status was confirmed on 93 (26%) out of 354 trees investigated [7]. The potential for diversity is definitely lower in dry tropical forests, where it has been

reported that vascular arbuscular mycorrhiza dominate and ectomycorrhizal species are usually absent or occur in low numbers [8].

The term “truffle” is used to describe the edible hypogeous fruiting bodies of mycorrhizal ascomycetes. The origin of the term “truffle” is thought to be from the Latin word *tubera*, which is defined as a “swelling” or a “lump”. It is thought that this became “tufer” and then gave rise to the numerous related European terms for truffle in different languages (*trufa*, *truffe*, *trufel*, etc.). Truffles have a variety of names within Africa. In North Africa, they are known by various local names such as Al-Kamaa, Al-Fag’a, gibbah, khlaasi, Zubaidi, Eblaj, Nahbaat alra’ad, Terfas, Faga Al toyoor, Nabat Al Radh, asqal, Bidat El Ardh, and Banat Ober [9–11]. In the Kalahari area, truffles are called n’abbas. These local names for truffles often relate to some aspect of the truffle fruiting pattern, for example, translations may refer to “crack” or “burst” or denote “hidden” or “to hide”. Such names become relevant when the fruiting of desert truffle species native to those areas is considered. As these fruit bodies swell, under the sand and soil they often cause cracks in the ground and sometimes appear almost epigeous, as if they have “burst” forth from the ground.

This review focuses on the most revered, reported, and utilized hypogeous mycorrhizal fungal species from continental Africa. Although the term “truffle” is primarily used for fruiting bodies from the *Tuber* genus, here, it is used to identify all hypogeous fruiting bodies of mycorrhizal fungi. Comparatively rare species are not dealt with in depth within this review. Rarity is used here to both denote infrequency of occurrence and a lack of representation in the academic literature. For example, although currently, there are three species of truffle known to exist that are endemic to the Kalahari, only one has been dealt with in depth. *Eremiomyces echinulatus* and *Mattirolomyces austroafricanus* have been reported in only a few studies [12,13], and are therefore not addressed in depth in this review. Key truffle species across six genera are now described in detail.

Tuber

The genus *Tuber* includes a collection of species that form ectomycorrhizal associations with a range of host tree species and woody shrubs. Currently, this genus is represented by five known species from North African countries: *T. aestivum* syn. *uncinatum*, *T. asa*, *T. borchii*, *T. oligospermum*, and *T. rufum*. A sixth species, *T. melanosporum*, is also known and its introduction to the continent is included in this review as the geographic spread and local importance of this species is increasing.

Tuber aestivum (syn. *uncinatum*) (Wulfen) Spreng.

This is predominantly a European species highly valued for culinary purposes but has been discovered occurring naturally in just one country within Africa, Morocco. Ascospores are subglobose and occasionally large (>400 µm), with a blackish-brown to black peridium and conspicuous warting, with pyramidal warts often depressed at the apex. The gleba is firm and solid, whitish when immature and ripening to light-brown to dark-brown at maturity, and marbled with white meandering veins that do not discolor when exposed to the air. Ascospores are 20–45 × 18–35 µm in size (excluding ornamentation) and ornamented with a coarse, irregular reticulum; one–six ascospores are present per asci. They were discovered in the Middle Atlas by Malençon [14] at an altitude of 1,600–2,000 m. The comparative rarity of this species means there is no record of its indigenous use, but recent attempts to cultivate this species in South Africa have been successful [15].

Tuber melanosporum Vittad.

This species has never been found to occur in continental Africa naturally. However, the global demand for this species has fueled a recent introduction of *T. melanosporum* cultivation from Europe, and consequently, this is now an important hypogeous species

within Africa. Ascumata are subglobose or irregular and occasionally large (>400 g) with a reddish-blackish-brown to black peridium and warting, with pyramidal warts often depressed at the apex. The gleba is firm and solid, whitish when immature and purplish-black at maturity, and marbled with white branching veins that redden when exposed to the air. Ascospores are 28–48 × 20–30 µm (excluding ornamentation), ellipsoid, and ornamented with pointed and often curved spines with one–five per asci. This species requires a climate with seasonal fluctuations not characterized by extremes [16,17] and has been successfully cultivated in Morocco at an elevation of 1,700 m [18]. More recently, this truffle has been introduced to South Africa and has produced fruiting bodies in a number of localities and with a range of non-native tree host species [15], forming the backbone of an embryonic local industry (Fig. 1). Newly established orchards take a number of years to reach maturation, after which fruiting bodies may be produced annually and are located with the aid of specially trained scent detection dogs. Nevertheless, cultivation of this species is spreading across Northern and Southern continental Africa and is included here due to its burgeoning socioeconomic importance.

