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First record of Streblidae, *Raymondia alulata* Speiser, 1908 (Diptera: Streblidae), in Swaziland and a review of the genus *Raymondia* and their hosts in Africa

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Species of the genus *Raymondia* (Diptera: Streblidae) are obligate ectoparasites of bats. They have a wide distribution across Africa and are associated with many different bat species. Here we present the first record of this family in Swaziland. The ectoparasites were of the species *Raymondia alulata* and were found parasitizing individuals of the species *Nycteris thebaica*. We review the status of *Raymondia* species known in Africa, including specimen records, hosts, and host distributions and provide an updated identification key for species in this genus.

Key words: distribution, Chiroptera, bat flies, ectoparasite, host-parasite relationships, parasitism

INTRODUCTION

Bats are known to host an exceptionally large number of ectoparasite species (Dick and Patterson, 2006), with the highest ectoparasite diversity of any mammalian order (Dittmar *et al.*, 2006). While in many cases ectoparasites appear to have very high host specificity (ter Hofstede *et al.*, 2004), some species may parasitize multiple hosts (e.g., Marshall, 1982; Dantas-Torres and Otranto, 2014). Similarly, infested bats often host multiple ectoparasite species (Marshall, 1982). What factors determine the species richness of ectoparasites for each host or the specificity of ectoparasites is still debated, but include roost type, roost fidelity, group size, and individual body size of hosts (Bordes *et al.*, 2008). Sex and reproductive state also appear to play an important role in rates of infestation (Sundari *et al.*, 2012). Further, there is limited information about the extent of occurrence and the possible overlap in distributions of many ectoparasite species.

Streblidae (Hippoboscoidea: Diptera) is a family of sanguivorous bat flies with a worldwide distribution that exclusively parasitize bats. The abundance

and richness of this family is greatest in tropical and subtropical regions of the world (Dick and Graciolli, 2008). The family comprises 33 known genera of which 26 occur in the New World and seven in the Old (Dick and Graciolli, 2008), with no common genera or subfamilies between the two regions. However, recent research suggests that Streblidae may be paraphyletic, with Old World Streblidae forming a clade with Old World Nycteribiidae separate from New World Streblidae (Dittmar *et al.*, 2006). For this reason, we focus our study only on Old World Streblidae.

Of the Old World Streblidae, *Raymondia* Frauenfeld, 1855 is the second most diverse genus after *Brachytarsina* (Speiser, 1900) (31 spp.), with 21 known species. *Raymondia alulata* Speiser, 1908 has a wide distribution over southern, central, and eastern Africa (Jobling, 1939; Maa, 1968; Theodor, 1968). It appears to be primarily associated with *Nycteris thebaica* E. Geoffroy, 1818 (Nycteridae) (Maa, 1968; Theodor, 1968), although it has also been recorded from *Cloeotis percivali* Thomas, 1901, *Hipposideros caffer* (Sundevall, 1846), and *Rhinolophus* spp., which belong to the suborder

Pteropodiformes (=Yinpterochiroptera) and are only distantly related to Nycteridae (Hutcheon and Kirsch, 2006).

A better understanding of bat ectoparasites could shed light on a variety of biological processes, such as evolution, competition, and community structure (Giorgi *et al.*, 2004; Patterson *et al.*, 2007; Tello *et al.*, 2008). Further, ectoparasites may impact the hosts' health, fitness, or body condition (Zahn and Rupp, 2004; Bordes *et al.*, 2008), potentially serving as a bioindicator (Palm and Ruckert, 2009; Palm *et al.*, 2011). There is also evidence that ectoparasites may play a role in the transmission of pathogens, including some that may be transmittable to humans (Megali *et al.*, 2011; Billeter *et al.*, 2012; Gay *et al.*, 2014).

However, it is impossible to make any such inferences without a better understanding of the ecology of ectoparasites. Presently, we lack even basic information on the distribution and hosts of many Streblidae species, especially in Africa. Many records from Africa in particular are decades old and may use outdated nomenclature for both ectoparasites and bat hosts. Therefore, here we organize an updated review of the genus *Raymondia*, including a new record for Swaziland, which is also the first record of any Streblidae in that country. This review also identifies geographic areas, bat and ectoparasite species that are especially lacking in information.

MATERIALS AND METHODS

Study Area

This study was carried out in the Lowveld region of eastern Swaziland bordered by the Drakensberg Mountains in the west and the Lubombo Mountains in the east. The area is a part of the Maputaland-Pondoland-Albany biodiversity hotspot (Steenkamp *et al.*, 2004). Elevation ranges from approximately 150 to 600 m above sea level. At lower elevations, land-use is dominated by commercial sugarcane plantations, subsistence maize fields, grazing lands for domestic livestock, rural villages, and several protected parks (Monadjem and Reside, 2008). The dominant natural vegetation type is open savanna or woodland (Roques *et al.*, 2001).

Bat Capture

The specimens of *R. alulata* were obtained from two individual bats of the species *Nycteris thebaica*. The first bat was a juvenile, non-reproductive male caught near the campsite in Mbuluzi Game Reserve (26.14°S, 32.00°E) in a harp trap on 6 January 2014 around 20:20 h. The second individual, an adult, non-reproductive female, was captured on 26 April 2014 in a mist-net exiting a roost in a culvert beneath a road running between Mbuluzi Game Reserve and Mlawula Nature Reserve (26.14°S, 32.00°E — Fig. 1).

Bats were identified according to Monadjem *et al.* (2010). *Nycteris thebaica* is the only member of the family Nycteridae currently known from Swaziland (Monadjem, 1998; Shapiro and Monadjem, 2015), and is identifiable by the shape of its tragus and ear and dental morphology (Monadjem *et al.*, 2010). Forearm length was measured with calipers to the nearest

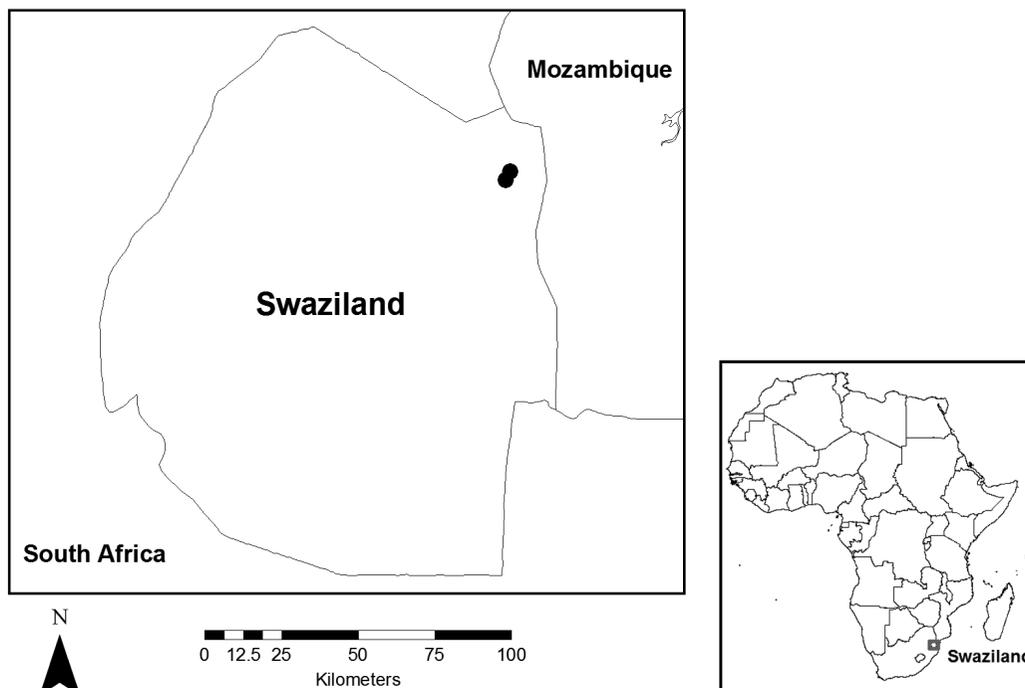


FIG. 1. Map of study area in Swaziland. Sites where *Raymondia alulata* were collected from *Nycteris thebaica* shown by the black circles

0.1 mm and mass taken with a spring balance. Reproductive status was noted and age (adult or juvenile) was determined by ossification of the epiphyseal joints.

