The Edible Mushrooms of Madagascar: An Evolving Enigma[1]

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The Edible Mushrooms of Madagascar: An Evolving Enigma. This paper on the most significant edible wild mushrooms of Madagascar is organized in the following four categories: (1) mushrooms of introduced eucalypt plantations, (2) mushrooms of introduced pine plantations, (3) mushrooms of native forests and woodlands, and (4) mushrooms found in fields, agricultural waste and other altered, non–forest habitats. *Eucalyptus robusta* plantations yield by far the bulk of edible mushrooms that are sold, especially species of *Russula* and *Cantharellus*. Some *Suillus* species of northern hemisphere origin have been introduced with pine plantations and are locally important, forming the basis of a small canning industry. In native woodland areas on the central plateau, several ectomycorrhizal mushrooms—very similar to those on the African mainland—are collected and consumed. With the exception of the widely marketed *Cantharellus platyphyllus* ssp. *bojeriensis*, these are only of local importance in the villages and smaller markets of the area. Denser forests in the mountains or on the east coast as well as manmade habitats such as fields, pastures, and agricultural wastes are searched for saprobic mushrooms of various types. Some of these saprobic mushrooms show considerable potential for cultivation. The variety of ectomycorrhizal mushrooms found in eucalypt plantations is unprecedented outside of Australia and, for the most part, do not appear to be of Australian origin. Possible reasons for this are briefly discussed. Two economically important species, *Russula prolifica* sp. nov. and *R. edulis* sp. nov., are newly described.

Les champignons comestibles de Madagascar: l'énigme se poursuit. Les champignons comestibles sauvages de Madagascar sont présentés d'après leur appartenance à quatre habitats différents: plantations exotiques d'Eucalyptus, plantations exotiques de pins, savanes et forêts indigènes et, enfin, champs cultivées, prairies et déchets agronomiques. Les plantations d'Eucalyptus (en particulier d'*E. robusta*) produisent de loin la majorité des champignons comestibles mis en vente, surtout chanterelles et russules. Quelques bolets du genre *Suillus*, manifestement introduits de l'hémisphère nord, pullulent localement sous des pins importés et font l'objet d'une industrie artisanale de conserves. Sur le Haut Plateau, plusieurs espèces de champignons ectomycorrhiziques, très similaires à celles décrites du continent africain, sont ramassées et consommées dans l'aire des savanes. A l'exception du *Cantharellus platyphyllus* ssp. *bojeriensis*—espèce très commune sur les marchés et le long des routes du Haut Plateau, ces différentes espèces ne représentent qu'un intérêt local. Les forêts denses d'altitude ou le long de la côte Est, ainsi que les habitats créés par l'homme (champs, prairies de pâturage, déchets de l'agriculture) sont explorées à la recherche d'un nombre de champignons comestibles saprophytes, dont certains à potentiel très prometteur pour la domestication. La diversité des champignons ectomycorrhiziques associés aux plantations d'eucalyptus dépasse de loin celle observée dans les autres pays ou les eucalyptus ont été introduits par l'homme. L'auteur discute sommairement quelques éléments qui ne semblent pas favoriser l'hypothèse d'une éventuelle origine australienne pour la plupart de ces champignons. Deux russules comestibles représentant un intérêt économique, *R. prolifica* sp. nov. et *R. edulis* sp. nov., sont sommairement décrites comme nouvelles.

Key Words: *Cantharellus*; *Russula*; *Eucalyptus*; eucalypts; *Pinus*; edibility; edible mushrooms; Madagascar; ectomycorrhizal.

Introduction

Madagascar is the fourth largest island in the world and is characterized by enormous climatic and ecological variation. The northern and southern tips of the island are 1,500 kilometers (km) apart and its surface area is equivalent to that of France, Belgium, Luxemburg, and the Netherlands combined. Along the east coast, prevailing winds rise

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rapidly from the narrow coastal plains over the slopes of the eastern escarpment to elevations of 1,000 to 1,500 meters (m), up to peaks of 2,876 m in the Massif de Tsaratanana. These winds bring abundant rains to the entire east coast of Madagascar, with total annual rainfall of over 3,500 millimeters (mm) for the wettest parts in the northeast. Immediately to the west of this north–south oriented mountain range, the landscape continues in the form of a hilly plateau, which occupies the central part of the island; this area is often referred to as the central highlands or central plateau (Fr: *les Hautes Terres*). To the south and west of this plateau, the landscape gradually becomes drier and the southwestern part of the island is semi–desert.