Tuber oligospermum (Tul. & C. Tul.) Trappe.

This indigenous species is found in acidic soils and associates with *Pinus pinaster* var. *atlantica* in arid zones of North Africa. In Morocco, this species can be found in the Mamora Forest, inland from Rabat, where host trees include the cork oak (*Quercus subra*) [19,20]. The 2–3-cm fruitbody is subglobose or irregular in form, with a 140–270-µm-thick peridium, and a gleba that ranges from whitish in immature specimens to grayish-brown at maturity and is marbled with numerous whitish veins. Asci contain one–three(four) globose spores that are 28–50 µm in diameter, excluding a 5–7-µm-high ornamented regular reticulum with four–six meshes across the spores [21]. Harvesting of this species contributes to the local economy. Occasionally, *T. oligospermum* is exported to Europe and may be fraudulently sold as the highly valuable European species *Tuber magnatum* or mixed into batches of truffles that are sold as *T. magnatum*. The mode of collection is by stick (see description for *Terfezia arenaria*) and by raking or digging of the ground in known productive areas. Due to the collection methods, the tubers are often immature and lacking in flavor. In productive areas, collectors can be seen selling their harvests at the sides of roads where the tubers are wrapped in damp sand or clay to preserve moisture and often stacked in pyramidal shapes to attract buyers. Unscrupulous sellers sometimes fail to include the tuber and balls of solid clay may be mixed into batches of genuine clay-covered fruiting bodies.

Tuber asa Tul. & C. Tul.

This is another *Tuber* species with a preference for sandy soils that is confined to northern Africa in its continental African distribution. The irregularly globose 2–5-cm fruiting body is ochraceous yellow with reddish-brown spots and a gleba with a color ranging from yellowish-grey to beige that is marbled with numerous whitish veins. Asci contain one–four(five) globose or broadly ellipsoid spores that are 25–45 × 22–40 µm in size, with a raised reticulum that is 1–3-µm tall [22]. With a whitish peridium, this species is found to be hosted by a number of *Helianthemum* species and may be found in the same vicinity as *Terfezia arenaria* and *T. leptoderma*. However, the actual identity of this species is currently debated, as it may be representative of another member of the *Puberulum* group of truffles [23].

Delastria

Delastria is a monospecific genus, meaning that it is represented by just one known species, *D. rosea* Tul. & C. Tul. This species has the interesting presentation of a gleba divided into isolated fertile pockets. Pockets contain asci, within which there are

