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ACARI (CHELICERATA) — PARASITES OF REPTILES

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ABSTRACT: A brief review of acari parasitizing reptiles (Reptilia) was presented. Reptilian mites are represented by 15 families of temporary and permanent parasites which belong to 3 orders: Mesostigmata (Entonyssidae, Heterozerconidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Omentolaelapidae, Paramegistidae), Metastigmata (Amblyommidae, Argasidae, Ixodidae) and Prostigmata (Cloacaridae, Harpirhynchidae, Leeuwenhoekiidae, Pterygosomatidae, Trombiculidae). The main aspects of host-parasite relationships were analyzed. Acari of six families (Acariformes: Cloacaridae, Harpirhynchidae, Pterygosomatidae and Parasitiformes: Entonyssidae, Ixodorhynchidae, Omentolaelapidae), i.e. 242 species were recorded as permanent parasites of reptiles. All hosts of these mites are summated in table format. The obtained results indicated that host-specificity among acariform mites is higher than that one in Parasitiformes. Differences in specificity between permanent endoparasitic and ectoparasitic mites were not significant. Most ectoparasitic mites occur under the host's scales or in sites not reached by itching activities of the reptiles e.g. the ear canals or elbow joints. Endoparasites live in the respiratory passages of their reptilian hosts or in the host cloaca and muscles. Available data show that permanent parasites are characterized by the low prevalence index (IP) while IP of temporary parasites is high. The effect of mites on host fitness is unclear. Most studies showed that acari may cause various diseases and debilitation in reptiles e.g. anemia, reduced activity or dermatitis what is very marked in captive collections of reptiles. Additionally, species belonging to five families, i.e. Amblyommidae, Argasidae, Ixodidae, Macronyssidae, and Pterygosomatidae were recorded as vectors of many pathogens.

KEY WORDS**:** Acari, host-parasite relationships, parasites, Reptilia

INTRODUCTION

Symbiotic relationships such as commensalism and parasitism are widely distributed among acari-like chelicerates named Acari or Acarina (Chelicerata) (Krantz and Walter 2009). Many monographic reviews concerning host-parasite relationships of mammal and bird-associated acari were published in the past 20 years (Balashov 1982, 2009; Kim 1985; Clayton and Moore 1997; Bochkov 2009, etc). At the same time, host-parasite relationships between acari and reptiles or amphibians received only limited attention (Balashov 1982, 2009) and special reviews about this topic are absent. In acari, the strongly limited number of taxa is associated with amphibians, whereas reptile-associated acari are numerous and belong to several families being known throughout the world. Moreover, mites of some families are associated exclusively with these hosts (Krantz and Walter 2009). Even studying a small fraction of the over 9000 extant reptile species described to date allowed for the recording of more than 400 species of parasitic acari.

In this paper, I try to briefly summarize our knowledge about host-parasite relationships of acari and reptiles.

MATERIAL AND METHODS

In relation to acari taxonomy I follow the system of Krantz and Walter (2009). Types of parasitism are accepted according to the classification by Balashov (1982, 2009). I am focused exclusively on parasitic relationships as defined by Dogel (1947) and Balashov (1982) and do not discuss micropredators attacking reptiles. Data about reptilian mites are summated in Table 1.

Reptile overall systematics and the species names used in this paper were obtained from the TIGR/JCVI Reptile Database (http://www.reptile-database.org as of 24 April 2012 (Uetz 2010).

For the analysis of host-specificity among permanent parasites of Reptilia 240 mite species from six families (Acariformes: Cloacaridae, Harpirhynchidae, Pterygosomatidae and Parasitiformes: Entonyssidae, Ixodorhynchidae, Omentolaelapidae) were used (see Table 2). To estimate of the host specificity level, parasitiform mites vs. acariform mites and ectoparasites vs. endoparasites were compared using Fisher's exact test. Confidence intervals (CI) for proportions were calculated using the binomial distribution.

I. Host taxonomy and phylogeny

Zug et al. (2001) grouped extant reptiles into three subclasses: Anapsida, Lepidosauria, and Archosauria. The first subclass Anapsida contains only one order of turtles, Testudines with two suborders: the hidden-neck turtles Cryptodira (248 species) and the side-necked turtles Pleurodira (79 species). This order is the oldest reptile group that evolved sometime prior to the Upper Jurassic or Cretaceous (Pyron 2010).

The second subclass Lepidosauria contains two orders, Rhynhocephalia (2 species) and Squamata. The second order includes Sauria (~4900

sp.), Ophidia (~3070 sp.), and Amphisbaenia (~200 sp.). The lepidosaurs appeared in the Upper Triassic (over 200 Myr) and diversified into numerous families during the Jurassic and Cretaceous period (Vidal and Hedges 2009).

The third subclass, Archosauria includes the order Crocodylia which contains crocodylians, alligators, and gharials (25 sp.). The order appeared in the Upper Cretaceous and includes the closest living relatives of birds (Brochu 2003).

Traditionally, the classical phylogeny divided living reptiles into two phylogenetic branches based on morphology and the fossil records: anapsid reptiles (with a single opening in their sculls i.e. Testudines) and diapsid reptiles (with two temporal openings in their sculls i.e. the Archosauria and Lepidosauria) (Hedges and Poling 1999).

Despite the series of taxonomic revisions (Zug et. al. 2001; Fujita et. al. 2004; Vidal and Hedges 2009; Pyron et. al. 2011) the phylogenetic relationships among the primary lineages of Reptilia remain still unclear. Both morphological and molecular studies have yielded multiple hypotheses for the phylogenetic relationships of Reptilia. Morphological studies show that Testudines may be the only extant anapsid amniotes and the sister taxon of the diapsids. On the other hand, recent molecular studies show that Testudines may be actually diapsid amniotes who have lost their temporal scull openings. Most molecular data confirms the hypothesis that Testudines are sisters of the Archosauria, however, Rieppel and Reisz (1999) placed turtles as the sister group to lepidosaurs rather than to archosaurs. Similarly, the phylogenetic links of snakes (Ophidia) among other Lepidosauria are uncertain. Some studies place them among lizards within Anguimorpha (Lee 2000), whereas others place snakes as sisters of a clade including all the lizards (Underwood 1970). Moreover, Rhynhocephalia is usually placed as a sister group to the Squamata based on morphology, although analyses of limited molecular data suggest that tuataras are closer to archosaurs and turtles (Rest 2003).

II. Host-parasite relationships

1. Facultative parasites

The only recorded example of this type of interaction is *Benoinyssus najae* Fain, 1958 (Eupodidae) found in the nasal cavities of *Naja melanoleuca* Hallowell, 1857 (Squamata: Elapidae) (Fain 1958). Subsequently, a large number of specimens belonging to this species were found in soil and leaf-litter samples. Later on, it has been shown that Fain's record was possibly accidental after he checked the nasal cavities of a related snake species. It is most probable that members of *Benoinyssus* are free-living soil mites and might resort to parasitic lifestyles if the opportunity occurs (Olivier and Theron 1997).

2. Obligate parasites

2.1. Temporary parasites

2.1.1. Temporary ectoparasites

PARASITIFORMES

Ixodoidea

Up to now, more than 100 hard and soft tick species belonging to eight genera of the families Argasidae and Ixodidae have been collected from reptiles worldwide (Pietzsch et al. 2006).

Ticks from above mentioned families have a wide geographical distribution and are described from all classes of terrestrial vertebrates (Amphibia, Reptilia, Aves and Mammalia). However, in many cases reptiles are the principal hosts of ticks (e.g. nearly all species of the genus *Aponomma* parasitize snakes, lizards, and tuatara; a lot of *Amblyomma* species show a marked preference for reptilian hosts). There are known a few cases when all stages are found exclusively on one reptile species (monoxenous parasitism) e.g. *Argas (Microargas) transversus* (Argasidae) from *Chelonoidis nigra* (Quoy et Gaimard, 1824) (Hoogstraal and Kohls 1966; Hoogstraal et al. 1973).

Macronyssidae

In the family Macronyssidae (Parasitiformes: Mesostigmata), only mites of the genus *Ophionyssus* are ectoparasites of reptiles, mainly lizards of various genera (Fain and Bannert 2000, 2002). The genus comprises 16 described species from Squamata (Sauria: Agamidae, Scincidae, Lacertidae, Cordylidae, Diplodactylidae, and Ophidia), although mammals have also been reported as hosts (Fain and Bannert 2002). Most frequently these ectoparasites are located on the soft tissues around the eyes, in the ears (tympanic membrane), under the scales or around the cloaca of their hosts (Bannert et. al. 2000). Protonymphs and females of these mites are parasitic. The larva and deutonymph do not feed and display only low activity (elatostatic forms). Females lay eggs whether or not they are inseminated. The virgin females produced male offspring exclusively (arrhenotokous parthenogenesis), while inseminated females produced offspring of both sexes (Bannert et. al. 2000). All *Ophionyssus* species have been found in the Old World, except for *O. natricis* which

is a cosmopolitan inhabitant of captive snakes (Wozniak and DeNardo 2000).

