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Nutritional and Possible Pharmaceutical Aspects of Tree Exudates Eaten by Lemurs of Madagascar's Dry Forests †

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† In memoriam of Fabien Génin and Judith Masters.

Abstract: Gums produced by trees after injuries are valuable food resources for several primate species. Yet, information on the chemical characteristics of gum is scant and inconsistent. We use gums consumed by lemurs (strepsirrhine primates of Madagascar) as an example to illustrate their possible nutritive and pharmaceutical properties. Exudates from 45 tree species of the dry forests of Madagascar contained 0.38–23.29% protein, 0.46–65.62% sugar, and 0.39–11.86 kJ/g of energy in dry matter. Exemplified by the lemur species *Microcebus griseorufus*, gum consumption increased with increasing sugar and energy content but was unrelated to protein. But lemurs also fed on gum with very low protein and energy content, suggesting that these exudates were consumed for other reasons. Disk diffusion tests with exudates from five out of 22 tree species consumed by lemurs showed antibacterial activity against *Micrococcus* spp. and/or *Staphylococcus aureus*. Exudates with antibacterial activity had lower protein, sugar, and energy contents than samples without antibacterial properties. GC-MS analyses revealed several components with antimicrobial effects that would have the potential for self-medication. This might explain the consumption of gum with very low nutritive value. Possible medicinal effects of tree exudates deserve further attention in view of their pharmaceutical applicability for animals and humans alike.

Keywords: plants; gum; resin; antibacterial effects; strepsirrhine primates; self-medication; *Microcebus*; *Phaner*

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1. Introduction

Exudates produced on tree trunks after injuries can be gums, resins, or latexes [1]. Gums can be important food items for primates and a variety of other mammalian species [2,3]. Following the classification of Bearder and Martin [4], gums are water-soluble and are produced to seal wounds from mechanical or insect damage. They can contain large amounts of di-, oligo-, and polysaccharides characterized by ß-glycoside linkages. ß-linked glycosides cannot be broken down by primate digestive enzymes, instead requiring microbial fermentation to turn them into energy that can be absorbed by primates. These gums represent important food items, especially in dry forest ecosystems, but are thought to be difficult to collect and to digest, requiring specific morphological adaptation for clinging to large tree trunks, possibly a tooth comb to scrape the exudate off the trunk, and specializations of the digestive tract to improve microbial fermentation (e.g., [4–10]). In contrast to gum, resins are not soluble in water but can be dissolved in lipophilic solvents. Resins are produced by specialized cells to seal wounds against infections and contain no or very low concentrations of metabolizable nutrient components [4]. Resins are not supposed to be eaten by primates [6], but, especially when produced due to wounds, gums and resins can be mixed, thus making categorization of the exudate difficult under field conditions. Both types of exudates (gums and resins) can contain a variety of plant secondary metabolites used for medicinal purposes by humans, such as terpenoids mixed with essential oils. Well-known examples are gum Arabic from *Acacia* spp. or myrrh from *Commiphora* spp. [11,12]. Due to these properties, tree exudates may not only provide nutrients [3,13], but have also been considered to be consumed for their pharmaceutical properties [14]. Despite (or because of) this complexity, exudates have not received similar attention to other primate food categories, such as leaves or fruit [15–19].

In this report, we apply the conventional approach used in studies on leaf and fruit selection by primates in relation to plant chemistry to the chemical composition of gum. In short, animals need protein and energy to survive. Micronutrients, vitamins, and minerals are certainly also important but will not be considered here [20]. As a rule of thumb, and not considering the quality of proteins (i.e., the composition of amino acids), primate food must contain 6–8% protein in dietary dry matter (equivalent to about 1.1% nitrogen) to cover their protein needs [21]. If protein concentrations are below this threshold, the diet must be supplemented with protein-rich items (e.g., insects) or consumers must have special morphological or physiological adaptations to compensate for the low-protein items [22]. A similar threshold cannot be defined for the energy content of food as requirements vary widely in relation to body mass and the physiological state of animals.

Gum-eating mammals, including primates, have been categorized as obligate, facultative, and opportunistic gum feeders [3]. Obligate feeders are expected to have specializations that optimize nutrient extraction from gum. Facultative and opportunistic feeders are not expected to have similar adaptations because they rely on different food categories, such as leaves and fruit. As a consequence, facultative and opportunistic feeders should feed on gum of higher quality (higher protein and/or higher energy content) than obligate gum feeders because the latter should be able to extract nutrients from gum more efficiently and therefore can extend the range of gums for consumption towards gum of low quality. If animals eat gum of lower quality than is believed to be needed to fulfill their nutritional needs, the consumption could be for other reasons, such as for minerals (e.g., [15]), or for pharmaceutical purposes (e.g., [23]). The latter is especially difficult to test under descriptive field conditions, but any evidence for pharmaceutical properties of gum might allow the design of further studies, similar to the phenomenon of chimpanzees feeding on leaves with antihelminthic properties [24,25].

Here, we use gum-eating lemur species (nonhuman primates of Madagascar) of the dry forest ecosystems of western Madagascar [26] to address the following questions:

1. Do facultative gum feeders consume gum of different nutritional quality than obligate gum-feeding species?
2. Are the protein, sugar, and energy content of gum relevant for food selection?

3. Are consumed gums with low protein, sugar, and/or energy content more likely to display antibacterial activity than gums of higher nutritional value?

2. Materials and Methods

2.1. Comparison of Obligate and Facultative Gum Feeders

During various studies carried out between 1990 and 2012, we collected 152 exudates from natural tree wounds of 45 different tree species at six dry and spiny forest sites in western Madagascar. We considered these exudates to represent gum. For this general comparison between lemur species, gums were collected at sites and from tree species where lemurs have been observed feeding on these tree species, but not always from the same tree or in the same season or year. The sites were (from north to south): Ankarafantsika [27], Analabe [28]; gum collected by F. Génin in November 2007), Kirindy (CNFEREF) [29,30], Zombitse [31]; gum collected by F. Génin in August 2011), Tsimanampetsotse [32,33]; Giertz unpubl., and Berenty [34,35] (Figure 1). Observed consumers of the tree exudates used here were *Microcebus griseorufus*, *M. murinus*, *M. ravelobensis*, and *Phaner pallescens* [7,27,29,36], supplemented with unpublished data from P. Giertz, Y. Ratovonamana, and O. Schuelke. All sites are part of Madagascar's dry and spiny forest ecosystem with annual precipitation decreasing from north to south from 1600 mm in Ankarafantsika to less than 400 mm per year in Tsimanampetsotse [31,37].

Figure 1. Sites of sample collection, marked by asterisks (base map from Google Maps).

2.2. Relevance of Protein, Sugar, and Energy Content for Gum Consumption of Microcebus griseorufus

To investigate the relevance of protein, sugar, and energy content for gum consumption, we studied the obligate gum-eating lemur species *Microcebus griseorufus* as an example. The case study was carried out in the Parc National de Tsimanampetsotse (24°03′–24°12′ S, 43°46′–43°50′ E), located about 85 km south of Toliara. Rainfall is highly seasonal, rarely exceeding 400 mm per year, and is mostly restricted to the time between December and February. During the last two decades, rainfall shifted towards March and April [33]. The

vegetation has a pronounced xerophytic character and belongs to Madagascar's spiny forest formations [31,37]. The different vegetation formations within Tsimanampetsotse National Park vary according to the underlying soils and their water-holding capacity. Two main formations were considered for the study reported here: (1) Dry forest on unconsolidated sands at the foot of the Mahafaly Plateau. This formation is characterized by *Didierea madagascariensis* (Didieraceae) and *Cedrelopsis grevei* (Rutaceae) and reaches a mean height of 6 m; (2) xerophytic, spiny bush on calcareous soil, characterized by *Alluaudia commosa* (Didieraceae), *Cassia meridionalis* (Fabaceae), and *Cedrelopsis gracilis* (Rutaceae). The spiny bush grows on limestone and reaches a maximum height of 4 m [33].

