Desert Truffles of the African Kalahari: Ecology, Ethnomycology, and Taxonomy[1]

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Desert Truffles of the African Kalahari: Ecology, Ethnomycology, and Taxonomy. The Khoisan people of the Kalahari Desert have used truffles for centuries. The extreme conditions in which desert truffles grow means that they fruit only sporadically when adequate and properly distributed rainfall occurs, and then only where suitable soil and mycorrhizal hosts occur. Truffles are hunted in the Kalahari by men and women; they look for cracks in the soil, often humped, caused by expansion of the truffles, which are then extracted with hands or digging sticks. The truffles are eaten raw or cooked (boiled, roasted over fire, or buried in hot ashes). Commercial harvest of Kalahari truffles has increased in the last decade and the quantities harvested have been observed to be declining where livestock have been concentrated.

Key Words: Hypogeous fungi, mycorrhizae, Ascomycota, Pezizales, Pezizaceae, Kalaharituber, Eremiomyces, Mattirolomyces.

Introduction

The nomadic peoples of the Kalahari in southern Africa have probably used desert truffles for millennia (Trappe 1990). The earliest documents recording the use of truffles for food date back as early as 300 years B.C. for the North African cradles of civilization (Chatin 1984; Mattirolo 1922; Pagnol 1973; Rayss 1959; Tulasne and Tulasne 1851). Desert truffles belonging to the genera *Terfezia* and/or *Tirmania* have been eaten by the indigenous peoples of North Africa and the Middle East from prehistoric times; in addition, they were probably served at royal feasts of the Pharaohs as described by Pliny and Theophrasis and mentioned in the Talmud (Pagnol 1973; Rayss 1959).

This article reviews current knowledge of the ecology, ethnomycology, and taxonomy of desert truffles used by the Khoisan people (sometimes referred to as Bushmen or San) of the Kalahari. In addition to the two genera discovered so far in the Kalahari of Namibia and Botswana, we include a third from west of Kimberly in Northern Cape Province of South Africa, because it is in the same arid savannah biogeographic zone as the southern Kalahari proper (Alcocks 1953). Each of these genera is represented by a single species in the area: *Kalaharituber pfeilii* (Henn.) Trappe & Kagan–Zur, *Eremiomyces echinulatus* (Trappe &

[1]Published online 23 October 2008.

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Marasas) Trappe & Kagan–Zur, and *Mattirolomyces austroafricanus* (Trappe & Marasas) Trappe & Kovacs. A key to and brief descriptions of these species are presented in the final section of this paper.

Kalaharituber pfeilii, commonly known in English as the Kalahari truffle (Figs. 1 and 2) has long been treated within the Mediterranean genus *Terfezia* until DNA sequencing showed it to be on a different evolutionary trajectory. Accordingly, it was assigned to the new genus *Kalaharituber* (Ferdman et al. 2005). In times past, it has been variously misidentified as *Terfezia boudieri* Chatin (Ceruti 1960; Pole-Evans 1918), *T. claveryi* Chatin (Doidge 1950; Marloth 1913; Pole-Evans 1918), or *Terfezia pinoyi* Maire (Mattirolo 1922).

A companion piece in this issue (Trappe et al. 2008) presents comparative information about the use of the taxonomically distinct truffles known to Aborigines of the central Australian Outback. Although the genera and species of desert truffles differ from continent to continent, many aspects of their ecology are similar, as are their uses by geographically distant, nomadic but culturally unrelated desert peoples.

Truffle Ecology in the Kalahari

Weather and Seasonality

Given the relatively sparse food resources in arid lands, human desert inhabitants have learned over the generations to locate and utilize all available resources, particularly water (Bayly 1999). Desert truffles manifest themselves to the careful observer and can be relatively easy to collect by people with traditional expertise.

Fig. 1. Uncleaned, sand–covered *Kalaharituber* specimens fresh from the field. (Photo by Adriaan Smit, all rights reserved).

Fig. 2. Sliced *Kalaharituber* truffles showing the pale brown outer peridium and interior whitish pockets of spore–bearing tissue separated by pale brownish veins. (Photo by Adriaan Smit, all rights reserved).

