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Review of the distribution and biology of the snake mite *Ophionyssus natricis* (Acari: Macronyssidae)

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Original research

ABSTRACT

The mite *Ophionyssus natricis* (Gervais, 1844) (Macronyssidae) is a widespread ectoparasite of reptiles and a vector of some important veterinary diseases. This paper reviews the geographic distribution and host range of *O. natricis* and the available information about its clinical significance. Some incorrect identifications and host records are also identified. The snake mite has been collected from 144 species of reptiles, mostly snakes, as well as one amphibian and three species of mammals. It has been recorded in 36 countries in Europe, Asia, Africa, North and South America, and Australia. Its geographic range has undoubtedly been extended by human activities. Our records of *O. natricis* on the lizards *Darevskia brauneri* (Méhely, 1909) and *Ophisops elegans* Ménétries 1832, and on the snake *Telescopus fallax* Fleischmann, 1831, are new host records.

Keywords reptile; lizard; snake; ectoparasite

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Introduction

Mites in the family Macronyssidae (Acari: Mesostigmata: Gamasina) are mostly obligate blood-sucking ectoparasites of mammals, birds and reptiles. The family currently includes 34 genera with approximately 240 species (Radovsky, 2010). The genus *Ophionyssus* Mégnin, 1884a currently includes 14 species worldwide (Beron, 2014). The most extensively studied species in the genus is the snake mite *Ophionyssus natricis* (Gervais, 1844), which naturally infests snakes and lizards in Africa (Till, 1957; Evans & Till, 1966), but in other parts of the world it is associated primarily with animals in captivity (Miranda *et al.*, 2017; Norval *et al.*, 2020). Our purpose in this paper is to review the published data on the geographic distribution and host range of the snake mite, and to summarise the available information about its clinical significance.

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Material and methods

Most of the information presented here was derived from a search of the literature using Web of Science ® and Google Scholar ®, and from the personal libraries of the authors. We collected new information by examining specimens in the Reptile Collection of the Zoological Museum of the Moscow State University (ZMMU) and in the terrarium of the Russian State Agrarian University – Moscow Agricultural Academy. Mites were collected from the body surface of lizards by forceps, transferred to 70% alcohol, and mounted on microscope slides in Faure-Berlese medium. Mites were identified based on keys and descriptions given by Bregetova (1956) and Moraza *et al.* (2009). Measurements of body parts of imaginal and pre-imaginal stages are presented in Table 1. External measurements were taken in micrometres (µm). Slide-mounted voucher specimens were deposited in the collection of the Parasitological Collection of the Tyumen State Medical University (Tyumen, Russia). The classification of reptiles is based on Uetz *et al.* (2023).

Table 1 Measurements of *Ophionyssus natricis* (Gervais, 1844) from different parts of the distribution area.

	Brazil (Micherdzinski, 1980)	**Japan** (Zhang & Uchikawa, 1993)	**Romania** (Miron & Ivan, 2003)	**Azerbaijan** (this study, n=5)
Female				
Idiosoma				
Length	990	–	985 (944–1056)	654 (622–689)
Width	667	–	–	314 (300–322)
Propodosomal shield				
Length	310	270–310	274 (252–289)	289 (271–294)
Width	263	265–325	–	261 (255–267)
Pygidial shield				
Length	–	50–60	70 (60–78)	55–61
Width	–	50–60	–	52–59
Sternal shield				
Length	45	40–45	46 (36–54)	49 (43–53)
Width	112	103–110	–	91 (86–94)
Genital shield				
Length	275	290–320	–	273 (267–279)
Width	288	–	–	–
Stigmata and peritreme				
Length	144	128–145	–	–
Anal shield				
Length	–	110–145	125 (114–144)	121 (120–123)
Width	–	68–85	–	67 (65–68)
Gnathosoma				
Length	180–183	–	–	176 (171–179)
Chelicera, fixed digit				
Length	–	45–50	–	44–50
Protonymph (n=2)				
Idiosoma				
Length	366–381	–	–	361, 369
Width	240–251	–	–	221, 227
Propodosomal shield				
Length	–	180–235	–	177, 181
Width	–	190–240	–	182, 189
Pygidial shield				
Length	–	50–75	–	48, 52
Width	–	75–90	–	71, 79
Sternal shield				
Length	–	110	–	101
Width	–	75–80	–	72
Anal shield				
Length	–	55–65	–	41, 48
Width	–	42–55	–	36, 38