Paramegistidae

Mites of the family Paramegistidae are usually associated with myriapods and insects. The genus *Ophiomegistus* is an exception and includes blood sucking parasites living on skinks and snakes. So far, 21 species of this genus are described from the Oriental and Australasian regions, with most of them found in New Guinea (13 species). Only adult mites have been described from reptiles, thus we may assume that immature individuals are free-living. Klompen and Agustin (2007) claimed that these mites may be limited to this region and associated with specific hosts occupying semi-fossorial areas.

Heterozerconidae

Most representatives of the family Heterozerconidae are associated with millipedes (Diplopoda) living in warm regions around the world. However, adults of three species have been found on snakes (Ophidia: Boidae and Colubridae) and lizards (Amphisbaenidae) in the Neotropical region (Lizaso 1979; Flechtmann and Johnston 1990).

ACARIFORMES

Trombiculoidea

Most species of the worldwide distributed families Trombiculidae and Leeuwenhoekiidae (>3000 species) are known from the larval stages (chiggers). The larvae parasitize arthropods and vertebrates (including reptiles). Most chiggers are not host specific. However, many of them are found exclusively in particular habitats (e.g. nests, burrows etc.) (Callaghan et al. 1994). Aside from species that have been reported from the soft parts of reptile skin (e.g axilla, groins, "pocket-like structures" etc.) specimens of *Babiangia bulbifera* Southcott, 1954 were found completely hidden under the scales of the skink *Lygosoma sp*. (Southcott 1954). It appears that this unique species begins the process of host adaptation by hiding completely under a scale of its lizard host, and by having a flattened body.

2.1.2 Temporary endoparasites

Up to now only a few mite species of the family Trombiculidae are known as temporary endoparasites of reptiles. It is worth mentioning that one species of the family Laelapidae (Parasitiformes), *Mabuyonyssus freedmani* Till, 1957, was taken from the African lizard *Trachylepis margaritifera* (Peters, 1854) by Till (1954) and it could be a parasite inhabiting the nasal cavities of these hosts (Fain 1961b).

Among trombiculids, representatives of two genera, *Vatacarus* (2 species) and *Iguanacarus* (4 species) are reptile endoparasites. Mites from both genera occur in the lungs and nasal passages of amphibious marine sea snakes (*Laticauda* sp.) and marine iguanas (*Amblyrhynchus* sp.) in coastal areas of the Pacific Ocean (Nadchatram 1980, 2006).

These mites are presumably host-specific parasites, which is atypical for the family Trombiculidae. Larvae of the genus *Vatacarus* increase 1. 500 times or more during feeding and assume a maggot-like shape with highly developed digitform papillae (neosomules) covering almost the entire idiosoma (neosome). These papillae enable the larvae to move in the tracheal mucosa of the host (Nadchatram 2006). The adult mites emerge directly from the larvae (tachygenesis), which is unique in the family Trombiculidae.

Additionally, their life cycle is closely correlated with the life cycle of their hosts; when sea snakes *Laticauda sp*. go ashore during the mating season the mites leave the host to continue with the free-living phase of their life cycle. Mites from the second parasitic genus, *Iguanacarus*, are not vermiform after feeding, do not have neosomules on idiosoma and are known only from larval forms (Nadchatram 1980).

2.2 Permanent parasites

This type of parasitism occurs in three mite orders and seven families of mites — Parasitiformes (including Entonyssidae, Ixodorhynchidae and Omentolalepidae), Acariformes (Cloacaridae and Harpirhynchidae), and Pterygosomatidae. In addition, in the family Argasidae (normally represented by temporary parasites) the species *Argas (Microargas) transversus (*Banks, 1902) spends its entire life on the giant tortoise *Chelonoidis nigra* (Quoy and Gaimard 1824) on the Galapagos Islands and even lays eggs directly onto this host (Hoogstraal and Kohls 1966; Hoogstraal et al. 1973).

2.2.1. Permanent ectoparasites

PARASITIFORMES

Ixodorhynchidae

This family includes 31 species of 6 genera associated exclusively with snakes of the families Colubridae, Elapidae, Lamprophiidae, and Viperidae. They are often found attached beneath the snake's scales, on the head and around the snake's eyes. The mites are distributed worldwide, excluding Australia (Fain 1962).

Omentolaelapidae

The family Omentolaelapidae contains only one species — *Omentolaelaps mehelyae* (Fain

1961) which infests snakes of the genus *Mehelya* (Lamprophiidae) from Central Africa (Fain 1961). The mites can hide beneath the host's scales entirely (idiosoma is greater in breadth than in length). Moreover, mites of this highly-specialized species have developed an organ on the ventral surface of the hysterosoma which acts as a sucker and helps it stay on the body surface of the host.

ACARIFORMES

Harpirhynchidae

Mites of the family Harpirhynchidae are permanent and highly specialized ectoparasites of birds and snakes. One of the subfamilies (Ophioptinae) is associated only with snakes belonging to three families: Colubridae, Elapidae, and Lamprophiidae (Ophidia: Colubroidea). At present this subfamily includes 16 species belonging to two genera: *Ophioptes* (14 species) and *Afrophioptes* (2 species) (Fain 1964; Lizaso 1981). All development of these mites proceeds within the scales. The life cycle consists of egg, larva and nymph (both stage are legless), and adults (which possess four pairs of fully developed legs and can move freely over the host's skin). The development of immatures occurs in the soft tissue at the base of the scales.

Most of them are recorded from tropical or subtropical regions, with only one mite species recorded on the European colubrid snake (Beron 1974). The ancestor of Ohioptinae probably migrated from passerine birds onto the colubroid snakes (Bochkov et al. 1999).

Pterygosomatidae

Most representatives of this family are known as external parasites of Reptilia (only the genus *Pimeliaphilus* contains species that are parasites of arthropods). The family includes 156 species and subspecies divided into eight genera (*Pterygosoma*; *Geckobia*; *Geckobiella; Zanurobia*; *Hirstiella*, *Ixodiderma, Scaphothrix,* and *Tequisistlana*). Mites from all these genera are permanent, highly specified ectoparasites of lizards (Sauria) (Bertrand et al. 2000; Bochkov and OConnor 2006). So far, only one species *Geckobia enigmatica* (Bertrand et Pedrono 1999) was described from the tortoise *Astrochelys yniphora* (Vaillant, 1885) (Testudines).

They spend their entire life on the host and the majority of the species are parthogenetic. Most of them can be found under the lizard's scales, particularly those belonging to the families Gekkonidae, Agamidae, Cordylidae, and Gerrhosauridae. Most representatives of this family are widely distributed throughout the world.

Bochkov and OConnor (2006) claimed in their paper that parasitism of the family on lizards probably developed as a result of switching from arthropod to reptile hosts.

2.2.2. Permanent endoparasites

The Entonyssidae (Parasitiformes) and Cloacaridae (Acariformes) are permanent endoparasites of Reptilia. However, the cloacal region is also used as a niche by some mites of the family Pterygosomatidae (Prostigmata). Two species of the family (*Pterygosoma tuberculata* Jack, 1962 and *P. gracilipalpis* Jack, 1962) were recorded from the cloaca of agamas despite the fact that most species in this family are ectoparasites (Jack 1962).

PARASITIFORMES

Entonyssidae

This family includes 24 species belonging to eight genera. All species have been found in the lungs of snakes belonging to the families Colubridae, Lamprophiidae, Elapidae, Homalopsidae, and Viperidae (Ophidia: Colubroidea). The life cycle consists of egg, larva, protonymph, deutonymph, and adults (Fain 1961b). They were recorded on most continents excluding Australia.

ACARIFORMES

Cloacaridae

In the family Cloacaridae, only mites of the subfamily Cloacarinae (14 species) are highly host-specific endoparasites of reptiles. They have been discovered exclusively in the cloaca and muscles of turtles living in North America, Asia, Australia and Africa (Fain 1968; Pence and Casto 1975; Pence and Wright 1998; Bochkov and OConnor 2008).