Desert truffles fruit only in years with adequate and properly distributed rainfall. In Kuwait, for example, species of *Terfezia* and *Tirmania* fruit in years with a minimum rainfall of about 180 millimeters (mm), well distributed from October through March (Awamah and Alsheikh 1979). Similar data have not been published for southern African and other Southern Hemisphere species, but the need for water to initiate fruiting is confirmed by tradition and experience.

A feature shared by all desert truffles is an abundance of large, inflated, thin–walled cells in the peridium and gleba (Alsheikh 1994; Alsheikh and Trappe 1983; Trappe 1990; Trappe and Weber 2001). These structures are not effective for water retention, as one might surmise, but instead appear to be integral to spore dispersal. The thin–walled cells take up large amounts of water, swelling in the process and providing the moisture needed for spore formation. The underground swelling of the fruiting bodies produces mounds visible on the surface of the sandy soil. These dry out and crack (Fig. 3), producing a clear visual cue to the presence of truffles below (Leistner 1967; Mshigeni 2001; Story 1958; see also Australian examples, e.g., Beaton and Weste 1982; Thomas 1974). Subsequently, the sand sloughs off and is blown away by the wind to expose the drying fruiting bodies (McLennan 1961), whereby the inflated cells collapse into powdery fragments, exposing the spores that are released by abrasion from blowing sand and become wind borne. Further evidence of the

Fig. 3. Cracked mounds on the soil surface formed by expanding Kalahari truffles beneath. (Photo courtesy of the South African Department of Agriculture, all rights reserved).

effectiveness of this dispersal method was discovered in Kuwait by Awamah and Alsheikh (1979, 1980): Spores from desert truffles that had been dried in the sun and stored for nine months germinated faster than spores taken from fresh fruiting bodies. Kagan-Zur et al. (1999) and Roth-Bejerano et al. (2004) extracted spores from dried specimens of Kalahari truffles and, after plating the spores on agar, observed germination.

As in other deserts, rainfall in the Kalahari is highly erratic; one year the precipitation may be less than a third of the average amount and the following year it may be more than double (Leistner 1967). Regarding truffle associations with rainfall, Story (1958) quotes G. Scholtz of Ghanzi, a town in the central Kalahari of Botswana:

> Nature appears to be against you this year. I even offered five shillings per truffle, but according to the San (my offer was just laughed at) no rain, no truffles. And we certainly have had no rain.

Long–term records from seven stations in the southern Kalahari ranged in annual average from 156 to 362 mm; the heaviest rainfall occurred during the months of November through April, averaging from 11 to 75 mm (Leistner 1967), with regional differences being highly pronounced. A minimum precipitation of 10 mm over a short time is required to noticeably affect vegetation, and two showers totaling 20 to 25 mm falling within two weeks markedly affect vegetation (Leistner 1967). In the southern Kalahari, truffles have been recorded as fruiting in April and May after late summer rains (Leistner 1967). Pole-Evans (1918) gives the fruiting season as March through June. Story (1958) reports the fruiting season to be from April into July for the central and northern Kalahari. Mshigeni (2001) found truffles in northern Namibia towards the end of the pearl millet growing season in June, i.e., at the end of the rainy season when air and soil temperatures are cooling (Leistner 1967).

Substrate

Pans of compact calcareous sand are common in the Kalahari and have a strikingly uniform, zoned vegetation. Leistner's (1967) diagrammatic illustration of vegetation zones on these pans has a remarkable resemblance to the representation of pans in Australia in the painting by Aboriginal artist Betsy Napangardi Lewis (see Fig. 1 in Trappe et al. 2008, this issue). In the southern Kalahari, the truffles grow on fairly compact to compact, pink or infrequently white, slightly calcareous sands (Leistner 1967). Analyses of Kalahari truffle–bearing sands from nine locations (two in Botswana and seven in Namibia) by Taylor et al. (1995) showed pH ranging from 5.5–6.5 in eight and 7.2 in one. $CaCo_3$ was also low, ranging from 0.3–3.1%. Story (1958) states that Kalahari truffles occur in the dips between sand dunes (Fig. 4). Although Kalahari truffles have been associated solely with calcareous sands in the literature as cited above, they also have been found in arenosol within the top 5–20 centimeters (cm) of the soil (D. Modise, pers. com.).