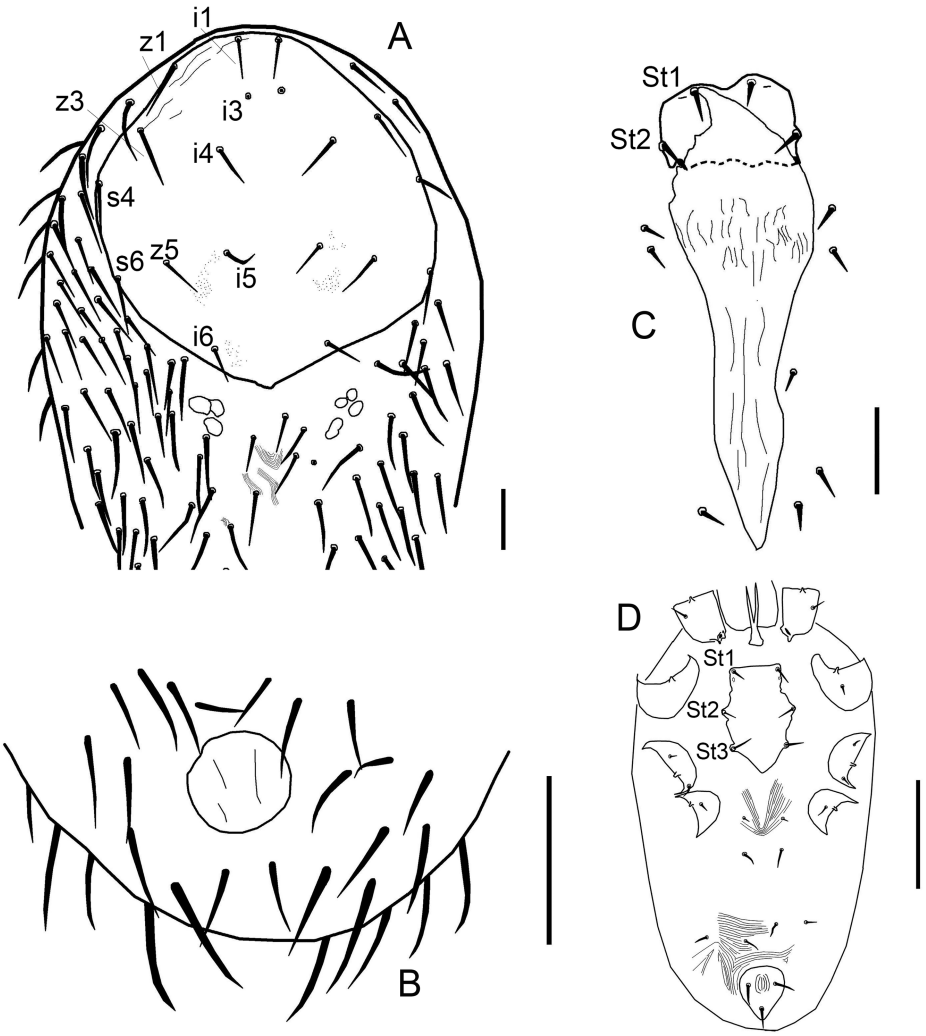

Figure 1 *Ophionyssus natricis* (ex *Ophisops elegans* from Azerbaijan): A – Female, propodosomal shield, scale bar = 50 µm; B – Female, pygidial shield, scale bar = 100 µm; C – Female, sternal and genital shields, scale bar = 50 µm; D – Protonymph, ventral idiosoma, scale bar = 100 µm.

New material examined

Five females, two protonymphs from *Ophisops elegans* Ménétries, 1832 from Azerbaijan, Lerik District, Zuvand settlement vicinity 38°47′ N, 48°25′ E, April 2009, leg. A.A. Kidov, identified by M.V. Orlova (Figure 1, Table 2). Additional specimens from *Darevskia brauneri* (Méhely, 1909) from Russia, Krasnodar region, Ubinskaya settlement, 44°42′N, 38°31′ E, leg. and det. A.A. Kidov; and from *Python regius* (Shaw, 1802) and *Telescopus fallax* Fleischmann, 1831, April 2009, from terrarium of Russian State Agrarian University (Moscow), identified by A.A. Kidov. It is most likely that the snakes and lizards acquired *O. natricis* during their stay in the terrarium in Moscow, so we attributed this record to Russia, not to Azerbaijan (Table 3). Our records of *O. natricis* for *Ophisops elegans*, *Darevskia brauneri* and *Telescopus fallax* are new host records.

Results

Taxonomic background

The first published reference to the snake mite appears to be that of Metaxa (1823), who observed undentified mites on captive snakes in Italy. Dugès (1834) found it in France and noted its similarity to the bird mite *Dermanyssus avium* Dugès, 1834. It was first named as *Dermanyssus natricis* by Gervais (1844), based on specimens collected on captive reptiles in Paris. The same species was also described by several other authors under different names. Camin (1949), Till (1957), Fain (1962) and Micherdzinski (1980) reviewed the earlier literature on the species and listed these junior synonyms, and that information need not be repeated here.

Table 2 Published records of *Ophionyssus natricis*. Non-reptile hosts are shown in square brackets.

