The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review

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by

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Abstract. While the key role of termites in the decomposition of litter in the tropics has been acknowledged for a long time, much less insight exists in their importance 50 for the recycling of dung of primary consumers, especially herbivores. A review of published studies shows that a diverse group of termites (at least 126 species) has been reported to feed on a wide range of mammalian dung (18 species). Predominantly, wood-feeding and polyphagous wood-litter feeding species were found to feed also substantially on dung. Moreover, we found that termites can 55 quickly remove large amounts of mammalian dung, especially in the dry season, when on average about 1/3-rd of the dung deposited in a given habitat is removed by termites within one month (with the highest rates observed in savannas). No distinctive preference for mammalian dung over other organic food sources was observed for fungus-growing termites (Macroterminitae), whereas the majority of the 60 studied non-fungus growing taxa prefer dung over alternative food items. As termites bring large quantities of dung below the soil surface, with associated substantial pedoturbation and nutrient enrichment of soils, dung feeding by termites appears to be a previously underestimated process that is important in order to understand the functioning of tropical ecosystems.

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INTRODUCTION

Termites are widely distributed throughout the tropical and subtropical regions of the world, with the highest diversity found in tropical forests (Eggleton, 2000).

Until the early 1970's approximately 1900 living and fossil species of termites had been described (Lee & Wood, 1971) and a constant flow of first descriptions is still increasing this number significantly. Termites (taxon-dependent) act as herbivores as well as decomposers, feeding on a wide range of living, dead or decaying plant materials (Adamson, 1943; Noirot & Noirot-Timothée, 1969; Lee & Wood, 1971;
Wood, 1976, 1978; Bignell & Eggleton, 2000; Traniello & Leuthold, 2000), including the consumption and turnover of large volumes of soil rich in organic matter and fungi. These feeding habits make termites important ecosystem engineers resulting in the long-term modification of physical soil properties such as texture, water infiltration rates and nutrient contents at various spatial scales (e.g. Dangerfield et al. 1998).

Previous overviews of the food and feeding habits of termites either only list mammalian dung as just one possible food item (Lee & Wood, 1971; Wood, 1976, 1978; Bignell & Eggleton, 2000; Traniello & Leuthold, 2000) or even do not mention mammalian dung as a food item of termites at all (Adamson, 1943; Noirot & NoirotTimothée, 1969). Only one older paper focuses on the utilization of mammalian dung by termites (Ferrar & Watson, 1970), but is restricted to data from the Australian region. It does not include the more recent work on the subject, and does not address the ecosystem consequences of dung feeding by termites (Ferrar & Watson, 1970). The lack of attention for the role of termites as dung feeders has been in strong contrast to the attention that has been paid to dung beetles in the comminution and decomposition of herbivore dung, emphasizing the importance of the latter group for nutrient cycling (e.g. Hanski & Cambefort, 1991). So far, the question to what extent and which species of termites consume mammalian dung and whether termites might

fulfil a similar ecosystem role as dung beetles, has remained largely unanswered. In

95 this paper we therefore review the existing literature on the processing of herbivore dung by termites, from both the termite autecological perspective, as well as its ecosystem consequences.

THE AUTECOLOGICAL PERSPECTIVE

- Consumption of mammalian dung. We identified 24 studies, dating between
 100 1955 and 2004, that contain detailed data on the consumption of mammalian dung by termites (Appendix). These studies report in total 126 taxa of termites to feed on dung. This number represents a conservative count and is most likely an underestimation: studies reporting a termite genus to utilize dung with no species specification were counted only once and omitted completely from the count if
 105 another publication provided a species-specific record of the same genus. Representatives of the families Mastotermitidae, Rhinotermitidae and predominantly Termitidae are involved in the removal of dung. In our list the genus *Amitermes*, family Termitidae, is remarkable, in that at least 35 species have been reported to use dung as a food source. This observation might be explained by the high diversity
 110 (Scheffrahn et al., 1999) as well as the polyphagous feeding style and tropicopolitan
- distribution of this genus (Eggleton, 2000), which is most diverse in semi-arid habitats (Scheffrahn & Su, 1987).

The majority of the findings were extracted from surveys of termite diversity, from a smaller number of field (using mostly cattle-dung/cattle-manure, exceptionally elephant dung) and one single laboratory experiment, which provided only descriptive data (Skaife, 1955). Incidents where termites foraged on mammalian dung were reported from around the globe: Africa, Asia, Australia and North-/Central-/South-America. Most observations were made in Australia and Africa, potentially mirroring a skewed emphasis to preferentially study feeding habits of termites in grass- andbush-lands on these continents.