Fig. 4. Typical Kalahari truffle habitat: sandy soil covered with shrubs and grasses. *Kalaharituber* often fruits in the dips between sand dunes (background); gemsbok (*Oryx gazella*) are in the foreground. (Photo by Adriaan Smit, all rights reserved).

Plant Associations

Plants associated with Kalahari truffles are as diverse as with the Australian truffles (see Trappe et al. 2008, this issue) and include both herbaceous and woody species (Leistner 1967). Typical habitats in the wild have shrub–grass–forb plant communities (Fig. 4), although they also fruit in cultivated fields of various food plants. Pole-Evans (1918) and Palmer and Pitman (1961) reported association with shrubs of *Acacia hebeclada* DC. In the area around Ghanzi in the central Kalahari, truffles were collected in a mixed grassveld of *Aristida* and *Eregrostis* species with scattered trees of *Acacia uncinata* (Story 1958).

Mycorrhiza formation with herbaceous plants appears probable. Mshigeni (2001) reports that northern Namibian villagers especially look for truffles in fields of pearl millet (*Pennisetum typhoides* [Burm.] Stapf & C. E. Hubb.). Kalahari truffles have been found recently in a field of sorghum (*Sorghum bicolor* [L.] Moench) in the Kweneng District of Botswana (K. Mogotsi, D. Modise, E. Khonga, and S. Machacha, pers. com.). They have also been observed to fruit in circles around *Grewia flava* DC. shrubs (Murphy 2007). Taylor et al. (1995) were the first to carefully examine roots associated with the basal "stalk" of densely interwoven hyphae, roots, and soil formed at the base of Kalahari truffles. They found evidence of Hartig nets (the hyphal network surrounding outer rootlet cortical cells, a structure typical of ectomycorrhizae) in the Bignoniaceae (*Rhigozum brevispinosum* Kuntze, *R. trichotomum* Burch.), Combretaceae (*Terminalia sericea* Burch. ex DC.), Mimosaceae (*Acacia hebeclada, A. mellifera* Benth., *Dichostachys cinerea* [L.] Wight & Arn.), Poaceae (*Enneapogon cenchroides* [Licht.] de Winter, *Eragrostis rigidor* Pilg., *Stipagrostis uniplumus* [Licht.] de Winter), and Tiliaceae (*Grewia flava*). Kagan-Zur et al. (1999) found Kalahari truffles in a cultivated field with the basal mycelium entangled with roots of tsammas, the wild ancestors of cultivated watermelons (*Citrullus lanatus* [Thunb.] Matsum. & Nakai, = *C. vulgaris* Schrad.). The roots were colonized with a septate mycelium, the hyphae seeming "to stream from one cell to the other, filling the cells rather densely at times. No Hartig net was observed." DNA from the colonized roots matched that of fruiting bodies of the truffle. *C. lanatus* is an annual indigenous in the Kalahari; evolution of a mycorrhizal association with Kalahari truffles is conceivable, especially in light of the similar mycorrhizal morphology formed by desert truffles in the genera *Terfezia* and *Tirmania* with annuals in the Arabian Peninsula (Awameh 1981; Awameh and Alsheikh 1979). These and related members of the Cucurbitaceae are used by the Khoisan as sources of both food and water. Much more research is needed to determine the Kalahari truffle's full range of hosts.

Predation by Animals

Animal dispersal of Kalahari truffle spores is little recorded. Mills (1990) observed a brown hyena (*Hyaena brunnea*) digging up and eating 21 truffles. Amy Schoeman (2008) reports that fruitings can be located by watching baboons (*Papio ursinus*),

> "which are particularly partial to them, as are bat–eared foxes (*Otocyon megalotis*) and meerkats (*Suricata suricata).* Half–eaten portions are sometimes seen lying around where animals had had their fill."

The Tswalu Kalahari Reserve News (2008) notes the above animals plus meerkats as truffle mycophagists and ventures that "the earliest humans in the region, the San and Nama peoples, probably learned about this earthly delight from watching the animals." Lester Levy (2008) watched a meerkat eat a truffle, observing that "he seemed to enjoy it immensely."