Madagascar is separated from Africa by the 460–km wide Mozambique Channel; it was connected to Africa until 140 million years ago. Before that, it was nestled between what is now Kenya and India as part of the supercontinent called Gondwana. One testament to this ancient history is the distribution pattern of mushrooms, such as the giant boletes of the genus *Phlebopus*, which were first described from Madagascar (Heim 1936) but also are known in tropical America, New Zealand, Australia, Southeast Asia, and Africa. Another example is the enigmatic pagoda fungus, *Podoserpula pusio* (Berk.) D. A. Reid, previously known only from a few collections in Venezuela and from New Zealand/Australia but recently discovered in one of the few protected forest areas near the capital of Madagascar, Antananarivo (Buyck 1997).

The Malagasy people (Fig. 1) are the result of the intermingling of immigrants including African peoples who crossed the Mozambique Channel, Malayo–Indonesians who introduced rice farming to Madagascar long ago, and much more recently, immigrants from Europe, China, India, and the Comores. The colonial period strengthened the political and intellectual domination of the Malayo–Indonesian ethnicities, especially the Merina, the ascendant ethnic group since the late 18th century. Merina (about 25% of the population) and the related Betsileo (about 12%) live in the central highlands, while the coastal peoples or "cotiers"—such as the Betsimisaraka, Tsimihety, and Sakalava—are of mixed African, Malayo–Indonesian, and Arab ancestry.

The affinities of the Malagasy plant flora are strongest, not surprisingly, with Africa, reflecting their proximity and the fact that the two land masses were once joined. The similarities to Africa are most pronounced in the drier western and southern parts of the island. Clear relationships are also evident with Asia (primarily India, Sri Lanka, and the Malaysian region), especially in the moister eastern portion of Madagascar. Other islands in the region (Comores, Réunion, and Mauritius) are of recent volcanic origin and have much less diverse and distinctive floras. Madagascar, on the other

Fig. 1. A family of chanterelle gatherers, ages one and one–half to twenty–eight, in a eucalypt plantation near their village outside the town of Fianarantsoa on the central plateau of Madagascar. (David Arora, all rights reserved).

hand, is noteworthy for its exceedingly high levels of endemism for very diverse groups of organisms, even at high taxonomic levels (Myers et al. 2000). Unfortunately, there is little left of Madagascar's original fauna and flora and the island is now listed among the top conservation priorities in the world because of the unique character of its rapidly vanishing biodiversity.

Until the late 19th century, the literature on Malagasy mushrooms consisted mostly of anecdotal reports using local Malagasy names for the species (Poisson 1952). The first scientific publications on Madagascar's mushrooms resulted from the great explorations in the late 19th and early 20th centuries (Cooke and Massee 1890; Hennings 1908). Several of these early publications reported on the consumption of edible mushrooms on the island, including the description of two new species in *Cantharellus*, many new boletes, and several edible mushrooms in the genera *Agaricus* and *Lepiota* sensu lato (Dufour 1913; Patouillard 1924, 1927; Dufour and Poisson 1926). Mycology in Madagascar was greatly advanced by Roger Heim, who initiated a series of monographs and papers based on his own six–month collecting expedition to Madagascar in 1934–1935. There was also a large number of collections sent to Paris by resident French collaborators, in particular phytopathologist Gilbert Bouriquet and Raymond Decary, an agronomist and keen naturalist with a special interest in gasteromycetes (Decary 1927, 1946). During the period between Heim's visit and the end of World War II, mycological collection and research continued in Madagascar (Boiteau 1944; Bouriquet 1944; Anon. 1947), resulting in a special exposition on mushrooms at Antananarivo in 1942 that was seen by more than 2,000 visitors—probably the first exhibit of its kind in any tropical country. Since Madagascar's independence in 1960 and Heim's retirement and subsequent death in 1979, the mushrooms of Madagascar have been more or less ignored by western scientists. It was not until 1996, when this author took a position as mycologist at the Parisian National Museum of Natural History (where Heim had formerly been director), that the study and inventory of Madagascar's mushrooms was resumed through frequent collecting trips with students and collaborators.