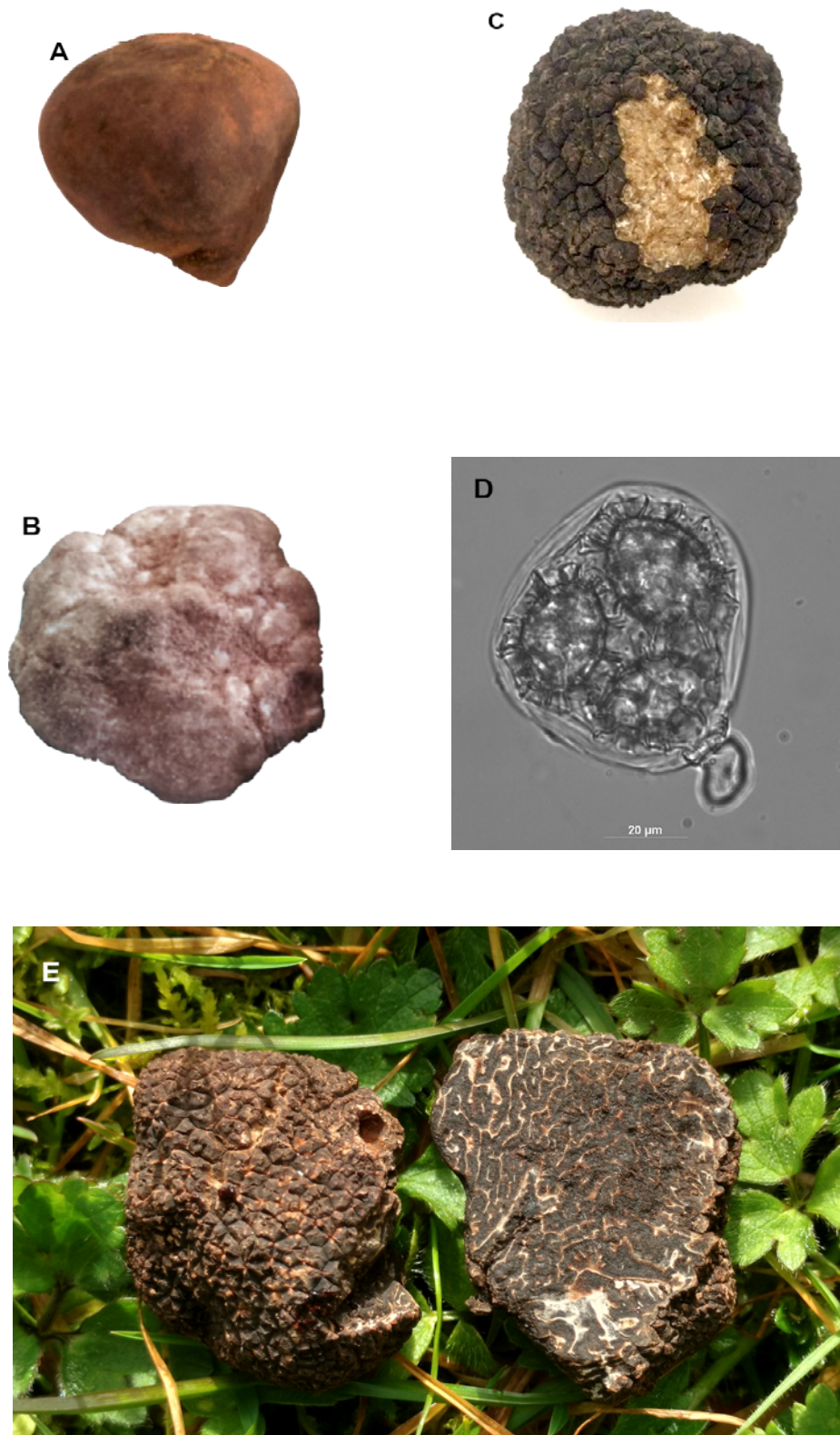


Fig. 1 Examples of truffles from continental Africa. *Terfezia clavaryi* (A) displaying a sterile tapered base and orange brownish-red peridium. *Tuber oligospermum* (B) displaying a subglobose fruitbody with a whitish peridium. *Tuber aestivum* (syn. *uncinatum*) displaying a warty peridium and light-brown gleba, spores (C) ornamented with a coarse irregular reticulum, and three ascospores per asci (D). *Tuber melanosporum* (E) displaying a warty peridium and gleba intersected by white veins, reddening with exposure to air. The photographs were taken by the corresponding author, excluding image (D), which was taken by Philip Schlur.

normally three–four spino-reticulated spores (alveolated spores) [24]. The peridium is whitish and similar in appearance to many other whitish truffle species but the gleba has a pinkish hue when fully ripe. Despite its attractive appearance, the odor is reported to be weak, with a bitter and displeasing taste [25]. This species is found across North Africa but due to its weak aroma and unpalatable taste it is not widely valued for culinary purposes and is known locally, in Morocco, as the “bitter Terfass of pine”. Host species are mainly pine (*Pinus pinaster* var. *atlantica*) and soils are typically acidic, with this truffle species sometimes growing in the same areas as *T. oligospermum* [20]. The harvesting period is also short, normally just from November to December, and the sporocarps form relatively high in the soil horizon, so much so that December rains may expose them.