Ethnomycology

Native terms for the Kalahari truffle include *mahupu* or *n'xaba* (locally in Khoisan, D. Modise, pers. com.); *dcoodcoò* (in Khoisan and Jul'hoansi, Leffers 2003); *kuutse* (in Khoisan, Tanaka 1980); *tkabba* (language unspecified, Leistner 1967); *mahupu* (in Botswana, language unspecified but presumably Setswana, Taylor and Parratt 1995); *omatumbula* (in Bantu and Oshidonga, Mshigeni 2001; W. Haacke, pers. com.); *hawan* or *haban* (in Khoe and Khoekhoegowab, W. Haacke, pers. com.); and *n/abba* (in Nama, Tswalu Kalahari Reserve News 2007). The other two truffle species treated in this paper are infrequent to rare, and no specific reference to them being used as food has come to our attention, although they quite likely would be eaten if found.

Both women and men search for truffles; the women keep an eye out for them when gathering firewood. Mshigeni (2001), Story (1958), and Thomas (1974) report villagers looking for cracks

or cracked humps in the soil to find truffles. Thomas (1974) describes hunting with a local woman:

> Keeping her eyes on the ground, Twikwe noticed a tiny crack in the sand. She scooped with the point of her digging–stick, tipped out a truffle, and picked it up almost without stopping. As we walked on, she broke it in half, put half in her kaross, and offered half to me.

According to Story (1958),

> A good deal of practice is needed before [the method] can be applied, for the cracks are slight, and are specially difficult to find where the surface has been disturbed by game or stock, or where they have been partly filled in by windblown sand, but matters are eased somewhat by the fact that there is seldom more than about three inches of sand covering the truffles and that they grow in patches.

The truffles may vary considerably in appearance; when extracted from the soil, they are covered with clinging sand (as can be seen in Fig. 1), which masks their true color. They may be rounded or irregular in shape. Mshigeni (2001) attributes such morphological differences to differences in soil hardness. Pole-Evans (1918) records a specimen as weighing 226 grams (g), but notes that the usual weights run 25 to 45 g. Specimens studied by Taylor et al. (1995) ranged from 10 to 200 g. One of the largest on record was found in May 2005 at Obobogorob, 200 kilometers (km) northwest of Upington in South Africa. The truffle weighed 400 g and measured 11×12 cm (Fig. 5). An even larger one, found in 2006 at Khokhotsa Village in Botswana, weighed 500 g and was hollow in the center: "The large size was due to the very good rains we had in the Kgalakgadi region of Botswana," according to Prof. E. B. Khonga (pers. com.).

Not only are Kalahari truffles considered a delicacy, but they are nutritious as well. Analysis of 24 vegetables for energy content (kj) revealed that, on a weight–for–weight basis, Kalahari truffles were second only to cooked maize among the numerous vegetables analyzed; both scored notably higher than the other vegetables (Nutrition Information Center, University of Stellenbosch 2008). The truffles also had considerably higher fat, phosphate, and potassium contents than maize or other vegetables.

Story (1958) reports that the truffles may be boiled or roasted. "The texture is like soft cheese. They are not aromatic and the flavour is far inferior to that of the best European truffles."

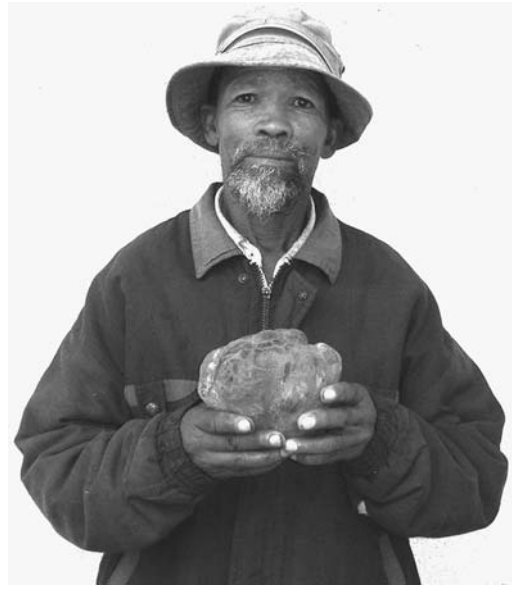

Fig. 5. Truffle hunter Hendrik Josop holding a Kalahari truffle that weighed 400 grams—one of the largest on record. (Photo by Rudi Botha, all rights reserved).