Most of Madagascar's mushroom species have yet to be described. Yet the thousands of collections deposited in the Paris Museum, first by Heim and his correspondents and more recently by the author and his collaborators, constitute a rich source of specimens and field data, especially for the larger forest mushrooms. These collections document a large number of wild, locally consumed and marketed species. Boa's (2004) recent global summary of edible and medicinal mushrooms lists 75 species for Madagascar based on published records. Remarkably, despite decades of ongoing research, most of the common wild edible mushroom species of Madagascar have not been formally described in the scientific literature and are thus missing from Boa's list. Also, several significant errors were found in Boa's source references for Madagascar, including the listing of one reputedly toxic species, *Amanita robusta* Bouriquet, as edible.

One unfortunate consequence of this neglect of mushrooms is that they have been ignored in the planning of conservation strategies for the rapidly degrading natural habitats of Madagascar. Forests and woodlands dominated by a low diversity of plant species have been systematically considered of low conservation priority. Yet it is precisely in these undervalued (from a conservation standpoint) habitats that important genera of larger forest mushrooms, such as *Russula, Lactarius, Amanita, Cantharellus*, and several genera of boletes, are especially prominent and prolific enough to warrant attention as a significant source of food and money for local people. As the above genera are well known as ectomycorrhizal root symbionts of northern temperate forests, they presumably play a crucial ecological role as obligate symbionts of some of the dominant, endemic forest trees in Madagascar. However, the diversity and importance of these ectomycorrhizal relationships have hardly been investigated in Madagascar. (Those readers familiar with temperate mushrooms will note the absence of other important temperate ectomycorrhizal genera such as *Cortinarius, Hebeloma, Tricholoma*, and *Inocybe*; these genera are principally "cold–adapted" mushrooms and are very rare in subtropical and tropical countries.)

Buyck (2002) provides a short overview of the various habitats and hosts for Madagascar's ectomycorrhizal mushrooms. For those interested in the origin, evolution, and specificity of ectomycorrhizal relationships, the island's mixture of native and exotic elements presents a challenging puzzle. The diversity of native and exotic ectomycorrhizal tree hosts includes recently imported Australian eucalypts (*Eucalyptus* spp.), imported northern hemisphere pines (*Pinus* spp.), endemic species in two

genera shared with Africa (*Monotes* in the Dipterocarpaceae, a family dominating Asian ectomycorrhizal forests, and *Uapaca* in the Phyllantaceae), two genera found throughout the Pacific (*Intsia*, a legume and *Pisonia* of the Nyctaginaceae), and a possibly considerable number of other trees and shrubs that belong to strictly endemic families (Buyck 2002; Ducousso et al. 2004).

This paper presents an overview of some of the more common edible mushrooms eaten by the Malagasy people. Since vegetation goes a long way toward determining the types of mushrooms present, the discussion is presented according to the following four categories: (1) mushrooms of introduced eucalypt plantations, (2) mushrooms of introduced pine plantations, (3) mushrooms of native forests and woodlands, and (4) mushrooms found in fields, agricultural waste and other altered, non–forest habitats.

Edible Mushrooms of Eucalypt Plantations

Eucalypts are not native to Madagascar. French colonists introduced the first eucalypts more than a century ago. Out of the approximately 180 introduced eucalypt species in Madagascar, some 12 have become extremely important to village economies as a source of timber and charcoal (Sutter 1990). Their presence now determines the general aspect of large parts of the island (Fig. 2), occupying over 70% of the total soil surface in large areas on the central plateau (Bertrand 1999). When traveling through the east coast and central plateau of Madagascar during the rainy season (November/December to March/April, with a short, second rainy season in June/July on the east coast), one is struck by the quantity of edible mushrooms offered for sale on plates or in baskets along the roads and at the numerous markets. Among these, the most common and abundant mushrooms are ectomycorrhizally associated with eucalypts, yet they are not known from native eucalypt populations in Australia (see Discussion). Regularly cut plantations of *Eucalyptus robusta* Sm. seem to be particularly favored by several *Russula* and *Cantharellus* species. These mushrooms are harvested in impressive quantities and transported for sale in the capital, Antananarivo, and other cities. Incredibly, nearly all of these economically important eucalypt–associated mushrooms remain undescribed in the scientific literature.