Kalaharituber

Kalaharituber is a monospecific genus represented by *Kalaharituber pfeilii* (Henn.) Trappe & Kagan-Zur [26]. First described in Namibia as *Terfezia pfeilii* [27], the fruiting body is turbinate to obpyriform or subglobose and 6.5 × 6 cm in size, with a wrinkled dark-brown peridium (1-mm thick). The gleba is soft and fleshy with sterile white veins and yellowish white-brown fertile pockets with a pleasant odor. Asci contain five–eight globose to ellipsoid or obovoid spores that are 70–100 × 50–80 μm in size, with surface ornamentation of densely crowded spines (0.5–1.5 × <0.5 μm) [26]. This is a common and valued species of truffle endemic to the Kalahari region, widely known as the Kalahari truffle. There are two other species that are endemic to the Kalahari, but both are infrequent and known only from a very small number of collections from Botswana, Namibia, and South Africa [26]. Kalahari truffles are widely respected and used by local peoples as a favored food source, having a well-documented history of use [28].

The sand sheets of the eastern Kalahari change little in elevation, with sand generally deeper than 60 m often being red or pink due to the presence of iron compounds. The distribution of iron compounds has been suggested as being a meaningful factor in the distribution of *K. pfeilii*. This species often occurs in compacted white or pinkish sands, across a wide range of pH (5.5–6.5; occasionally as high as 7.2) and is sometimes found in agricultural fields that contain herbaceous plants [29,30]. Although many host plants have been suggested, the primary host plant of this species is currently unknown, although Kagan-Zur et al. have presented compelling evidence for an association of this fungus with wild watermelon plants (*Citrullus vulgaris*) [29]. Animal vectors may be important in spore dispersal, with meerkats, baboons, bat-eared foxes, and hyenas all having been observed consuming the fruiting bodies of this fungus [28]. Fruiting bodies can be found from January to June and display regional variation in maturation dates depending on localized rainfall events. The link with rainfall is displayed in Khoisan oral mythology, where Kalahari truffles are known as eggs of the lightning bird because they appear so close after spring’s thunderstorms [13].

Further, the Kalahari truffle supposedly has medicinal properties. It has been attributed to possess strong curative powers by local peoples; some San hunters carry dried pieces of its fruiting bodies in the belief that they may be used as an oral antidote to the poison of their arrows [12]. The Khoisan people have also claimed aphrodisiac properties of the fruiting bodies [13]. In Botswana, dried and powdered fruiting bodies are also reportedly used medicinally to induce birth in humans and livestock [31]. As is the case in several regions where quantities of wild valuable fungi are harvested, there are reports of the exploitation of local peoples. Truffle distributors are reported to pay local peoples, such as San hunters, to be taken to the wild production sites. Once there, the location is GPS-tagged, and then, the distributors return annually to harvest the fruiting bodies without the involvement of local peoples. Such activities create tension and also diminish the harvest of this fungus for traditional uses. Khoisan Kalahari truffle gatherers have also shown an unwillingness to profit from the sale of this species. One hunter claimed that low prices are asked because desert truffles are God’s given gift from the soil; they emerge from it entirely on their own and without toil [30].

Picoa

Picoa is a genus of appreciated edible species, known to be high in antioxidants and containing compounds with antimutagenic and anticarcinogenic properties [32]. Species within the *Picoa* genus may also be surprising high in protein, with the following nutritional profile having been reported: 22.54% protein, 19.94% fat, 36.66% carbohydrate, 13.04% fiber, and 8.21% ash [32].

Picoa juniperi Vittad.

Picoa juniperi is the type species of *Picoa*, with the genus first being proposed by Vittadini [33]. *Picoa juniperi* displays an unusual external similarity to *Tuber aestivum* syn. *uncinatum*, with a blackish brown peridium with polygonal warts. The gleba is white with fertile tissue separated by sterile veins [34] and a sweet smell and coconut-like flavor that is altered when parasitized by *Melanospora zobelii*. With six–eight oval ascospores per asci, *P. juniperi* is differentiated from *P. lefebvrei* by its smooth appearance [34]. The small size of ascocarps, i.e., 1–3 cm, limits the market potential of this species but it is readily consumed when found with other desert truffle species. In Morocco, *P. juniperi* is often called *Ed doukar*, where it favors calcareous soils and is rare; however, it is harvested in February, and its hosts are *Terfezia claveryi* and *Helianthemum lipii* [20,35]. In Tunisia, the harvest season is similar, with this species being found in February with its hosts *H. lipii*, *H. sessiliflorum*, and *Rhanterium suaveolens* [34–36].