Bats were visually examined for ectoparasites, including gently blowing on the fur to expose ectoparasites below the surface of the fur. Ectoparasites were removed using soft forceps and placed in vials with 70% ethanol. Bats were collected under a permit from the Swaziland National Trust Commission. Handling methods were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Florida (Protocol #201508751).

Identification of Ectoparasites

Flies of the family Streblidae were identified according to Jobling (1939) and confirmed by Dr. Gustavo Gracioli at the Department of Zoology, Federal University of Mato Grosso do Sul (Universidade Federal de Mato Grosso do Sul, UFMS). The specimens were deposited in the collections of the Federal University of Mato Grosso do Sul (ART 1767 — 3 ♂♂ and 1 ♀) and the Federal University of Pernambuco (Universidade Federal de Pernambuco, UFPE CE 100793 — 1 ♂ and 1 ♀) (see Fig. 2).

Literature Search

We conducted a literature search using the key words ‘Streblidae’ and ‘*Raymondia*’ in Google Scholar (<https://scholar.google.com>), Web of Science (<http://www.webofknowledge.com>) and Periódicos CAPES (<http://www.periodicos.capes.gov.br>). For the compilation of species of *Raymondia*, we used data from studies conducted on the African continent and reviews of African bat ectoparasites (see Appendix I).

Many of the studies we consulted were conducted 50–90 years ago. Nomenclature for both ectoparasite and bat species has changed since then and we provide updated names below.

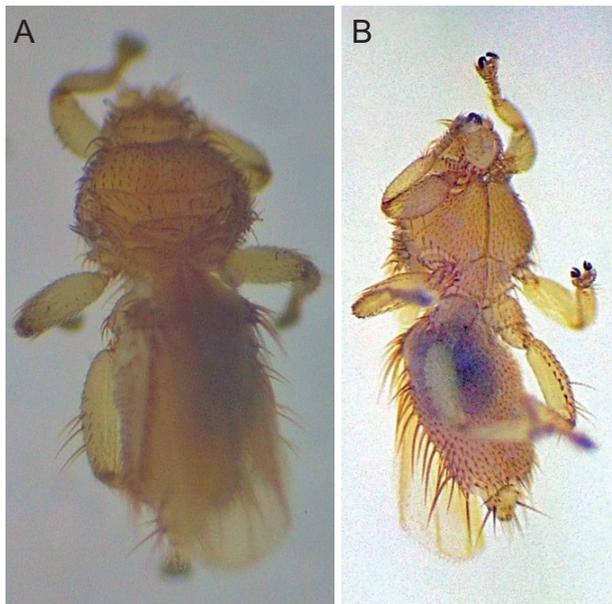


FIG. 2. Dorsal (A) and ventral (B) view of female *R. alulata* specimen (UFPE CE 100793) taken from *N. thebaica* in Swaziland

Names of locations have also changed since many of the original studies were published. Below, we use the currently accepted names for the location of each record. The names of each location at the time each study was conducted are included in Appendix I. In addition, we reviewed descriptions of all *Raymondia* species occurring in Africa and provide an updated identification key. The key is primarily based on Maa (1968) and Theodor (1968, 1973) with relevant updates to nomenclature (see Appendix II).

Mapping Bat Host Distributions

Host distributions were plotted using shapefiles compiled by the IUCN (2012) for each host species with modifications based on Monadjem *et al.* (2010) and A. Monadjem (unpublished data). Distributions for all host bat species have been merged into a single ‘host distribution.’ Specific host species recorded at each site can be seen in Appendix I. Since the publication of earlier studies, there have been significant changes in nomenclature, and cryptic species in several species-complexes have been described. We have updated the bat host species based on currently known distributions. We call attention in particular to the *Hipposideros caffer-ruber* species complex. In the studies we consulted, there appear to be frequent misidentifications or questionable identifications of *Hipposideros caffer*, *H. ruber* (Noack, 1893), and cryptic *H. caffer-ruber* complex species (Vallo *et al.*, 2008; Monadjem *et al.*, 2013b). Current, accurate distribution maps of *H. caffer*, *H. ruber*, and the unnamed cryptic species belonging to this species complex do not yet exist. Hence, we use a combined distribution for the *H. caffer-ruber* species complex, with slight modifications based on Monadjem *et al.* (2010) for any host species within this complex. We refer to this species complex as the ‘*Hipposideros caffer-ruber* complex’ throughout this paper and use ‘*Hipposideros caffer*’ only for individuals recorded from southern Africa (Vallo *et al.*, 2008). Similarly recent research suggests that the species *Rhinolophus clivosus* Cretzschmar, 1828 may represent two cryptic species, *R. clivosus* (northeast Africa) and *R. augur* K. Andersen, 1904 (southern and eastern Africa) (Benda and Vallo, 2012). Here, we use the IUCN’s (2012) distribution of *Rhinolophus clivosus* (sensu lato). Additionally, we use the African range of *Triaenops persicus* Dobson, 1871 as portrayed by the IUCN (2012) to denote the distribution of *T. afer* Peters, 1876 (considered a subspecies of *T. persicus* by the IUCN, 2012), which was recently elevated to species status (Benda and Vallo, 2009). Finally, a shapefile for the distribution of *Miniopterus africanus* Sanborn, 1936 was not available because the IUCN (2012) considers it a subspecies of *M. inflatus* Thomas, 1903. When species distributions were not available, as in the case of newly described species or species not recognized by the IUCN (2012), distributions were plotted based on an unpublished database (A. Monadjem, unpublished data). Only bat hosts identified to the level of species are included in the distribution maps.

Statistical Analysis

In order to determine whether species richness of *Raymondia* was simply an artifact of the number of studies conducted in each country, we tested if there was a correlation between the number of studies per country and the number of *Raymondia* species recorded in each country. We used the packages *corrplot* (Wei, 2015), *corrgram* (Wright, 2015) and *Hmisc* (Harrell, 2006) in the program R (R Core Team, 2013) to test for correlation.