As part of a radio-tracking and capture-mark-recapture study of *Microcebus griseorufus* [32,33,38–40]; Giertz unpubl., we recorded feeding events of 16 *M. griseorufus* in the Tsimanampetsotse National Park for a total of 108 h in the dry forest on sand and 102 h on the limestone plateau between March 2008 and March 2009.

2.3. Antibacterial Properties and Chemical Composition of Consumed Gum

For the study of possible interactions between antibacterial properties and the concentrations of protein, sugar, and the energy content of gum consumed by lemur species, we restricted the analyses to samples linked to actual feeding observations and took samples from the same trees where the animals had been observed feeding or from a conspecific tree nearby within a day of the feeding observations.

2.3.1. Chemical Analyses

Samples were dried in the air (if needed) and stored away from sunlight in a cool place, and ground into powder using a mortar and pestle prior to analyses. We analyzed 101 samples for total nitrogen using the Kjeldahl method. The Kjeldahl procedure digests samples in a mixture of sulfuric acid and a commercially available catalyst, followed by transformation of nitrogen into ammonium and titration to measure the amount of nitrogen in the sample. Nitrogen can serve as a proxy for protein. The factor for the conversion of nitrogen into protein can vary between different food categories and the conversion factor is unknown for exudates [41]. For the calculation of the energy content of protein in gum, we use a conversion factor of 6.25.

We analyzed 152 samples of soluble sugar concentrations as equivalent to galactose after acid hydrolyzation of 50% methanol extract. The concentrations of the resulting monosaccharides were measured photometrically at 490 nm using a phenolic reagent (2.5 g phenol in 50 mL H_2O) [42]. Though this represents a rather indiscriminate method, the results are well correlated with enzymatic analyses of distinct sugars, such as glucose and fructose, analyzed by lab-kits from Boehringer Mannheim. Due to the small quantities of sample material available, we could run chemical analyses only once per sample.

For the 101 samples for which nitrogen and sugar analyses were available, we estimated the energy content (kJ/g dry matter) derived from the protein and sugar concentrations as E = [(% Protein x 16.736) + (% Sugar x 16.736)]/100 [43].

We assayed methanol extracts of exudates from 17 tree species using gas chromatography followed by mass spectrometry using a GCMS-QP2010S of Shimadzu and a DB5 column. Since we only wanted to assess the composition of the exudates qualitatively, we did not aim for any quantification of the components. We produced methanol extracts with 200–300 mg of sample in 2 mL of methanol using an Ultra-Turrax for 2 min. The resulting solution was filtered. We considered blank samples for comparison. We identified the components with the FFNSC library (Flavor and Fragrance Natural and Synthetic Compounds) provided by Shimazdu. We considered only components that were identified by the library with a probability $\geq$98%. Due to the large number of components, we did not add internal standards to the samples. We took information on possible pharmaceutical properties of the substances identified using the GC-MS from The Merck Index [44] and the NIH National Library of Medicine (https://www.nlm.nih.gov/; accessed 20 June 2023).

2.3.2. Antibacterial Activity

We conducted disk diffusion tests according to Bauer et al. [45] to test the exudates for antibacterial activity. We dissolved the exudate powders in water, methanol, and olive oil with concentrations of 3 to 33.3 mg/100 µL. Some of the samples did not seem to dissolve well in the solvent and therefore we added powder in a non-standardized way, hoping that some components might come into solution. This qualitative approach certainly prohibits any direct pharmaceutical application of our results. We prepared base plates for bacterial growth tests by pouring 20 mL of yeast-extract-peptone-glucose agar into sterile Petri dishes. We poured 7 mL of semisolid agar medium (Luria-Bertani- and yeast-extract-peptone-glucose medium), inoculated with 100–300 µL of the specific test organisms, over the base plate to obtain a homogenous bacteria layer. We placed 25 µL of oil-dissolved exudates or 15 µL of water- and methanol-dissolved exudates on a sterile filter paper clip (9 mm diameter) on the agar plates. Controls consisted of the solvents without exudates. After incubating the test plates for 24–48 h at 28–37 °C, depending on the optimal growth conditions of the test organisms, we measured antibacterial activity as the diameter of the zones of inhibition around the filter paper (including the filter paper).

Since there is little information available on the bacterial composition of the digestive tract of lemurs and the microbiome of *Microcebus griseorufus* can vary substantially under different conditions [46–50], and viruses can show regional co-evolution with hosts with unknown consequences for co-infections [51], we used standard laboratory bacteria for our antibacterial tests. The test organisms were the gram-negative *Escherichia coli* (ESCH 006) and *Pseudomonas aeruginosa* (PSMN 028), and the gram-positive *Micrococcus* sp. (MICO 001), *Micrococcus roseus* (MICO 003), *Micrococcus luteus* (MICO 004), *Micrococcus* sp. (MICO 005), *Micrococcus lysodeicticus* (MICO 006), *Staphylococcus aureus* (SFCO 002), and *Enterococcus faecalis* (STCO 001). IDs in brackets refer to bacteria strains provided by the Department of Microbiology and Biotechnology, Institute of Plant Science and Microbiology, University of Hamburg, Germany.

2.3.3. Statistics

For the comparison of the chemical composition of gum consumed by obligate or facultative gum feeders, we calculated the mean nitrogen, sugar, and energy content per tree species across all study sites. Some trees could not be identified. Since they were different from the known tree species, they were considered as distinct species. For the regional study, samples were collected at the different study sites between 1989 and 2012. Since gums were collected at different sites and over many years, we calculated means per tree species and used these means to characterize the chemical composition of gums consumed by the different lemur species. The components of gums consumed by the different species were compared via single-factor analyses of variance.

To study the relevance of protein, sugar, and energy content for gum consumption of *Microcebus griseorufus*, we log-transformed the number of feeding records to improve normality and correlated the number of feeding records with the protein, sugar, and energy content per food species using Pearson correlations. For these analyses, we considered the data from the dry forest and the spiny bush and from the dry and the wet season as being independent. We used only food tree species for which we had collected gum in the respective habitat and season.

To study possible differences of chemical properties of gums with and without antibacterial activity, we used the mean concentrations of the 22 species for which we had carried out the antimicrobial tests. If different individuals of the same tree species produced either positive or negative results, we restricted the calculation of the mean protein, sugar, and energy content to the samples for which we had run the antibacterial tests and calculated the means separately for individuals with or without antibacterial activity. This applied to two tree species: *Albizia tulearensis* and *Terminalia disjuncta*. Since residuals deviated from normality, we used non-parametric Mann-Whitney U tests for comparisons of the samples with and without antibacterial activity.

The p values are two-tailed. Statistical tests were performed with SPSS 25.0.

2.4. Ethical Note

All animal work has been conducted according to Malagasy and German guidelines. Our research was conducted in collaboration with the Département Biologie Animale and the Département Biologie et Ecologie Végétale of the Université d'Antananarivo. Authorization to enter Tsimanampetsotse National Park, as well as to capture and handle small mammals, were delivered by the Ministère de l'Environement, des Eaux et Forêts et du Tourisme of Madagascar in accordance with Madagascar National Parks (MNP, former ANGAP; permit n° 057/07 issued on March 12, 2007, permit n° 009/08 issued on 15 January 2008, and permit n° 261/08 issued on 9 October 2008). We hereby confirm that our study was conducted in accordance with the recommendations of the Weatherall report "The use of non-human primates in research".

3. Results

3.1. Regional Study

The 152 gum samples belonged to 45 different tree species. The chemical composition (mean per tree species) ranged from 0.38 to 23.29% protein (n = 42), 0.46–65.62% sugar (n = 47), and 0.39–11.86 kJ/g of energy (n = 42; Appendix A, Table 1). Gums consumed by the facultative gum feeder, *Microcebus murinus*, had higher contents of proteins, sugars, and energy than the obligate gum feeding species, but the chemical concentrations and the energy content did not differ significantly between the four lemur species (ANOVA: $F < 1.17$ for all three components; $p > 0.05$).

Table 1. Chemical composition and energy content of gum consumed by four lemur species of the dry deciduous and spiny forests of Madagascar. Values are means ± standard deviations and sample size. For *M. ravelobensis*, only two samples were available. We list the values for these two samples rather than calculating standard deviations. The classification of specialization on gum follows [3].