Across studies, termites were observed to feed on dung of in total 18 mammalian species: black rhinoceros (*Diceros bicornis*), African buffalo (*Syncerus caffer*), cattle (*Bos taurus*), camel (*Camelus* sp.), dikdik (*Madoqua* sp.), donkey (*Equus asinus asinus*), African elephant (*Loxodonta africana*), goat (*Capra aegagrus*)

- 125 hircus), horse (Equus caballus), hyrax (Hyracoidea), impala (Aepyceros melampus), kudu (Tragelaphus sp.), kangaroo/wallaby (Macropodidae), sheep (Ovis aries), duiker (Cephalophinae), springbok (Antidorcas marsupialis), wombat (Vombatidae) and zebra (Equus quagga ssp). We found no references for a clear specialization where particular termite species would feed mainly on the dung of one particular mammalian
- herbivore species. When we analyzed the collective records with regard to feeding-types, we found that predominantly wood-feeding (42 species = 39%) as well as polyphagous wood-litter feeding termite species (27 = 25%) also forage on mammalian dung. In comparison to that, 17 litter- (= 16%) and 22 (= 20%) soil-feeding termite species were documented to show the same behavior. Given that, we
 may hypothesize that the consumption of mammalian dung by termites is of more than mere incidental importance. The question arises, how termites manage to locate

Locating dung. Johnson & Whitford (1975) studied the foraging behavior of unidentified subterranean termites in the Chihuahuan desert and found that *Yucca elata* logs and cattle dung, which provided large surface area contact with the soil, were preferred over small twigs and surface litter. They conclude that the modified

this spatial and temporal heterogeneously distributed food source?

environment under a large object on the soil surface (e.g. increased moisture content) is a necessary factor in food suitability, at least for subterranean termites. Ettershank

et al. (1980) conducted baiting field experiments to see if this modified environment

- 145 is also used for locating the food. They conclude that desert subterranean termites locate relatively large size surface food such as cattle dung and *Yucca* sp. logs by sensing the thermal shadows cast by such items. A next question is whether dung is particularly attractive to termites from a nutritional perspective, or whether it is just an accumulation of organic matter?
- Nutrition. As Higashi et al. (1992) outlined, as termites generally feed on dead plant material that has a carbon to nitrogen ratio much higher than their own tissues', they have to balance their C and N inputs. The same authors list two classes of such C-N balancing mechanisms: adding N to inputs or selectively eliminating C, both achieved with the aid of microbial symbionts. But the lower the C/N ratio of the 155 diet, the less urgently this balancing is needed. Matsumoto (1976) reports C/N ratios of 4 to 12 for termite tissues, whereas fresh dead wood has C/N ratios as high as 350 to 1000 (LaFage & Nutting, 1978). For comparison, Ouédraogo et al. (2004) provide data on the C/N ratio of the baits they presented to termites: *Andropogon* straw = 153 (0.32% N), cattle dung = 40 (0.95% N), maize straw = 59 (0.77% N). Accordingly, at least the cattle dung provided to the termites in this study has a much more favorable
- C/N ratio than the alternative food items and might, therefore, be attractive to termites. In spite of this, and the clearly increased phosphorous levels of the used cattle dung (1.06% vs. 0.03% in *Andropogon* straw and 0.18% in maize straw), the involved soil macrofauna preferentially removed the straw over the cattle dung (Table
- 165 2, later discussion). This may mean that the symbiotic opportunities of termites that allow them to compensate for very low food quality simply overrule the need to be highly selective in food selection from a C/N ratio perspective. Despite the various

biochemical processes involved, this may accordingly hold true for both – endo- and ectosymbiotic (fungus-growing) termites.

- 170 Alternatively, or additionally, it might be that the physical parameters bulk density, texture and spatial location of dung make this food source attractive to termites. Seen in comparison to the alternatives, such as standing, dead grass, dung pats are an easily available local accumulation of litter and organic matter, aggregated by large herbivores. Termites might simply benefit energetically by exploiting dung 175 pats with a comparable high mass per volume ratio, instead of feeding on grass litter
- that needs to be collected over a wider spatial range in a more unfavorable microclimate. Moreover, the mammalian herbivores and their endosymbionts mechanically (fragmentation) and biochemically 'preprocessed' the plant materials and in this way may have facilitated the further utilization by termites.

180 THE ECOSYSTEM PERSPECTIVE

Dung deposited naturally on the soil surface by mammalian herbivores needs to be broken down and eventually incorporated into the soil layer to reenter the nutrient cycle. It has been suggested for a long time (e.g. Adamson, 1943), that termites are of crucial importance to the fertility of tropical soils and the productivity of ecosystems. Besides that termites promote aeration, drainage and penetration of roots, as well as contribute to pedoturbation via their epigeal lifestyle, termites accelerate the formation of humus and the cycling of mineral elements by consuming dead wood and other plant remains (Adamson, 1943). The question arises, whether the comminution of mammalian dung by termites is not only of autecological importance but also impacts the functioning of the ecosystem, i.e. the nutrient cycling

dynamics, and if so how these effects may be qualified and quantified.