These mites have been found on turtles belonging to the suborders Cryptodira and Pleurodira. Cloacarines are probably transmitted venereally between turtles, however, Casto et. al. (1975) suggested that arrhenotoky also might be a method of reproduction among these mites. The deep morphological specialization among of cloacarin and their wide distribution among host taxa indicate that the relationship between cloacarines and turtles has ancient origin. Most authors suggest that the common ancestor of cloacarines appeared before the divergence of the Pleurodira and Cryptodira in the Upper Jurassic or Cretaceous (Pence and Casto 1975; Bochkov and OConnor 2008).

III. Host specificity

From the 15 families of reptilian mites, six families are restricted to particular host orders.

This strict host specificity is mostly observable in permanent parasites of reptiles (Omentolaelapidae, Ixodorhynchidae, Entonyssidae, Pterygosomatidae, Harpirhynchidae, and Cloacaridae). Thus, in Table 3 I gathered information about host-specifity at different levels to determine (1) if the current data shows if the degree of host specificity at family, generic and species levels in members of the Parasitiformes and Acariformes is the same and (2) if host-specificity among permanent endoparasites and ectoparasites of reptiles varies.

(1) As seen in Table 3, all permanent mite species show a tendency to infest hosts belonging to the same family or the same genus (closely related hosts). For the analyzed Parasitiformes and Acariformes species (N=56, N=184 respectively) the number of mite species specific to one host species was 31 for Parasitiformes and 138 for Acariformes. Using available data on described species and recorded hosts, it appears that Acariformes are more specific than Parasitiformes. However, these results show that this is true only at the family level of host-specificity ($\chi2 = 9.78$, df (1) $p = 0.0018$; CI calculated using the binominal distribution, $p = 0.0035$). At the species level specificity is not significantly different ($\chi2 = 1.47$, df (1) $p = 0.02246$; CI calculated using the binominal distribution, $p = 0.2695$). A similar conclusion can be reached when we compare specificity at the generic level ($\chi2 = 0.01$, df(1) $p = 0.9080$, CI calculated using the binominal distribution, $p = 1.000$).

The maximum number of host species and subspecies recorded per mite species was: 20 for the *Geckobiella texana* (Pterygosomatidae) and nine for *Ixobioides butantanensis* (Ixodorhynchidae) and *Pterygosoma draconensis* (Pterygosomatidae) (see Table 2). Considering the proportions of species with the highest host specificity (i.e. monoxenous), Ixodorhynchidae seems to be the least host-specific, and Cloacaridae the most.

(2) These results show that host-specificity between permanent endoparasites and ectoparasites is not significantly different at the family level ($\chi2 = 9.78$, df (1) $p = 0.0018$; CI calculated using the binominal distribution, $p = 0.0035$), generic ($\chi2 = 9.78$, df (1) $p = 0.0018$; CI calculated using the binominal distribution, $p = 0.0035$) and species level ($\chi2 = 9.78$, df (1) $p = 0.0018$; CI calculated using the binominal distribution, $p = 0.0035$).

It is worth mentioning that the majority of the mite-reptile relationships analyzed here (see Table 2) are based on single records in the literature, most frequently from the description of new species. We should be aware that upcoming research may show that in many cases host-specificity has been overestimated by researches.

IV. Habitat preference

Reptile mites are capable of occupying a wide range of parasitic niches and most species are strongly specific with respect to their location in or on a reptilian host. As we see in Table 1 most ectoparasites from both megaorders the Parasitiformes (Omentolaelapidae, Ixodorhynchidae, Paramegistidae, Heterozerconidae) and Acariformes (Pterygosomatidae, Harpirhynchidae) occur under the host's scales.

Mites from the families Omentolalepidae, Argasidae (*Argas transversus*), Pterygosomatidae, and Trombiculidae (*Babiangia bulbifera*) live completely hidden under the host's scales. Their idiosoma is flattened dorso-ventrally and is greater in breadth than in length (convergent evolution) (Fain 1969). In turn, mites of the subfamily Ophioptinae (Harpirhynchidae) which occur in the same habitat have rounded bodies with a reduced number of setae on idiosoma, large coxae and strong legs that help them live in the pits which they cause at the distal end of host's scales.

Unlike mites from the above mentioned families, the Paramegistidae, Ixodorhynchidae and Heterozerconidae cannot hide beneath the scales entirely. Mites of the genus *Ophiomegistus* (Paramegistidae) live partially lodged under the scales of their hosts (Klompen and Austin 2007). Ixodorhynchidae and Heterozerconidae prefer the lateral or ventral scales of snakes and can also be found near the head (Fain 1962, Finnegan 1931).

A typical niche for ectoparasites that cannot hide under the scales are sites not reached by itching activities of the reptiles. Sites of attachment for ticks and ophionyssids (Macronyssidae) on lizards are the head, including the nasal passages and ear canals, the legs including the axillae, the elbow joints, between toes and in the cloacal region. On snakes they are commonly found around the eyes, under the scales and shields, on the underside of a host's head or in loreal pits (Ophidia: Crotalinae) (Bannert et al. 2000; Simonov and Zinchenko 2010).

Mites from the family Trombiculidae are most frequently found in the "pocket-like structures" (folds of skin on the host's body where mites tend to aggregate) and in the joint regions, especially armpits (Arnold 1986; Audy 1954). Leeuwenhoe-

kiidae are most frequently collected from the external ear canals and axillary regions of the legs (Audy 1954).

Moreover, despite living beneath the scales, Pterygosomatidae may also occur in "pocket-like structures" (Bertrand and Modry 2004) and in completely unprotected sites on the host's body. For example, a few species from the genus *Pterygosoma* attach to the wing-like membranes of agamid lizards from the South-Asian genus *Draco* while other mites (genus *Geckobiella*, *Hirstella, Cyclurobia*) most frequently use sites like the axilla, groin, neck or host's tail (Jack 1962, Bertrand 2000).

Endoparasitic mite species live in the respiratory tracks of their reptilian hosts (Parasitiformes: Entonyssidae; Acariformes: Trombiculidae), the nasal passages (Parasitiformes: Laelapidae) or in the cloaca and muscles of reptiles (Acariformes: Cloacaridae) (Fain 1961b; 1968).

V. Prevalence

Permanent parasites are characterized by the low prevalence index (IP) e.g. *IP* for examined snakes parasitized by Entonyssidae was 2% (N=2000) (Fain 1961) while the overall percentage of snakes (N=2180) parasitized by Ixodorhynchidae was 3.3 % (Fain 1962). However, these studies were conducted on museum material (the snakes were preserved in alcohol) and these records might be too low.

It seems that IP for temporary parasites on reptiles is higher than for permanent ones. Unfortunately we do not have enough data for solid conclusions. For example, the highest and most varied *IP* is noted for temporary parasites of reptiles. For example, *IP* for *Tropidurus hispidus* (Spix, 1925) parasitized by *Eutrombicula alfreddugesi* (Trombiculidae) was 100% (Delfino et al. 2011). It is worth mentioning that these surveys were conducted by examining hosts taken directly from the field.

VI. Impact of mites on reptiles fitness

Acari may cause various diseases and debilitation in reptiles. However, despite a growing body of research, the direct impact of mites on the health condition of reptiles is still unclear (Reardon and Norbury 2004). Even for ticks and chiggers, which have been the subjects of many thorough studies, evidence of damage to host fitness is often ambiguous. For example, several papers have shown that high ectoparasitic loads have a metabolic cost (lizards with high-mite infestation had the smallest gain in body mass (Klukowski and Nelson 2001), physical endurance, reduced activity, focal inflammation of the skin and swelling observed around the site of attachment (Reardon and Norbury 2004). But, on the other hand, Goldberg and Bursey (1991) showed no histological evidence that a load of chiggers causes significant damage to the hosts — if it was present, it must have been minimal. Other long-term studies made by Bull and Burzacott (1993) on the lizards *Taliqua rugosa* Gray, 1825 have shown that lizards with the largest numbers of ticks reach the largest body size and are more likely to be in mating pairs than those with low tick loads. Moreover, according to the Red Queen hypothesis of Leigh van Valen, parthenogenetic individuals should be more vulnerable to parasitism than their sexual relatives. Surveys made by Moritz et al. (2001) on the clonal lineages of gecko, *Heteronotia binoei* Gray, 1945 and its sexual relatives provides strong support for this idea, but later study of the gecko *Lepidodactylus* Fitzinger, 1843 showed that the sexual individuals have a higher load of hematophagous mites than asexual gecko living in the same habitat (Hanley et al. 2005).