Lemur Species	Gum Specialization	Protein (%)	Sugar (%)	Energy (kJ/g)
Microcebus griseorufus	Obligate	6.43 ± 5.66 N = 25	27.06 ± 19.53 N = 26	5.62 ± 3.41 N = 25
M. murinus	Facultative	6.90 ± 6.12 N = 10	33.96 ± 12.29 N = 10	6.84 ± 2.24 N = 10
M. ravelobensis	Obligate	1.75/10.31 N = 2	21.93/28.21 N = 2	3.96/6.45 N = 2
Phaner pallescens	Obligate	4.96 ± 4.73 N = 12	21.58 ± 13.92 N = 16	4.90 ± 2.65 N = 12

3.2. Relevance of Protein, Sugar and Energy Content for Gum Consumption of *Microcebus griseorufus*

During the 210 h of focal animal observations, we recorded 189 feeding events, including 37 cases of exudate feeding, representing 19.6% of all feeding records. During the focal observations, *M. griseorufus* consumed exudates from eight different tree species. Exudates were consumed most often during the dry season in the spiny thicket on limestone (Appendix B). *Operculicarya hyphaenoides* is also known to be eaten but this was not observed during the systematic observations.

The number of feeding observations per vegetation formation and season was not correlated significantly with the protein concentrations in the exudates ($r = -0.43$; $p = 0.084$, $n = 17$), and was significantly positively correlated with the sugar concentrations and the energy content ($r = 0.57$, $p = 0.014$, $n = 18$, and $r = 0.51$, $p = 0.037$, $n = 17$). Samples with antibacterial properties were low in protein, sugar, and energy and were consumed only twice during the systematic observations (Figure 2).

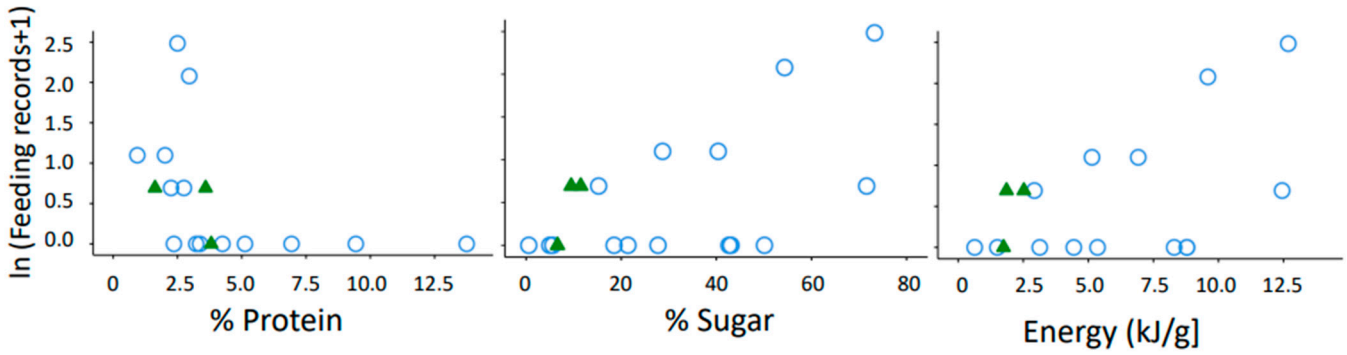

Figure 2. Frequency of exudate consumption by *Microcebus griseorufus* in relation to protein, sugar, and energy content, and antibacterial properties of the exudate; ○ no antibacterial effect; ▲ antibacterial effect.

3.3. Antibacterial Properties and Chemical Composition of Consumed Gum

Six of the 40 samples from 22 different tree species analyzed for antibacterial activity showed clear antibacterial inhibition and three showed indications of antibacterial activity against bacteria used in the assays (Appendix C, Appendix D, Appendix E). No exudate in any of the solvents showed antibacterial activity against *Escherichia coli* (ESCH 006), *Pseudomonas aeruginosa* (PSMN 028), *Micrococcus* sp. (MICO 006), *Micrococcus lysodeicticus* (MICO 006), and *Enterococcus faecalis* (STCO 001). It should be kept in mind that we could not use extracts from all samples in all assays due to the low quantities of exudate available for some of the samples.

Water-dissolved samples showed no antibacterial effect (Appendix C). We found clear antibacterial activity in five oil-dissolved samples of *Commiphora simplicifolia* (Figure 3a) against *Micrococcus luteus* (MICO 004), *Micrococcus* sp. (MICO 005), *M. Roseus* (MICO 003), and *Staphylococcus aureus* (SFCO 002, Appendix D). The exudate from an unidentified tree species collected at Zombitse (F11-11) showed clear activity in *M. luteus* (Figure 3b) and a faint inhibition against *Micrococcus* sp. (MICO 005). Oil-dissolved extracts of *Quivisianthe papinae* and *Terminalia disjuncta* indicated an inhibition against *M. luteus* (MICO 004) and *Micrococcus* sp. (MICO 005).

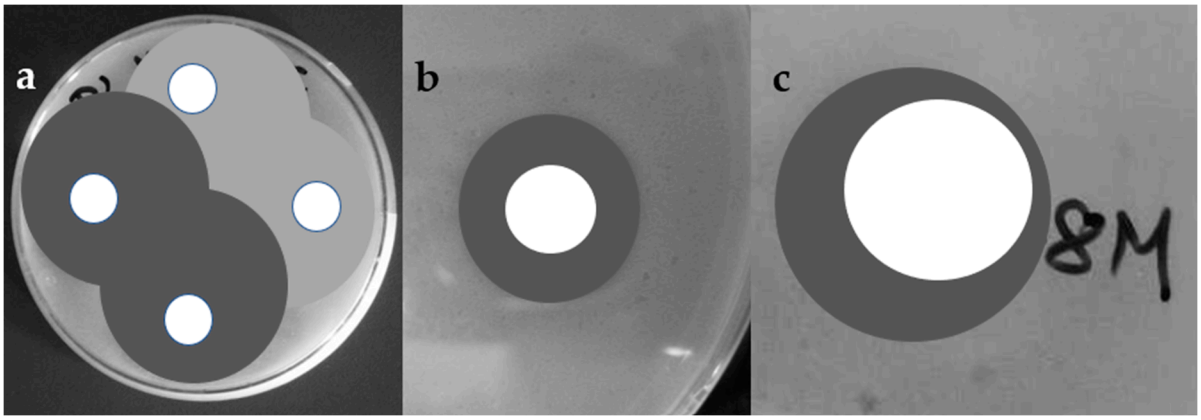

Figure 3. Zones of inhibition against *Micrococcus luteus* of oil-dissolved samples, (**a**) *Commiphora simplicifolia* (sample P08-125), (**b**) Sample F11-11 from an unknown tree species consumed by *Phaner pallescens* in Zombitse, (**c**) Indication of antibacterial activity of methanol dissolved gum from *Quivisianthe papinae* against *Staphylococcus aureus*. Upper part: photos of the original plates. Lower part: schematic representation; white circles are the disks of filter paper soaked in gum extracts; grey circles represent zones of bacterial inhibition due to diffusion of antibacterial components from the white disks.

Methanol dissolved exudates showed some antibacterial activity (Appendix E). Clear antibacterial activity was found in the exudate of *Commiphora simplicifolia*. *Quivisianthe papinae* showed some indication of inhibition against *S. aureus* (SFCO 002, Figure 3c) and some species of the genus *Micrococcus*. *Albizia tulearensis* inhibited *Micrococcus luteus*.

Of the 22 tree species tested, three showed clear antibacterial activity in the disk diffusion tests. Two species (*Albizia tulearensis* and *Terminalia disjuncta*) showed antibacterial activity in some samples but not in others. Extracts from gum of 17 species did not show any antibacterial activity (Table 2).

Table 2. Antibacterial activity according to disk diffusion tests and the protein, sugar, and energy contents of exudates from lemur food plants. Values are means from gum collected from 1–5 different trees, tested individually. Information on the utilization of the tree species in traditional medicine are from [52] (A), [39] (R), and [53] (F); na = not applicable because of unclear species identification.