Removal rates. The results of five studies reporting dung removal rates of termites as measured in field experiments are summarized (Table 1). Since the removal rates, as reported in the original publications, were measured over different time intervals, we standardized them to: % dung removed/month. The five studies report that termites removed between 12-57% of available dung within one month. Overall, higher removal rates were measured in the dry than in the wet season (Coe, 1977; Omaliko, 1981; Whitford et al., 1982; Ouédraogo et al., 2004). Measured removal rates were 12 %/month for a desert, 36-57 %/month in savannas, 31 %/month in an agricultural field and 12 %/month in a pasture. Despite the low sample size, savannas tend to have the highest removal rates. Over all studies, the average dung removal rate by termites was around 30% per month of the dung placed in a given habitat in the field by experimentators.

- Preferences and seasonality. Another important aspect is the occurrence of
 food preferences and the differentiated role of termites vs. dung beetles. The results shown in Table 1 are quantitative ones reflecting a general, qualitative trend though: higher removal rates are found during the dry season for a given habitat. As mentioned earlier, Ferrar & Watson (1970) also reach the conclusion that termites prefer dry dung pats. One single study (Herrick & Lal, 1996) documents an increased
 comminution of cattle dung by *Amitermes beaumonti* and *Hoplotermes* sp. nov. in a Neotropical pasture ecosystem in the wet season. Many authors, e.g. Weir (1971), detected the overall pattern that dung beetles are responsible for the removal and burial of almost all dung during the wet season. This has led various authors to state that dung beetles are generally responsible for nutrient recycling from dung (e.g. Losey & Vaughan, 2006). It appears that this is however only true for the wet season:
 - since adult dung beetles feed exclusively on the liquid component of the dung by

means of specialized filtering mouthparts (Cambefort, 1991), they rely on the availability of dung with high water content. In addition, some dung beetle species (e.g. Onthophagus binodis) produce significantly fewer brood balls under dry soil 220 conditions (Barkhouse & Ridsdill-Smith, 1986). This means that in the dry season termites seem to gain in importance - relative to dung beetles. But dung is not only a temporally but also spatially very heterogeneous resource; it is not permanently available to termites, based on the mobile lifestyle of its producers, while termites are sessile and bound to their nests. This is an important contrast to dung beetles, which are mobile. These factors might be of explanatory nature to the findings regarding 225 food-preferences (dung vs. other, natural items) of termites (Table 2). Overall, termites show no clear, distinct preference for mammalian dung over other plant food items. A very interesting pattern becomes apparent though if the 12 fungus-growing taxa (Macrotermitinae) are compared to the remaining ten species that do not grow 230 fungi: while half of the Macrotermitinae taxa show a preference for the alternative plant food items (50%) or no clear preference at all (33%), the greater part (70%) of the non-fungus-growers prefers dung (Table 2). The finding regarding the fungusgrowers is surprising on the one hand, given the advantageous nutritional characteristics of dung as argued earlier. On the other hand, feeding on mammalian 235 dung might be even disadvantageous to a certain extent for termites, especially the Macrotermitinae: about 330 termite species in this subfamily are known to cultivate a specialized fungus, genus Termitomyces, for food (Mueller et al., 2005). The nest of a single termite species can have different, but few, symbiotic species (Aanen et al., 2002). Since termite nests provide conditions (high humidity, stable temperature) that 240 favor this required microbial growth (Roy et al., 2006), termite nests also are favorable habitats for entomopathogenic fungi and bacteria, which hypothetically can

be contained in herbivore dung. Social insects are known to show host-mediated behavior such as increased grooming, increased nest cleaning, secretion of antibiotics, dispersal of infected individuals and relocation of the entire colony in order to reduce
pathogen transmission (Roy et al., 2006). The finding that fungus-growing termites do not clearly prefer herbivore dung might be therefore an expression of pathogen avoidance. From the fungal symbionts' perspective, it may be more beneficial that termites feed it the same type of organic matter (e.g. a dominant grass) throughout the year, rather than vary greatly the type of food. It might be the case, that termites
exploit mammalian dung opportunistically in case it becomes available as a food source to them, but potentially the spatial and temporal heterogeneity of the availability of this food source counteracted the evolutionary development of a distinct behavioral preference for this food source, at least in some groups of termites.

Impacts on nutrient cycling. Despite the lack of evidence for a preferential 255 feeding on dung by termites as a whole, support can be found for the concept that the comminution of mammalian dung by termites impacts the ecosystem's functioning via the nutrient cycle dynamics.