Country	Host	References	Notes	Species range
		Europe		
Norway	Not stated	Mehl, 1979		
Sweden	Not stated	Ahl, 1994		
Denmark	[*Homo sapiens*]	Schultz, 1975		
Bulgaria	*Natrix tessellata*	Beron, 1966		Native species
Romania	**Snakes**			
	Natrix natrix	Feider & Solomon, 1963		Native species
	Natrix tessellata	Miron & Ivan, 2003	Mite as *Ophionyssus viperae*	Native species
	Zamenis longissimus	Miron & Ivan, 2003	As *Elaphe longissima*	Native species
	Dolichophis caspius	Miron & Ivan, 2003	As *Coluber jugularis caspius*	Native species
	Vipera ursinii	Miron & Ivan, 2003		Native species
Great Britain	**Lizards**			
	Uta stansburiana hesperis	Burrage, 1966		Non-native species
	Sceloporus occidentalis occidentalis	Burrage, 1966		
	Pogona vitticeps	Castro, 2019		Non-native species
	Not identified	Evans & Till, 1966		
	Snakes			
	Thamnophis ordinoides	André, 1937	As *Uta stansburiana elegans*	Non-native species
	Cerastes vipera	André, 1937	As *Cerastes aegyptiacus*	Non-native species
	Malayopython reticulatus	André, 1937	As *Python reticulatus*	Non-native species
	Epicrates cenchria	Mendoza-Roldan *et al* ., 2019		Non-native species
	Turtles			
	Testudo hermanni boettgeri	Castro, 2019		Non-native species
Poland	**Snakes**			
	Boa constrictor	Pawełczyk *et al* ., 2016		Non-native species
Germany	**Lizards**			
	Iguana iguana	Beck & Pantchev, 2006; Beck & Pfister, 2006		Non-native species
	Turtles			
	Testudo hermanni boettgeri	Wiechert, 2007		Non-native species
France	**Snakes**			
	Natrix natrix	André, 1937	As *Tropidonotus natrix*	Native species
	Hemorrhois hippocrepis	André, 1937	As *Periops hippocrepis*	Non-native species
Netherland	Snakes (not identified)	Buitendijk, 1945		
Austria	Captive snakes, occasionally captive Agamidae (not identified)	Hassl, 2016		
Switzerland	**Snakes**			
	Vipera aspis	Schweizer, 1961		Native species
Italy	**Snakes**			
	Pantherophis guttatus	Cervone *et al* ., 2016		Non-native species
	Python regius	Cervone *et al* ., 2016		Non-native species
	P. bivittatus	Cervone *et al* ., 2016		Non-native species
	Epicrates cenchria	Cervone *et al* ., 2016		Non-native species
	Morelia spilota	Mendoza-Roldán *et al* ., 2019		Non-native species
	Eunectes murinus	Mendoza-Roldán *et al* ., 2019		Non-native species
	Boa constrictor	Mendoza-Roldán *et al* ., 2019		Non-native species
	Podarcis siculus	Mendoza-Roldán *et al* ., 2019		Native species
	Podarcis siculus klemmeri	Mendoza-Roldán *et al* ., 2019		Native species
Spain (Canary islands)	**Snakes**			
	Lampropeltis californiae	Santana-Hernández *et al* ., 2021		Non-native species
Slovenia	**Snakes**			
	Boa constrictor	Rataj *et al* ., 2011		Non-native species

Ophionyssus natricis has been throughly described and illustrated several times, notably by Camin (1953) and Micherdzinski (1980). Moraza *et al.* (2009) provided detailed information on how *O. natricis* can be distinguished from other species of *Ophionyssus*. The morphological recognition of the species is supported by molecular sequence data (Alfonso-Toledo & Paredes-

Table 2 Continued.

Country	Host	References	Notes	Species range
		Asia		
Armenia	**Lizards**			
	Darevskia sp.	Arutunian & Ohandjanian, 1983	As *Lacerta saxicola*	
	Snakes			
	Natrix natrix	Arutunian & Ohandjanian, 1983		Native species
Uzbekistan	**Snakes**			
	Natrix tessellata	Abdushukurova *et al* ., 1966		Native species
Turkmenistan	**Snakes**			
	Psammophis lineolatus	Markov & Bogdanov, 1960		Native species
(Soviet Central Asia)	**Snakes**			
	Echis carinatus	Bogdanov, 1965		Native species
	Spalerosophis diadema	Bogdanov, 1965		Native species
Turkey	**Snakes**			
	Natrix tessellata	Dik, 2012		Native species
	Pantherophis guttatus	Keskin, 2021		Non-native species
Iran	[*Homo sapiens*]	Amanatfard *et al* ., 2014		
	Snakes			
	Python sp.	Amanatfard *et al* ., 2014		Non-native species
Israel	**Snakes**			
	Hemorrhois nummifer	Costa, 1966	As *Coluber ravergieri*	Native species
	Snakes (not identified)	Shulov, 1957		
Korea	**Snakes**			
	Snakes (not identified)	Whan, 1966		
Japan	**Snakes**			
	Chondropython viridis	Zhang & Uchikawa, 1993		Non-native species
Malaysia	**Snakes**			
	Python bivittatus	Mariana *et al* ., 2011	As *Python molurus bivittatus*	Native species
India	**Snakes**			
	Naja naja naja	Khaire *et al* ., 1987		Native species
	Daboia russelii	Khaire *et al* ., 1987	As *Vipera russelii*	Native species
	Chrysopelea ornata	Khaire *et al* ., 1987		Native species
Pakistan	**Snakes**			
	Python molurus	Sumaira *et al* ., 2020		Native species
		Africa		
Egypt	**Snakes**			
	Platyceps florulentus	Keegan, 1956; Yunker, 1956	As *Coluber florulentus*	Native species
	Psammophis leightoni	Keegan, 1956; Yunker, 1956	As *Psammophis sibilans*	Native species
	Psammophis schokari	Keegan, 1956; Yunker, 1956		Native species
	Spalerosophis diadema cliffordii	Keegan, 1956; Yunker, 1956	As *Spalerosophis cliffordii*	Native species
	Naja haje	Keegan, 1956; Yunker, 1956		Native species
	Telescopus obtusus	Keegan, 1956; Yunker, 1956	As *Telescopus dhara obtusus*	Native species
Morocco	[*Sclerophrys mauritanica*]	Blanc & Ascione, 1959	As [*Bufo mauritanicus*]	
	Lizards			
	Mesalina simoni	Er-Rguibi *et al* ., 2023		Native species
	Snakes			
	Malpolon monspessulanus	Blanc & Ascione, 1959		Native species
	Natrix maura	Blanc & Ascione, 1959		Native species
	Coluber hippocrepis	Blanc & Ascione, 1959		Native species
Congo	**Snakes**			
	Bothrophthalmus lineatus	Fain, 1962		Native species
Republic of South Africa	**Snakes**			
	Bitis arietans	Till, 1957		Native species
	Boaedon lineatus	Till, 1957		Native species
	Causus rhombeatus	Till, 1957		Native species
	Dispholidus typus	Till, 1957		Native species
	Naja nivea	Till, 1957		Native species
	Psammophis leightoni	Till, 1957	As *Psammophis sibilans trinasalis*	Native species
	Hemachatus haemachates	Till, 1957		Native species
West Africa (country not stated)	**Snakes**			
	Boodon fuliginosus	Phisalix, 1914		Native species