Of the two most widely collected *Russula* species associated with eucalypts, one has been described: *Russula madecassense* Heim, while the other, which is by far the most abundant and

Fig. 2. The original forests and woodlands of Madagascar's central plateau have largely been replaced by rice paddies and eucalypt plantations. (David Arora, all rights reserved).

commonly marketed species, has not. This latter species was referred to as *Russula pseudovesca* nom. prov. in Buyck (2002), but use of that species name is pre–empted by Ying (1989); it is described here as *R. prolifica sp. nov*. (see Appendix). It is a mystery how this species could have escaped the attention of Heim, Decary, or other mycologists in the past unless it was absent or rare at that time. Several facts suggest that the species was very recently introduced into Madagascar or at least was not common until long after the eucalypts were introduced. First, the mushroom is not known in Australia. Second, Heim (1938a) notes a general dislike among Malagasy people for species of *Russula* and *Lactarius*, something that is absolutely not the case today. On the contrary, *Russula* is at present the most commonly consumed and economically important mushroom genus in Madagascar, closely followed by *Cantharellus*. Third, *R. prolifica* occurs nowadays side by side under eucalypts with the much less abundant *R. madecassense*, a species which Heim (1938 a,b) has described and which is easily distinguishable by the darker and more homogeneous cap color and less firm texture. It seems highly unlikely that Heim could have missed *R. prolifica* in his own and his collaborators' collections if, in fact, it was as common in the 1930s and 1940s as it is today. Fourth, russulas are usually stripped of their cap cuticle before selling them, a tradition not found where russulas are eaten in Africa, and a practice likewise not mentioned by Heim. One possible explanation for this exceptional practice is that it was recently developed in response to the preference of resident European clients for white, clean mushrooms such as *Agaricus bisporus* (J. E. Lange) Pilát; skinning the russulas not only removes dirt clinging to the cap cuticle but also reveals the white flesh underneath.

The second most important edible mushroom that occurs under eucalypts, and again particularly with *E. robusta*, is a yellow or golden chanterelle (Figs. 1, 3) generally marketed as *girolle*, the French name for the common European species, *C. cibarius* Fr. It is easily separated from the northern temperate *C. cibarius* by the initially brownish–grayish cap surface that usually develops numerous concentrically arranged scales that are also found on the upper half of the stipe. This characteristic places it close to *C. rufopunctatus* (Beeli) Heinem., a very similar, commercially valuable species of the Zambezian woodlands on the African mainland. Another, much smaller, eucalypt–associated chanterelle ranges in color from bright red to pink to orange or egg–yellow (Fig. 4) and occurs in groups of up to several hundred mushrooms closely aggregated around the bases of *E. robusta*. It is offered regularly for sale along the roadsides on the central plateau but is not typically sold in the cities. Similar species on other continents that warrant comparison before describing this taxon as a new species include the following: North America's *C. cinnabarinus* (Schwein) Schwein. and its Australian counterpart *C. cinnabarinus* var. *australiensis* (Cleland) Corner; *C. concinnus* Berk.; *C. madagascariensis* Pat., one of the first chanterelles described from Madagascar (Patouillard 1924); the very similar but less variable, pale pinkish *C. decolorans*, only recently described from native mountain forests in Madagascar (Eyssartier and Buyck 1999); and the smaller, always bright reddish *C. floridulus* Heinem. from the miombo woodlands of Africa. Finally, a fourth prominent chanterelle of Madagascar's eucalypt plantations is *Cantharellus avellaneus* Pat. (Patouillard 1924). It often blankets the ground under eucalypts but is drab in color and usually well hidden by a thick layer of similarly colored leaves. *C. avellaneus* is morphologically extremely close to *C. congolensis* Beeli, a species originally described from the African rain forest but widely distributed in tropical Africa. However, while *C. congolensis* is widely eaten on the mainland, *C. avellaneus* has not found favor in Madagascar.

Other, less significant edible mushrooms that occur under Madagascar's eucalypts include *Laccaria edulis* Bouriquet and several boletes. In general, the age of the plantation, and especially the absence of human interference (e.g., trimming the trees back to their bases every three to five years or so to produce charcoal *in situ*), has a very positive effect on the diversity of the associated mushrooms.

Edible Mushrooms of Pine Plantations

Several species of pine—principally *P. elliotii* Englem., *P. kesiya* Royle ex Gordon and *P. patula* Schiede ex Schltdl. & Cham.—have been imported and planted all over Madagascar and are regenerating abundantly. Most if not all of the mushrooms associated with pines in Madagascar are of northern hemisphere origin. So far, these mushrooms have been unable to colonize native woodlands or forests in Madagascar, nor have we observed typical Malagasy ecto-

Fig. 3. This undescribed, commercially-harvested golden chanterelle is abundant in Madagascar's eucalypt plantations. (Bart Buyck, all rights reserved).