Coe (1977) estimates for the Tsavo (East) National Park (Kenya), that during a year termites may remove up to 8.7 x 10³ kg faeces per km² from the surface of the
soil. This equals a nitrogen turnover of about 12 kg/ha/year based on a nitrogen content of 1.39% for fresh elephant dung as reported by Anderson & Coe (1974). This estimation gives a quantitative impression of the role of termites in facilitating the return of nutrients below the soil surface after they passed through the primary consumer (mammalian herbivores) component of the nutrient cycle. Without direct comparable data on the equivalent removal of dung by dung beetles though, the overall, quantitative importance of this process remains elusive. Herrick & Lal (1996)

studied the dung removal by termites associated with the transport of soil, both within the profile and to the soil surface (pedoturbation). They found a strong linear relationship between dung removal and soil accumulation at the original soil surface, 270 with an average of 2.0 g soil accumulated for every gram of dung which was removed. For their Neotropical pasture system, they give the minimum estimate of 2450 kg ha⁻¹ year⁻¹ of soil turnover in association with dung produced by two animal units ha⁻¹ (Herrick & Lal, 1996). Basappa & Rajagopal (1990) examined physical and chemical properties of termite modified soils in India. The results were that the water holding capacity, pH, organic carbon, organic matter, total nitrogen, the cation 275 exchange capacity, as well as the exchangeable cations like calcium, magnesium, potassium and sodium were higher in termite modified soils than in surrounding soils (Basappa & Rajagopal, 1990). Some of these findings (e.g. regarding phosphorous) may be explained by the incorporation of organic matter and left-over dung into the 280 termite modified soil. Similar findings are to be expected for non-dung feeding termites as well. Independent of the actual source of nutrients or the processes underlying the enrichment, termite modified soils are richer in nutrients; nutrients that in turn may facilitate primary productivity. This second process may be temporarily delayed: Weir (1971) used radioactive P₃₂ to study the removal of dung by termites in 285 Zimbabwe. The author could document that termites (unknown species) consumed the dung, but no radioactivity was detected in the adjacent vegetation during five months of the dry season in which the measurements were taken. Thus, the removal of nutrients by termites to their mounds did not result in this material becoming accessible to plants during the dry season (Weir, 1971). This process might be 290 delayed until the point in time when a given termite colony dies and the mound or the nest eventually is subject to erosion; e.g. shown by Coventry et al. (1988).

Furthermore, studies document that the consumption of mammalian dung influences the spatial distribution of termites. Gould et al. (2001) found Amitermes beaumonti to be more abundant in the stratum ranging from 0-3.5 cm below their 295 cattle dung baits they used in Costa Rica (vs. the 3.5-7.0 cm stratum). Exactly the opposite pattern was found in control areas, indicating that at least this termite species adjusts its subterranean foraging behavior according to the accessibility of dung used as a food source. From the mammalian perspective, Coe & Carr (1978) report that blesboks (Damaliscus dorcas phillipsi) appear to deliberately place their middens in 300 the vicinity of mounds of harvester termites (Trinervitermes trinervoides). They hypothesize that this is due either to the fact that termite mounds provide a spot of bare ground and therefore an increased visibility helping to detect predators and/or that blesboks are attracted to the mounds due to the increased foraging quality of the surrounding vegetation. The later reasoning could therefore be of the nature of a 305 positive feedback loop involving foraging behavior of termites and mammalian herbivores, but it awaits further clarification.

With respect to the overall nutrient cycling dynamics, termites may be seen as the crucial connective component between the dung producing herbivores and the microbial decomposers in savannas by further fragmenting, and maybe even more important, spatially redistributing the dung particles. From temperate regions it is known that invertebrates, such as earthworms, are of critical importance: they comminute and ingest the plant debris, resulting in the incorporation of organic matter into the soil, as well as a significant increase in its surface area, but little chemical change (Burges, 1967). If herbivore dung is regarded as partially decomposed plant material, it becomes apparent that termites and earthworms fulfil comparable ecological roles in these ecosystem dynamics. The major difference between termites

and other invertebrate decomposers is that – especially in savannas – considerable quantities of plant materials are consumed by wood-, grass- and fresh litter-feeding termites before and not after it has been attacked by saprophytic micro-organisms

320 (Wood, 1976). In the case of herbivore dung, this distinction does not hold anymore, since the plant material already has been attacked by the herbivores' own gut-endosymbionts. In contrast to the equivalent feeding guild of earthworms in temperate regions though, mound-building, fungus-growing termites (e.g. *Macrotermes*) are capable of engineering their own soil microclimate in order to facilitate the 325 decomposition of plant materials by their symbiotic fungi.