León, 2021). We now provide a list of some of the major taxonomic references to the species, including the important recent works by Moraza *et al.* (2009), Radovsky (2010) and Beron (2014).

Table 2 Continued.

Country	Host	References	Notes	Species range
		America		
Canada	[*Condylura cristata*]	Micherdzinski, 1980		
	Snakes			
	Heterodon platirhinos	Thomasson & Blouin-Demers, 2015		Native species
USA (including Hawaii)	**Lizards**			
	Uta stansburiana	Goldberg & Bursey, 1991		Native species
	Elgaria multicarinatus	DeNardo & Wozniak, 1997; Wozniak & DeNardo, 2000		Native species
	Tiliqua scincoides	DeNardo & Wozniak, 1997; Wozniak & DeNardo, 2000		Non-native species
	Snakes			
	Malayopython reticulatus	André 1937	As *Python reticulatus*	Non-native species
	Boa constrictor	Radovsky 1971; DeNardo & Wozniak, 1997		Non-native species
	Crotalus ruber	Schroeder, 1934		Native species
	Crotalus oreganus	Schroeder, 1934	As *C. confluentus oreganus*	Native species
	Masticophis flagellum	Schroeder, 1934		Native species
	Thamnophis sirtalis infernalis	Schroeder, 1934		Native species
	Thamnophis hammondii	Schroeder, 1934	As *Thamnophis ordinoides hammondii*	Native species
	Pituophis catenifer annectens	Schroeder, 1934		Native species
	Drymarchon couperi	Reeves *et al* ., 2006		Native species
	Antaresia maculosa	Reeves *et al* ., 2006		Native species
Mexico	**Lizards**			
	Iguana iguana	Salazar, 2014		Native species
	Snakes			Native species
	Crotalus triseriatus	Paredes-Leon *et al* ., 2008		Native species
	Crotalus durissus	Rodriguez & Lazcano, 1992		Native species
	Crotalus cerastes cercobombus	Rodriguez & Lazcano, 1992		Native species
	Crotalus lepidus lepidus	Rodriguez & Lazcano, 1992		Native species
	Crotalus atrox	Rodriguez & Lazcano, 1992		Native species
	Crotalus ravus	Rodriguez & Lazcano, 1992		Native species
	Pituophis deppei deppei	Rodriguez & Lazcano, 1992		Native species
	Boa constrictor	Rodriguez & Lazcano, 1992		Native species
	Gerrhonotus liocephalus	Rodriguez & Lazcano, 1992		Native species
	Lampropeltis triangulum	Rodriguez & Lazcano, 1992		Native species
	Barisia imbricate	Rodriguez & Lazcano, 1992		Native species
	Barisia ciliaris	Rodriguez & Lazcano, 1992		Native species
	Corytophanes cristatus	Rodriguez & Lazcano, 1992		Native species
	Laemanctus serratus	Fuantos-Gámez *et al* ., 2020		Native species
	Python bivittatus	Fuantos-Gámez *et al* ., 2020	As *Python molurus bivittatus*	Non-native species
	Turtles			
	Staurotipus triporcatus	Paredes-León *et al* ., 2008		Native species
	Trachemys scripta elegans	Paredes-León *et al* ., 2008		Native species
	Trachemys venusta	Paredes-León *et al* ., 2008		Native species
Panama	**Snakes**			
	Boa constrictor	Miranda *et al* ., 2017		Native species
	Epicrates maurus	Miranda *et al* ., 2017		Native species
	Corallus ruschenbergerii	Miranda *et al* ., 2017		Native species
	Corallus caninus	Miranda *et al* ., 2017		Native species
	Python regius	Miranda *et al* ., 2017		Non-native species
Nicaragua	**Snakes**			
	Boa constrictor	Rimbaud *et al* ., 2006		Non-native species
Antigua	**Snakes**			
	Alsophis antiguae	Daltry *et al* ., 2001		Native species
Brazil	[*Mesomys ecaudatus*]	Ferreira da Silva *et al* ., 2018		
	Lizards			
	Enyalius iheringii	Mendoza-Roldan *et al* ., 2020b		Native species
	Pogona vitticeps	Mendoza-Roldan *et al* ., 2020b		Non-native species
	Snakes			
	Boa constrictor constrictor	Barbosa *et al* ., 2006	As *Python reticulatus*	Native species
	Malayopython reticulatus	Fonseca, 1933; Micherdzinski, 1980		Non-native species
	Corallus hortullana	Mendoza-Roldan *et al* ., 2020b	As *Corallus hortullanus*	Native species
	Crotalus durissus	Mendoza-Roldan *et al* ., 2020b	As *Crotalus durissus terrificus*	Native species
	Pantherophis guttatus	Almeida Pereira *et al* ., 2019	As *Pantherophis guttata*	Native species