The negative effect of mites on host fitness is very marked in captive collections of reptiles. e.g. *Ophionyssus natricis* cause anemia and debility when living on snakes. The skin around chronically attached mites often becomes reddened and swollen. Moreover, the mites also attract the attention of the affected animals. The snakes appear to be extremely irritated and can be seen rubbing affected areas frequently and/or spending long periods of time soaking in water (Wozniac et al. 2000).

VII. The transmission of blood-parasites

In addition to the direct parasitic influence described above, reptile mites may be involved in the transmission of blood parasites. Acari species belonging to five families (Macronyssidae, Ixodidae, Amblyommidae, Argasidae, Pterygosomatidae) have been recorded as vectors of many pathogens.

Mites from the genus *Hirstiella* (Pterygosomatidae) may serve as a vector of the hemogregarinae *Hepatozoon sauromali* Lewis et Wagner, 1964 (Apicomplexa: Hepatozoidae), or even as a potential vector of *Plasmodium* sp. (Newell and Ryckman 1964) (Apicomplexa: Plasmodiidae). *Geckobiella texana* Banks, 1904 (Pterygosomatidae) is a vector of the protozoarian *Schellackia oc-*

cidentalis Bonorris et Ball, 1955 (Apicomplexa: Lankesterellidae) (Bonorris and Ball 1955), while mites from the genus *Ophionyssus* (Macronyssidae) are known as vectors for the bacteria *Proteus hydrophilus* (Chester, 1901) (Gammaproteobacteria: Aeromonadaceae) (Camin 1948) or haemogregarine protozoon *Karyolysus sp*.(Apicomplexa: Haemogregarinidae) which parasitize the lacertid lizards (Bannert et. al. 2000).

Furthermore, some research has shown that lizards may also be reservoirs of *Borrelia burgdorferi* Johnson et al., 1984 (with ticks serving as vectors) and play a role in the maintenance of this pathogen (Ekner at. al. 2011). Consequently, reptile-feeding ticks which are also known to be vectors for and reservoirs of many other pathogens have recently been investigated by many authors (Burridge 2001; Burridge and Simons 2003; Nowak 2010). The focus of this work has been on ticks spreading outside of their natural range (especially via the international trade in pet reptiles). Some populations of ticks can adapt to new climates and cause the spread of human and animal tick-borne diseases (possibly an important zoogeographical and epidemiological problem).

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Table 1.
Parasitic mites (Acari) of reptiles

Mite family (Subfamily)	No. of species	No. of genera	Order, suborder and the family of the hosts	Locality on/in the hosts	Type of parasitism	Distribution
PARASITIFORMES: MESOSTIGMATA						
Paramegistidae Tragardh, 1946	21	1	Squamata: Sauria: Scincomorpha (Scincidae); Ophidia: Phytonoidea (Pythonoidae); Colubroidea (Colubridae, Elapidae)	EC (partially lodged under the scales)	T	Australia, Asia
Heterozerconidae Berlese, 1892	3	2	Squamata: Sauria: Amphisbaenia (Amphisbaenidae); Ophidia: Booidea (Boidae); Colubroidea (Colubridae)	EC (on the head)	T	South America
Macronyssidae Oudemans, 1936	16	1	Squamata: Sauria: Iguania (Agamidae); Gekkota (Diplodactylidae); Scincomorpha (Cordylidae, Lacertidae, Scincidae)	EC (around the eyes, in the ears, in the skin folds, on the legs)	T	Europe, Africa, Asia, Australia (cosmopolitan Ophionyssus natricis Gervalis, 1844 recorded on captive reptiles).
Entonyssidae Ewing, 1922	24	8	Squamata: Ophidia: Colubroidea (Colubridae, Elapidae, Viperidae)	EN (lungs)	P	Europe, Africa, Asia, North and South America
Laelapidae Berlese, 1892	1	1	Squamata: Sauria: Scincomorpha (Scincidae)	EN (nasal passages)	T	Africa
Ixodorhynchidae Ewing, 1923	31	6	Squamata: Ophidia: Colubroidea (Colubridae, Elapidae, Viperidae)	EC (under the scales on or near the head region)	P	Europe, Africa, Asia, North and South America
Omentolaelapidae Fain, 1961	1	1	Squamata: Ophidia: Colubroidea (Lamprophiidae)	EC (under the scales)	P	Africa
PARASITIFORMES: METASTIGMATA						
Ixodoidea (Ixodidae Koch, 1844 and Argasidae Koch, 1844)	>100	8	Testudines: Cryptodia; Rhynhocephalia: Sphenodontia; Squamata: Sauria, Ophidia; Crocodylia: Eusuchia	EC (around the head, skin folds, around the cloaca)	T	Europe, Africa, Asia, Australia, North and South America
ACARIFORMES: PROSTIGMATA						
Pterygosomatidae Oudemans, 1910	156	8	Squamata: Sauria: Iguania (Agamidae, Iguanidae, Liolaemidae, Liolaemidae Phrynosomatidae); Gekkota (Gekkonidae, Carphodactylidae, Diplodactylidae, Eublepharidae, Phyllodactylidae); Scincomorpha (Gerrhosauridae, Cordylidae, Lacertidae); Testudines: Cryptodira: Testudinoidea (Testudinidae)	EC (mainly under the scales); EN (2 species only) (cloaca)	P	Europe, Africa, Asia, Australia, North and South America

EC — ectoparasites; EN — endoparasites; P — permanent parasites, T — temporary parasites

Table 1. Continued

Trombiculoidea (Trombiculidae Ewing, 1929 and Leeuwenhoekiidae Womersley, 1944)	>40	18	Squamata: Iguania (Agamidae); Scincomorpha (Scincidae); Gekkota (Gekkonidae, Phyllodactylidae); Varanoidea (Varanidae); Rhynhocephalia: Rhynchocephalia (Sphenodontidae); Ophidia: Colubroidea (Colubridae)	EC (mite-pockets", armpits, around the head); EN (6 species) (respiratory tracks)	T	Europe, Africa, Asia, Australia, North and South America
Harpirhynchidae Dubinin, 1957 (Ophioptinae)	16	2	Squamata: Ophidia: Colubroidea (Colubridae, Lamprophiidae, Elapidae)	EC (within the scales)	P	Europe, Asia, Africa, Australia, North and South America
Cloacaridae Camin, Moss, Oliver et Singer, 1967 (Cloacarinae)	14	6	Testudines: Cryptodira (Chelydridae, Emydidae, Geoemydidae, Trionychidae, Testudinidae, Cheloniidae); Pleurodira (Chelidae, Pelomedusidae)	EN (cloaca)	P	North and South America, Asia, Africa, Australia

Table 2.
Permanent parasites (Acari) of reptiles (Reptilia)

Mite genus (in bold), mite species	Host species	Host family	Host order	Region
ENTONYSSIDAE				
Entonyssus Ewing, 1923				
halli Ewing, 1923	*Pituophis* sp.	Colubridae	Ophidia	North America
	Pituophis melanoleucus Daudin, 1803			
colubri (Hubbard, 1938)	*Coluber flagellum* Shaw, 1802			
	Coluber constrictor constrictor Linneaus, 1758			
	Coluber constrictor flaviventris Say, 1823			
	Coluber constrictor foxii (Baird et Girard, 1853)			
asiaticus Fain, 1960	*Rhabdophis chrysargos* (Schlegel, 1837)			Asia
javanicus Fain, 1961	*Xenochrophis vittatus* (Linnaeus, 1758)			
squamatus Fain, 1983	*Elaphe schrenckii* Strauch, 1873			
philippinensis Fain, 1961	*Fordonia leucobalia* (Schlegel, 1837)	Homolopsidae		
rileyi Ewing, 1923	*Crotalus* sp.	Viperidae		North America
	Crotalus atrox Baird et Girard, 1853			
Entophionyssus Fain, 1960				
hamertoni Radford, 1939	*Thamnophis sirtalis parietalis* (Say, 1823)	Colubridae	Ophidia	North America
	Thamnophis sirtalis sirtalis (Linnaeus, 1758)			
glasmacheri (Vitzthum, 1935)	*Pantherophis alleghaniensis* (Holbrook, 1836)			
	Pantherophis obsoletus (Say, 1823)			
	Pantherophis emoryi (Baird et Girard, 1853)			
	Pituophis catenifer sayi (Schlegel, 1837)			
	Lampropeltis getula (Linnaeus, 1766)			
natricis Keegan, 1943	*Nerodia fasciata* (Linnaeus, 1766)			
	Nerodia sipedon sipedon (Linnaeus, 1758)			
fragilis Keegan, 1946	*Lampropeltis getula* (Linnaeus, 1766)			
heterodontos Keegan, 1943	*Heterodon platirhinos* Latreille, 1801 *Lampropeltis calligaster* (Harlan, 1827)			