Picoa lefebvrei (Pat.) Maire.

Originally, this species was reported from Tunisia and placed within a newly erected monospecific genus, *Phaeangium*, and named *Phaeangium lefebvrei* [37]. This species has a peridium that is brown to black, sometimes with reddish tones, and has small polygonal warts. The fruiting bodies are small, often 1–3 cm in size, with a sweet coconut smell at maturity. The gleba is white with white veins, although black markings may appear when the fungi are parasitized by *Melanospora zobelii*. Oval spores occur as four–eight per asci, with a diameter of around 30 µm, and may be verrucose or ornamented (warty) [34,38]. After recent morphological and phylogenetic analysis, this species is now known to be closely related to *Picoa juniperi* and is now named *Picoa lefebvrei* [38]. Within continental Africa, this species is confined to the north, with sighting reports from Tunisia [34]. Forming an association with species of the genus *Helianthemum* [9], mycorrhiza have also been produced in greenhouse conditions with *Helianthemum almeriense* [39].

An unusual aspect of *P. lefebvrei* as a hypogeous fungus is that birds may be important spore dispersal vectors. Observations of this species being unearthed and consumed by a number of migratory avian species have been recorded in gravelly calcareous deserts, and it is also sometimes used by the Bedouin people as bait when hunting birds [40,41]. This possible long-range dispersal mechanism suggests that this species may be more widespread than is currently reported within English speaking literature. *Picoa lefebvrei* is also known as *hberi* and is readily consumed by Bedouin children as treats [40,41]. Despite its agreeable taste, the size of the fruiting bodies limits the market potential of this species, although it has excellent antioxidant properties [32].

Leucangium

Leucangium carthusianum (syn. *Picoa carthusiana*) (Tul. & C. Tul.) Paol.

Pico carthusiana was originally described by Tulasne [42]. However, based on morphological analysis it was later reassigned as *Leucangium carthusianum* by Trappe [43]. Li [44] provided an in-depth study on the ultrastructure of this species, revealing multinuclei lemon-shaped spores (apiculate) that are distinctly different than those of

Picoa spp. When ripe, the sporocarps release a sweet aroma, often described as a cross between pineapple and chocolate. The peridium is black with varied morphology and sometimes exhibits pronounced pyramidal warts, superficially resembling some black tuber species. The gleba is firm with grey pockets of spore-bearing tissue separated by white veins and spores are 65–80 × 25–40 µm, fusoid, and smooth [45]. Recent phylogenetic analysis has provided a molecular position for *L. carthusianum* within the Morchellaceae–Discinaceae lineage, excluding this species from the genus *Picoa* [46]. In North Africa, *L. carthusianum* is found growing near *Rhanterium suaveolens* and *Helianthemum lipii* in calcareous soils in February and its primary value seems to be as an indicator species for *Terfezia* and *Tirmania* species [35,36]. Known as zouber in Tunisia [35,36], it has also been collected in Egypt [47], where it is primarily found in alkaline soils. This species is very widely distributed and has been observed from not only Africa, but also Asia, Europe, and North America. Despite morphological and scent similarities, the North American populations have a distinctly contrasting ecological niche, with different climatic, edaphic, and host-plant preferences compared to the North African populations. Molecular studies have only been conducted on samples from North American populations [46], so it is possible that the North African populations may be distinct to those in North America.

Terfezia

Terfezia have a long history of use domestically and as exports. Truffles from this genus are very widely consumed and appreciated. During Greek and Roman eras, truffles were imported from Libya and sold in the markets of Southern Europe [48].

Terfezia arenaria (syn. *Terfezia leonis*) (Moris) Trappe.