Ophionyssus natricis (Gervais, 1844)

Dermanyssus natricis Gervais, 1844: 223.
Ophionyssus natricis Mégnin, 1884a: 617; 1884b: 110; André, 1937: 62; Vitzthum, 1943; 771; Fonseca, 1948: 313; Camin, 1949: 583; 1953; 3; Zemskaya, 1951: 49; Baker *et al.*, 1956: 33; Bregetova, 1956: 223; Keegan, 1956: 219; Womersley, 1956: 599; Till, 1957: 126; Schweizer,

Table 2 Continued.

Country	Host	References	Notes	Species range
		America		
Argentina	**Lizards**			
	Leiosaurus bellii	Mauri, 1967	As *Ophiodes striatus*	Native species
	Teious teyou	Mauri, 1967		Native species
	Ophiodes fragilis	Mauri, 1967		Native species
	Snakes			Native species
	Epicrates cenchria crassus	Mauri, 1967		Native species
	Helicops leopardine	Mauri, 1967		Native species
	Chironius carinatus	Mauri, 1967		Native species
	Erythrolamprus poecilogyrus	Mauri, 1967	As *Leimadophis poecilogyrus*	Native species
	Xenodon merremii	Mauri, 1967		Native species
	Lystrophis dorbignyi	Mauri, 1967		Native species
	Lystrophis semcinctus	Mauri, 1967		Native species
	Dipsas turgida	Mauri, 1967	As *Sibynomorphus turgidus*	Native species
	Imantodes cenchoa	Mauri, 1967		Native species
	Leptodeira annulata annulata	Mauri, 1967		Native species
	Clelia clelia	Mauri, 1967	As *Pseudoboa cloelia*	Native species
	Oxyrhopus rhombifer	Mauri, 1967	As *Pseudoboa rhombifera*	Native species
	Tomodon dorsatus	Mauri, 1967		Native species
	Tachymenis ocellata	Mauri, 1967	As *Tomodon ocellatus*	Native species
	Philodryas baroni	Mauri, 1967		Native species
	Philodryas patagoniensis	Mauri, 1967	As *Philodryas schotti*	Native species
	Erhythrolamptus aesculapii	Mauri, 1967		Native species
	Micrurus frontalis	Mauri, 1967		Native species
	Micrurus lemniscatus	Mauri, 1967		Native species
	Bothrops alternata	Mauri, 1967		Native species
	Bothrops ammodythoides	Mauri, 1967		Native species
	Bothrops jararacussu	Mauri, 1967		Native species
	Bothrops neuwiedii meridionalis	Mauri, 1967		Native species
	Crotalus terrificus terrificus	Mauri, 1967		Native species
		Australia and Oceania		
Australia	**Lizards**			
	Amphibolurus muricatus	Domrow, 1988		Native species
	Carlia longipes	Domrow, 1988		Native species
	Chlamydosaurus kingie	Domrow, 1988		Native species
	Lacerta viridis	Domrow, 1988		Non-native species
	Tiliqua rugosa	Norval *et al* ., 2020, 2021		Native species
	Tiliqua scincoides	Norval *et al* ., 2020, 2021		Native species
	Snakes			
	Acanthophis antarcticus	Norval *et al* ., 2020, 2021		Native species
	Antaresia children	Norval *et al* ., 2020, 2021		Native species
	Aspidites ramsayi	Norval *et al* ., 2020, 2021		Native species
	Hoplocephalus bitorquatus	Norval *et al* ., 2020, 2021		Native species
	Hoplocephalus stephensii	Norval *et al* ., 2020, 2021		Native species
	Liasis fuscus	Norval *et al* ., 2020, 2021		Native species
	Morelia viridis	Norval *et al* ., 2020, 2021		Native species
	Morelia spilota metcalfei	Norval *et al* ., 2020, 2021		Native species
	Notechis scutatus	Norval *et al* ., 2020, 2021		Native species
	Pseudechis porphyriacus	Norval *et al* ., 2020, 2021		Native species
	Pseudonaja textilis	Norval *et al* ., 2020, 2021		Non-native species
	Python bivittatus	Norval *et al* ., 2020, 2021	As *Python molurus bivittatus*	Native species
	Tropidechis carinatus	Norval *et al* ., 2020, 2021		Native species
New Zealand	**Lizards**			
	Tiliqua scincoides	Heath, 1986		Non-native species
Country not stated	**Lizards**			
	Sceloporus graciosus graciosus	Radford, 1950		
	Snakes			
	Hierophis viridiflavus	Radford, 1950	As *Coluber viridiflavus viridiflavus*	

1961: 155; Fain, 1962: 107; Domrow, 1963: 214; 1974: 17; 1985: 152; 1988: 857; Evans & Till, 1966: 337; Beron, 1966: 52; Costa, 1966: 75; Hallas, 1978: 28; Mehl, 1979: 33; Arutunjan & Ohandjanian, 1983: 312; Zhang & Uchikawa, 1993: 76; Moraza *et al.*, 2009: 65; Radovsky, 2010: 108; Beron, 2014: 130.