Hamertonia Turk, 1947				
bedfordi (Radford, 1937)	*Dendroaspis angusticeps* (Smith, 1849)	Elapidae	Ophidia	Africa
psammophis Till, 1957	*Psammophis trinasalis* Werner, 1902	Lamprophiidae		
	Psammophis sibilans (Linnaeus, 1758)			
	Rhamphiophis oxyrhynchus (Reinhardt, 1843)			
	Psammophis lineatus (Bibron et Duméril, 1854)			
	Meizodon coronatus (Schlegel, 1837)	Colubridae		
radfordi Fain, 1960	*Hapsidophrys smaragdina* (Schlegel, 1837)			
Entophiophaga Fain, 1960				
congolensis Fain, 1960	*Dasypeltis scabra* (Linnaeus, 1758)	Colubridae	Ophidia	Africa
	Crotaphopeltis hotamboeia (Laurenti, 1768)			
scaphiophis Fain, 1960	*Scaphiophis albopunctatus* Peters, 1870			
natriciterei Fain, 1960	*Natriciteres olivacea* (Peters, 1854)			
colubricola Fain, 1960	*Dolichophis cassius* (Gmelin, 1789)			Europe
Viperacarus Fain, 1960				
europaeus Fain, 1960	*Vipera berus* (Linnaeus, 1758)	Viperidae	Ophidia	Europe
Cobranyssus Fain, 1960				
schoutedeni (Radford, 1953)	*Naja naja* (Linnaeus, 1758)	Elapidae	Ophidia	Asia
Pneumophionyssus Fonseca, 1940				
aristoterisi Fonseca, 1940	*Erythrolamprus aesculapii* (Linnaeus, 1758)	Colubridae	Ophidia	South America
jellisoni Fain et Junker 1972	?snake	?		
Entophioptes Fain, 1960				
liophis Fain 1960	*Lygophis anomalus* (Günther, 1858)	Colubridae	Ophidia	South America
IXODORHYNCHIDAE				
Hemilaelaps Ewing, 1923				
triangulus Ewing, 1923	*Pantherophis obsoletus* (Say, 1823)	Colubridae	Ophidia	North America
	Lampropeltis calligaster (Harlan, 1827)			
	Lampropeltis triangulum (Lacépède, 1789)			
	Coluber schotti (Baird et Girard, 1853)			
	Drymarchon couperi (Holbrook, 1842)			
piger (Berlese, 1918)	*Hierophis gemonensis* (Laurenti, 1768)			Europe
	Zamenis situla (Linnaeus, 1758)			
	Natrix natrix natrix (Linnaeus, 1758)			
feideri Fain, 1962	*Natrix natrix helvetica* (Lacépède 1789)			
radfordi (Feider et Salomon, 1959)	*Dolichophis caspius* (Gmelin, 1789)			
	Natrix natrix (Linnaeus, 1758)			
imphalensis (Radford, 1947)	*Coelognathus radiatus* (Boie, 1827)			Asia
tanneri (Tibbetts, 1954)	*Rhabdophis tigrinus* (Boie, 1826)			Oceania
javanensis Fain, 1961	*Lycodon subcinctus* Boie, 1827			
evansi Fain, 1961	*Coelognathus flavolineatus* (Schlegel, 1837)			
novae-guineae Fain, 1961	*Dendrelaphis calligastra* (Günther, 1867)			
dipsadoboae Fain, 1962	*Dipsadoboa unicolor* Günther, 1858			Africa

farreri (Tibbetts, 1954)	*Boaedon lineatus* Duméril, Bibron et Duméril, 1854	Lamprophiidae	Ophidia	Africa
	Bothrophthalmus lineatus (Peters, 1863)			
	Platyceps florulentus (Geoffroy, 1827)	Colubridae		
	Dasypeltis scabra sabra linneaus (Linnaeus, 1758)			
	Elaphe dione (Pallas, 1773)			
	Philothamnus carinatus (Andersson, 1901)			
	Scaphiophis albopunctatus Peters, 1870			
congolensis Fain, 1962	*Causus rhombeatus* (Lichtenstein, 1823)	Viperidae		
causicola Fain, 1961	*Causus rhombeatus* (Lichtenstein, 1823)			
ophidius (Lavoipierre, 1958)	*Causus lichtensteinii* (Jan, 1859)			
caheni Fain, 1961	*Bitis nasicornis* (Shaw, 1802)			
	Naja melanoleuca Hallowell, 1857	Elapidae		
schoutedeni (Fain, 1961)	*Boaedon fuliginosus* (Boie, 1827)	Lamprophiidae		
	Bothrophthalmus lineatus (Peters, 1863)			
upembae (Fain, 1961)	*Boaedon fuliginosus* (Boie, 1827)			
	Boaedon lineatus Duméril, Bibron et Duméril, 1854			
Strandtibbettsia Fain, 1961				
gordoni (Tibbetts, 1957)	*Natrix stolata* Stejneger, 1907	Colubridae	Ophidia	Asia
	Rhabdophis subminiatus (Schlegel, 1837)			
	Rhabdophis tigrinus (Boie, 1826)			
brasiliensis Fain, 1961	*Siphlophis cervinus* (Laurenti, 1768)			South America
Ixodorhynchus Ewing, 1923				
liponyssoides Ewing 1923	*Leptophis mexicanus* Duméril, Bibron et Duméril, 1854	Colubridae	Ophidia	North America
	Storeria dekayi (Holbrook, 1839)			
	Thamnophis ordinoides (Baird et Girard, 1852)			
	Thamnophis sauritus sauritus (Linnaeus, 1766)			
	Thamnophis sirtalis parietalis (Say, 1823)			
	Thamnophis sirtalis sirtalis (Linnaeus, 1758)			
johnstoni Fain, 1961	*Heterodon platirhinos* Latreille, 1801			
leptodeirae Fain, 1962	*Leptodeira maculata* (Hallowell, 1861)			
cubanensis Fain, 1962	*Caraiba andreae* (Reinhardt et Lütken, 1862)			
Ixobioides Fonseca, 1934				
butantanensis Fonseca, 1934	*Philodryas chamissonis* (Wiegmann, 1835)	Colubridae	Ophidia	South America
	Mastigodryas bifossatus (Raddi, 1820)			
	Xenodon merremi (Wagler, 1824)			
	Tomodon dorsatus Duméril, Bibron et Duméril, 1854			
	Lygophis anomalus (Günther, 1858)			
	Liophis poecilogyrus (Wied-Neuwied, 1825)			
	Erythrolamprus aesculapii (Linnaeus, 1758)			
	Erythrolamprus venustissimus (Wagler)			
	Carollia sp.			
fonsecae Fain, 1961	*Xenodon guentheri* Boulenger, 1894			
brachispinosus Lizaso, 1983	*Xenodon neuwiedii* Gunther, 1863			
	Chironius bicarinatus (Wied, 1820)			