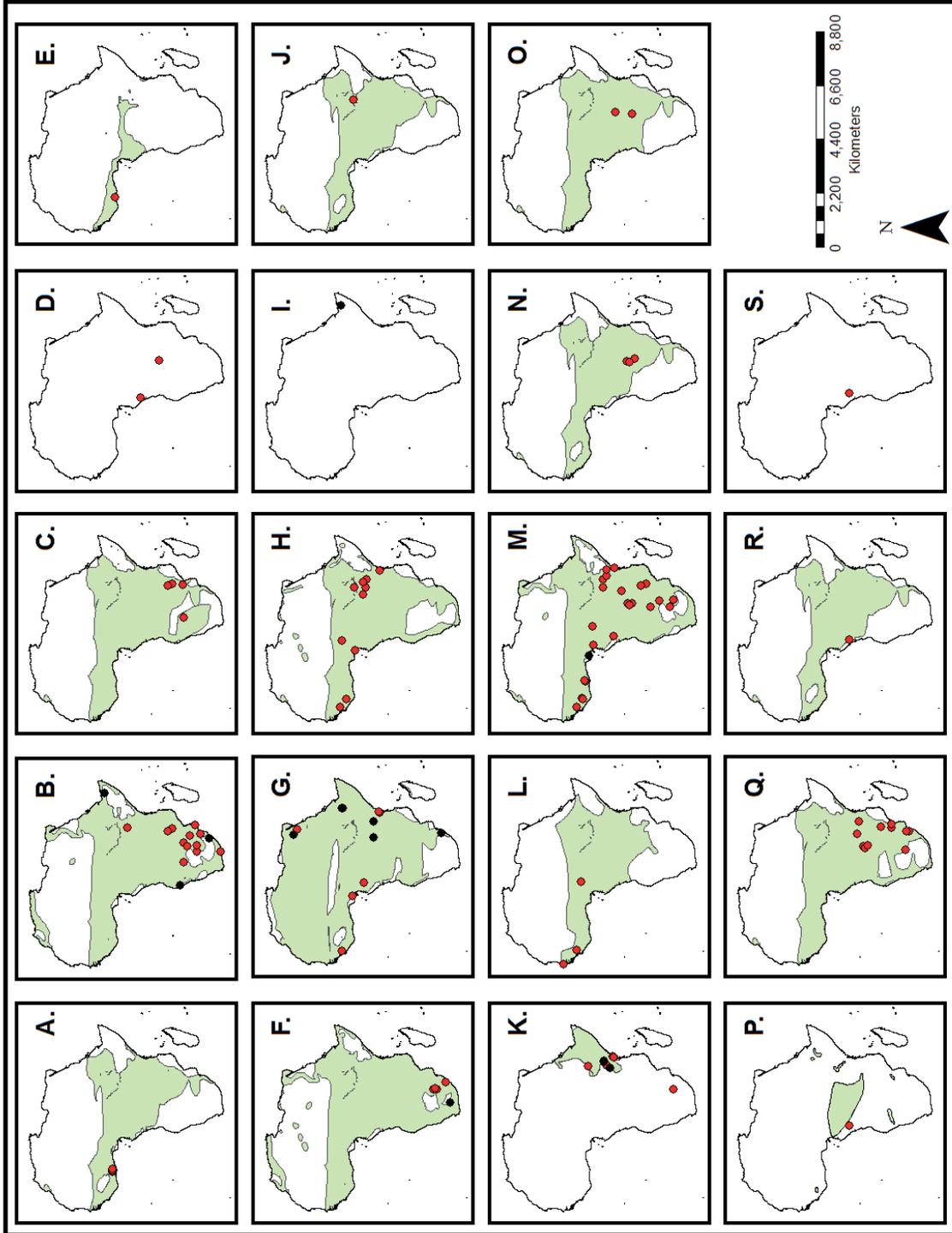


FIG. 3. Maps showing specimen records and host distributions in Africa for each species of *Raymondia*. Distributions of all host bat species have been merged. Circles in black indicate records for which only a country, territory, or region were indicated, without a specific town, village, mountain, or cave. A — *R. allisoni*; B — *R. atulata*; C — *R. aspera*; D — *R. brachyphysa*; E — *R. boquienii*; F — *R. hardyi*; G — *R. huberi huberi*; H — *R. intermedia*; I — *R. lobulata*; J — *R. planiceps*; K — *R. scopigera*; L — *R. seminuda*; M — *R. setiloba*; N — *R. simplex*; O — *R. waterstoni*; P — *R. tauffliebi*; Q — *Raymondia* sp. A; S — *R. sp. B*

RESULTS

We recorded 17 species of Streblidae in the genus *Raymondia* across all of continental Africa (Appendix I, Fig. 3), as well as two *Raymondia* species not identified to the level of species and identified here as *Raymondia* sp. A and *Raymondia* sp. B. *Raymondia* has been recorded parasitizing 28 different species of bats in 10 genera distributed across the families Emballonuridae, Hipposideridae, Megadermatidae, Nycteridae, Rhinolophidae and Vespertilionidae. The greatest number of host species were in the genera *Rhinolophus* (12 spp.), *Hipposideros* (seven spp.), and *Miniopterus* (four spp.). *Raymondia* has been recorded parasitizing only one species in the families Emballonuridae, Megadermatidae, and Vespertilionidae. The bats recorded hosting the greatest number of *Raymondia* species are *Hipposideros caffer-ruber* complex (eight spp.), *Hipposideros caffer* (sensu stricto) (six spp.), *Cloeotis percivali* (four spp.), *R. landeri* Martin, 1838 (four spp.), and *Triaenops afer* (four spp.).

Raymondia huberi huberi Frauenfeld, 1855, *Raymondia hardyi* Fiedler, 1954, and *R. seminuda* Jobling, 1954 were each found parasitizing bats in four different families, making them generalists. All *Raymondia* species recorded from multiple bat species included hosts from at least two different families. About half of the *Raymondia* species (47%) were recorded parasitizing only a single bat family and species. The host species of *R. lobulata* Speiser, 1900 is still unconfirmed as Kessel (1925) did not specify the bat species on which it was found. Two *Raymondia* specimens collected from the *H. caffer-ruber* complex and *Rhinolophus* sp., in caves in the Congo (Brazzaville), were not identified to the species-level (*Raymondia* sp. A and *Raymondia* sp. B).

At the country level, *R. seminuda* and *R. huberi huberi* had the widest distributions and were collected in 14 and 10 different countries, respectively. At the other end of the spectrum, 47% of *Raymondia* species (excluding *Raymondia* sp. A and B) had only been recorded within a single country. The Democratic Republic of Congo was the country with the greatest number of *Raymondia* species recorded, with eight. Of the 23 countries with records of *Raymondia*, 35% were of only one species. We found no correlation between the number of *Raymondia* species per country and the number of studies conducted per country ($r = 0.21$, $n = 23$, $P = 0.33$).

Below, we list the known species of *Raymondia* in Africa, including their distributions within the

continent, their hosts, relevant observations and anecdotal remarks.

REVIEW OF *RAYMONDIA* SPECIES*Raymondia allisoni* Theodor, 1968

Country

Ghana.

Hosts

Hipposideros caffer-ruber complex, *Rhinolophus alcyone* Temminck, 1852.

Comments

Theodor (1968) records *R. allisoni* parasitizing *Hipposideros caffer* in Ghana. This locality is not within the currently recognized distribution of *H. caffer* (sensu stricto), but the host species is likely to be within the *H. caffer-ruber* complex (Vallo *et al.*, 2008; Monadjem *et al.*, 2013b).

Raymondia alulata Speiser, 1908

Countries

Botswana, Democratic Republic of Congo, Mozambique, Namibia, South Africa (*R. bedfordi*), Somalia (*R. quadriceps*), Swaziland (present study), Uganda, Zimbabwe.

Hosts

Cloeotis percivali, *Hipposideros caffer*, *Nycteris thebaica*, *Rhinolophus blasii* Peters, 1867, *Rhinolophus* sp.

Comments

Here we include records of *R. bedfordi* and *R. quadriceps* described in Jobling (1939) as synonyms of *R. alulata*. We consider *Nycteris capensis* A. Smith, 1829 (Jobling, 1939; Theodor, 1968) and *N. damarensis* Peters, 1870 (Ferris, 1930; Bedford, 1932; Jobling, 1939) synonyms of *N. thebaica* (Monadjem *et al.*, 2010). This is the first record of Streblidae for Swaziland (Fig. 2).

Raymondia aspera

Maa, 1968

Country

Mozambique.

Hosts

Hipposideros caffer, *Miniopterus mossambicus* Monadjem *et al.*, 2013a, *Rhinolophus mossambicus* Taylor *et al.*, 2012, *Rhinolophus landeri*, *Rhinolophus* sp., *Triaenops afer*.

Comments

Maa (1968) records *R. aspera* parasitizing *Miniopterus schreibersii* (Kuhl, 1817) in Tete, Mozambique, but this region is not part of the range of *M. schreibersii* (sensu stricto). Based on the locality, we consider this a record of the newly described *M. mossambicus* (Monadjem *et al.*, 2013a). Similarly, the record of *R. aspera* parasitizing *R. hildebrandtii* Peters, 1878 in Tete, Mozambique is outside this species' distribution, and most likely refers to the recently described species *R. mossambicus* (Taylor *et al.*, 2012). Maa (1968) records three species of widely distributed Muridae (Rodentia) *Acomys* sp., *Grammomys dolichurus* (Smuts, 1832), and *Mastomys natalensis* (Smith, 1834) hosting *R. aspera*. However, we doubt the validity of these records and consider them errors since bats are the only recognized hosts of Streblidae ectoparasites (Wenzel *et al.*, 1966; Dick and Patterson, 2006).