At least five other species names are now considered to be junior synonyms of *O. natricis* (see Beron, 2014 for details).

Misidentifications of *Ophionyssus natricis*

Some published records of *O. natricis* actually refer to other species. Biological Services (2015) includes an illustration of a mite on the head of a snake, but the mite appears to be *Ophiomegistus* Banks, 1914 and not *Ophionyssus*. The illustration of a snake mite in Maxwell (2022) shows an oribatid mite. Sabu *et al.* (2002) reported a mite they identified as *O. natricis* on snakes in India. Their illustration shows an unidentified species of Astigmata, not *O. natricis*, and the occurrence of *O. natricis* inside nodules of necrotic tissue as they reported would be extremely unusual.

Geographic distribution

The data listed in Table 2 show that *Ophionyssus natricis* is near cosmopolitan, and has been found in every continent except Antarctica. Records for Russia are listed in more detail in Table 3. The apparent absence of *O. natricis* in China is surprising. Su *et al.* (2010) and Ma & Bai

Table 3 Records of *Ophionyssus natricis* in Russia.

Date	Locality	Host	References	Notes	Species range
1950	Moscow Zoo, host was captured in Middle Asia	**Snakes**			
		Echis carinatus	Zemskaya, 1951		Non-native species
Undated	Moscow Zoo	**Snakes**			
		Macrovipera lebetinus	Bregetova, 1956	As *Vipera lebetina*	Native species
		Platiceps karelini		As *Coluber karelini*	Non-native species
1954–1955	Damchik section, Astrakhan' Nature Reserve, Astrakhan' oblast' (Lower Volga region)	**Snakes**			
1959–1960		*Natrix natrix*	Markov et al., 1964		Native species
		Natrix tessellata			Native species
		Elaphe dione			Native species
1973–1976	Manure pile, Cherniy Mys settlement, Kolyvan' district, Novosibirsk oblast' (Western Siberia)	**Snakes**			
		Natrix natrix	Belova & Grigoriev, 1981		Native species
2005	Bogdinsk-Baskunchak Nature Reserve, Astrakhan' oblast' (Lower Volga region)	**Snakes**			
		Dolichophis caspius	Bakiev, 2007		Native species
23–30 August 2008	South-Eastern part of Novosibirsk oblast' (Western Siberia)	**Snakes**			
		Gloydius halys	Simonov & Zinchenko, 2010		Native species
Undated	Moscow Zoo	**Snakes**			
		Simalia boeleni	Vasiliev & Balakina, undated	As *Morelia boeleni*	Non-native species
April 2009	Moscow	**Lizards**			
		Darevskia brauneri	this paper, new record		Native species
		Ophisops elegans	this paper, new record		Native species
		Snakes			
		Python regius			Non-native species
		Telescopus fallax	this paper, new record		Native species

(2012) reported other species of *Ophionyssus* in China, and *O. natricis* will almost certainly be found there when further studies are carried out.

Life cycle and behaviour

The life cycle and behaviour of *Ophionyssus natricis* were examined in detail by Camin (1953). Individuals pass through the egg, larva, protonymph, and deutonymph stages before developing into adult males and females. Protonymphs and adults are hematophagous, feeding on the host and then molting in the environment, but larvae and deutonymphs do not feed. The life cycle can be completed within 7 to 14 days when environmental and host conditions are optimal, in temperatures ranging from 20º C to 30º C and humidity higher than 75%. Oliver (1971) summarised previous results showing that *O. natricis* reproduces by arrhentokous parthenogenesis, with nine chromosomes in males and 18 in females. Aspects of the biology and behaviour of *O. natricis* are described in a large number of publications, including the useful summaries by Reinert & Brandstätter (1993), Wozniak & DeNardo (2000), Fitzgerald & Vera (2006) and Schilliger *et al.* (2013).

Bannert *et al.* (2000) provided a detailed description of the life cycle of *Ophionyssus galloticolus* Fain & Bannert, 2000, which appears to be very similar to that of *O. natricis*.