Species	Protein	Sugar	Energy	Used in Traditional Medicine
No antibacterial activity				
Acacia bellula	8.78	34.48	7.24	A, F
Albizia mainaea	11.31	28.35	6.64	
Albizia tulearensis	3.38	0.61	0.67	A
Commiphora arafy	15.25	30.81	7.71	F
Commiphora guillaumini		32.82		
Commiphora marchandii		37.81		A
Commiphora sp3	4.38	74.52	13.20	
Delonix floribunda	2.61	44.40	7.87	A, R
Hymenodictyon decaryi	3.50	5.55	1.51	
Neobeguea mahafaliensis	3.58	12.88	2.76	A, R, F
Operculicarya gummifera		0.63		F
Operculicarya hyphaenoides	3.19	11.43	2.45	R
Poupartia sylvatica	27.25	7.95	5.89	
Rhopalocarpus sp	3.94	38.15	7.04	
Terminalia disjuncta	2.75	73.77	12.81	A
Terminalia mantaliopsis	1.44	25.15	4.45	
Terminalia mantaly	2.38	26.06	4.76	
Terminalia ulexoides	13.75	4.98	3.08	A
Zanthoxylum sp	4.13	54.39	9.79	
Antibacterial activity				
Albizia tulearensis	2.94	0.47	0.57	A
Commiphora simplicifolia	3.58	8.37	2.11	A, F
Quisvianthe papinae	2.38	0.46	0.47	
Terminalia disjuncta	1.63	9.48	1.86	A
Unknown tree species consumed by *Phaner pallescens*	5.31	12.01	2.90	na

Sugar concentration and the energy content of exudates showing antibacterial activity were significantly lower than in exudates that did not show antibacterial activity (Mann-Whitney U test: sugar: $z = 2.24$, $p = 0.025$; energy: $z = 2.64$, $p = 0.008$). Protein concentrations did not differ between samples with and without antibacterial activity ($z = 1.24$, $p = 0.215$; Figure 4).

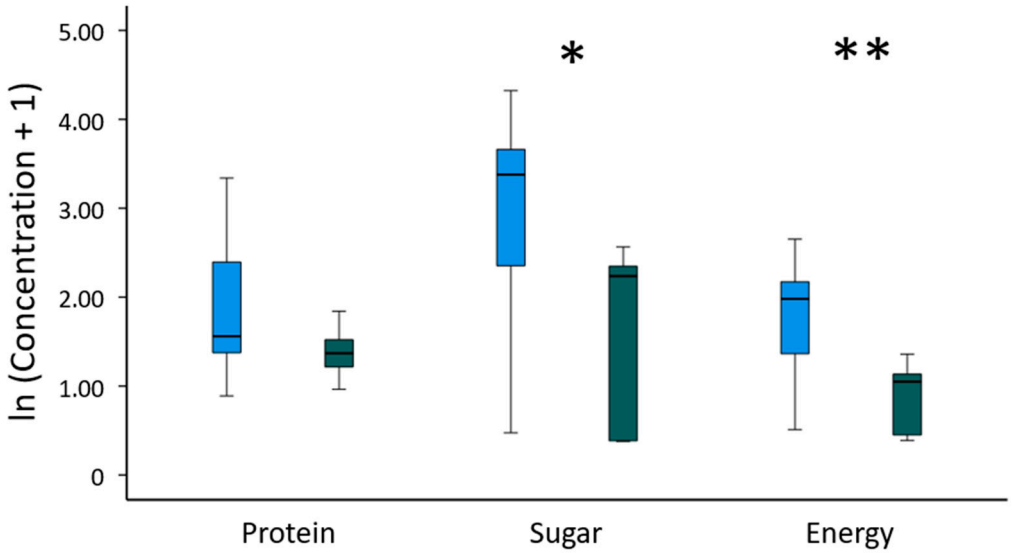

Figure 4. Protein and sugar concentrations (% dry matter) and energy content (kJ/g dry matter) of exudates without antimicrobial effect (blue) and exudates with antimicrobial activity (green). Values are medians, quartiles, and ranges. * $p < 0.05$; ** $p < 0.01$.

In the GC-MS analyses, we identified a total of 75 different components matching the library with a probability ≥98% from the methanol extracts of the exudate samples from 17 different tree species (Appendix F). There is no general pattern in the number of different components between species with or without antibacterial effect. The two species of *Commiphora* stand out for their large number of components, but one of them (*C. simplicifolia*) showed very strong antibacterial effects, while *C. arafy* had no effect in our assays. *Terminalia* spp. did not produce a single component identified in the library.

Many of the components identified have some pharmaceutical properties and are used for medical purposes. Others are irritants or are added to human food as flavors. The consequences of consuming the substances are highly dependent on their concentrations and thus cannot be generalized. Some components are listed as having antimicrobial effects, such as andrographolide, caprylic acid, eugenol, pelagonic acid, salicylic acid, and viriflorol. Apart from salicylic acid, all these components occur predominantly in exudates that had shown antibacterial activity in our disk diffusion tests.

4. Discussion

As well as fruits, leaves, insects, and nectar, primate species from all radiations eat tree exudates. The notion of the role of these components for primate nutrition ranges from exudates being a fallback resource consumed when nothing else was available to being a staple food resource, or a required source of plant secondary metabolites with pharmaceutical properties needed to maintain the animals' health [2,3,14]. Different conclusions might be drawn as this dietary category combines different plant products derived from different plant parts and with different properties, such as gums, saps, resins, or latexes, that may be difficult to distinguish under field conditions [2,4,6,54–56]. In order to reduce additional complexity introduced by evolutionary adaptations of the different primate radiations, we used obligate and facultative gum consumers among lemurs from the dry and spiny forests of Madagascar to explore possible drivers of exudate consumption that we considered to be gum.

The gums consumed by three of the four lemur species (i.e., the three species of *Microcebus*) contained average protein concentrations that match the recommended protein concentrations of 6–8% protein in primate foods. Gum consumed by the most specialized gum eater, *Phaner pallescens*, had lower protein concentrations that would not be sufficient to cover the species' protein needs. *Phaner* spp. have a rather differentiated gut and other gum-eating primates with similar specializations are known for their long food

passage time that allows efficient extraction of nutrients (mainly through fermentation products produced in the hindgut, i.e., after the small intestine where amino acids can be absorbed) [3,13,57,58]. Thus, the low-protein concentrations in gum are unlikely to be compensated for by morphological adaptations, but rather through supplementing their diet with insects [28]. Contrary to their response towards protein concentrations, *Microcebus griseorufus* increased their consumption of gum with increasing energy content. This matches the findings and interpretations of other studies that gum is primarily a source of energy [3,13,55].

As a yet unresolved phenomenon, some of the exudates consumed by the lemurs contained very low concentrations of protein, sugars, and energy content, but were still eaten by lemurs. It is questionable whether or not these exudates were gums or rather resins, but this issue cannot be resolved. In any case, the lemurs consumed these exudates. This resembles the phenomenon of the consumption of leaves with low nutrient content but high pharmaceutical properties by other non-human primates, summarized under the issue of self-medication [23,25,59–61]. Gum-eating lorises were also suggested to consume exudates for their medicinal effects, with negative effects if these components are not provided in captivity [3,13,14,62].

Though our sample size is small, it is noticeable that some of the extracts with very low protein and energy contents showed antibacterial activity against gram-positive bacteria (*Micrococcus* spp. and *Staphylococcus aureus*), while none of the exudates with high protein or energy content had similar activities. Most notably, extracts from *Commiphora simplicifolia* showed pronounced antibacterial activity. Antibacterial inhibition was obtained with oil- and methanol- dissolved samples, but not with water-dissolved samples. These results are consistent with the distinction between water-soluble "gum" and non-water-soluble "resin" and their properties, with antibacterial properties that are more prominent components of the lipophilic but not the water-soluble fraction of tree exudates [4,63]. The feeding behavior of *Microcebus griseorufus* on exudates with antibacterial properties could be interpreted as ingestion of exudates with positive medicinal effects because the nutritional value of these exudates was extremely low. Alternatively, it could be interpreted as "sampling" exudates by *M. griseorufus* to monitor sources of exudates.