brachispinosus Lizaso, 1983	*Thamnodynastes strigatus* (Günther, 1858)	Colubridae	Ophidia	South America
truncatus (Johnson, 1962)	*Pantherophis vulpinus* (Baird et Girard, 1853)	Colubridae	Ophidia	North America
	Pantherophis obsoletus (Say, 1823)			
	Thamnophis sirtalis (Linnaeus, 1758)			
Chironobius Lizaso 1983				
alvus Lizaso, 1983	*Chironius bicarinatus* (Wied, 1820)	Colubridae	Ophidia	South America
nordestinus Lizaso, 1983	*Chironius carinatus* (Linnaeus, 1758)			
Ophiogongylus Lizaso 1983				
rotundus Lizaso, 1983	*Xenodon neuwiedii* Günther, 1863	Colubridae	Ophidia	South America
	Erythrolamprus aesculapii (Linnaeus, 1758)			
	Leptodeira annulata (Linnaeus, 1758)			
breviscutum Lizaso, 1983	*Liophis poecilogyrus* (Wied-Neuwied, 1825)			
OMENTOLAELAPIDAE				
Omentolaelaps Fain, 1961				
mehelyae Fain, 1961	*Gonionotophis capensis* (Smith, 1847)	Lamprophiidae	Ophidia	Africa
	Gonionotophis savorgnani (Mocquard, 1887)			
PTERYGOSOMATIDAE				
Pterygosoma Peters, 1849				
annectans Jack, 1962	*Acanthocercus annectens* (Blanford, 1870)	Agamidae	Sauria	Africa
	Agama lionotus Boulenger, 1896			
annectans circularis Jack, 1962	*Agama lionotus* Boulenger, 1896			
transvaalense Lawrence, 1935	*Acanthocercus atricollis* (Smith, 1849)			
	Acanthocercus cyanogaster (Rüppell, 1835)			
agamae Peters, 1849	*Agama armata* Peters, 1855			
	Agama agama Linnaeus, 1758			
agamae aculeatum Lawrence, 1936	*Agama aculeata distanti* (Boulenger 1902)			
	Agama aculeata aculeata Merrem, 1820			
	Agama armata Peters, 1855			
	Agama kikii Boulenger, 1885			
agamae agamae Peters, 1849	*Agama mossambica* Peters, 1854			
	Agama armata Peters, 1855			
	Agama kirkii Boulenger, 1885			
	Agama agama Linnaeus, 1758			
	Agama montana Barbour et Loveridge, 1928			
armatum Lawrence, 1936	*Agama armata* Peters, 1855			
aculetum Lawrence, 1935	*Agama hispida aculeate* Loveridge, 1936			
bedfordi Lawrence, 1936	*Agama atra* Daudin, 1802			
benguellae Jack, 1961	*Agama aculeate* Merrem, 1820			
	Agama anchietae Bocage, 1896			
bibronii Jack, 1962	*Agama impalearis* Boettger, 1874			
	Laudakia stellio (Linnaeus, 1758)			
bibronii pseudorbicularis Jack, 1962	*Agama impalearis* Boettger, 1874			

crewei Lavoipierre, 1955	*Agama agama* Linnaeus, 1758	Agamidae	Sauria	Africa
	Agama atra Daudin, 1802			
fimbriata Lawrence, 1951	*Agama planiceps* Peters, 1862			
fimbriata problematica Jack, 1962	*Agama planiceps* Peters, 1862			
phillipsi Jack, 1961	*Acanthocercus phillipsii* (Boulenger, 1895)			
hirsti Lawrence, 1936	*Agama aculeata* Merrem, 1820			
longipalpe Lawrence, 1936	*Agama hispida aculeate* Loveridge, 1936			
	Agama atra Daudin, 1802			
melanum Hirst, 1917	*Agama atra* Daudin, 1802			
melanum capensis Jack, 1962	*Agama atra* Daudin, 1802			
melanum longipalpe Lawrence, 1936	*Agama atra* Daudin, 1802			
melanum angolae Jack, 1962	*Agama planiceps* Peters, 1862			
	Agama aculeata Merrem, 1820			
	Agama anchietae Bocage, 1896			
neumanni (Berlese, 1910)	*Calotes versicolor* (Daudin, 1802)			
	Calotes liocephalus Günther, 1872			
	Calotes liolepis Boulenger, 1885			
	Calotes mystaceus Duméril et Bibron, 1837			
serrata Jack, 1961	*Agama rueppelli* Vaillant, 1882			
	Agama rueppelli occidentalis Parker 1932			
singularis Jack, 1961	*Agama agama* Linnaeus, 1758			
spinosa Jack, 1961	*Agama spinosa* Gray, 1831			
spinosa orbicularis Jack, 1962	*Agama agama* Linnaeus, 1758			
tenuisetis Jack, 1962	*Agama agama* Linnaeus, 1758			
	Agama aculeata Merrem, 1820			
triangulare Lawrence, 1936	*Agama hispida* (Kaup, 1827)			
	Agama hispida hispida (Kaup 1827)			
livingstonei Bertrand et Modry 2004	*Agama caudospinosa* Meek, 1910			
neumanni (Berlese, 1910)	*Agama agama* Linnaeus, 1758			Africa, Asia
	Agama doriae Boulenger, 1885			
inermis (Tragardh, 1905)	*Laudakia stellio* (Linnaeus, 1758)			
	Laudakia stoliczkana (Blanford, 1875)			
tuberculata Jack, 1962	*Laudakia tuberculata* (Gray, 1827)			Asia
	Laudakia himalayana (Steindachner, 1867)			
gladiator Bertrand, Paperna et Finkelman 1999	*Calotes versicolor* (Daudin, 1802)			
pseudotrapelus Bochkov, Mielnikov et Nazarov, 2009	*Pseudotrapelus sinaitus* (Heyden, 1827)			
dracoensis Jack, 1962	*Draco beccarii* Peters et Doriae, 1878,			
	Draco blandfordii Blandford, 1878			
	Draco cornatus Günther, 1864			
	Draco lineatus Daunin, 1802			
	Draco maculatus Gray, 1845			

dracoensis Jack, 1962	*Draco ornatus* Gray, 1845	Agamidae	Sauria	Asia
	Draco reticulates Günther, 1864			
	Draco spilopterus Wiegmann, 1834			
	Draco timorensis Kuhl, 1820			
caucasica Jack, 1961	*Laudakia caucasia* (Eichwald, 1831)			
dayana Jack, 1962	*Laudakia dayana* (Stoliczka, 1871)			
expansum Bertrand, Paperna et Finkelman 1999	*Laudakia stellio* (Linnaeus, 1758)			
gracilipalpis Jack, 1962	*Laudakia tuberculata* (Gray, 1827)			
adramitana Jack, 1961	*Acanthocercus adramitanus* (Anderson, 1896)			
persicum Hirst, 1917	*Laudakia nupta* (De Filippi, 1843)			
sinaita Jack, 1961	*Trapelus mutabilis* (Merrem, 1820)			
mutabilis Jack, 1961	*Trapelus mutabilis* (Merrem, 1820)			
rhipidostichata Bertrand, Paperna et Finkelman, 1999	*Trapelus mutabilis* (Merrem, 1820)			
foliosetis Jack, 1961	*Psammophilus dorsalis* (Gray, 1831)			
patagonica de la Cruz, Morando et Avila, 2004	*Liolaemus* sp.	Liolaemidae		?
bicolor Lawrence, 1935	*Gerrhosaurus flavigularis* Wiegmann, 1828	Gerrhosauridae		Africa
	Gerrhosaurus nigrolineatus Hallowell, 1857			
	Gerrhosaurus multilineatus Bocage, 1866			
gerrhosauri Lawrence, 1935	*Gerrhosaurus validus* Smith, 1849			
	Gerrhosaurus major Duméril, 1851			
hystrix Lawrence, 1935	*Gerrhosaurus flavigularis* Wiegmann, 1828			
Geckobia Megnin, 1878				
pachydactyli Lawrence, 1936	*Chondrodactylus bibronii* (Smith, 1846)	Gekkonidae	Sauria	Africa
damarensis Lawrence, 1951	*Pachydactylus montanus* Methuen et Hewitt, 1914			
hewitti Lawrence, 1936	*Pachydactylus maculatus* Gray, 1845			
fitzsimonsi Lawrence, 1951	*Afroedura karroica* (Hewitt, 1925)			
karroica karroika Lawrence, 1951	*Afroedura karroica* (Hewitt, 1925)			
karroica draconensis Lawrence, 1951	*Afroedura ni varia* (Boulenger, 1894)			
tasmani Lawrence, 1936	*Hemidactylus mabouia* (Moreau De Jonnès, 1818)			
homopholis Lawrence, 1936	*Homopholis walbergii* (Smith, 1849)			
phyllodactyli Lawrence, 1936	*Afrogecko porphyreus* (Daudin, 1802)			
socotrensis Hirst, 1917	*Pristurus rupestris* Blanford, 1874			
infanadianaensis Haitlinger, 1988	*Phelsuma* sp.			