Moris, in 1829, was the first to describe a *Terfezia* species. Observed in Sardinia and originally termed *Tuber arenarium*, the species was later renamed *Terfezia leonis* by Tulasne [49]. Renamed again by Trappe in 1971 [43], this species is now known as *Terfezia arenaria*. With a whitish peridium that takes on brown hues at maturity, the gleba is also white with fertile pockets becoming pink with pale sterile veins. This species produces large (3–15 cm) ascomata that are subglobose, turbinate, and obpyriform, often with a tapered, sterile base. The ascospores are globous with a diameter of 25–30 µm that ornamented with separate, truncated or rounded warts and the scent is very weak. *Terfezia arenaria* is highly prized for culinary use and is harvested, in large quantities in Morocco from March until May; it is then exported to Kuwait and Saudi Arabia [20]. This species is found across North Africa frequently associating with *Helianthemum guttatum* and has been recorded in Algeria [50]. This species is also a cultivation candidate as mycorrhized plants can be successfully cultivated [51].

The antimicrobial properties of an aqueous extract of this and other *Terfezia* species has been investigated, and in contrast to other *Terfezia* species, thus far, there does not appear to be any noteworthy antibacterial activity by this species [52].

In rural Morocco, the tuber is collected by some unusual practices. Collectors use a sturdy stick or wooden pole with a pointed end to strike the ground around host plants. The sound of the stick striking the ground is noted and subtle differences are detected by the collector as being indicative of subterranean fruiting bodies (see Fig. 2). This labor-intensive harvesting method also means that fruiting bodies are often unripe at collection. Despite the extremely small size of host plants, wild sites can be very productive, with yields of 1,000 kg/Ha per annum being reported.

Terfezia boudieri Chatin.

Originally described using Algerian samples by Chatin [53], this species is now known to be widely distributed in North Africa. African countries with documented populations include Algeria, Tunisia, Egypt, Libya, and Morocco [20,53–55].

Ascomata are subglobose, turbinate, and obpyriform but this species differs from *T. arenarium* and has a darker peridium that is often cracked and is dark brown. The gleba is composed of salmon-pink fertile pockets divided by paler sterile veins. Ascospores (20–26 µm) are globose and decorated by truncated warts and conical spines. In contrast to *T. arenarium*, *T. boudieri* generally occurs in alkaline limestone soils, rather than acidic sites. It is often harvested under *Helianthemum* spp., such as *H. lipii*, *H. apertum*, *H. ledifolium*, and *H. sessiliflorum* in Morocco [20]. In Tunisia, it occurs under *H. lipii*, *H. sessiliflorum*, and sometimes *Rhanterium suaveolens* [35,36], and occasionally large larvae may be found in close proximity (see Fig. 3). Fruiting bodies are collected from January to May, with the majority of the harvest occurring between February to April [55].

Like *T. arenaria*, *T. boudieri* is a widespread and widely consumed *Terfezia* species in North Africa. Slama et al. [36] reported that in the northern Sahara (Tunisia), *T. boudieri* forms endomycorrhiza with *H. sessiliflorum*, whereas elsewhere the same partners may form ectomycorrhiza [56]. The impact on the plant partner may be positive, as mycorrhization has been shown to alter plant physiology by increasing CO₂ assimilation rates and water use efficiency, allowing the plant partner to adapt to the harsh environmental conditions of deserts [57].

Nutritionally, *T. boudieri* is one of the most studied of all the truffles occurring within Africa. Containing all the essential amino acids and being high in antioxidants, the composition of *T. boudieri* is 14% protein, 8% fat, and 54% carbohydrates [58]. Slama et al. [59] also observed that the fruit bodies are rich in Ca²⁺ (1,423), K⁺ (1,346), P (346), Mg²⁺ (154), and Na⁺ (77 mg/100 g dry weight).

This species also appears to have significant antimicrobial properties. In 2013, Dođan and Aydin [60] tested extracts of *T. boudieri* against nine different bacteria and one yeast. Extracts showed antimicrobial properties against all tested bacteria, although the most pronounced reported impact was on the yeast *Candida albicans*.

Terfezia claveryi Chatin.