CONCLUDING REMARKS

From an autecological point of view, we found a previously underestimated diversity of termite taxa to feed on a wide range of mammalian dung.

- From the ecosystem perspective, we conclude that termites remove 330 substantial quantities of mammalian dung and associated soil, over relatively short times and preferably in the dry season. The foraging on dung appears to be of only opportunistic importance to termites. No distinctive preference for mammalian dung could be detected for termites as a whole group and for fungus-growers in particular, but was found for no-fungus-growing termites. By removing large quantities of dung 335 from above to below the soil surface, by being responsible for substantial pedoturbation and nutrient enrichment of soils as well as by causing changes in the spatial distribution of termites and even the mammalian dung producers themselves, this feeding behavior appears to be of great importance on the ecosystem level.
- Coming back to our initial question whether termites, by foraging on 340 mammalian dung, might fulfil a comparable ecological role as dung beetles do in the context of nutrient cycling dynamics, we can conclude that the currently existing body

of literature supports qualitatively the view that these two feeding guilds are both of ecological significance, but no sufficient, quantitative information exists to ultimately answer this question at the current point in time.

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TABLE 1. Dung removal rates of termites measured in field experiments. Standardized removal rates were computed assuming a linear removal-time relation as e.g. found by Coe (1970). Abbreviations: d = days, m = months.

Original	System	Standardized	Reference
removal rate		removal rate	
		(% dung	
		removed/month)	
100% / 80-85 d	savanna, Kenya	ca. 36 %/m	Coe 1977
	dry season		
	elephant dung		
	Odontotermes sp.		
	Microtermes sp.		
80-85% / 5-9 m	pasture, Costa Rica	ca. 12 %/m	Herrick & Lal
	dry + wet season		1996
	cattle dung		
	Amitermes beaumontii		
	Hoplotermes sp. nov.		
80% / 42 d (dry)	derived savanna, Nigeria	ca. 57 %/m	Omaliko 1981
50% / 42 d (wet)	dry + wet season	(dry)	
	cattle dung	ca. 36 %/m	
	unknown termite sp.	(wet)	
92% / 3 m	sorghum field, Burkina Faso	ca. 31 %/m	Ouédraogo et
	wet season		al. 2004
	cattle dung		
	Macrotermes sp.		
	Trinervitermes sp.		
42.2% / 3 ½ m	Chihuahuan desert, USA	ca. 12 %/m	Whitford et al.
	cattle dung		1982
	Gnathamitermes		
	tubiformans		
	Amitermes wheeleri		

TABLE 2. Food preferences of termites with respect to the consumption of mammalian dung. Abbreviations: ca = cattle dung, el = elephant dung, ho = horse dung, to = tortoise droppings, M = measurement taken.

Food Preference	Species	Reference
el dung ="other" dung=dead roots	Amitermes sciangallorum	Buxton 1981
grass=ground wood>el dung	Macrotermes subhyalinus	M: semi-
el dung=grass	Odontotermes badius	quantitative
el dung=grass =ground wood>"other" dung	Odontotermes zambesiensis	(minor vs.
el dung=grass=ground wood>"other" dung	Odontotermes mediocris	major
ground wood>el dung	Microtermes allaudanus	consumption)
ground wood>el dung	Synacanthotermes zanzibarensis	
el dung>litter	Odontotermes sp.	Coe 1977
	Microtermes sp.	M: # plots with termites
woody litter>mammalian dung	Macrotermes michaelseni	Dangerfield &
	Microtermes sp.	Schuurman 2000 M: descriptive
cattle dung>mesquite wood	Gnathamitermes tubiformans	Ettershank et al.
	Amitermes wheeleri	1980
		M: # termite
		attack holes
cattle dung> control (litter etc.)	Amitermes beaumonti	Gould et al. 2001
	Hoplotermes sp. nov.	M: individuals/plo
cattle dung> control (litter etc.)	Amitermes beaumonti	Herrick & Lal 199
	Hoplotermes sp. nov.	M: termites/l of so
cattle dung>litter	unknown	Johnson & Whitfor
Yucca wood>litter		1975
		M: foraging
		groups/source/ha
Andropogon or maize straw >cattle dung	Macrotermes sp.	Ouédraogo 2004
	Trinervitermes sp.	M: individuals/bait
millet (canes or ground)>cattle manure	Macrotermes subhyalinus	Rouland et al. 2003
millet (canes)>manure>ground millet	Odonotermes nilensis	M: mass of soil sheeting
litter (Restionaceae)>ca,el,ho,to dung	Amitermes hastatus	Skaife 1955
		M: descriptive (lab