Kalotus (1996) characterizes the Australian desert truffles similarly. But Hein Botha (pers. com.) of South Africa, who grew up in the Kalahari, emphatically disagrees:

> I can assure you that Kalahari truffles are *very* aromatic. I have only had a European truffle once, at a restaurant in Cape Town. That evening we smelled both European and Kalahari truffles and were all convinced that the Kalahari truffle had a significantly stronger aroma than the European one.

Other descriptions of its aroma include "ultra mushroomy" and "like the Kalahari smells after rain" (Tswalu Kalahari Reserve News 2008). Leistner (1967) notes the Kalahari truffles are eaten boiled or baked in ashes. They may also be fried (Smits, pers. com.). Sometimes they are eaten fresh out of the ground and are said to have a delicious, salty flavor (Thomas 1974). Just as in other parts of the world, some regard truffles as aphrodisiacs.

Although Kalahari truffles are now harvested for sale, they are not even close to being as expensive as European truffles are. Mshigeni (2001) reports that when Kalahari villagers marketed their truffles on the roadsides, the average price at that time was USD 4.00 for 25 kilograms (kg) (USD 0.16 per kg). When he asked them why they sold their truffle harvest at such a low price, the villagers

responded, "*Omatumbula* are God's given manna from the soil. You don't grow them—they come up from the soil on their own."

Taylor and Parratt (1995) point out that in Botswana, truffle harvesters in rural communities earn cash by selling raw truffles to intermediaries and processors, but could earn more if they had better access to even low–level technology.

In traditional Khoisan mythology, Kalahari truffles were regarded as eggs of the "lightning bird" because they appeared after thunderstorms (Murphy 2007). According to Tanaka (1980), some Khoisan hunters believe that desert truffles (*kuutse* or *n'xaba*) counteract the effects of poisoned arrows in animals they have shot and, until the hunter "confirms the death of the animal, he can take no food or drink other than water, for the San believe that if the archer eats food, the wounded animal will regain its health and escape. Most importantly, the hunter must not eat *kuutse*, because the poison in the body of a wounded animal will be weakened. The hunters keep a piece of dried *kuutse* to eat as an antidote in case they accidently cut themselves with a poisoned arrow."

Discussion

Unlike the situation of rapidly declining traditional knowledge and use of desert truffles in Australia (see Trappe et al. 2008, this issue), the Khoisan of the Kalahari continue to use and value the Kalahari truffle. However, truffle production appears to be declining, at least where livestock are concentrated. Taylor et al. (1995) note:

> Truffles used to be prolific in the Kalahari when appropriate rainfall conditions prevailed. Owing to disturbance of the sandy soils around the Kalahari villages by cattle and goats, the truffle harvest is steadily declining. An important natural complement of the local diet is thus being endangered.

These observations raise the possibility that some land use practices introduced by Europeans may conflict with Kalahari truffle production, especially on fragile sandy soils. This possibility certainly calls for developing good information on the ecological requirements of these desirable mushrooms.

Commercial harvest of Kalahari truffles is well underway. An Internet search revealed numerous sites advertising Kalahari truffles for international sale. Exploitation of desert truffles should be conducted with care to ensure sustainability, and with the best interests of the original custodians of these fascinating mushrooms a foremost consideration. Again, sound knowledge of the truffle's habitat requirements is needed. Mshigeni et al. (2005) assert that, if indigenous people such as the Khoisan are to be the primary beneficiaries of desert truffles, not only must sound biological information be developed, but also the people themselves must be made aware of the value of this unique desert resource and how to market it.

Keys and Descriptions

The Kalahari truffle species have been described in detail elsewhere (Ferdman et al. 2005; Marasas and Trappe 1973; Trappe et al. n.d.). The Kalahari truffle, formerly *Terfezia pfeilii*, was demonstrated by molecular phylogenetic techniques to belong in its own genus, not with the Northern Hemisphere *Terfezia* spp. (Ferdman et al. 2005). Its updated name is *Kalaharituber pfeilii*. The second Kalahari truffle, formerly termed *Choiromyces echinulatus*, similarly deserves its own genus (Ferdman et al. 2005), so now it is named *Eremiomyces echinulatus*. In the descriptions below, the accepted name is followed by an equals sign and the earlier, superceded name. All three truffle species described here belong to the family Pezizaceae. The key below emphasizes macroscopic characters, but microscopic characters, especially those of spores, are generally useful to confirm identification of truffles.