Many studies have postulated or demonstrated that animals eat specific plants to combat or control disease [23,25,60,64–66]. Experimental evidence for self-medication is lacking from free-ranging primates, but the phenomenon that primate species eat plant parts with very low nutritive quality suggests another role for these items, such as fighting against diseases [61]. The African great apes (Hominidae) are especially well studied in terms of self-medication [23,25,65,67,68]. Chimpanzees show a reduction in intestinal parasite load after chewing the bitter pith of *Vernonia amygdalina*, and many plants consumed by *Macaca fuscata* inhibit protozoan parasites that are relevant for humans [61]. Some studies on strepsirrhine primates have also postulated antiparasitic effects of plants consumed, such as in *Eulemur fulvus* [69], peripartum sifaka females (*Propithecus verreauxi*) [70], and *Eulemur* spp., that might use millipede secretions against ectoparasites and intestinal parasites [71,72].

Antibacterial, antiviral, and other pharmaceutical effects have been described for all tree genera for which we have found inhibiting effects against the bacteria used in our assays (e.g., *Commiphora*: [73,74]; *Quivisianthe*: [75]; *Terminalia*: [76]. Pharmaceutical effects of *Commiphora* species are especially well known, such as *C. mukul*, with its antiphlogistic [77], hypolipidemic, and antioxidant effects [78]. The commonly known Myrrh, which is the gum of different *Commiphora* species, is used as a mouth wash and as an antibacterial and antifungal drug [79]. Chewing on *C. africana* provides a positive effect on Massai's health [80], and sesquiterpenes of *C. molmol* have been proven to have antibacterial and antifungal properties [79]. Madagascar's *Commiphora* spp. have not been studied extensively. A search in the Web of Science with the topic "*Commiphora*" produced 799 hits worldwide, many addressing pharmaceutical properties. In contrast, "*Commiphora*" and "Madagascar" produced only 15 hits, none of which addressed any pharmaceutical aspect (accessed 10 May 2020). *Quivisianthe papinae* is poorly covered by the international literature, but

other members of the family Meliaceae (e.g., *Neobeguea mahafaliensis*, which did not show antibacterial properties in our assays) have some pharmaceutical properties appreciated by the local population that might also be present in *Quivisanthe* [52,81]. Parts of *Terminalia* are used against tumors, HIV-1, fungal and microbial diseases, malaria, diarrhea, or as a painkiller. Similarly, as with *Commiphora*, the majority of pharmaceutical properties documented stem from species outside of Madagascar [76].

5. Conclusions

The study started out with the observation that lemurs eat gum with nutritive values too low to cover the energy or protein needs of the consumers. Following the findings that gum consumed by Asian loris have pharmaceutical properties [13,14,23], we postulated that gum is either consumed for its energy and protein content, or, if the energy or protein content was very low, gum could also be consumed for its pharmaceutical properties. Though our sample size was small, gum with antibacterial activity had lower protein, sugar, and energy contents than samples without antibacterial properties, thus supporting the idea that pharmaceutical properties play a role in food selection of lemurs when feeding on gum. Due to the small sample size and opportunistic rather than systematic sampling, the present study has to be considered a pilot study on possible reasons for the consumption of gum without obvious nutritive value, possibly hinting towards pharmaceutical properties of gum that is of low nutritive value. Without experimental approaches, it is difficult to compile convincing evidence for self-medication by animals. But the large number of bio-active components found in exudates of the various tree species studied here indicates an unexplored source for pharmaceutical applications. Given the widespread occurrence of exudate feeding among Malagasy strepsirrhines and the limited information on ethnobotanical applications and pharmaceutical properties [75], more detailed analyses of this phenomenon might offer promising options for future studies.

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Data Availability Statement: All data generated or analyzed during this study are included in this published article and its Appendix A.

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Appendix A

Protein, sugar, and energy content of tree exudates consumed by lemurs of the dry and spiny forests of western Madagascar. The year of exudate collection and the lemur species listed as consumer do not match in all cases. Consumer species: *Mg = Microcebus griseorufus*, *Mm = M. murinus*, *Mr = M. ravelobensis*, *Pp = Phaner pallescens*. Consumer species not occurring at the site of sample collection but known to feed on exudates from the same tree species elsewhere are listed in brackets.

Tree Species	Site of Collection	Year Collected	Consumer Species	Protein %	Sugar %	Energy kJ_g
Acacia bellula	Tsimanampetsotse	2008	*Mg*	10.44	34.55	7.53
Acacia bellula	Tsimanampetsotse	2008	*Mg*	7.13	34.40	6.95
Acacia bellula	Tsimanampetsotse	2008	*Mg*	3.31	59.00	10.43
Alantsilodendron alluaudianum	Berenty	2006	*Mg*	21.38	10.01	5.25
Alantsilodendron alluaudianum	Berenty	2006	*Mg*	19.81	41.00	10.18
Alantsilodendron alluaudianum	Berenty	2006	*Mg*	19.06	27.49	7.79
Alantsilodendron alluaudianum	Berenty	2006	*Mg*	18.44	47.63	11.06
Alantsilodendron alluaudianum	Berenty	2006	*Mg*	12.88	48.68	10.30
Albiza tulearensis	Tsimanampetsotse	2012	*Mg*	4.13	0.65	0.80
Albiza tulearensis	Tsimanampetsotse	2012	*Mg*	2.94	0.47	0.57
Albiza tulearensis	Tsimanampetsotse	2012	*Mg*	2.63	0.57	0.53
Albizia mainaea	Analabe	2007	*Mm, Pp*	11.31	28.35	6.64
Albizia microphylla	Berenty	2011	*Mg*	2.19	8.04	1.71
Astrotrichilia asterotricha	Ankarafantsika	2009	*Mm, Mr*	1.75	21.93	3.96
Azima tetracantha	Berenty	2004	*Mg*	5.25	65.62	11.86
Commiphora 1	Berenty	2004	*Mg*	4.00	32.23	6.06
Commiphora 3	Berenty	2004	*Mg*	2.81	31.37	5.72
Commiphora 5	Berenty	2004	*Mg*	2.75	30.42	5.55
Commiphora aprevalii	Berenty	2006	*Mg*	4.56	59.08	10.65
Commiphora arafy	Analabe	2007	*Mm, Pp*	15.25	30.81	7.71
Commiphora arafy	Kirindy	2000	*Pp*		32.82	
Commiphora arafy	Kirindy	1990	*Pp*		16.70	

Tree Species	Site of Collection	Year Collected	Consumer Species	Protein %	Sugar %	Energy kJ_g
Commiphora arafy	Kirindy	1989	*Pp*		17.10	
Commiphora humbertii	Tsimanampetsotse	2008	*Mg*		6.05	
Commiphora humbertii	Berenty	2006	*Mg*	1.94	28.98	5.17
Commiphora lamii	Tsimanampetsotse	2008	*Mg*	9.44	41.53	8.53
Commiphora lamii	Berenty	2006	*Mg*	5.00	31.4	6.09
Commiphora marchandii	Tsimanampetsotse	2008	*Mg*	9.44	53.73	10.57
Commiphora marchandii	Tsimanampetsotse	2008	*Mg*		25.67	
Commiphora marchandii	Tsimanampetsotse	2008	*Mg*		49.94	
Commiphora monstruosa	Tsimanampetsotse	2008	*Mg*		24.66	
Commiphora orbicularis	Berenty	2006	*Mg*	11.38	39.33	8.49
Commiphora orbicularis	Berenty	2006	*Mg*	11.31	55.94	11.26
Commiphora orbicularis	Berenty	2006	*Mg*	10.06	32.51	7.12
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*	4.69	9.17	2.32
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*	4.31	15.22	3.27
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*	4.00	9.88	2.32
Commiphora simplicifolia	Tsimanampetsotse	2012	*Mg*	3.81	4.90	1.46
Commiphora simplicifolia	Tsimanampetsotse	2012	*Mg*	3.81	6.02	1.65
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*	2.94	12.35	2.56
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*	1.38	17.39	3.14
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*		4.76	
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*		5.81	
Commiphora simplicifolia	Tsimanampetsotse	2012	*Mg*		8.92	
Commiphora simplicifolia	Tsimanampetsotse	2008	*Mg*		10.7	