Fig. 4. This small, colorful chanterelle of uncertain identity is abundant in Madagascar's eucalypt plantations and is often sold along roads. (Bart Buyck, all rights reserved).

mycorrhizal mushrooms associated with pines or other conifers.

Amanita muscaria (L.) Lam., *Scleroderma citrinum* Pers., *Lactarius* cf. *hepaticus* Plowr. and many other typical northern hemisphere mushrooms can be observed under pine and some occur locally in abundance, especially *Suillus granulatus* (L.) Roussel, *S. luteus* (L.) Roussel, and *S. bovinus* (Pers.) Roussel. The *Suillus* species are of some importance as food, especially for the canning industry. Canned mushrooms are destined principally for export but canned *Suillus* spp. are also found for sale at Antananarivo. Closely related to *Suillus* is *Rhizopogon* cf. *luteolus* Fr., which fruits hypogeously or semi–hypogeously under pines. It is consumed locally but is of no commercial importance. Though highly prized porcini (*Boletus edulis* Bull.) are harvested commercially from pine plantations in southern Africa, this

Fig. 5. Roadside mushroom vendors near Antsirabe vie with each other to sells bowls of *Cantharellus platyphyllus ssp. bojeriensis*, a common chanterelle of native woodlands. (David Arora, all rights reserved).

species has not been found in Madagascar. Other boletes, particularly in the genus *Tylopilus*, are quite common in pine plantations in the mountainous areas of Madagascar but are not eaten because of their bitterness.

Even though Madagascar's pine plantations are more susceptible to fire than are eucalypts, they do not give rise to massive growth of morels (*Morchella* spp.) after being burned as do their counterparts in the northern hemisphere. To our knowledge—and, in our opinion, most unfortunately—commercially valuable ascomycetes such as morels and truffles (*Tuber* spp.) are either entirely absent or else exceedingly rare in Madagascar. *Morchella intermedia* Boud. was reported from gardens near Antsirabe and Antananarivo in central Madagascar (Bouriquet 1942a) as being most likely associated with introduced *Mimosa* spp. The Malagasy people did not recognize this morel as edible at the time (Heim 1934b; Bouriquet 1942b), and more recent records of its presence are lacking. *Tuber* species have never been reported, but the endemic truffle, *Terfezia decaryi* Heim has been described from southern Madagascar and from the central plateau where it was reported as growing "near garden fences" (Heim 1934a). More recent records of this species are lacking.

Edible Mushrooms of Native Woodlands and Forests

The edible mushrooms associated with the native woodland and forests of Madagascar are very diverse, but greater diversity presumably means greater competition between ectomycorrhizal symbionts. The result is that few mushroom species occur in native woodlands in quantities comparable to those found in plantations of exotic trees. This also explains why most of the native woodland and forest mushrooms are not commercially valuable except locally. Both the woodlands on the central plateau and the dense, *Uapaca*–dominated forests of the east–coast lowlands and mountain crests are home to at least a dozen species of *Cantharellus*, many of which remain to be described. Most of these bear a strong resemblance to African species and all are recognized by local people as being edible. They are consumed when available but are of no particular economic importance with one prominent exception: the beautiful *Cantharellus platyphyllus* ssp. *bojeriensis* Eyssartier & Buyck, always found in *Uapaca bojeri* Baill. woodlands on the central plateau. This chanterelle—a sister taxon of the common African species, *C. platyphyllus* Heinem. (Eyssartier and Buyck 1999)—is sold along the main roads (Fig. 5) and at most markets of Madagascar's central plateau. Other edible woodland mushrooms of lesser importance include *Clavulina albiramea* (Corner) Buyck & Duhem (Duhem and Buyck 2007) and *Afroboletus luteolus* (Heinem.) Pegler & T. W. K. Young.

In the open woodland areas, *Russula* is the other major genus of edible mushrooms (second to *Cantherellus* in terms of local importance), owing to the relative abundance of a few edible species originally described from the African miombo woodlands, such as *R. cellulata* Buyck s.l., *R. porphyrocephala* Buyck, and *R. liberiensis* Singer. All of these species—or at least extremely similar sister–taxa—are also consumed in Madagascar. Some of these, such as *R. cellulata*, are locally very common both in Madagascar and in African woodlands (Härkönen et al. 1993; Buyck 1994; Buyck and Nzigidahera 1995; Bourdeaux et al. 2004). On the other hand, *Russula edulis* Buyck *sp. nov.* (Appendix) is an example of a locally consumed mushroom on Madagascar's central plateau that is extremely rare in Africa; despite many years of collecting, the author knows this taxon from only two localities on the African mainland.