This is a common species in sub-Saharan regions, often producing a large subglobose to turbinate ascomata (often with a sterile tapered base), with weights of 350 g not uncommon. The peridium is yellow-orange but matures to a brownish-reddish-black. The gleba is fleshy, with salmon-pink pockets of fertile tissue separated by whitish pink, sterile veins. Ascospores are globose reticulate, often ornamented with rounded truncated warts, and are 16–20 µm in diameter with six–eight asci [61]. This species primarily occurs in sandy, limestone soils and associates with a range of *Helianthemum* spp. [18]. This is another sought after *Terfezia* species that has a large market value and was the first desert truffle species to be successfully cultivated [62]. Widely harvested between March and May, it is often called “red Terfass of Tafilalet” [20]. Nutritionally, Murcia et al. [32] reported a composition of 16% protein, 7% fat, 65% carbohydrate, 8% crude fiber, and 4% ash. *Terfezia claveryi* has been shown to be relatively rich in thiamin and very rich in riboflavin, niacin, pantothenic acids, and pyridoxine [63]. The species is also a very rich source of Fe and a reasonably rich source of Zn and Mg²⁺ [63]. Extracts of this species have displayed good antimicrobial activities, with particularly noteworthy impacts on *Chlamydia trachomatis* and the healing of open wounds and stomach ulcers [64].

Terfezia canariensis Bordallo & Ant. Rodr.

Although not endemic to mainland Africa, this species exists on the Canary Islands just 100 km from the coast of Morocco and within the African continent. This species was previously misidentified as *T. claveryi* and was only identified as *T. canariensis* in 2012 [65].

With subglobose to turbinate ascomata 2–8 cm in size and a short obconic base, the peridium is reddish brown and blackens with age. The gleba is fleshy with pockets of fertile tissue separated by whitish pink, sterile veins. Ascospores are globose, 21–23 µm in diameter, and ornamented with a small-meshed reticulum with eight per asci [65].



Fig. 2 Desert truffles (*Terfezia arenaria*) being located in Morocco using the “stick” method (left) and freshly unearthed fruiting bodies (right). The photographs were taken by the corresponding author.



Fig. 3 Desert truffle (*Terfezia arenaria*) in the soil (left) in Morocco and an example of larvae (unidentified) that are occasionally found in close proximity to the fruiting body (right). Note: these larvae do not seem to damage the truffle, but may benefit from the locally elevated moisture levels. The photographs were taken by the corresponding author.



Fig. 4 *Helianthemum canariensis*, a host plant for *Terfezia canariensis*, growing in the mountains of Betancuria on the island of Fuerteventura. The photograph was taken by the corresponding author.

Endemic to the islands and associating with the local *Helianthemum* species, *H. canariensis*, this species can occur from coastal sites to as high as 600 m elevation (see Fig. 4). As with other desert truffle species, this truffle fruits after rainfall events, which is when locals can often be seen gathering them in some quantities. Despite the recent volcanic history of the Canary Islands, *H. canariensis* seems to favor soils derived from sedimentary rocks and especially those with a high calcium content.

Terfezia leptoderma Tul. & C. Tul.

Subglobose to turbinat ascumata with a sterile tapered base, smaller than some *Terfezia* species, and with a peridium that is light colored in the immature phase, ripening to a reddish-brown to blackish-brown at maturity and that is often cracked. The gleba is solid and fleshy, with fertile pockets of pinkish-grey to dark brown and separated with sterile yellowish-cream veins. Ascospores are globose (occasionally subglobose), 18–28 μm in diameter, ornamented with narrow cones or spines, and with eight per asci [55].

Growing in North Africa on acidic soil, this species associates with both *Helianthemum guttatum*, *Cistus*, oak, and pine (*Pinus pinaster* var. *atlantica*) and is primarily harvested between February and May [18,66]. Although edible and collected in its own right, this species is also valued as an indicator species for the arrival of the more valuable *T. arenaria* season. *Terfezia leptoderma* is reported to be often sold together with *T. arenaria* and is also sold as *T. arenaria* [20].

Terfezia olbiensis (Tul. & C. Tul.) Sacc.

Malençon [14] considers *T. olbiensis* to be an immature form and synonymous with *T. leptoderma*. In contrast, Alsheikh [55] maintains that *T. olbiensis* is a distinct species.

This conflict in the literature demonstrates the similarities of this spiny spore species to *T. leptoderma* to the extent that morphological (ascocata, ascospores, spore-ornamentation) and ecological descriptions are often the same. However, Kovács et al. [66] have clearly separated *T. olbiensis* from *T. leptoderma* using morphological and molecular characteristics, although the morphological differences are slight.