Tree Species	Site of Collection	Year Collected	Consumer Species	Protein %	Sugar %	Energy kJ_g
Commiphora sp.	Berenty	2006	*Mg*	2.63	50.17	8.84
Commiphora stellulata	Kirindy	1990	*Pp*		26.10	
Commiphora trifolia	Berenty	2003	*Mg*	16.88	2.13	3.18
*Commiphora*_Anka1	Ankarafantsika	2009	*Mm*	17.75	38.17	9.36
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	4.56	21.99	4.44
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	4.25	26.71	5.18
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	2.75	71.61	12.44
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	2.50	58.14	10.15
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	1.44	8.03	1.58
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	1.31	50.69	8.70
Delonix floribunda	Tsimanampetsotse	2012	*Mg*	1.25	56.03	9.59
Delonix floribunda	Tsimanampetsotse	2008	*Mg*	0.75	34.12	5.84
Delonix floribunda	Tsimanampetsotse	2012	*Mg*	0.63	24.77	4.25
Delonix floribunda	Tsimanampetsotse	2008	*Mg*		20.59	
Delonix floribunda	Tsimanampetsotse	2008	*Mg*		35.93	
Delonix floribunda	Analabe	2007	*Mm, Pp*	3.88	47.59	8.61
Dichrostachys	Berenty	2004	*Mg*	30.94	18.68	8.30
Dichrostachys	Berenty	2004	*Mg*		11.88	
Dichrostachys	Berenty	2004	*Mg*	22.94	18.49	6.93
Dichrostachys	Berenty	2004	*Mg*	18.19	32.39	8.46
Dichrostachys	Berenty	2004	*Mg*		22.83	
Dichrostachys	Berenty	2004	*Mg*	22.31	21.21	7.28
Dichrostachys	Berenty	2004	*Mg*		22.19	
Dichrostachys	Berenty	2004	*Mg*		21.67	
Dichrostachys	Berenty	2004	*Mg*		30.85	
Dichrostachys	Berenty	2004	*Mg*		19.55	
Dichrostachys	Berenty	2004	*Mg*		28.20	
Dichrostachys	Berenty	2004	*Mg*		24.91	
Dichrostachys	Berenty	2004	*Mg*		22.61	
Dichrostachys	Berenty	2004	*Mg*		2.63	

Tree Species	Site of Collection	Year Collected	Consumer Species	Protein %	Sugar %	Energy kJ_g
Dichrostachys	Berenty	2004	*Mg*		21.13	
Dichrostachys	Berenty	2004	*Mg*	22.81	26.51	8.25
Dichrostachys	Berenty	2004	*Mg*	22.56	32.3	9.18
Dichrostachys	Berenty	2004	*Mg*		38.53	
Grewia_Tabarike	Berenty	2004	*Mg*	7.00	16.64	3.96
Grewia_Tabarike	Berenty	2004	*Mg*	7.50	14.01	3.60
Grewia_Taolankafotsy	Berenty	2004	*Mg*	11.25	2.49	2.30
Hymenodictyon decaryi	Kirindy	2000	*Pp*	3.50	5.55	1.51
Neobeguea mahafaliensis	Tsimanampetsotse	2012	*Mg*	5.13	21.42	4.44
Neobeguea mahafaliensis	Tsimanampetsotse	2008	*Mg*	3.38	11.08	2.42
Neobeguea mahafaliensis	Tsimanampetsotse	2008	*Mg*	2.25	6.15	1.41
Neobeguea mahafaliensis	Tsimanampetsotse	2008	*Mg*	2.00	10.71	2.13
Neobeguea mahafaliensis	Tsimanampetsotse	2008	*Mg*		0.17	
Neobeguea mahafaliensis	Tsimanampetsotse	2008	*Mg*		2.70	
Neobeguea mahafaliensis	Tsimanampetsotse	2008	*Mg*		9.53	
Neobeguea mahafaliensis	Kirindy	2000	*Pp*		37.25	
Neobeguea mahafaliensis	Analabe	2007	*Pp*	3.38	2.83	1.04
Operculicarya gummifera	Kirindy	2001	*Pp*		0.63	
Operculicarya gummifera	Kirindy	2001	*Pp*		0.81	
Operculicarya gummifera	Kirindy		*Pp*		26.01	
Operculicarya hyphaenoides	Tsimanampetsotse	2008	*Mg*	2.44	65.60	11.39
Operculicarya hyphaenoides	Tsimanampetsotse	2008	*Mg*	2.13	74.72	12.86
Operculicarya hyphaenoides	Tsimanampetsotse	2008	*Mg*	1.69	40.67	7.09
Operculicarya hyphaenoides	Tsimanampetsotse	2008	*Mg*		58.18	
Operculicarya hyphaenoides	Tsimanampetsotse	2008	*Mg*		73.64	

Tree Species	Site of Collection	Year Collected	Consumer Species	Protein %	Sugar %	Energy kJ_g
Operculicarya hyphaenoides	Tsimanampetsotse	2008	*Mg*	3.19	11.43	2.45
Poupartia silvatica	Ankarafantsika	2009	*Mm, Mr*		28.21	6.45
Poupartia silvatica	Kirindy	2000	*Pp*	27.25	7.95	5.89
Poupartia silvatica	Kirindy	1999	*Pp*	2.31	56.64	9.87
Poupartia silvatica	Kirindy	1999	*Pp*	1.38	25.08	4.43
Poupartia silvatica	Kirindy	1990	*Pp*		16.70	
Poupartia silvatica	Kirindy	1990	*Pp*		23.30	
Poupartia silvatica	Kirindy	1993	*Pp*		39.59	
Quivisianthe papinae	Berenty	2011	*(Mg)*	2.38	0.46	0.47
Rhopalocarpus lucidus	Zombitse	2011	*(Mg)*	2.75	13.51	2.72
Rhopalocarpus similis	Ankarafantsika	2009	*Mm*	2.56	64.76	11.27
Rhopalocarpus sp	Analabe	2007	*Mm*	3.94	38.15	7.04
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*	3.94	78.76	13.84
Terminalia disjuncta	Tsimanampetsotse	2012	*Mg*	3.69	48.66	8.76
Terminalia disjuncta	Tsimanampetsotse	2012	*Mg*	3.19	62.86	11.05
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*	3.13	61.60	10.83
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*	3.00	80.63	14.00
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*	2.38	85.94	14.78
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*	2.13	53.25	9.27
Terminalia disjuncta	Tsimanampetsotse	2012	*Mg*	2.00	51.57	8.97
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*	1.63	9.48	1.86
Terminalia disjuncta	Tsimanampetsotse	2008	*Mg*		55.76	
Terminalia mantaliopsis	Analabe	2007	*Mm, Pp*	2.38	26.06	4.76
Terminalia mantaly	Analabe	2007	*Mm, Pp*	1.44	25.15	4.45