Key to Kalahari Truffles

1. Truffle surface brown; interior white in youth, at maturity with yellowish to brown pockets separated by white veins. Spores ornamented with minute, crowded spines.....*Kalaharituber pfeilii.*
1. Truffle white to cream color; interior pale, marbled with meandering veins. Spores ornamented with blunt rods and cones or a honeycomb mesh.
   2. Spores ornamented with openly spaced, blunt rods and cones.....*Eremiomyces echinulatus.*
   2. Spores ornamented with a honeycomb mesh.....*Mattirolomyces austroafricanus.*

Kalaharituber pfeilii (Henn.) Trappe & Kagan–Zur (Figs. 1, 2, 5)
= *Terfezia pfeilii* Henn.

Truffles Top–shaped to subglobose, up to 7 (–11) × 9 (–12) cm, with a basal tangle of hyphae, roots, and soil dense enough to form a stalk–like structure. Surface minutely velvety and covered with soil or sand but often becoming smooth on exposed areas, yellowish brown to dark brown with yellowish wrinkles or cracks. Interior solid, white in youth, at maturity with yellowish to brown fertile pockets separated by white veins. **Spores** Globose, 16–22 (–26) micrometers (µm) broad excluding the ornamentation of densely crowded, acute spines 0.5–1.5 (–2) × ≤0.5 µm. **Asci** Not reactive to iodine solution.

Etymology: Kalahari + Latin *tuber* (truffle), the "Kalahari truffle," and *pfeilii*, in honor of Count Joachim von Pfeil, German colonial politician, traveler, and author who obtained the type collection in the 1890s.
Distribution, habitat, and season: Kalahari and adjacent arid areas of Botswana, Namibia, and Northern Cape Province of South Africa; typically in sandy soil, April through July.

Eremiomyces echinulatus (Trappe & Marasas) Trappe & Kagan–Zur
= *Choiromyces echinulatus* Trappe & Marasas

Truffles Subglobose, brown as dried but probably pale when fresh. Interior pale, marbled with meandering veins. **Spores** Globose, 10–14 µm broad excluding the ornamentation of straight, somewhat distant, obtuse rods and cones 1–2 × 0.5–1 (–1.5) µm. **Asci** Not reacting to iodine solution.

Etymology: Greek, *eremio–* (desert) + *–myces* (fungus), the "desert fungus," and Latin, *echinulatus* (spiny) in reference to the spore ornamentation.
Distribution and season: Kalahari of Botswana and Northern Cape Province of South Africa, June.

Mattirolomyces austroafricanus (Trappe & Marasas) Trappe & Kovacs
= *Terfezia austroafricanus* Trappe & Marasas

Truffles Subglobose, surface as dried orange brown, probably pale when fresh. Interior as dried ochraceous, marbled with pale, meandering veins and pockets. **Spores** Globose, 25–30 µm broad excluding the ornamentation of straight, truncate to obtuse spines (2–) 3–5 (–6) × 1–3 µm connected by walls to form a partial to complete, honeycomb–like configuration. **Asci** Not reactive to iodine solution.

Etymology: Mattirolo– (renowned Italian mycologist who discovered the first species of the genus) + Greek, *–myces* (fungus), "Mattirolo's fungus," and Latin, *austro–* (southern) + *–africanus*, (African), "southern African."
Distribution, habitat, and season: Northern Cape Province of South Africa, in arid savannah; April.

Acknowledgements

These studies were supported in part by the U.S. Forest Service, Pacific Northwest Research Station, Forestry Science Laboratory, Corvallis, Oregon. Magda Nel of the University of Pretoria granted permission to use the photo of *Kalaharituber pfeilii* by G. C. A van der Westhuizen and Albert Eicker. Professors Keto Mshigeni, Wilfrid Haacke of the University of Namibia, and Dean Elenimo Khonga of the Botswana College of Agriculture shared valuable insights on the traditions, hunting and native names of Kalahari truffles. Professor David Modise of the University of South Africa provided information and reviewed the manuscript on very short notice. Hein Botha shared his personal knowledge of Kalahari truffles with us, and Rudi Botha provided the photograph of Hendrik Josop holding an unusually large specimen. The South African Department of Agriculture permitted use of Fig. 3.

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