Occurrence on aquatic hosts

Captive snakes infested by *O. natricis* seek relief from irritation by immersing themselves in water (for example Page, 1966; Šlapeta *et al.*, 2018), and dead mites can be found floating in water bowls in terraria, suggesting that mites are easily killed by immersion in water. It therefore seems unlikely that reptiles that spend significant time in water would be acceptable hosts for this parasite. We conducted a Web of Science® search for records of *O. natricis* on marine and aquatic snakes in the following genera: *Acrochordus* Hornstedt, 1787; *Afronatrix* Rossman & Eberle, 1977; *Agkistrodon* Palisot de Beauvois, 1799; *Aipysurus* Lacépède, 1804; *Cerberus* Cuvier, 1829; *Emydocephalus* Krefft, 1869; *Enhydris* Sonnini & Latreille, 1802; *Ephalophis* Smith, 1931; *Farancia* Gray, 1842; *Fowlea* Theobald, 1868; *Grayia* Günther, 1858; *Helicops* Wagler, 1828; *Homalopsis* Kuhl & Hasselt, 1822; *Hydrelaps* Boulenger, 1896; *Hydrophis* Latreille, 1801; *Hydrops* Wagler, 1830; *Laticauda* Laurenti, 1768; *Leptodeira* Fitzinger, 1843; *Myron* Gray, 1849; *Myrrophis* Kumar *et al.*, 2012; *Natrix* Laurenti, 1768; *Nerodia* Baird & Girard, 1853; *Opisthotropis* Günther, 1872; *Parahydrophis* Burger & Natsuno, 1974; *Pseudoeryx* Fitzinger, 1826; *Ptychophis* Gomes, 1915; *Tretanorhinus* Duméril *et al.*, 1854; *Trimerodytes* Cope, 1895. Positive results were returned for *Helicops*, *Leptideira*, and *Natrix*. Mauri (1967) reported *O. natricis* on *Helicops leopardinus* (Schlegel, 1837) and *Leptodeira annulata* (Linnaeus, 1758) in Argentina. Both these species have been referred to as water snakes, but they are not completely aquatic (Ávila *et al.*, 2006; Thaler *et al.*, 2022). Feider & Solomon (1963), Markov *et al.* (1964), Bogdanov (1965), and Beron (1966) reported the snake mite on *Natrix tessellata* Laurenti, 1768 in Uzbekistan, Bulgaria, Romania and Russia (Astrakhan') but did not provide detailed collecting data. Chiodini *et al.* (1983) and Dik (2012) reported *O. natricis* on *Natrix* spp. in captivity but these hosts also cannot be considered as fully aquatic.

Some documents report the occurrence of *O. natricis* on crocodiles, but these all appear to be the result of mistakes or misunderstandings. Dhooria (2016) reported this host association without any reference to its source. It is also found on many internet sites including Biological Services (2015), Maxwell (2022), and Reptiles Cove (2022), but these records are not supported by evidence.

Wozniak & DeNardo (2000) referred to the host range of *O. natricis* as follows "The mite has been shown to thrive on most snakes and some lizards including southern alligator lizards, *Elgaira mulicarnata* (Wozniak, personal observations), blue-tongue skinks *Tiliqua scincoides* (Wozniak, personal observations) and side-blotched lizards *Uta stansburiana* (Goldberg and Bursey, 1991)". Mendoza-Roldan (2019) misquoted that information when describing *O.*

natricis as "a cosmopolitan inhabitant of captive snakes, but also infest captive lizards, turtles, crocodiles and other reptiles (Wozniak & DeNardo, 2000)". This incorrect information was not repeated in Mendoza-Roldan *et al.* (2020a, 2020b), who reported *O. natricis* only on snakes and lizards.

Numerous publications refer to ectoparasites of crocodilians, including ticks and leeches, but none of these mention *Ophionyssus* sp. on this host (e.g. Jacobson, 1984; Magnusson, 1985; Huchzermeyer, 2003; Leslie *et al.*, 2011; Tellez, 2013; Divers & Stahl, 2019; Partyka, 2019; Pereira & Colli, 2023). We have been unable to find any confirmed records of *Ophionyssus* sp. on any species of crocodilian.

Pest control

Snake mites are highly mobile, and can quickly infest and re-infest terraria or enclosures. They can survive for extended periods without feeding (Wozniak & DeNardo, 2000), so routine environmental hygiene alone is not an effective method of control. Fitzgerald & Vera (2006) reviewed the chemical pesticides used for control of snake mites, as well as a variety of cultural methods for limiting their populations. Commonly used insecticides and acaricides, including those previously reviewed by Camin *et al.* (1964), are potentially harmful to reptiles, and are not recommended for control of snake mites. Alternative methods of mite control have included the use of sorptive dust, which operates by causing dehydration (Tarshis, 1960). Fitzgerald (2019) listed the currently available methods for controlling snake mites, and the methods and materials that are no longer recommended. A new generation of isoxazoline compounds appears to have considerable potential to provide safe and effective mite control when administered to snakes orally without side effects and without the need to treat the environment of the snake (Fuantos-Gámez *et al.*, 2020; Gobble, 2022; Mendoza-Roldan *et al.*, 2023).

Some authors have proposed the use of predatory mites to control *O. natricis* on captive reptiles. Rotter (1963) used *Cheyletus eruditus* Schrank, 1781 (Acari: Cheyletidae) to control the snake mite on captive lizards, and *C. eruditus* is now available commercially for that purpose (Schilliger *et al.*, 2013; APPI Biological Control, 2021). *Stratiolaelaps scimitus* (Womersley, 1956) (Acari: Laelapidae) may also have some effect as a predator in terraria, but its value is limited by its low tempertature optimum (Mendyk, 2015). Maslova & Dochevoy (2016) reported a carabid beetle (*Carabus granulatus telluris* Bates, 1883) moving around on the scales of a pitviper (*Gloydius ussuriensis* (Emelianov, 1929)) and feeding on ectoparasites, apparently including *O. natricis*.