Raymondia boquieni Vermeil, 1965

Countries

Congo (Brazzaville), Democratic Republic of Congo.

Host

Rhinolophus sp.

Raymondia brachyphysa Jobling, 1956

Country

Ivory Coast.

Host

Hipposideros cyclops (Temminck, 1853).

Raymondia hardyi Fiedler, 1954

Country

South Africa.

Hosts

Cloeotis percivali, *Hipposideros caffer*, *Myotis tricolor* (Temminck, 1832), *Nycteris thebaica*,

Rhinolophus blasii, *R. clivosus*, *R. cohenae* Taylor *et al.*, 2012, *R. simulator* K. Andersen, 1904, *R. smithersii* Taylor *et al.*, 2012.

Comments

Raymondia hardyi was considered a subspecies of *R. waterstoni* Jobling, 1931 by Theodor (1968). Later morphological examination confirmed that *R. hardyi* was in fact a distinct species restricted to South Africa (Theodor, 1973). Theodor (1973) states that all specimens previously identified as *R. waterstoni* from South Africa in Theodor (1968) are in fact *R. hardyi*. Therefore we consider all South African specimens of *R. waterstoni* in Theodor (1968) to be *R. hardyi*. We also consider specimens of *R. waterstoni* identified by Jobling (1939) in South Africa as *R. hardyi*. We consider *Nycteris capensis* (Theodor, 1968) a synonym of *N. thebaica* (Monadjem *et al.*, 2010). *Raymondia hardyi* has been recorded parasitizing *Rhinolophus hildebrandtii* in South Africa (Theodor, 1968), which is outside this species' distribution. Based on this location, this record is most likely *R. cohenae* or *R. smithersii* (Taylor *et al.*, 2012).

Raymondia huberi huberi Frauenfeld, 1855

Countries

East Africa, Egypt, Eritrea, Ethiopia, Gabon, Kenya, Nigeria, Sierra Leone, South Africa, Tanzania.

Hosts

Asellia tridens (É. Geoffroy, 1813), *Cardioderma cor* (Peters, 1872), *Cloeotis percivali*, *Coleura afra* (Peters, 1852), *Hipposideros caffer*, *H. vittatus* (Peters, 1852), *H. fuliginosus* (Temminck, 1853), *Rhinolophus* sp., *Triaenops afer*.

Comments

We consider *Megaderma cor*, cited in Kessel (1925) and Jobling (1930) a synonym of *Cardioderma cor* and *Hipposideros tridens* (Jobling, 1930) a synonym of *Asellia tridens*. *Hipposideros comersoni* (É. Geoffroy, 1813), as cited by (Theodor, 1968), is restricted to Madagascar (Goodman, 2011). As the record was made in savanna habitat in Kenya, we consider this to be a record of *H. vittatus* (Patterson and Webala, 2012). Similarly Jobling (1930, 1939) and Theodor (1968) record *R. huberi* from *Triaenops persicus*. This species does not occur in Africa and we consider it a record

of *T. afer* (Benda and Vallo, 2009). The record for Egypt is the northernmost record of *Raymondia* in Africa.

Raymondia intermedia Jobling, 1936

Countries

Cameroon, Congo (Brazzaville), Democratic Republic of Congo, Kenya, Liberia, Sierra Leone, South Sudan, Tanzania, Uganda.

Hosts

Hipposideros caffer, *Miniopterus africanus*, *Rhinolophus clivosus*, *R. eloquens* K. Andersen, 1905, *R. fumigatus* Rüppell, 1842, *R. hildebrandtii*, *R. landeri*, *Rhinolophus* sp.

Comments

We consider *Rhinolophus lobatus* (Jobling, 1939) a synonym of *R. landeri* (Brown and Dunlop, 1997). Theodor (1968) records *R. intermedia* parasitizing *R. ferrumequinum* (Schreber, 1774) in Kenya, but this species does not occur in sub-Saharan Africa and we consider this species to be *R. clivosus* (Patterson and Webala, 2012).

Raymondia lobulata Speiser, 1900

Country

Somalia.

Host

Unknown bat species.

Comments

Kessel (1925: 24) cites only “bats ... from British Somaliland” as the host of *R. lobulata* in Africa, as well as *Megaderma lyra* É. Geoffroy, 1810 in Sri Lanka (Ceylon) and further unspecified bats in Chennai (Madras), India.

Raymondia pagodarum Speiser, 1900

Country

Uganda.

Hosts

Hipposideros caffer-ruber complex.

Comments

Ferris (1930) records *R. pagodarum* parasitizing *Hipposideros ruber* in Uganda. However, *H. ruber*

(sensu stricto) is not known to occur there and we refer to this a record of *Hipposideros caffer-ruber* complex.

Raymondia planiceps Jobling, 1930

Countries

East Africa, Kenya, South Africa.

Host

Cardioderma cor.

Comments

Cardioderma cor is the only confirmed host of *R. planiceps*. However, there are several records from unspecified bat hosts in East Africa, Kenya, South Africa (Jobling, 1939; Theodor, 1968). As South Africa is well outside the range of *Cardioderma cor* or any Megadermatidae species (Theodor, 1968; Monadjem *et al.*, 2010), *R. planiceps* may be hosted by other bat species in this part of its range. Alternatively, this could be a misidentification of *R. planiceps*.

Raymondia scopigera Jobling, 1954

Countries

Cameroon, Senegal, Sierra Leone.

Host

Nycteris macrotis Dobson, 1876.

Comments

We consider *Nycteris aethiopica* (Jobling, 1954; Theodor, 1968) a synonym of *N. macrotis* (Wilson and Reeder, 2005).

Raymondia seminuda Jobling, 1954

Countries

Botswana, Cameroon, Congo (Brazzaville), Democratic Republic of Congo, Ghana, Guinea, Kenya, Liberia, Mozambique, Nigeria, Sierra Leone, South Africa, Tanzania, Uganda.

Hosts

Clootis percivali, *Hipposideros caffer*, *H. caffer-ruber* complex, *Miniopterus africanus*, *M. inflatus*, *Nycteris thebaica*, *Rhinolophus eloquens*, *Rhinolophus* sp., *Triaenops afer*.

Comments

Theodor (1968) records *R. seminuda* parasitizing *Hipposideros caffer* across West Africa. Since *H. caffer* (sensu stricto) does not occur in West Africa, we consider these to refer to the *H. caffer-ruber* complex. In several other cases, it is not clear whether the host bat was indeed *H. caffer* (sensu stricto) or within the *H. caffer-ruber* complex. Similarly, we consider the record of *Hipposideros ruber guineensis* to also be a member of the *H. caffer-ruber* complex. Whitaker and Mumford (1978) record *R. seminuda* from *Triaenops persicus*. This species does not occur in Africa and we consider it a record of *T. afer* (Benda and Vallo, 2009). As in the case of *R. aspera*, Maa (1968) records a rodent *Mastomys natalensis* (Muridae) as a host of *R. seminuda*. As noted above, we consider this record an error because only bats are considered hosts of Streblidae ectoparasites (Wenzel *et al.*, 1966; Dick and Patterson, 2006).

Raymondia setiloba (Jobling, 1954)

Country

Democratic Republic of Congo.

Hosts

Hipposideros caffer-ruber complex, *Miniopterus* sp., *Rhinolophus* sp.

Comments

Theodor (1968) records *R. setiloba* parasitizing *Hipposideros caffer* and *Rhinolophus hildebrandtii* in the Democratic Republic of Congo. We refer to the former as the *H. caffer-ruber* complex. It is unclear which species within the *R. hildebrandtii* complex occurs in the DRC as no genetic or morphological studies of this bat group have been conducted there. We correct the date for the description of *R. setiloba* as 1954 (Jobling, 1954), not 1955 as indicated in Dick and Graciolli's (2008) worldwide checklist of the family Streblidae.