Though Madagascar's ectomycorrhizal mushrooms are strongly reminiscent of those described from the African mainland, some of the continent's most important and commercially valuable mushrooms are noticeably absent from Madagascar. Examples are *Lactarius kabansus* Pegler & Piearce and *Amanita loosii* Beeli (=*A. zambiana* Pegler & Piearce). The same applies to the highly prized genus *Termitomyces*, so common on the mainland but absent from Madagascar. Madagascar's termites, it seems, associate only with mushrooms such as *Podaxis, Xylaria*, and some agarics (Jumelle and Perrier de la Bathie 1907, 1910; Heim 1938c).

In the denser types of native forest, especially in the mountains, ectomycorrhizal mushrooms are rarely collected for food. However, some saprobic or parasitic wood–inhabiting species are gathered very occasionally. Examples include *Tremella fuciformis* Berk., *Collybia aurea* (Beeli) Pegler, several species of *Auricularia*, as well as some species of *Oudemansiella*, *Lentinus* and *Pleurotus*, in particular *Lentinus sajor–caju* (Fr.) Fr (=*Pleurotus sajor–caju* [Fr.] Singer), a well–

known pantropical species that fruits abundantly on dead tree trunks at lower altitudes. *Auricularia* spp. are among the best–known edible mushrooms in Madagascar, and are also imported from Asia in dried form and commonly sold in markets.

A very recent but interesting finding from our most recent excursions to Madagascar is the shiitake, *Lentinula edodes* (Berk.) Pegler, or more likely a morphological twin (i.e., a closely related, undescribed species). It has been found in humid, mixed mountain forests at higher elevations of the central plateau and eastern escarpment on a *Eucalyptus robusta* log and on an unidentified native tree. Although only found twice so far, the large number of fruiting bodies produced on the logs suggests a certain commercial potential for local production of this shiitake look–alike.

Edible Mushrooms of Fields, Agricultural Waste, and Cultivated Land

Agricultural wastes are well known as substrates for the spontaneous development and cultivation of many kinds of mushrooms around the world (Oei 2003). Especially on Madagascar's warm, humid east coast, saprobic edible mushrooms that appear spontaneously on agricultural wastes have been highly appreciated for many years. Two well–known examples are *Coprinus molestus* Bouriquet on rice straw and *Volvariella volvacea* (Bull.) Singer on a variety of wastes including rice straw, manioc, coffee pulp, and fallen baobab (Bouriquet 1943). The latter mushroom, widely known in Asia as the (paddy) straw mushroom, is known in Madagascar as the "mushroom of the clove tree" because of its frequent presence on distillation residues of clove (*Eugenia caryophyllata* Thunb.). Cultivation experiments with different mushroom species have met with variable success in Madagascar (Bouriquet 1942a, 1942b).

During the colonial period, horse riding was very popular and the widespread use of horse manure in gardens and fields led to the spontaneous production of wild agarics that were collected for consumption (Bouriquet 1942a). Several species of *Agaricus*, *Lepiota*, and *Macrolepiota* were mentioned frequently in the early literature (Dufour 1913; Bouriquet 1943) as being collected for the table, but with the decline in equestrian sports, which, in part, is probably due to the end of the French colonial occupation, these agarics have become much less common today. The familiar, manure–dwelling button mushroom, *Agaricus bisporus* (J.E. Lange) Pilát, also has been cultivated in Madagascar, especially near Antsirabe where horse riding was once very popular. On the east coast, *Gymnopus tamatavae* (Bouriquet) Antonin, Buyck, Randrianjohany & Duhem, growing in circles or large groups in pastures (Antonin et al. 2005), is collected near the port city of Tamatave and sold in local markets there.

On the central plateau, the edible but difficult–to–digest *Phlebopus colossus* (Heim 1935) Singer makes an impressive appearance. It occurs mostly near ornamental trees (coffee, mango, legumes, etc.), even those left standing in the middle of planted fields. The genus *Phlebopus* is believed to be facultatively ectomycorrhizal (Miller et al. 2000) and includes the world's largest boletes: an Australian specimen shown in a newspaper weighed 27 kilograms (kg) (D. Arora, pers. com.). Another giant species of altered habitats, *Macrocybe spectabilis* (Peeraly & Sutra) Pegler, has whitish gills and prefers the nutrient–rich soils of rural roadsides, compost, palm plantations, and gardens near the coast. It is reputed to be delicious in Africa and Mauritius (Buyck 1994), but we have found no evidence for its consumption in Madagascar. Since a related species, *M. crassa* (Berk.) Pegler & Lodge, is cultivated in Southeast Asia, it would be very interesting to study the potential of *M. spectabilis* for cultivation in Madagascar.