mananjaryensis Haitlinger, 1988	*Phelsuma lineata* Gray, 1842	Gekkonidae	Sauria	Africa
ardoharonomailsoensis Haitlinger, 1988	*Phelsuma* sp.			
samambavyensis Haitlinger, 1988	*Hemidactylus frenatus* Schlegel, 1836			
australis Hirst, 1917	*Lygodactylus capensis* (Smith, 1849)			
oedurae Lawrence, 1936	*Afroedura transvaalica* (Hewitt, 1925)			
transvaalensis Lawrence, 1936	*Lygodactylus capensis* (Smith, 1849)			
	Pachydactylus capensis (Smith, 1846)			
	Chondrodactylus angulifer Peters, 1870			
natalensis Lawrence, 1936	*Lygodactylus capensis* (Smith, 1849)			
ovambica Lawrence, 1936	*Rhoptropus barnardi* Hewitt, 1926			
	Rhoptropus boultoni Schmidt, 1933			
rhoptropi Lawrence 1936	*Rhoptropella ocellata* (Boulenger, 1885)			
	Lygodactylus capensis (Smith, 1849)			
namaquensis Lawrence, 1936	*Pachydactylus namaquensis* (Sclater, 1898)			
	Pachydactylus acuminatus Fitzsimons, 1941			
capensis capensis Lawrence, 1951	*Pachydactylus capensis* (Smith, 1849)			
capensis hostata Lawrence, 1951	*Pachydactylus purcelli* Boulenger, 1910			
	Pachydactylus acuminatus Fitzsimons, 1941			
capensis lanceolata Lawrence 1951	*Pachydactylus punctatus* Peters, 1854			
hemidactyli Lawrence, 1936	*Hemidactylus mabouia* (Moreau De Jonnès, 1818)			Africa, Asia, Mediterranean, Central and South America, Caribbean
	Hemidactylus tasmani Hewitt, 1932			
	Hemidactylus frenatus Schlegel, 1836			
	Hemidactylus mercatorius Gray, 1842			
malayana Hirst, 1917	*Cyrtodactylus pulchellus* Gray, 1827			Asia
turkestana Hirst, 1926	*Mediodactylus russowii* (Strauch, 1887)			
hirsti Bochkov et Mironov, 2000	*Cyrtopodion caspium* (Eichwald, 1831)			
?*uenoi* Kawashima et Kamo, 1960	*Goniurosaurus kuroiwae splendens* Rösler, 1995			
philippinensis Lawrence, 1953	?*Haplodactylus* sp.			
	Hemidactylus frenatus Schlegel, 1836			
indica Hirst, 1917	*Hemidactylus brookii* Gray, 1845			
boulengeri Hirst, 1917	*Hemiphyllodactylus yunnanensis* (Boulenger, 1903)			
glebosum Bertrand, Paperna et Finkelman, 1999	*Hemidactylus platyurus* (Schneider, 1792)			
parvulum Bertrand, Paperna et Finkelman, 1999	*Mediodactylus kotschyi* (Steindachner, 1870)			
dubium Bertrand, Paperna et Finkelman, 1999	*Hemidactylus frenatus* Schlegel, 1836			
hindustanica Hirst,1926	*Hemidactylus leschenaultii* Duméril et Bibron, 1836			

orientalis Abdussalam, 1941	*Hemidactylus leschenaultii* Duméril et Bibron, 1836	Gekkonidae	Sauria	Asia
	Hemidactylus flaviviridis Rüppell, 1835			
morum Bertrand, Paperna et Finkelman, 1999	*Hemidactylus turcicus* (Linnaeus, 1758)			
nipponica Kawashima, 1962	*Gekko japonicus* (Schlegel, 1836)			
simplex Hirst, 1926	*Hemidactylus leschenaultii* Schlegel, 1836			
diversipelis Hirst, 1926	*Hemidactylus leschenaultii* Schlegel, 1836			
kasurensis Abdussalam, 1941	*Hemidactylus flaviviridis* Rüppell, 1835			
bataviensis Vitzhum, 1926	*Hemidactylus brookii* Gray, 1845			
	Hemidactylus frenatus Schlegel, 1836			New Guinea
gymnodactyli Womersley, 1941	*Heteronotia binoei* (Gray, 1845)			Australia
	Phyllodactylus marmoratus Loveridge, 1934			
cayennensis Floch et Fauran, 1955	*Platydactylus* sp.			Oceania
manaensis Floch et Abonnenc, 1945	*Platydactylus* sp.			
guyanensis Floch et Abonnenc, 1945	*Platydactylus* sp.			
carcinoides Bertrand et Ineich, 1989	*Gehyra oceanica* (Lesson, 1830)			
blanci Bertrand et Ineich, 1986	*Gehyra oceanica* (Lesson, 1830)			
voraci Bertrand et Ineich, 1986	*Gehyra vorax* Girard, 1858			
gibbsoni Bertrand et Ineich, 1987	*Lepidodactylus* sp.			
gehyrae Hirst, 1926	*Gehyra oceanica* (Lesson, 1830)			
grasipes Bertrand et Ineich, 1987	*Gehyra vorax* Girard, 1858			
papuana Hirst, 1917	*Cyrtodactylus louisiadensis* (De Vis, 1892)			
terentoale de la Cruz, 1973	*Tarentola american* (Gray, 1831)			North America (Cuba)
squameum Bertrand, Paperna et Finkelman, 1999	*Ptyodactylus guttatus* Heyden, 1827	Phyllodactylidae		Asia
leonilae Hoffman et Morales-Malacara, 1985	*Phyllodactylus lanei* Smith, 1935			America
tarentulae Tragardth, 1906	*Tarentola annularis* (Geoffroy De St-Hilaire, 1827)			Africa
loricata Berlese, 1812	*Tarentola mauritanica* (Linnaeus, 1758)			
latasti Megnin 1878	*Tarentola mauritanica* (Linnaeus, 1758)			Africa, Europe
canariensis Zapatero-Romos et. al. 1989	*Tarentola delalandii* (Duméril et Bibron, 1836)			Europe
tinerfensis Zapatero-Romos et. al. 1989	*Tarentola delalandii* (Duméril et Bibron, 1836)			Oceania
clelandi Hirst, 1917	*Phyllurus platurus* (Shaw, 1790)	Carphodactylidae		Australia
manzanelli Domrow, 1983	*Phyllurus cornutus* Günther 1897			

haplodactyli Womersley,1941	*Naultinus* sp.	Diplodactylidae	Sauria	New Zeland
naultina Womersley, 1941	*Naultinus* sp.			
anocellatus Bochkov et Mironov 2000	*Eublepharis angramainyu* Anderson et Leviton, 1966	Eublepharidae		Asia
enigmatica Bertrand et Pedrono 2000	*Astrochelys yniphora* (Vaillant, 1885)	Testudinae	Testudines	Africa
Hirstiella Berlese, 1920				
tenuipes (Hirst, 1917)	*Gonatodes albogularis* (Duméril et Bibron, 1836)	Sphaerodactylidae	Sauria	North America
pyriformis Newell et Ryckman, 1964	*Sauromalus darius* Dickerson, 1919	Iguanidae		
	Sauromalus ater Duméril, 1856			
	Sauromalus ater ater Duméril, 1856			
	Sauromalus hispidus Stejneger, 1891			
trombidiformes Berlese, 1920	*Sauromalus ater* Duméril, 1856			
bakeri Cunliffe, 1952	?iguana			
boneti Cunliffe, 1952	*Ctenosaura multispinis* Cope, 1886			
javieri (de la Cruz) 1984	*Cyclura nubila* (Gray, 1831)			
stamii Jack, 1961	*Iguana iguana* (Linnaeus, 1758)			? South America (collected from iguanas in the Amsterdam Zoo, Holland)
diolii Baker, 1998	*Brachylophus vitiensis* Gibbons, 1981			South America (Caribbean region)
	Brachylophus fasciatus (Brongniart, 1800)			
	Cyclura cornuta (Bonnaterre, 1789)			Australia (Toronga Zoo)
palaezi Cunliffe, 1949	*Sceloporus ferrariperezi* Cope, 1885	Phrynosomatidae		North America
jimenezi Parades-Leon et Morales-Maracara, 2009	*Phyllodactylus bordai* Taylor, 1942			
sharifi (Abdussalam, 1941)	*Hemidactylus flaviviridis* Rüppell, 1835	Gekkonidae		Asia
insignis (Berlese 1892)	*Tarentola mauritanica* (Linnaeus, 1758)			Europe, Africa
otophila Hunter et Loomis 1966	*Coleonyx variegatus* (Baird, 1858)	Eublepharidae		North America
Geckobiella Hirst, 1917				
texana (Banks), 1905	*Sceloporus undulatus* (Bosc et Daudin, 1801)	Phrynosomatidae	Sauria	North America
	Sceloporus undulatus undulatus (Bosc et Daudin 1801)			
	Sceloporus spinosus Wiegmann, 1828			
	Sceloporus torquatus Wiegmann, 1828			
	Sceloporus torquatus melanogaster Cope 1885			
	Sceloporus poinsettii Baird et Girard, 1852			
	Sceloporus clarkii Baird et Girard, 1852			
	Sceloporus horridus Wiegmann, 1834			
	Scloporus occidentalis bocourtii Boulenger 1885			
	Sceloporus occidentalis occidentalis Baird et Girard, 1852			