APPENDIX

505	Termites reported to forage on dung. Dung consumed: br = black rhinoceros, bu =
	buffalo, ca = cattle, cam = camel, di = dikdik, do = donkey, el = elephant, em = emu,
	go = goat, ho = horse, hy = hyrax, im = impala, ku = kudu, kw = kangaroo/wallaby, sh
	= sheep, sm = small buck, sp = springbok, to = tortoise, wo = wombat, ze = zebra;
	Country: Au = Australia, BF = Burkina Faso, Bo = Botswana, Br = Brazil, CR =
510	Costa Rica, In = India, Ke = Kenya, Na = Namibia, SA = South Africa, Se = Senegal,
	Tz = Tanzania, USA, Zi = Zimbabwe; Habitat: AF = agricultural field, Bu = bush
	land/ wood land, De = desert, Pa = pasture, Sa = savanna; Study: Ex = experiment in
	field, La = laboratory, Su = survey; Other diet: W = wood-feeding, L = litter-feeding,
	S = soil-feeding.

Taxon	Dung	Country	Habitat	Study	Other Diet	Reference
MASTOTERMITIDAE						
Mastotermes darwiniensis	са	Au	?	Su	WL	Ferrar&Watson 1970 Gay&Calaby 1970
RHINOTERMITIDAE						,,
Heterotermes cf. tenuis	са	Br	Sa	Ex	W	DeSouza 1993
Heterotermes ferox	ca,ho	Au	?	Su	W	Ferrar&Watson 1970
Heterotermes longiceps	ca	Br	Sa	Ex	W	DeSouza 1993
Heterotermes paradoxus	ca,ho	Au	?	Su	W	Ferrar&Watson 1970
Psammotermes allocerus	br,ca,	Na	Bu,Sa	Su	W	Coaton&Sheasby 1972
	cam,do, el,go, ho,sh,	Zi	Bu	Su	W	Mitchell 1980
	sp,ze					
Psammotermes hybostoma	?	?	?	?	?	Harris 1970
Schedorhinotermes actuosus	са	Au	?	Su	WL	Ferrar&Watson 1970
Schedorhinotermes seclusus	ho	Au	?	Su	W	Ferrar&Watson 1970
TERMITIDAE Apicotermitinae						
Anoplotermes spp. a,b	са	Br	Sa	Ex	S	DeSouza 1993
Grigiotermes sp. a,s	ca	Br	Sa	Ex	S	DeSouza 1993
Hoplotermes sp. nov	ca	CR	Pa	Ex	?	Herrick&Lal 1996
	04		14		•	Gould et al. 2001
<i>Ruptitermes</i> spp. a,d	са	Br	Sa	Ex	S	DeSouza 1993
Macrotermitinae					-	
Allodontermes sp.	ca,do,	Na	Bu,Sa	Su	WL	Coaton&Sheasby 1972
···· ·····	el,ho, ku,ze	Zi	Bu,Sa	Su	WL	Mitchell 1980