Raymondia simplex Jobling, 1955

Country

Democratic Republic of Congo.

Hosts

Hipposideros caffer-ruber complex, *Rhinolophus landeri*.

Comments

We consider *Rhinolophus lobatus* (Jobling, 1939; Theodor, 1968) a synonym of *R. landeri* (Brown and Dunlop, 1997). As noted above, the species of the host within the *Hipposideros caffer-ruber* complex recorded is unknown (Theodor, 1968).

Raymondia tauffliebi Theodor, 1968

Country

Congo (Brazzaville).

Host

Miniopterus inflatus.

Raymondia waterstoni Jobling, 1931

Countries

Botswana, Congo (Brazzaville), Democratic Republic of Congo, Mozambique, Tanzania.

Hosts

Hipposideros caffer-ruber complex, *Miniopterus natalensis* (A. Smith, 1834), *Rhinolophus hildebrandtii*, *R. landeri*, *R. mossambicus*, *R. simulator*, *Rhinolophus* sp., *R. swinnyi* Gough, 1908, *Triaenops afer*.

Comments

We consider *Rhinolophus lobatus* (Theodor, 1968) a synonym of *R. landeri* (Brown and Dunlop, 1997). *Raymondia waterstoni* has been recorded parasitizing *Rhinolophus hildebrandtii* in Mozambique (Maa, 1968), which is outside this species' distribution. Based on location, this record is most likely *R. mossambicus* (Taylor *et al.*, 2012). As in the case of *R. aspera* and *R. seminuda*, Maa (1968) mentions *Mastomys natalensis*, a rodent, hosting *R. waterstoni*. As in the above mentioned cases, we consider this host to be an error (Wenzel *et al.*, 1966; Dick and Patterson, 2006) and do not include it.

Raymondia sp. A

Country

Congo (Brazzaville).

Hosts

Hipposideros caffer-ruber complex.

Comments

Theodor (1968) records *Raymondia* sp. A from *Hipposideros caffer centralis*. Based on the locality, the host is most likely within the *Hipposideros caffer-ruber* complex.

Raymondia sp. B*Country*

Congo (Brazzaville).

Hosts

Rhinolophus sp.

Comments

Theodor (1968) notes that this species shares some morphological similarities to *R. intermedia* and could possibly be a subspecies of it.

DISCUSSION

There are clear research gaps in our knowledge of *Raymondia*, particularly in northern Africa (Fig. 4). Although nearly 86% of known *Raymondia* species have been recorded in Africa (see Dick and Graciolli, 2008), about half the countries are understudied or without any information about ectoparasites at all. Most countries in Africa have four or less species that have been recorded. Even the Democratic Republic of Congo and South Africa, with eight and six species, respectively, have a relatively small number of species recorded compared to their size and the diversity of their bat fauna. For one ectoparasite species, *R. lobulata*, the specific bat host species in Africa are still unknown, and the hosts are known only to the level of genus for two other species (*R. boquieni* and *Raymondia* sp. B), both of which are hosted by *Rhinolophus* sp.

Raymondia species with the greatest number of hosts (*R. intermedia*, *R. huberi huberi*, *R. seminuda*) were also those with specimen records in the largest number of countries, which supports the niche-breadth hypothesis, in which parasites with lower host specificity also have greater geographic ranges (Krasnov *et al.*, 2005). However, in general there seems to be virtually no correlation between ectoparasite distribution and host distribution. The host distribution of certain species, such as *R. pagodarum*, *R. scopigera*, or *R. simplex* (Fig. 3), extends far beyond where records have been made. This could indicate a small distribution of the ectoparasite within their hosts' distributions, perhaps as a result

of a certain region's environment or alternatively geographic variations in behaviour and roosting in the host species. However, the more likely explanation is that this lack of correlation is a result of under-sampling of the ectoparasites; the current records probably underestimate the range of *Raymondia* species.

While Streblidae are generally highly host specific (Dick, 2007), *Raymondia* species in Africa appear to be more generalist. About half (53%) have been recorded parasitizing multiple bat species and families. Furthermore, due to the rarity of *Raymondia* records, the percentage could be higher still. *Raymondia huberi huberi* (nine species, four families), *R. hardyi* (eight species, four families) *R. intermedia* (eight species, four families) can be considered true generalists (polyxenous, sensu Wenzel *et al.*, 1966). Many ectoparasite species have rarely been found parasitizing species of different genera, while our review indicates that nine (47%) *Raymondia* species have been recorded on bat species of different genera. In fact, nearly every *Raymondia* species recorded from multiple species of bats was found from multiple genera, and in many cases, in different families. In the Americas, Streblidae

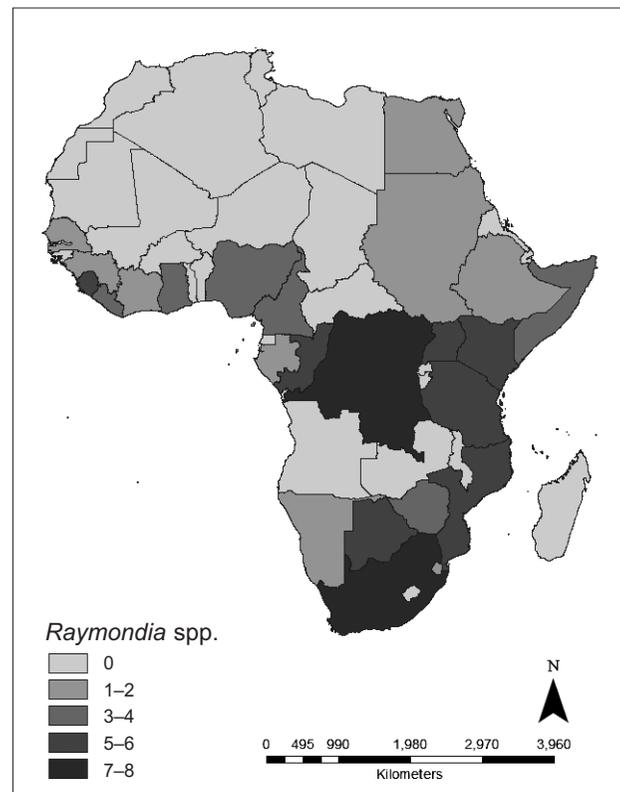


FIG. 4. Heat map of *Raymondia* species richness, by country

species tend to have very high host specificity and monoxenous behaviour; the genus *Mastoptera* seems to be an exception, with low specificity, parasitizing bats principally in the subfamily Phyllostominae (see ter Hofstede *et al.*, 2004; Dick and Gettinger, 2005; Gracioli *et al.*, 2010; Dick, 2013).

The large number of *Raymondia* species with low host specificity in Africa may be related to their evolutionary history with hosts (Poulin and Mouillot, 2003). It could also be due to similarities in habitat or roost type preference between different bat species (Adamson and Caira, 1994) or an indication of frequent contact between bats of different species, such as roosting together. A better understanding of the true host specificity could shed light on both host and parasite phylogeny and evolution (Adamson and Caira, 1994). In addition, host specificity is directly related to parasite mobility (ter Hofstede *et al.*, 2004). Ectoparasites with restricted mobility tend to be more host-specific, due to the difficulty in encountering new hosts (Wenzel *et al.*, 1966; Marshall, 1981). Mobility does not seem to present a barrier for *Raymondia* spp. because they have retained well-developed wings, allowing them to move relatively easily between hosts, potentially those of different species. A further explanation for the low level of host specificity of African *Raymondia* species may be that the taxonomy of this group is poorly known. In general, there are still many uncertainties in Streblidae taxonomy (Dick and Patterson, 2006; Dittmar *et al.*, 2006). It may well be that what is currently regarded as a generalist species (e.g., *R. intermedia*), may in fact represent multiple cryptic species, each one being host specific to a particular bat species. Supplementing classical taxonomic identification with molecular identification could further clarify these relationships and potentially reveal cryptic *Raymondia* species.