Tree Species	Site of Collection	Year Collected	Consumer Species	Protein %	Sugar %	Energy kJ_g
Terminalia sp.	Kirindy	2001	*Pp*	2.69	17.88	3.44
Terminalia sp.	Kirindy	2001	*Pp*	2.44	26.91	4.91
Terminalia sp.	Kirindy	2000	*Pp*	1.56	64.70	11.09
Terminalia sp.	Kirindy	2000	*Pp*	1.44	1.41	0.48
Terminalia sp.	Kirindy	2000	*Pp*		2.28	
Terminalia sp.	Kirindy	2000	*Pp*		6.32	
Terminalia sp.	Kirindy	2000	*Pp*		6.67	
Terminalia sp.	Kirindy	2001	*Pp*		8.40	
Terminalia sp.	Kirindy	2000	*Pp*		11.21	
Terminalia sp.	Kirindy	2000	*Pp*		12.19	
Terminalia sp.	Kirindy	2000	*Pp*		15.48	
Terminalia sp.	Kirindy	2000	*Pp*		19.32	
Terminalia sp.	Kirindy	2001	*Pp*		21.89	
Terminalia sp.	Kirindy	2000	*Pp*		26.66	
Terminalia sp.	Kirindy	2001	*Pp*		51.5	
Terminalia sp.2	Kirindy	2000	*Pp*		0.66	
Terminalia ulexoides	Tsimanampetsotse	2012	*Mg*	13.75	4.68	3.08
Terminalia ulexoides	Tsimanampetsotse	2008	*Mg*	3.00	11.90	2.49
Terminalia ulexoides	Tsimanampetsotse	2008	*Mg*	1.75	9.86	1.94
Terminalia ulexoides	Tsimanampetsotse	2008	*Mg*	1.50	18.60	3.36
Terminalia ulexoides	Tsimanampetsotse	2012	*Mg*		5.28	
Terminalia ulexoides	Tsimanampetsotse	2008	*Mg*		18.50	
unknown sp1	Kirindy	1999	*Pp*	0.38	23.52	4.00
unknown sp2	Kirindy	2000	*Pp*	1.50	0.84	0.39
unknown sp3	Zombitse	2011	*Pp*	5.31	12.01	2.90
Zanthoxylum sp.	Kirindy	1999	*Pp*	4.13	54.39	9.79
Zanthoxylum sp.	Kirindy	2001	*Pp*	3.50	45.21	8.15
Zanthoxylum sp.	Kirindy	2001	*Pp*		60.65	

Appendix B

Exudate consumption of *Microcebus griseorufus* in Tsimanampetsotse National Park; chemical composition of exudates is represented by the mean per tree species derived from Appendix A, assigned to different vegetation formations and seasons. Freq. = Frequency of consumption, N% = % nitrogen, Sugar % = % sugar; AB = antibacterial effect.

	Dry Season				Wet Season				Dry Season				Wet Season			
	Freq.	**N %**	**Sugar %**	**AB**	**Freq.**	**N**	**Sugar**	**AB**	**Freq.**	**N %**	**Sugar %**	**AB**	**Freq.**	**N**	**Sugar**	**AB**
Acacia bellula	0	1.11	42.65	0	1			0	0			0	0			0
Albizia tulearensis	2			0	0	0.52	0.56	0	0			0	1			0
Commiphora marchandi	0	1.51	43.11	0	1			0	0			0	0			0
Commiphora simplicifolia	1	0.58	11.49	1	0	0.61	6.61	1	0			1	0			1
Delonix floribunda	0	0.68	27.74	0	1	0.44	71.61	0	2	0.32	28.71	0	2	0.15	40.40	0
Neobeguea mahafaliensis	0	0.54	5.63	0	0	0.82	21.42	0	3			0	0			0
Operculicarya hyphaenoides	0				0				0	0.38	50.12	0	0			
Terminalia disjuncta	1	0.26	9.48	1	7	0.47	54.36	0	11	0.40	73.27	0	3			0
Terminalia ulexoïdes	1	0.36	15.25	0	0	2.2	4.98	0	0		18.50	0	0			0

Appendix C

Antibacterial activity of water dissolved gum.

Tree Species	Sample No.	ESCH 006	PSMN 028	MICO 004	SFCO 002
Acacia bellula	P08-127	0	-	-	-
Acacia bellula	P08-128	0	-	-	-
Acacia burkei	F11-4	-	-	0	-
Albizia tulearensis	B12-10	-	-	0	-
Albizia tulearensis	B12-11	-	-	0	-
Albizia tulearensis	B12-12	-	-	0	-
Combretum molle	F11-5	0	-	-	-
Commiphora simplicifolia	P08-120	0	0	0	0
Commiphora sp.	F07-7	0	-	0	-
Commiphora sp.	F07-8	0	-	0	-
Delonix floribunda	B12-15	-	-	0	-
Delonix floribunda	B12-16	-	-	0	-
Harpephyllum caffrum	F11-7	0	-	-	-
Neobeguea mahafaliensis	P08-104	-	-	0	-
Neobeguea mahafaliensis	B12-13	-	-	0	-
Neobeguea mahafaliensis	B12-14	-	-	0	-
Quivisianthe papinae	F11-8	-	0	0	-
Terminalia disjuncta	P08-78	-	-	0	-
Terminalia mantaliopsis	F07-3	-	-	0	-
Terminalia ulexoides	B12-1	-	-	0	-
Terminalia ulexoides	B12-2	-	-	0	-
Terminalia ulexoides	B12-3	-	-	0	-
Unknown species	F11-11	-	-	0	-

All zones of inhibition measured as diameter including the filter paper with a diameter of 9 mm. 0: No zone of inhibition; -: No test performed.

Appendix D

Antibacterial activity of gum dissolved in olive oil.

Tree Species	Sample No.	ESCH 006	PSMN 028	MICO 001	MICO 003	MICO 004	MICO 005	MICO 006	SFCO 002	STCO 001
Acacia bellula	P08-127	-	-	-	-	0	-	-	-	-
Acacia bellula	P08-128	-	-	-	-	0	-	-	-	-
Acacia burkei	F11-4	-	-	-	-	0	-	-	-	-
Acacia robusta	F11-6	-	-	-	-	0	-	-	-	-
Albizia mainaea	F07-5	0	-	0	0	0	0	0	0	0
Albizia tulearensis	B12-10	0	-	-	-	0	-	-	-	-
Albizia tulearensis	B12-11	0	-	-	-	0	-	-	-	-
Albizia tulearensis	B12-12	0	-	0	0	0	0	0	0	0
Combretum molle	F11-5	-	-	0	0	0	0	0	0	0
Commiphora guillaumini	S00-19	-	-	0	0	0	0	0	0	0
Commiphora marchandii	P08-111	-	-	0	0	0	0	0	0	0
Commiphora marchandii	P08-114	-	-	-	-	0	-	-	-	-
Commiphora simplicifolia	P08-119	0	-	-	-	2	-	-	-	-
Commiphora simplicifolia	P08-120	0	0	0	1	2	1	0	0	0
Commiphora simplicifolia	P08-125	0	-	-	-	2	-	-	-	-
Commiphora simplicifolia	B12-7	-	-	-	2	2	1	-	1	-
Commiphora simplicifolia	B12-8	0	0	-	1	2	1	-	1	-
Commiphora sp.	F07-7	-	-	0	0	0	0	0	0	0
Commiphora sp.	F07-8	-	-	-	-	0	-	-	-	-
Delonix floribunda	F07-4	-	-	-	-	0	-	-	-	-
Delonix floribunda	P08-76	-	-	-	-	0	-	-	-	-
Delonix floribunda	P08-51	-	-	-	-	0	-	-	-	-
Delonix floribunda	B12-15	0	-	-	-	0	-	-	-	-
Delonix floribunda	B12-16	0	-	-	-	0	-	-	-	-
Harpephyllum caffrum	F11-7	-	-	-	-	0	-	-	-	-
Hymenodictyon decaryi	S00-3	-	-	-	-	0	-	-	-	-
Neobeguea mahafaliensis	P08-100	-	-	-	-	0	-	-	-	-
Neobeguea mahafaliensis	P08-104	-	-	0	0	0	0	0	0	0
Neobeguea mahafaliensis	B12-13	0	-	-	-	0	-	-	-	-

Tree Species	Sample No.	ESCH 006	PSMN 028	MICO 001	MICO 003	MICO 004	MICO 005	MICO 006	SFCO 002	STCO 001
Neobeguea mahafaliensis	B12-14	0	-	-	-	0	-	-	-	-
Operculicarya gummifera	S00-10	-	-	-	-	0	-	-	-	-
Operculicarya hyphaenoides	P08-108	-	-	-	-	0	-	-	-	-
Poupartia silvatica	S00-2	-	-	-	-	0	-	-	-	-
Quivisianthe papinae	F11-8	0	0	0	0	nr	nr	0	0	0
Rhopalocarpus sp.	F07-6	-	-	-	-	0	-	-	-	-
Terminalia disjuncta	P08-30	-	-	-	-	nr	-	-	-	-
Terminalia disjuncta	P08-53	-	-	-	-	0	-	-	-	-
Terminalia disjuncta	P08-78	-	-	-	-	0	-	-	-	-
Terminalia mantaliopsis	F07-3	-	-	-	-	0	-	-	-	-
Terminalia mentaly	F07-2	-	-	-	-	0	-	-	-	-
Terminalia ulexoides	B12-1	0	-	-	-	0	-	-	-	-
Terminalia ulexoides	B12-2	0	-	-	-	0	-	-	-	-
Terminalia ulexoides	B12-3	0	-	-	-	0	-	-	-	-
Zanthoxylum sp.	S00-13	-	-	-	-	0	-	-	-	-
Unknown species	F11-11	0	0	-	-	2	nr	-	0	0

All zones of inhibition measured as diameter including the filter paper with a diameter of 9 mm. 0: No zone of inhibition, 1: Zone of inhibition of 10–15 mm, 2: Zone of inhibition of 16–50 mm, nr: Inhibition suggested but not replicable, -: No test performed.