Ancistrotermes latinotus	ca,el,	Zi	Bu,Sa	Su	WL	Mitchell 1980
Maaratarmaaan	ku,sm	SA		Su	14/1	Uys 2002
<i>Macrotermes</i> sp.	ca,el	Na	Bu,Sa AF	Su	WL	Coaton&Sheasby 1972
<i>Macrotermes</i> sp.	ca	BF		Ex	WL	Ouédraogo et al. 2004 Mitchell 1980
Macrotermes falciger	ca,el	Zi	Bu,Sa	Su	WL	Dangerfield&Schuurman
Macrotermes michaelseni	ca,el	Bo,Zi	Bu,Sa	Su	WL	2000, Mitchell 1980
Macrotermes subhyalinus	ca,el	Ke,Zi	Bu,Sa	Su	WL	Buxton 1981, Mitchell 1980
Macrotermes subhyalinus	ca	Se	Sa	Ex	WL	Rouland et al. 2003
Macrotermes ukuzii	bu,cal,	Zi	Bu,Sa	Su	WL	Mitchell 1980
Microtermes sp.	bu,ca,do,	Na	Bu,Sa	Su	W	Coaton&Sheasby 1972
	el,ho,	Ke	Bu,Sa	Ex	W	Coe 1977
	, ,		,			Dangerfield&Schuurman
	ku,sh	Во	Bu,Sa	Su	W	2000
		Zi	Bu,Sa	Su	W	Mitchell 1980
Microtermes allaudanus	el	Ke	Bu,Sa	Su	W	Buxton 1981
Odontotermes sp.	ca,do,	Na	Bu,Sa	Su	W	Coaton&Sheasby 1972
	el,ho,	Ke	Bu,Sa	Ex	W	Coe 1977
	ku,ze					
Odontotermes amaniensis	?	Ke	?	Ex	W	Burchard 1989
Odontotermes badius	ca,el	Ke,Zi	Bu,Sa	Su	WL/L	Buxton 1981, Mitchell 1980
Odontotermes boranicus	el	Tz	Bu	Su	W	Kemp 1955
Odontotermes horni	?	In	?	Ex	?	Basappa&Rajagopal 1990
Odontotermes latericius	ca,el	Zi	Bu,Sa	Su	W	Mitchell 1980
Odontotermes mediocris	el	Ke	Bu,Sa	Su	WL	Buxton 1981
Odontotermes nilensis	са	Se	Sa	Ex	WL	Rouland et al. 2003
Odontotermes obesus	?	In	?	Ex	?	Basappa&Rajagopal 1990
Odontotermes patruus	са	Tz	Bu	Su	W	Kemp 1955
Odontotermes stercorivorus	?	Ke	?	Ex	W	Burchard 1989
Odontotermes transvaalensis	са	Zi	Bu,Sa	Su	W	Mitchell 1980
Odontotermes wallonensis	?	In	?	Ex	?	Basappa&Rajagopal 1990
Odontotermes zambesiensis	el	Ke	Bu,Sa	Su	WL	Buxton 1981
Pseudacanthotermes militaris	са	Zi	Bu	Su	WL	Mitchell 1980
Synacanthotermes		SA		Su		Uys 2002
zanzibarensis	el	Ke	Bu,Sa	Su	W	Buxton 1981
Nasutitermitinae	CI	NC	Du,Oa	Ou	••	Buxton 1901
Armitermes spp. a,b,c	са	Br	Sa	Ex	S	DeSouza 1993
Atlantitermes stercophilus	ca	Br	Sa	Ex	S	Constantino&DeSouza1997
Baucaliotermes hainesi	ca	Na	Bu,De,Sa	Su	L	Coaton&Sheasby 1972
Cornitermes sp.	ca	Br	Sa	Ex	Ŵ	DeSouza 1993
Diversitermes diversimiles	ca	Br	Sa	Ex	W	DeSouza 1993
Embiratermes heterotypus	ca	Br	Sa	Ex	S	DeSouza 1993
Embiratermes spissus	ca	Br	Sa	Ex	S	DeSouza 1993
Fulleritermes coatoni	ca	Zi	Bu,Sa	Su	WL	Mitchell 1980
		SA	,	Su		Uys 2002
Labiotermes spp. a,b	ca	Br	Sa	Ex	S	DeSouza 1993
Nasutitermes coxipoensis	са	Br	Sa	Ex	W	DeSouza 1993
Nasutitermes eucalypti	са	Au	?	Su	W	Ferrar&Watson 1970
Nasutitermes kemneri	са	Br	Sa	Ex	W	DeSouza 1993
Nasutitermes kimberleyensis	ca	Au	?	Su	W	Ferrar&Watson 1970
Nasutitermes longipennis	са	Au	?	Su	WL	Ferrar&Watson 1970
Nasutitermes torresi	ca,ho	Au	?	Su	?	Ferrar&Watson 1970
Paracornitermes laticephalus	ca	Br	Sa	Ex	S	DeSouza 1993
Procornitermes sp.	?	?	?	?	?	Araujo 1970