Bat ectoparasites in Africa have long been neglected. The vast majority of references to *Raymondia* on the continent were published at least forty years ago. Since then nomenclature for both bats and ectoparasites has changed considerably. Within these references, authors frequently change species and subspecies designations (e.g., Theodor, 1968, 1973, regarding *R. hardyi* and *R. waterstoni*). This study presents the most current, accurate list of *Raymondia* species and hosts in Africa. We updated the bat host species for 70 records of 13 different *Raymondia* species. However, these studies are largely based on classic taxonomy. Supplementing traditional taxonomy with phylogenetic studies of *Raymondia* could further clarify species identities

and distributions, especially in cases where distinguishing features, such as size of specimens or appendages, exist on a continuum.

Ectoparasites may play an important role in disease ecology, including some pathogens that may affect humans, such as *Bartonella* (Billeter *et al.*, 2012). Diverse Streblidae and Nycteribiidae occupying multiple hosts across the globe appear to carry *Bartonella* and may be important vectors for this disease (Morse *et al.*, 2012). *Bartonella* and *Rickettsia* have recently been detected in bats in our study area in Swaziland (Markotter *et al.*, under review). The role that ectoparasites may play in the transmission and prevalence of these pathogens requires further study. In addition, ectoparasite species diversity could have a positive correlation with viral species richness (Gay *et al.*, 2014). The potentially high ectoparasite species richness of many bat species in Africa may indicate the potential virus loads and guide investigations of pathogen discovery in bats.

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APPENDIX I

Summary of specimen records of *Raymondia* species in Africa. Original location name indicates the name used for the country in the original publication. Many names have been changed since then. A town or province is included when such information was provided in the original publication. Host indicates the bat host. Species with a question mark indicate cases where the host species is unclear, based on the location of the record. In cases where we have updated the bat host, based on currently known species distributions, the host cited in the article is listed under Original Host. In some cases, bat hosts were not identified with Latin names in the article and in such cases we list the name used by the author under Original Host

Ectoparasite	Reference	Country / Region	Town / Province	Original location name	Host	Original host
<i>Raymondia allisoni</i>	Theodor (1968)	Ghana	Miradani Oboum mine Bibiani		<i>Hipposideros caffer-ruber</i> complex <i>Rhinolophus alcyone</i> <i>Rhinolophus alcyone</i>	<i>Hipposideros caffer</i>
<i>Raymondia alulata</i>	Ferris (1930) Jobling (1930) Bedford (1932)	Namibia Somalia Namibia	Kakaoveld, Southwest Africa British Somaliland Kakaoveld, Southwest Africa		<i>Nycteris thebaica</i> Unspecified bat <i>Nycteris thebaica</i>	<i>Nycteris damarensis</i> <i>Nycteris damarensis</i>
	Jobling (1939)	Somalia	British Somaliland		Unspecified bat	<i>Nycteris damarensis</i>
	Maa (1968)	Namibia Somalia South Africa Botswana	Kakaoveld, Southwest Africa British Somaliland Port Elizabeth Drotsky's Cave		<i>Nycteris thebaica</i> Unspecified bat <i>Nycteris thebaica</i> <i>Nycteris thebaica</i>	<i>Nycteris capensis</i> <i>Nycteris thebaica</i>
	Theodor (1968)	Mozambique Botswana	Gamito, Tete Muchena, Tete Kanye	Bechuanaland Bechuanaland	<i>Nycteris thebaica</i> <i>Hipposideros caffer</i> <i>Nycteris thebaica</i> <i>Cloeotis percivali</i> <i>Nycteris thebaica</i> <i>Nycteris thebaica</i> <i>Rhinolophus</i> sp.	<i>Nycteris thebaica</i>
		Democratic Republic of Congo Namibia South Africa	Machanenga mine Lusolo Cave Ontje Bishopstowe Hol Kaenstartboom Parfuri		<i>Nycteris thebaica</i> <i>Nycteris thebaica</i> <i>Nycteris thebaica</i> <i>Nycteris thebaica</i> <i>Rhinolophus</i> sp. <i>Rhinolophus blasii</i>	<i>Nycteris capensis</i> <i>Nycteris capensis</i> <i>Nycteris capensis</i> <i>Nycteris capensis</i>
		Uganda	Pietermaritzburg Roofberg Kaina Mine, Ankole Tororo		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer</i> "Long-eared bat"
<i>Raymondia aspera</i>	Maa (1968)	Zimbabwe This study Botswana Mozambique	Bulawayo Swaziland Drotsky's Cave Muchena, Tete	Rhodesia Mbuluzi Game Reserve Bechuanaland	<i>Nycteris thebaica</i> <i>Nycteris thebaica</i> <i>Rhinolophus denti</i> <i>Miniopterus mossambicus</i> <i>Rhinolophus landeri</i> <i>Rhinolophus mossambicus</i> <i>Rhinolophus</i> sp.	<i>Miniopterus schreibersii</i> <i>Rhinolophus hildebrandtii</i> <i>Trienops afer</i>
<i>Raymondia boquieni</i>	Theodor (1968)	Congo (Brazzaville)	Vila Gamito, Tete Loudima Cave		<i>Hipposideros caffer</i> <i>Rhinolophus</i> sp.	

APPENDIX I. Continued

Ectoparasite	Reference	Country / Region	Town / Province	Original location name	Host	Original host
<i>Raymondia brachyphysa</i>	Theodor (1968)	Ivory Coast	Democratic Republic of Congo	Mulungwishi Cave	Unspecified bat	
<i>Raymondia hardyi</i>	Jobling (1939)	South Africa	Abidjan Krugersdorp		<i>Hipposideros cyclops</i> <i>Cloeotis percivali</i> <i>Rhinolophus blasii</i> <i>Rhinolophus clivusos</i> Unspecified bat <i>Hipposideros caffer</i> <i>Myotis tricolor</i> <i>Nycteris thebaica</i> <i>Rhinolophus clivusos</i> <i>Rhinolophus blasii</i> <i>Rhinolophus cohenae</i> or <i>Rhinolophus smithersi</i> ? <i>Rhinolophus simulator</i>	<i>Rhinolophus empusa</i> <i>Rhinolophus augur geoffroyi</i>
	Theodor (1968)	South Africa	Pretoria Sierkfontein Caves Bishopstowe		<i>Nycteris thebaica</i> <i>Rhinolophus blasii</i> <i>Rhinolophus cohenae</i> or <i>Rhinolophus smithersi</i> ? <i>Rhinolophus simulator</i>	<i>Nycteris capensis</i> <i>Rhinolophus clivusos augur</i> <i>Rhinolophus blasii empusa</i> <i>Rhinolophus hildebrandtii</i>
<i>Raymondia huberi huberi</i>	Kessel (1925)	East Africa Egypt	Rooiberg Luxor Unspecified location	British East Africa	Unspecified bat <i>Rhinolophus</i> sp. <i>Cardioderma</i> cor <i>Hipposideros</i> sp. <i>Cardioderma</i> cor <i>Hipposideros</i> sp. <i>Hipposideros caffer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor <i>Coleura afra</i> <i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor	Horseshoe-nosed bat <i>Megaderma</i> cor <i>Phyllorhina</i> sp <i>Megaderma</i> cor <i>Phyllorhina</i> sp. <i>Hipposideros tridens</i> <i>Megaderma</i> cor
	Jobling (1930)	South Africa East Africa	KwaZulu-Natal	Abyssinia Zululand	<i>Cardioderma</i> cor <i>Coleura afra</i> <i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor	<i>Trienops persicus</i> <i>Hipposideros tridens</i> <i>Megaderma</i> cor
		Egypt		Abyssinia	<i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor <i>Coleura afra</i> <i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor <i>Coleura afra</i> <i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor	<i>Trienops persicus</i> <i>Hipposideros tridens</i> <i>Megaderma</i> cor
		Ethiopia		Abyssinia	<i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor <i>Coleura afra</i> <i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor	<i>Trienops persicus</i> <i>Hipposideros tridens</i> <i>Megaderma</i> cor
		South Africa			<i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor <i>Coleura afra</i> <i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor	<i>Trienops persicus</i> <i>Hipposideros tridens</i> <i>Megaderma</i> cor
		South Africa			<i>Hipposideros caffer</i> <i>Trienops afer</i> <i>Asellia tridens</i> <i>Cardioderma</i> cor	<i>Trienops persicus</i> <i>Hipposideros tridens</i> <i>Megaderma</i> cor