Pleurotus tuber–regium (Rumph. ex Fr.) Singer (=*Lentinus tuber–regium* [Fr.] Fr.) is another example of an edible, nitrophilous mushroom that can attain impressive dimensions (on one occasion, the author observed a cap reaching nearly 50 centimeters [cm] in diam.). It fruits from underground sclerotia on cultivated land, rarely in the forest, and once located, the sclerotia are often gathered and transplanted close to the villages for easier collection of future fruiting bodies. The fruiting bodies as well as the sclerotia are locally consumed in Africa as well as in Madagascar (where it is referred to as *ola tafa*); there is also considerable literature on its use (particularly of the sclerotia) in witchcraft in Madagascar as well as in Africa (for a synthetic overview, see Buyck 1994). Besides various and ubiquitous species of *Auricularia*, some undescribed *Psathyrella* spp. and some collybioid mushrooms are collected locally in and around villages, especially on the mountain slopes of the eastern escarpment.

Discussion

For centuries, the forests and woodlands of Madagascar have provided local people with firewood, timber, medicinal plants, fiber, oil, resins, fodder, vegetables, nuts, and fruits as well as edible mushrooms. Without a doubt, wild mushrooms are an important seasonal and traditional supplement to the daily food of Malagasy people, most of whom still live in or at the edge of extreme poverty. But as a result of the changing countryside and the ability of Madagascar's mushrooms to exploit the eucalypt habitat on a scale unseen elsewhere, the menu of mushroom species used in Madagascar has changed dramatically in the last century, and will probably continue to change.

As Madagascar's native woodlands and forests have dwindled dramatically in the last century, eucalypt and pine plantations and fields have come to dominate the landscape. The most striking feature of most of Madagascar's commercially valuable mushrooms is that they are associated with imported eucalypts. Many dozens, perhaps even hundreds, of different mushroom species can be found in older eucalypt stands in Madagascar. In this respect, Madagascar is unusual compared to other places where eucalypts have been introduced because Madagascar's eucalypts seem to have acquired a diverse ectomycorrhizal mycoflora that is not primarily Australian in origin. Why is Madagascar unusual in this respect? Which species among the many imported eucalypt species support the highest mushroom diversity and production and under what conditions? These are fruitful questions to be investigated in the future. Even the origin of Madagascar's most abundant commercial species, *Russula prolifica sp. nov.* (Appendix), remains unclear; though exclusively associated with eucalypts in Madagascar, it has not been reported from Australia nor has it been found in the native forests of Madagascar or Africa.

As noted earlier, however, some of the edible eucalypt associates belonging to *Cantharellus* and *Russula* are closely related to species that exist on the African mainland. This makes it likely that these edible, eucalypt–associated species are of Malagasy or African origin, but perhaps were not prominent until the ectomycorrhizal eucalypts provided a largely unoccupied, newly available or "free" niche, which the mushrooms opportunistically seized. This is a scenario that is made more plausible by a recent study on fungal associates of *Eucalyptus robusta* in the Seychelles (Tedersoo et al. 2007).

Many other questions about Madagascar's mushrooms remain unanswered. Madagascar's native mycoflora features a number of abundant, edible species that are very closely related – or even identical – to those found in similar habitats on the African mainland (Buyck et al. 2007). On the other hand, certain prominent African species are entirely absent from similar habitats in Madagascar. Finally, certain ectomycorrhizal species (e.g., *Russula gossypina* Buyck and *Lactarius rubroviolascens* Heim) are present but equally rare both in Africa and Madagascar. These observations raise fundamental questions about the dispersal and evolutionary history of ectomycorrhizal forest mushrooms that are associated with entirely different, indeed 100% endemic, host tree floras on opposite sides of the Mozambique Channel.

Edible mushrooms appear to be an important component of the local rural economies in Madagascar, though market studies on this subject are lacking. They are certainly of special interest as a food source for rural people living in close relationship to the forest. Future inventories will undoubtedly reveal even more species of wild mushrooms collected and eaten by the Malagasy people, especially in smaller settlements far from the major towns. As more and more people migrate from rural areas to the cities, knowledge of forest resources may decline and indifference toward them may grow. More research documenting the diversity, ecology, and cultural and economic importance of wild mushrooms in Madagascar is most urgently needed.