Procornitermes sp.	ca	Br	Sa	Ex	S	DeSouza 1993
Rhadinotermes coarctatus	ca	Zi	Bu,Sa	Su	WL	Mitchell 1980
Rhynchotermes nasutissimus	са	Br	Sa	Ex	L	DeSouza 1993
Rhynchotermes sp. a						
Subulitermes sp.	ca	Br	Sa	Ex	S	DeSouza 1993
Syntermes sp.	са	Br	Sa	Ex	L	DeSouza 1993
Trinervitermes sp.	ca,el,ho	Na	Bu,Sa	Su	L	Coaton&Sheasby 1972
•	ca	Zi	Bu,Sa	Su	L	Mitchell 1980
	ca	BF	AF	Ex	L	Ouédraogo et al. 2004
Tumulitermes comatus	ca	Au	?	Su	WL	Ferrar&Watson 1970
Tumulitermes dalbiensis	ho	Au	?	Su	L	Ferrar&Watson 1970
Velocitermes paucipilis	ca	Br	Sa	Ex	L	DeSouza 1993
Velocitermes spp. 1,2,g	са	Br	Sa	Ex	L	DeSouza 1993
Termitinae	Ca	DI	Sa	LA	L	De3002a 1993
	hr co	Ne		<u></u>	14/	Contant Charachy 1070
<i>Amitermes</i> sp.	br,ca,	Na	Bu,Sa	Su	W	Coaton&Sheasby 1972
	do,el,	Au	?	?	?	Gay&Calaby 1970
	go,ho,					
	sh,ze					
Amitermes abruptus	ca,ho,	Au	?	Su	WL	Ferrar&Watson 1970
	kw,sh					
Amitermes agrilus	ca	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes beaumonti	са	CR	Ра	Ex	?	Herrick&Lal 1996
						Gould et al. 2001
Amitermes boreus	ca,ho	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes capito	ca	Au	?	Su	W	Ferrar&Watson 1970
Amitermes colonus	ho,sh	Au	?	Su	W	Ferrar&Watson 1970
Amitermes darwini	ca,ho,	Au	?	Su	WL	Ferrar&Watson 1970
	sh					
Amitermes dentosus	ca,ho,	Au	?	Su	W	Ferrar&Watson 1970
	sh					
Amitermes deplenatus	ho	Au	?	Su	W	Ferrar&Watson 1970
Amitermes eucalypti	са	Au	?	Su	Ŵ	Ferrar&Watson 1970
Amitermes exilis	ca,ho	Au	?	Su	Ŵ	Ferrar&Watson 1970
Amitermes germanus	ca,ho	Au	?	Su	W	Ferrar&Watson 1970
-			? ?	Su	?	Ferrar&Watson 1970
Amitermes gracilis	ca	Au	? ?			
Amitermes hartmeyeri	ca,ho,	Au	ſ	Su	W	Ferrar&Watson 1970
	kw	<u> </u>				Skeife 1055
Amitermes hastatus	ca,el,	SA	Bu,Sa	La	L	Skaife 1955
.	ho,to		0	•		
Amitermes herbertensis	са	Au	?	Su	W	Ferrar&Watson 1970
Amitermes heterognathus	са	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes lanceolatus	ca,ho	Au	?	Su	W	Ferrar&Watson 1970
Amitermes latidens	са	Au	?	Su	W	Ferrar&Watson 1970
Amitermes lativentris	ca,ho	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes laurensis	ca	Au	?	Su	L	Ferrar&Watson 1970
Amitermes modicus	са	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes neogermanus	cam,ca	Au	?	Su	WL	Ferrar&Watson 1970
	ho					
Amitermes obtusidens	ca,ho	Au	?	Su	W	Ferrar&Watson 1970
Amitermes perarmatus	ca,em	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes sciangallorum	el	Ke	Bu,Sa	Su	?	Buxton 1981
Amitermes vitiosus	ca,ho	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes westraliensis	ca	Au	?	Su	WL	Ferrar&Watson 1970
Amitermes wheeleri	са	USA	De	Ex	W	Ettershank et al. 1980
		2011	20		••	

						Whitford et al. 1982
Amitermes xylophagus	wo	Au	?	Su	W	Ferrar&Watson 1970
Amitermes spp. I-V	са	Au	?	Su	L	Ferrar&Watson 1970
Angulitermes sp.	ca,el,	Na	Sa	Su	WL	Coaton&Sheasby 1972
	ho,sh					
Angulitermes truncatus	di	Tz	Bu	Su	L	Kemp 1955
Anoplotermes sp.	?	?	?	?	?	Weesner 1970
Cubitermes sp.	ca,el,	Na	Bu,Sa	Su	S	Coaton&Sheasby 1972
	im,ze					
Eremotermes sp.	?	?	?	?	?	Roonwal 1970
Gnathamitermes tubiformans	са	USA	De	Ex	L	Ettershank et al. 1980
						Whitford et al. 1982
Lepidotermes sp.	ca,el	Na	Bu,Sa	Su	S	Coaton&Sheasby 1972
Microcerotermes sp.	bu,ca,do,	Na,Tz,Zi	Bu,Sa	Su	W	Coaton&Sheasby 1972
	el,ho,					Kemp 1955
	hy,ze					Mitchell 1980
Microcerotermes cavus	са	Au	?	Su	W	Ferrar&Watson 1970
Microcerotermes distinctus	са	Au	?	Su	W	Ferrar&Watson 1970
Microcerotermes nervosus	са	Au	?	Su	W	Ferrar&Watson 1970
Microcerotermes serratus	ca,ho	Au	?	Su	W	Ferrar&Watson 1970
Neocapritermes sp.	?	?	?	?	?	Araujo 1970
Neocapritermes spp. a,b,c	са	Br	Sa	Ex	S	DeSouza 1993
Neocapritermes araguaia	са	Br	Sa	Ex	S	DeSouza 1993
Promirotermes sp.	ca,el,	Na	Bu,Sa	Su	W	Coaton&Sheasby 1972
	ze					
<i>Synhamitermes</i> sp.	?	?	?	?	?	Araujo 1970
Termes boultoni	el	Zi	De	Su	W	Mitchell 1980