APPENDIX I. Continued

Ectoparasite	Reference	Country / Region	Town / Province	Original location name	Host	Original host
	Bedford (1932)	East Africa		British East Africa	Unspecified bat	
		Egypt		Abyssinia	Unspecified bat	
		Ethiopia		Zululand	Unspecified bat	
		South Africa	'KwaZulu-Natal		<i>Hipposideros caffer</i>	
			Onderstepoort		Unspecified bat	
	Jobling (1939)	Democratic Republic of Congo		Belgian Congo	Unspecified bat	
		East Africa		British East Africa	<i>Hipposideros caffer?</i>	<i>Hipposideros caffer</i>
		East Africa		German East Africa	<i>Coleura afra</i>	<i>Triatenops persicus</i>
				German East Africa	<i>Triatenops afer</i>	<i>Hipposideros tridens</i>
		Egypt		Abyssinia	<i>Asellia tridens</i>	
		Ethiopia			Unspecified bat	
		Kenya	Mt.Elgon		Unspecified bat	
			Unspecified location		Unspecified bat	
		Nigeria	Old Calabar		Unspecified bat	
		South Africa	KwaZulu-Natal	Zululand	<i>Hipposideros fuliginosus</i>	
			Onderstepoort		<i>Hipposideros caffer</i>	
			Transvaal		Unspecified bat	
			Transvaal		<i>Hipposideros caffer</i>	
		Zimbabwe		South Rhodesia	<i>Cloeotis percivali</i>	
		Unknown country		Solomona Habesch	Unspecified bat?	
	Jobling (1949)	Sierra Leone	Makeni		<i>Cardioderma cor</i>	<i>Hipposideros caffer</i>
	Theodor (1968)	Egypt			<i>Hipposideros caffer-ruber</i> complex	
		Kenya	Ngombeni Cave		<i>Cardioderma cor</i>	
			Shimoni Caves		<i>Cardioderma cor</i>	
		Tanzania	Kulumuzi Cave		<i>Hipposideros vittatus</i>	<i>Hipposideros commersoni</i>
	Maganga <i>et al.</i> (2014)	Gabon	Belinga		<i>Triatenops afer</i>	<i>Triatenops persicus</i>
					<i>Coleura afra</i>	
<i>Raymonida intermedia</i>	Jobling (1936)	Democratic Republic of Congo	Rutschurie	Belgian Congo	<i>Rhinolophus</i> sp.?	<i>Rhinolophus hildebrandtii</i>
	Jobling (1939)	Democratic Republic of Congo	Rutschurie	Belgian Congo	<i>Rhinolophus</i> sp.?	<i>Rhinolophus hildebrandtii</i>
		Republic of Congo	Mount Elgon		<i>Rhinolophus landeri</i>	<i>Rhinolophus lobatus</i>
		Kenya			Unspecified bat	
		Cameroon	Haute Benoue, Mbé		<i>Rhinolophus</i> sp.	
	Theodor (1968)		Wildi Cave, near Buéa		<i>Rhinolophus</i> sp.	
		Democratic Republic of Congo	Mount Hoyoy		<i>Rhinolophus</i> sp.	
		Kenya	Mt. Elgon		<i>Rhinolophus clivovus</i>	<i>Rhinolophus ferrumequinum keniensis</i>
			Koru		<i>Miniopterus africanus</i>	

APPENDIX I. Continued

Ectoparasite	Reference	Country / Region	Town / Province	Original location name	Host	Original host
		Sierra Leone	Musala		<i>Rhinolophus hildebrandtii</i>	
		South Sudan	Torit		<i>Rhinolophus fumigatus</i>	
		Tanzania	Amani	Sudan	<i>Rhinolophus eloquens</i>	
		Uganda	Entebbe	Tanganyika	<i>Hipposideros caffer</i>	
	Wolton <i>et al.</i> (1982)	Liberia	Tokadeh		<i>Rhinolophus eloquens</i>	
					<i>Rhinolophus clivosus</i>	
<i>Raymondia lobulata</i>	Kessel (1925)	Somalia		British Somaliland	Unspecified bat	
<i>Raymondia pagodarum</i>	Ferris (1930)	Uganda	Gondokoro		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros ruber</i>
<i>Raymondia planiceps</i>	Jobling (1930)	East Africa		British East Africa	Unspecified bat	
	Jobling (1939)	Kenya	Nairobi	British East Africa	Unspecified bat	
			Unspecified location		<i>Cardioderma cor</i>	
		South Africa	Krugersdorp		Unspecified bat	
	Theodor (1968)	East Africa	Kilifi Creek		Unspecified bat	
		Kenya	Ngombeni Cave		<i>Cardioderma cor</i>	
			Tseikuru		<i>Cardioderma cor</i>	
			Mago National Park		<i>Cardioderma cor</i>	
	Kanuch <i>et al.</i> (2015)	Ethiopia				
<i>Raymondia scopigera</i>	Jobling (1954)	Cameroon	Ngaouyanga		<i>Nycteris macrotis</i>	<i>Nycteris aethiopica aethiopica</i>
	Carnicas (1968)	Senegal	Forêt de Bandia, Thiès		<i>Nycteris macrotis</i>	
	Theodor (1968)	Cameroon			<i>Nycteris macrotis</i>	<i>Nycteris aethiopica</i>
		Sierra Leone	Musala		<i>Nycteris macrotis</i>	
		Botswana	Kasane	Bechuanaland	<i>Hipposideros caffer</i>	
	Maa (1968)	Mozambique	Gaza		<i>Rhinolophus</i> sp.	
			Tete		<i>Hipposideros caffer</i>	
			Vila Gamito, Tete		<i>Hipposideros caffer</i>	
					<i>Nycteris thebaica</i>	
		Nigeria	Abá		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer</i>
	Theodor (1968)	Botswana	Kanye	Bechuanaland	<i>Cloeotis percivali</i>	
			Ksane, Ngamiland		Unspecified bat	
			Francistown		<i>Nycteris thebaica</i>	
		Cameroon	Akok-Bekoé cave, near Yaoundé		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer</i>
			Bukoko		Unspecified bat	
		Congo (Brazzaville)	Meya Cave		<i>Mintopterus inflatus</i>	
		Democratic Republic Congo	Kaboyaboya	Cave, Lubudi	<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer</i>
				Kakanga Cave	<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer ruber</i>
			Kasoma Cave, Upemba National Park		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer ruber</i>
			Kyasala Cave, Lubudi		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer ruber</i>

APPENDIX I. Continued

Ectoparasite	Reference	Country / Region	Town / Province	Original location name	Host	Original host
			Kakontwe		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer</i>
			Kasoma cave, Upemba National Park		<i>Rhinolophus</i> sp.	
			Kyasala Cave, Lubudi		<i>Rhinolophus</i> sp.?	<i>Rhinolophus hildebrandtii</i>
			Losolo Cave, Lubudi		<i>Rhinolophus landeri</i>	<i>Rhinolophus lobatus</i>
			Goba		<i>Rhinolophus swinnyi</i>	
		Mozambique	Rukwa Valley	Tanganyika	<i>Rhinolophus</i> sp.	
		Tanzania			<i>Rhinolophus</i> sp.	
<i>Raymondia</i> sp. A	Theodor (1973)	Congo (Brazzaville)			Unspecified bat	
<i>Raymondia</i> sp. B	Theodor (1968)	Congo (Brazzaville)	Loudima Caves		<i>Hipposideros caffer-ruber</i> complex	<i>Hipposideros caffer centralis</i>
	Theodor (1968)	Congo (Brazzaville)	Meza Cave		<i>Rhinolophus</i> sp.	