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Appendix

Two commercially valuable species of *Russula* discussed in the main body of this article are described here as new species. More detailed and illustrated descriptions of both species will be provided elsewhere.

Russula edulis sp.nov.

Pileo saturate brunneo mox fissurato duro. Stipite breve albido duro pleno. Lamellis albidis saepe furcatis. Sporis verrucis minutissimis densissime dispositis ornatis, macula suprahilare inamyloidea. Pileipelle subpelle dense ac suprapelle extremitatibus 4–6 um latis plus minusve dense septatis ascendentibus ramosis in apice saepe inflatis composita. Pileocystidiis nullis. Holotypus: Madagascar. Central plateau, prope Arivonimamo, sub Uapaca bojeri, Buyck 97.264 (PC)

Cap up to 15 cm diam., smooth up to the very margin but usually becoming rapidly and sometimes profoundly cracked and fissured, exposing the whitish and firm underlying flesh, the surface layer glabrous, homogeneously dark brown to grayish brown, sometimes with very faint greenish tinges toward the margin, locally discoloring or off–white from the beginning, easily separable up to mid–radius, dull and never viscid. Gills adnate to subfree, 4–6 mm high, ivory, sometimes with faint pinkish tint when viewing at an angle, turning somewhat brownish where bruised, close, even but with many bifurcations at various distances between stipe and cap margin, not fragile; edges entire and concolorous. Flesh whitish but rapidly graying (although never very intensely) when exposed, also with faint pinkish tints when cut; very hard and thick (approx. 10–15 mm in center of cap); surface and interior of stipe turning slowly orange–brown with iron sulfate salts, and the

Fig. 6. Baskets of *Russula edulis* for sale. (Bart Buyck, all rights reserved).

interior then fading progressively to greenish gray. Taste mild or refreshing, not acrid. Odor strong, agreeable. Stipe sometimes slightly eccentric, very firm and solid, cylindrical or almost so, whitish in upper part but grayish–brown downward because of a dense, minute fibrillose covering. Spore print whitish. Spores minutely verrucose. Pileocystidia absent. Holotype: Madagascar. Central plateau, at Arivonimamo, in Uapaca bojeri woodland, 5 Feb. 1997, Buyck 97.264 (PC). Illustration: Fig. 6.

Russula prolifica sp.nov.

Russula vesca valde similis sed praesertim differt carne duriora statura compactiora consociatione Eucalyptu robusta crinibus crassotunicatis pilei suprapelle nullis pileocystidiis nullis sporis dense subreticulatis. Holotypus: Madagascar. Central plateau, prope Antananarivo, sub Eucalyptus robusta, 6 Feb. 2006, leg. B.Buyck and V. Hofstetter, Buyck 06.161 (PC).

Cap up to 12 cm diam., often irregular, surface layer separable up to mid–radius, smooth and glabrous, but when young profusely pruinose, continuous or minutely cracked–areolate, becoming striate at the margin with age; surface dull, viscid when wet, in every aspect very strongly reminiscent of *Russula vesca* Fr. by the nature and variability of its color patterns (mixtures of pinkish, vinaceous, brownish, cream to yellowish or even greenish tints) and presence of rusty brownish spots, but more often cracking or even deeply fissuring (from drought ?). Gills adnate, 4–8 mm high, brittle, not remarkably crowded but dense, even or with rare shorter lamellulae of variable length, frequent bifurcations only near the extreme margin and very close to the stipe, cream–colored, with local yellowish discolorations or rusty spots; edges entire and concolorous. Flesh whitish, very firm, unchanging, but turning rapidly and strongly carrot orange with iron sulfate. Taste and odor mild, but after a while both faintly spermatic. Stipe more or less cylindrical, sometimes curved in lower part, stout, smooth and glabrous, whitish or sometimes with pinkish to brownish–yellowish tints, browning when touched. Spore print dark cream. Spores minutely subreticulate–warty. Pileocystidia absent. Holotype: Madagascar. Central plateau, 20 km from Antananarivo on the N1, near the road in Eucalyptus robusta plantation, 6 Feb. 2006, leg. B. Buyck and V. Hofstetter, Buyck 06.161 (PC). Illustration: Fig. 7.

Fig. 7. *Russula prolifica.* (Bart Buyck, all rights reserved).