Clinical significance

Infestation of reptiles with *Ophionyssus natricis* can cause dehydration, lethargy, growth impairment (Wozniak & DeNardo, 2000) and in severe infestations, anaemia and dysecdysis (DeNardo & Wozniak, 1997; Mendoza-Roldan *et al.*, 2023). Affected individuals suffer hyperaemic and oedematous skin, and seek relief from the resulting pruritus by soaking in water (Wozniak & DeNardo, 2000). There have been reports of loreal pit inflammations and impactions associated with heavy infestations (Garrett & Harwell, 1991). Histopathologic evaluation of feeding sites shows infiltration with neutrophils, lymphocytes and plasma cells, with multifocal perivascular aggregates of lymphocytes and plasma cells in the adjacent dermis (DeNardo & Wozniak, 1997).

Ophionyssus natricis is a mechanical vector of *Aeromonas hydrophila* Chester, 1901, the causative agent of hemorrhagic disease in reptiles (Mendoza-Roldan *et al.*, 2021). It can be a vector of blood-borne protozoa and viral pathogens of snakes (Camin, 1948; Chiodini *et al*, 1983; Schumacher *et al*, 1994; Mendoza-Roldan *et al.*, 2023). In South America it was identified as a vector of *Hepatozoon* sp. and *Rickettsia* sp. (Mendoza-Roldan *et al.*, 2020a, b). It has also been implicated as vector of *Arenavirus* sp., the etiological agent of the Inclusion Body Disease in boid snakes (Chang & Jacobson, 2010; Divers & Stahl, 2019). *Ophionyssus*

natricis collected from *Boa constrictor* in Italy also contained *Wolbachia* sp. (Manoj *et al.*, 2021). Further vector competency studies are needed to characterise the overall role of this parasite in the transmission of other infectious agents, such as filariids.

This parasite can become a pest to humans due to the aggressive feeding of the protonymphs, which swarm and bite humans, causing papular vesiculo-bullous eruptions in the skin (Schultz, 1975; McClain *et al.*, 2009), other bite-associated dermatitis (Beck, 1996; Amanatfard *et al.*, 2014), and the risk of zoonotic transmission of pathogens.

Ecological significance

Schroeder (1934) presented a very clear description of the life cycle of *O. natricis*, and its importance as a pest of snakes in captivity. He also pointed out the agricultural value of snakes as a natural means of reducing rodent populations. Fonseca (1948), citing Schroeder (1934), speculated that *O. natricis* was harmful to wild snake populations, and therefore indirectly influenced wild rodent populations. That conclusion is not supported by the observation that *O. natricis* rarely reaches heavy levels of infestation of snakes in natural habitats.

Discussion

The catalogue of the family Macronyssidae by Beron (2014) provides a good taxonomic background to the systematics of *Ophionyssus natricis*. The genus *Ophionyssus* currently includes 14 valid species. Several other species have been placed in *Ophionyssus* at some time, but have since been transferred to other genera, including *Thigmonyssus myrmecophagus* (Fonseca, 1954), *Trichonyssus ehmanni* (Domrow, 1985), *T. galeotes* (Domrow *et al.*, 1980), and *T. scincorum* (Domrow *et al.*, 1980).

Most species of *Ophionyssus* have a limited geographic distribution but *O. saurarum* (Oudemans, 1901) is widespread in Europe, Asia, and Africa, and *O. natricis* is cosmopolitan. If we exclude *O. natricis*, the highest level of species diversity in the genus is found in Africa, with five species in southern Africa and a further three in the Canary Islands. Two species have been described from the Indo-Australian Region, and four occur in Europe and the Western Palaearctic.

Ophionyssus natricis occurs on a very wide range of snake and reptile hosts, while other species of *Ophionyssus* parasitise lizards in the families Lacertidae, Scincidae, Cordylidae, Agamidae, and Pygopodidae. Reptilian hosts of *O. natricis* include three families of turtles, 10 families of lizards, and seven families of snakes. The snake family with the largest number of infested species (46) is Colubridae, reflecting the fact that it is the most numerous group of modern snakes, with more than half of all known species. Approximately 20% of the hosts are terrarium species that are not typical of the countries where the infested specimens were found.

The evolutionary history of *O. natricis* has been obscured by human-assisted dispersal. Till (1957) recorded its presence on both snakes and lizards in wild conditions in South Africa. Field records of *O. natricis* in other countries are rare, suggesting that the species may have arisen in southern Africa, possibly following a host shift from a lizard to a snake. Nieri-Bastos *et al.* (2011) and Gomes-Almeida & Pepato (2021) demonstrated the potential value of molecular systematics in Macronyssidae. The required sequence data is not yet available for *Ophionyssus*, so a molecular analysis of the phylogenetic background of the snake mite is not yet possible.

Ophionyssus natricis has recently been found on wild populations of lizards in Australia (Norval *et al.*, 2020, 2021). Research is needed to determine whether this parasite represents a serious threat to wild populations of reptiles, both in Australia and elsewhere.

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