texana (Banks), 1905	*Sceloporus orcutti* Stejneger, 1893	Phrynosomatidae	Sauria	North America
	Sceloporus pyrocephalus Cope, 1864			
	Sceloporus cupreus Bocourt, 1873			
	Sceloporus siniferus Cope, 1870			
	Sceloporus acanthinus Bocourt, 1873			
	Sceloporus ornatus Baird, 1859			
	Sceloporus formosus Wiegmann, 1834			
	Sceloporus variabilis Wiegmann, 1834			
	Sceloporus utiformis Cope, 1864			
	Sceloporus jarrowi Cope, 1875			
harrisi Davidson, 1958	*Plica plica* (Linnaeus, 1758)	Tropiduridae		South America
Tequisistlana Hoffmann et Sanchez (1980)				
oaxacensis Hoffmann et Sanchez (1980)	*Lepidophyma flavimaculatum tehuanae* Smith, 1942	Xantusiidae	Sauria	North America
Zanurobia Lawrence, 1935				
circularis Lawrence, 1935	*Platysaurus guttatus* Smith, 1849	Cordylidae	Sauria	Africa
var. *latior* Lawrence, 1935	*Cordylus vittifer* (Reichenow, 1887)			
var. *spiniventer* Lawrence, 1935	*Platysaurus minor* Fitzsimons, 1930			
var. *capensis* Lawrence, 1935	*Platysaurus capensis* Smith, 1844			
var. *longipilis* Lawrence, 1935	*Platysaurus guttatus* Smith, 1849			
var. *transvaalensis* Lawrence, 1935	*Platysaurus intermedium* Matschie, 1891			
cordylensis Lawrence, 1935	*Cordylus cordylus* (Linnaeus, 1758)			
polyzonensis Lawrence, 1935	*Karusasaurus polyzonus* (Smith, 1838)			
	Namazonurus piersi (Hewitt, 1932)			
semilunaris Lawrence, 1935	*Pseudocordylus microlepidotus* (Cuvier, 1829)			
debilipes Lawrence, 1935	*Smaug warreni* (Boulenger, 1908)			
debilipes Lawrence, 1935 spp.	*Smaug warreni* (Boulenger, 1908)			
mossambica Lawrence, 1959	*Smaug warreni* (Boulenger, 1908)			
transvaalensis Lawrence, 1935	*Smaug vandami* (Fitzsimons, 1930)			
sanguinea Lawrence 1935	*Ninurta coeruleopunctatus* (Hewitt et Methuen, 1913)			
subquadrata Lawrence, 1935	*Hemicordylus capensis* (Smith, 1838)			
montana Lawrence, 1935	*Namazonurus namaquensis* (Methuen et Hewitt, 1914)			
Scaphorix Lawrence, 1935				
convexa Lawrence, 1935	*Karusasaurus polyzonus* (Smith, 1838)	Cordylidae	Sauria	Africa
	Namazonurus peersi (Hewitt, 1932)			
	Cordylus cordylus (Linnaeus, 1758)			
Ixoderma Lawrence, 1935				

inverta Lawrence, 1935	*Pseudocordylus subviridis* (Smith, 1838)	Cordylidae	Sauria	Africa
	Pseudocordylus microlepidotus (Cuvier, 1829)			
pilosa Lawrence, 1935	*Pseudocordylus subviridis* (Smith, 1838)			
	Gerrhosaurus major Duméril, 1851			
lacerate Lawrence, 1935	*Scapteira depressa* Merrem, 1820	Lacertidae		
	Pedioplanis inornata Roux, 1907			
	Pedioplanis undata (Smith, 1838)			
	Tropidosaura gularis Hewitt, 1927			
HARPIRHYNCHIDAE				
Ophioptes Sambon, 1928				
parkeri Sambon, 1928	*Erythrolamprus aesculapii* (Linnaeus, 1758)	Colubridae	Ophidia	South America
	Liophis poecilogyrus poecilogyrus (Wied-Neuwied, 1825)			
	Lygophis anomalus (Günther, 1858)			
	Clelia rustica (Cope, 1878)			
tropicalis Ewing, 1933	*Chironius carinatus* (Linnaeus, 1758)			
longipilis Lizaso, 1981	*Oxyrhopus trigeminus* Duméril, Bibron et Duméril, 1854			
	Liophis poecilogyrus (Wied-Neuwied, 1825)			
	Oxyrhopus petolarius (Linnaeus, 1758)			
brevipilis Lizaso, 1981	*Philodryas olfersii* (Lichtenstein, 1823)			
	Mastigodryas bifossatus (Raddi, 1820)			
	Lygophis meridionalis (Schenkel, 1902)			
	Liophis poecilogyrus (Wied-Neuwied, 1825)			
	Chironius flavolineatus (Boettger, 1885)			
coluber Radford, 1947	*Coelognathus radiatus* (Boie, 1827)			Asia
southcotti Fain, 1962	*Macropisthodon rhodomelas* (Boie, 1827)			
lycodontis Fain, 1964	*Lycodon subcinctus* Boie, 1827			
dromicus Allred, 1958	*Caraiba andreae orientalis* (Barbour et Ramsden, 1919)			North America
	Caraiba andreae (Reinhardt et Lütken, 1862)			
beshkovi Beron, 1974	*Platyceps najadum* (Eichwald, 1831)			Europe
samboni Southcott, 1956	*Simoselaps fasciolatus* (Günther, 1872)	Elapidae		Australia
congolensis Fain, 1962	*Philothamnus hoplogaster* (Günther, 1863)			Africa
najae Fain, 1962	*Naja melanoleuca* Hallowell, 1857			
boaedoni Fain, 1962	*Boaedon fuliginosus* (Boie, 1827)	Lamprophiidae		
schoutedeni Fain, 1962	*Boaedon lineatus* Duméril, Bibron et Duméril, 1854			
Afrophioptes Fain, 1962				
whartoni Fain, 1962	*Psammophis sibilans* (Linnaeus, 1758)	Lamprophiidae	Ophidia	Africa
rhodesiensis Fain, 1962	*Psammophylax tritaeniatus tritaeniatus* (Günther, 1868)			
CLOACARIDAE				
Cloacarus Camin et Singer, 1967				
faini Camin et Singer, 1967	*Chelydra serpentina* (Linnaeus, 1758)	Chelydridae	Testudines	North America
beeri Camin et Oliver, 1967	*Chrysemys picta* (Schneiderm 1783)	Emydidae		
Caminacarus Fain, 1968				

theodori Fain, 1968	*Clemmys caspica* (Wagler, 1830)	Geoemydidae	Testudines	Asia
costai Fain, 1968	*Clemmys caspica* (Wagler, 1830)			
sinensis Fain, 1968	*Trinyx sinensis* Boulenger 1889	Trionychidae		
pelusios Fain, 1968	*Pelusios castaneus* (Schweigger, 1812)	Pelomedusidae		Africa
pelomedusae Fain, 1968	*Pelomedusa subrufa* (Bonnaterre, 1789)			
deirochelys Fain, 1968	*Deirochelys reticularia* (Latreille, 1801)	Emydidae		North America
chrysemys Pence et Casto, 1975	*Chrysemys scripta elegans* Boulenger, 1889			
terrapenae Pence et Casto, 1975	*Terrapene carolina* (Linnaeus, 1758)			
dawsoni Bochkov et OConnor 2008	*Graptemys pseudogeographica* (Gray, 1831)			
Emyduracarus Fain, 1968				
australis Fain 1968	*Emydura latisternum* Boulenger, 1889	Chelidae	Testudines	Australia
Theodoracarus Fain, 1968				
testudinis Fain, 1968	*Testudo graeca ibera* Pallas, 1814	Testudinidae	Testudines	Asia
Chelonacarus Pence et Wright, 1998				
elongatus Pence et Wright, 1998	*Chelonia mydas* Linnaeus, 1758	Cheloniidae	Testudines	Central America

Table 3.

Host-specificity among permanent parasites of reptiles. Number of mites specific to host order, family, genus and species, respectively.

	No. species	Host specificity			
		To order	To family	To genus	To species
PARASITIFORMES					
Omentolaelapidae	1	0	0	1	0
Ixodorhynchidae	31	1	11	2	17
Entonyssidae	24	0	4	6	14
ACARIFORMES					
Pterygosomatidae	154*	0	12	30	112
Harpirhynchidae	16	0	3	1	12
Cloacaridae	14	0	0	0	14

*2 mite species not included (unknown hosts)