Tirmania

Across Saharan and sub-Saharan regions of Africa, *Tirmania* species are common and frequently abundant.

Tirmania nivea (Desf.) Trappe.

A highly regarded and widespread species, ascocarps are subglobose or pyriform, often with a basal mycelial attachment visible. The smooth peridium is off-white or light brown and smooth. The soft gleba is white or yellowish white, becoming yellowish brown with age. Ascospores are ellipsoid, 15–18 × 11–14 µm in diameter, and often eight per asci [55,61].

Tirmania nivea is found growing primarily in calcareous soils; it is harvested from December until March and hosted by many different *Helianthemum* species [18]. This species is very abundant in Northern Africa including parts of Algeria [51], Morocco [20], Tunisia [36], Libya, and Egypt [67]. Local names include “white Terfass of Tafilalet” and “Zubaidi” [18]. *Zubaidi* translates as “butter-like”, which is a reflection of both the color of this species and its historical value as a food stuff. This appreciation extends to the modern day and in some cases when a Bedouin finds a large *T. nivea* fruiting body, it is gifted to a local authority figure [40].

Nutritionally, *T. nivea* is reported to contain 40–60% carbohydrate, 20–27% protein, 2.4–7.5% lipid, 7–13% crude fiber, and 7.4–9.6% ash [68]. Al-Laith [10] concluded that the antioxidant levels of this species are particularly high. Similar to *Tirmania pinoyi* and *T. claveryi*, this species contains all essential amino acids, including those that are often limiting in foods of plant origin, such as the sulfuric amino acids (methionine, cysteine, tryptophan, and lysine).

Tirmania pinoyi (Maire) Malençon.

Ascocarps are subglobose to turbinate, often cracked and with a basal mycelial attachment. The peridium may be yellow to brown or reddish brown and the gleba is white to pale pink and veined. Ascospores are globose with often eight per asci, 16–18 µm in diameter, and with a smooth surface. Ascospores differ from those of *T. nivea*, with the inner side of wall being minutely roughened [55,61]

Tirmania pinoyi are harvested from December until March, are hosted by *Helianthemum* species, and may be found growing in more acidic conditions than *T. nivea* [69]. *Tirmania pinoyi* may also be known by the same local names such as *T. nivea*, “white Terfass of Tafilalet”, and “Zubaidi” [18]. They are very abundant in Northern Africa including parts of Algeria [51], Morocco [20], Tunisia [36], Libya, and Egypt [67] and are capable of forming ectomycorrhiza (in high phosphate substrates) as well as endomycorrhiza (in low phosphate substrates) [51].

Nutritionally, *T. pinoyi* has some similarity to *T. nivea*, containing all essential amino acids as well as having significant antioxidant activity [70]. Extracts of this fungus have also been shown to exhibit potent antimicrobial activities against gram-positive bacteria (*B. subtilis* and *S. aureus*) that are known to cause eye infections [71]. Omer et al. [72] reported that desert truffles (*Tirmania* and *Terfezia* spp.) have a history of utilization in folk medicine for the treatment of ophthalmic diseases.

Conclusion

Knowledge of truffle diversity and documented appreciation/use by local populations is largely confined to the northern and southern areas of Africa, with little known occurrence along the central equatorial belts. More knowledge exists on truffle species of Northern Africa than Southern Africa and this reflects a bias within the literature. Regardless, the majority of known truffles occurring within Africa are desert species that grow in mycorrhizal association primarily with members of the *Helianthemum* genus. Knowledge about the indigenous use of African fungi has largely been passed orally between generations and due to the fragmentation of many populations, much of this knowledge may have been lost. Urgent communication is needed with local populations to ensure that such knowledge is retained, and surveying work is essential to assess the diversity of hypogeous fungi across the continent. Truffle species that have been identified and tested have shown a range of promising attributes as sources of medicinally active compounds, and their extracts have shown a range of antimicrobial properties; thus, any newly discovered species may prove to be an important source of novel active compounds. Furthermore, although we know that many desert truffle species are mycorrhizal, very little is known about their ecological roles and primary spore vectors; additionally, whether there are threats to their populations from anthropogenic (or other) factors is unknown. It is clear that much remains to be uncovered about the hypogeous fruiting bodies of mycorrhizal fungi across Africa.

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