Appendix E

Antibacterial activity of methanol dissolved gum.

Tree Species	Sample No.	ESCH 006	PSMN 028	MICO 003	MICO 004	MICO 005	SFCO 002
Albizia tulearensis	B12-12	-	-	-	nr	-	0
Commiphora guillaumini	S00-19	-	-	0	0	-	-
Commiphora simplicifolia	P08-120	0	0	1	2	nr	1; 2
Commiphora simplicifolia	B12-8	-	-	nr	1	Nr	nr
Quivisianthe papinae	F11-8	-	-	nr	nr	Nr	nr
Terminalia disjuncta	P08-30	-	-	-	0	-	0

All zones of inhibition measured as diameter including the filter paper with a diameter of 9 mm. 0: No zone of inhibition, 1: Zone of inhibition of 10–15 mm, 2: Zone of inhibition of 16–50 mm, nr: Inhibition suggested but not replicable, -: No test performed.

Appendix F

Components identified by GC-MS in methanol extracts of exudates investigated in the present study; shaded columns species abbreviations are: *Ab* = *Acacia bellula*, *Am* = *Albizia mainaea*, *At* = *Albizia tulearensis*, *Df* = *Delonix floribunda*, *Ca* = *Commiphora arafy*, *Cs* = *C. simplicifolia*, *Hd* = *Hymenodictyon decaryi*, *NM* = *Neobeguea mahafaliensis*, *Oh* = *Operculicarya hyphanoides*, *Ps* = *Poupartia sylvatica*, *Qp* = *Quivisanthe papinae*, *Rs* = *Rhopalocarpus* sp., *Td* = *Terminalia disjuncta*, *Tm* = *Terminalia mantalis*, *Tma* = *Terminalia mantaliopsis*, *Tu* = *Terminalia ulexoides*, *Zsp* = *Zanthoxylum* sp. Parts used in traditional medicine according to [52,53]: Ar = Aerial parts, Gum, Sb = Subterranean parts, Lx = Sap or latex, Tr = Trunk, Br = stem barks.

	Ab	*Am*	*At*	*Df*	*Ca*	*Cs*	*Hd*	*Nm*	*Oh*	*Ps*	*Qp*	*Rs*	*Td*	*Tm*	*T ma*	*Tu*	*Z sp*	**Pharmacology [44]**	**Pharmacology NIH National Library of Medicine https://pubchem.ncbi.nlm.nih.gov/ (accessed on 1 November 2023)**
Antimicrobial effect in the present study	0	0	0/1	0	0	1	0	0	0	0	1	0	0/1	0	0	0	0		
Part used according to [52,53]	Ar		Br	Lx	Gur	Ar		Sb,Tr					Ar			Sb	Sb		
Acetophenone					1											1		None	Photosensitizing
Allocimene			1															Not listed	Possibly toxic
Andrographolide			1															Anti-inflammatory	Antiprotozoal Anti-inflammatory Antiviral Platelet Aggregation Inhibitor
Anethole																1		Antitussive; flavoring agent in food	Flavoring agent
Anisic acid																1		Condiment and flavor in foods; carminative; expectorant	Flavoring agent
Aromadendrene			1															Not listed	None
trans-α-Begamoten									1									Not listed	None
Benzaldehyd																1			
Bourbonene					1	1												Not listed	Flavouring agent
Bulnesene						1												Not listed	None
Cadinene					1		1											None	None
Calorene					1													Not listed	Not listed
Camphen									1									None	None
Caprylic acid (Octanoic Acid)						1												Antifungal Toxic	Possibly against seizures
Caryo-phyllene			1			1	1											None	Flavouring agent
Cendrene					1													Not listed	Not listed
Chamigrene					1	1												Not listed	None
Chavicol						1										1		None	None
Copaene					1		1											None	None

	Ab	*Am*	*At*	*Df*	*Ca*	*Cs*	*Hd*	*Nm*	*Oh*	*Ps*	*Qp*	*Rs*	*Td*	*Tm*	*Tma*	*Tu*	*Z sp*	**Pharmacology [44]**	**Pharmacology NIH National Library of Medicine https://pubchem.ncbi.nlm.nih.gov/ (accessed on 1 November 2023)**
Cubebene						1												Urinary antiseptic; expectorant	None
Curcumene					1													None	None
Curzene					1													Not listed	Not listed
Cyclolanost-24en-3ol								1										Not listed	Not listed
Cymen									1									None	None
Elemene			1		1	1												Not listed	None
Elemol					1													Not listed	None
Enanthic acid						1												Not listed; Enanthotoxin highly toxic	None
Ergostene			1															None	Not listed
Eudesmol					1													Not listed	None
Eugenol						1										1		Toxic	Anti-infective agent
Falcarinol							1											Not listed	Unclear
Farnesene					1	1												None	None
Germacrene					1													Not listed	None
Guaiacol																1		Expectorant	Not listed
Himachalene					1													Not listed	None
Hydrochinon																1		Not listed	Antioxidant Mutagen
Isoeugenol						1												None	None
Isoledene					1													Not listed	None
Isolongifolene					1													Not listed	None
Lauric acid						1												None	None
Limonene					1				1		1							None	None
Longifolenaldehyde								1										None	None
Maltol												1						Flavoring agent	None
p-Mentadien			1		1				1									Not listed	Not listed
Muurolen							1											Not listed	None
Myrcene						1												None	None
Myristic acid						1												Antifoaming	None
Neoisolongifolene					1													Not listed	None
Nerolidol			1			1												None	None
Palmitic acid						1												None	Enzyme inhibitor
Pelargonic acid						1												Strong irritant	Antifungal
Pelargonaldehyde						1												Not listed	None
Phenanthrene			1															Photosensitization of skin	None
Phenanthrenol			1															Not listed	None
α-Pinene									1									Toxic	None
ß-Pinene									1									None	None
Pinocarveol									1									Not listed	None
Podocarp 7-en-3one			1															Not listed	Not listed
Resorcinol				1														Toxic; antiseptic	Unclear
Salicylic acid																1		Antireumatic, analgesic	Anti-infective Antifungal Keratolytic
Santolinatriene			1															Not listed	None

	Ab	*Am*	*At*	*Df*	*Ca*	*Cs*	*Hd*	*Nm*	*Oh*	*Ps*	*Qp*	*Rs*	*Td*	*Tm*	*T ma*	*Tu*	*Z sp*	Pharmacology [44]	Pharmacology NIH National Library of Medicine https://pubchem.ncbi.nlm.nih.gov/ (accessed on 1 November 2023)
Selinene					1													Not listed	None
Spathulenol			1		1													Not listed	Part of essential oils
Syringol						1										1		Not listed	None
Tetradecanal											1							Not listed	None
Valeric acid						1												None	None
Valerolactone											1							Not listed	None
Veratraldehyde																1		None	None
Veratric acid																1		None	Prevention of neoplasm associated with HPV
Veratril						1										1		Not listed	None
Verbenone									1									None	Not listed
Vertraldehyde						1												Not listed	Not listed
Viridiflorol			1		1	1												Not listed	Growth inhibitor (animal cells, micro-organisms)

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