APPENDIX II

Key to *Raymondia* species occurring in Africa. Here we present an identification key to all species of the genus *Raymondia* which occur in Africa. This key was adapted from and based on Maa (1968), Theodor (1968, 1973) with relevant updates to nomenclature

1. Occiput with a row of setae. Posterior gular row of short setae reaching to the setae of the laterovertex. Mesonotal suture complete. Mesonotum completely covered with microtrichia. Scutellum with short setae in the middle of the surface. Alula with 4–9 setae. Apodeme of aedeagus very long, curved backwards. Digitiform processes fused at the base. Anterior processes of the anal frame with setae 2
 - Occiput without a row of setae. Posterior gular row of short setae reduced, not reaching setae of laterovertex, or absent. Mesonotal suture broadly interrupted in the middle. Microtrichia on mesonotum forming a broad stripe before the scutellar suture. Scutellum without short setae in the middle of the surface. Alula with one seta or without seta. Apodeme of aedeagus long or short, but not curved backwards. Digitiform processes separate. Anterior processes of anal frame without setae 3
2. Occipital row consisting of 8–9 setae. Sternal plate of thorax without microtrichia. No setae at the anterior margin of the anterior triangular processes of the mesosternum. R_{2+3} only slightly curved. Only one seta on abdomen of female lateral to tergite 10. Right paramere of male broad and short. Aedeagus broad, bifid . . . *R. alulata*
 - Occipital row consisting of 13–15 setae. Sternal plate of thorax completely covered with microtrichia. Setae present at the anterior margin of the anterior triangular processes of the mesosternum. R_{2+3} strongly curved towards wing margin. Three setae on abdomen of female lateral to tergite 10; a dense group of setae at ventral end of abdomen before proctiger. Right paramere and aedeagus of male long and slender *R. scopigera*
3. Head wider than anterior margin of mesonotum, rounded. Theca of labium markedly wider than long, with two lateral concavities at the posterior margin. Only one row of gular setae, the median setae very short. Microtrichia on sternal plate of thorax long, forming groups of 5–8, covering greater part of mesosternum. Alula with one seta *R. planiceps*
 - Head not wider than anterior margin of thorax, quadrangular or rounded-trapezoidal. Theca narrower, without lateral concavities at the posterior margin. A gular row of long setae and a posterior row of short setae present. Microtrichia on sternal plate not forming groups . . . 4
4. Sternal plate of thorax completely covered to the anterior margin with microtrichia, which are short and form distinct, dense transverse rows. Setae in cell r_1 not forming triangular group. Alula with one seta. Sternite 7 of female oblong, with two anterior and two posterior setae 5
 - Sternal plate of thorax covered with microtrichia in greater or smaller part or microtrichia absent. Microtrichia longer, more widely spaced. Setae in cell r_1 forming triangular group. Alula markedly reduced, without seta. Sternite 7 of female triangular 7
5. Anterior part of mesonotum bare, setae in posterior part as long as distance between them or shorter. Theca of labium as wide as long. Tergite 10 of female broadly rectangular or rounded anteriorly *R. seminuda*
 - Setae on anterior part of mesonotum present, longer than the distance between them 6
6. Setae on anterior part of mesonotum relatively widely spaced. Theca slightly longer than wide. Tergite 10 of female triangular anteriorly, with six setae. Right paramere of male with long, truncate apex *R. huberi huberi*
 - Transverse mesonotal suture oblique, widely interrupted at middle. Prescutellars 1/3 as long as scutellar bristles, generally not interspaced by small setae. Surface of prescutum finely setose. Bare area of prescutum less extensive, dorsolateral fence of female abdomen clearly composed of two columns of setae. Alula with one apical seta. Lobe of tergite 1 with few setae *R. aspera*
7. Lateral lobes of tergite 1 of abdomen with numerous setae in several rows *R. setiloba*
 - Lateral lobes of tergite 1 with only a single row of 4–10 setae 8
8. Microtrichia on mesonotum forming usual broad stripe before scutellar suture, as in *R. intermedia* 9
 - Distribution of microtrichia on sternum of thorax markedly reduced or absent 15
9. The row of setae on dorsum of abdomen next to the bare space consisting of very short spines anteriorly, a double row of about seven long setae posteriorly. Aedeagus shallowly S-shaped. Apodeme only little longer than aedeagus *R. waterstoni*
 - One or two rows of long setae on dorsum of abdomen next to the bare space 10

APPENDIX II. Continued

10. Gular row with eight short median setae. Posterior row of gular setae much reduced, consisting only of a short seta lateral to the second seta from the middle and 1–2 short setae markedly further laterally. Microtrichia covering greater part of sternal plate of thorax, forming regular transverse rows. Tergite 10 triangular, with only four posterior setae in a row *R. boquienni*
 – Median setae of gular row longer or shorter, posterior row of short setae well developed, consisting of 4–8 setae in the middle. Microtrichia on sternal plate not forming regular transverse rows. Tergite 10 with four posterior and two anterior setae 11
11. Tergite 10 triangularly produced anteriorly . . . 12
 – Tergite 10 rounded or rectangular anteriorly 13
12. Anterior process of tergite 10 narrow, much longer than the distance between the two anterior and the four posterior setae. Sternite 7 very large, with four long and several short setae . . . *R. allisoni*
 – Anterior process of tergite 10 broadly triangular, not much longer than the distance between the anterior and the two posterior setae. Sternite 7 small, with only four setae *R. tauffliebi*
13. Sternite 7 large, triangular. Tergite 10 broadly rectangular or rounded anteriorly, reaching further beyond the anterior setae than the distance between the anterior and posterior setae *R. intermedia*
 – Sternite 7 small 14
14. Sternite 7 with four setae more or less in a row. Anterior margin of tergite 10 close to the anterior setae *R. simplex*
 – Sternite 7 with two setae posteriorly and two setae markedly anteriorly. Tergite 7 with posterior row of four setae and two anterior setae. Aedeagus shorter, not S-shaped and with a posterior process *R. hardyi*
15. Apodeme of aedeagus much longer than apodeme of the parameres 16
 – Apodeme of aedeagus little or no longer than apodeme of the parameres 17
16. Right paramere long and broad . *R. intermedia*
 – Right paramere markedly less curved at tip (less curved than in *R. waterstoni*), bearing fewer and longer setae, left paramere with a blunt, rounded end *R. hardyi*
17. Right paramere twisted near junction with apodeme. Aedeagus broad, with pointed apex . . . 18
 – Right paramere with basal hump, but not twisted, aedeagus narrow 19
18. Sternal plate of thorax without microtrichia. Aedeagus 0.25 mm long, straight. Right paramere short, with narrow, pointed apex. Digitiform processes short and thick *R. brachyphysa*
 – Sternal plate of thorax covered with microtrichia in its greater part. Aedeagus 0.35 mm long, curved apically. Right paramere very large, curved nearly at a right angle, with long, truncate apex. Digitiform processes long and slender *R. allisoni*
19. Right paramere narrow, with only 7–8 setae at the outer margin. Digitiform processes long and slender. Aedeagus S-shaped *R. simplex*
 – Right paramere broader, with more numerous hairs. Digitiform processes shorter and thicker 20
20. Aedeagus short, curved dorsally, with sharp, triangular apex. Right paramere markedly curved, hook-shaped *R. tauffliebi*
 – Aedeagus longer, curved ventrally at the base or S-shaped. Right paramere with slightly curved or straight apical process *R. waterstoni*