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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

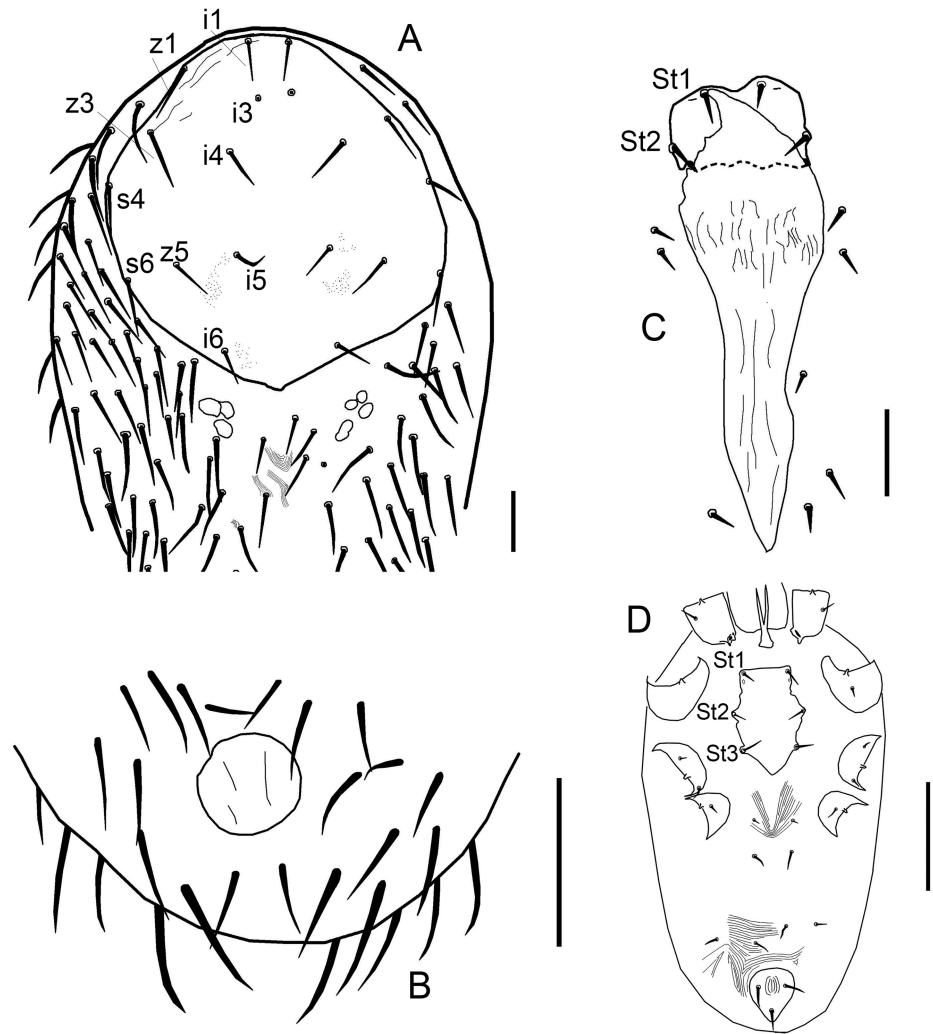


Figure 1 *Ophionyssus natricis* (ex *Ophisops elegans* from Azerbaijan): A – Female, propodosomal shield, scale bar = 50 μ m; B – Female, pygidial shield, scale bar = 100 μ m; C – Female, sternal and genital shields, scale bar = 50 μ m; D – Protonymph, ventral idiosoma, scale bar = 100 μ m.

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

Ophionyssus natricis has been thoroughly 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 <i>Darevskia</i> sp.	Arutunian & Ohandjanian, 1983	As <i>Lacerta saxicola</i>	
	Snakes <i>Natrix natrix</i>	Arutunian & Ohandjanian, 1983		Native species
Uzbekistan	Snakes <i>Natrix tessellata</i>	Abdushukurova <i>et al.</i> , 1966		Native species
Turkmenistan	Snakes <i>Psammophis lineolatus</i>	Markov & Bogdanov, 1960		Native species
(Soviet Central Asia)	Snakes <i>Echis carinatus</i>	Bogdanov, 1965		Native species
	<i>Spalerosophis diadema</i>	Bogdanov, 1965		Native species
Turkey	Snakes <i>Natrix tessellata</i>	Dik, 2012		Native species
	<i>Pantherophis guttatus</i>	Keskin, 2021		Non-native species
Iran	[<i>Homo sapiens</i>]	Amanatfard <i>et al.</i> , 2014		
	Snakes <i>Python</i> sp.	Amanatfard <i>et al.</i> , 2014		Non-native species
Israel	Snakes <i>Hemorrhois nummifer</i>	Costa, 1966	As <i>Coluber ravergieri</i>	Native species
	Snakes (not identified)	Shulov, 1957		
Korea	Snakes Snakes (not identified)	Whan, 1966		
Japan	Snakes <i>Chondropython viridis</i>	Zhang & Uchikawa, 1993		Non-native species
Malaysia	Snakes <i>Python bivittatus</i>	Mariana <i>et al.</i> , 2011	As <i>Python molurus bivittatus</i>	Native species
India	Snakes <i>Naja naja naja</i>	Khaira <i>et al.</i> , 1987		Native species
	<i>Daboia russelii</i>	Khaira <i>et al.</i> , 1987	As <i>Vipera russelii</i>	Native species
	<i>Chrysopelea ornata</i>	Khaira <i>et al.</i> , 1987		Native species
Pakistan	Snakes <i>Python molurus</i>	Sumaira <i>et al.</i> , 2020		Native species
Africa				
Egypt	Snakes <i>Platyceps florulentus</i>	Keegan, 1956; Yunker, 1956	As <i>Coluber florulentus</i>	Native species
	<i>Psammophis leightoni</i>	Keegan, 1956; Yunker, 1956	As <i>Psammophis sibilans</i>	Native species
	<i>Psammophis schokari</i>	Keegan, 1956; Yunker, 1956		Native species
	<i>Spalerosophis diadema cliffordii</i>	Keegan, 1956; Yunker, 1956	As <i>Spalerosophis cliffordii</i>	Native species
	<i>Naja haje</i>	Keegan, 1956; Yunker, 1956		Native species
	<i>Telescopus obtusus</i>	Keegan, 1956; Yunker, 1956	As <i>Telescopus dhara obtusus</i>	Native species
Morocco	[<i>Sclerophrys mauritanica</i>]	Blanc & Ascione, 1959	As [<i>Bufo mauritanicus</i>]	
	Lizards <i>Mesalina simoni</i>	Er-Rguibi <i>et al.</i> , 2023		Native species
	Snakes <i>Malpolon monspessulanus</i>	Blanc & Ascione, 1959		Native species
	<i>Natrix maura</i>	Blanc & Ascione, 1959		Native species
	<i>Coluber hippocrepis</i>	Blanc & Ascione, 1959		Native species
Congo	Snakes <i>Bothrophthalmus lineatus</i>	Fain, 1962		Native species
Republic of South Africa	Snakes <i>Bitis arietans</i>	Till, 1957		Native species
	<i>Boaedon lineatus</i>	Till, 1957		Native species
	<i>Causus rhombeatus</i>	Till, 1957		Native species
	<i>Dispholidus typus</i>	Till, 1957		Native species
	<i>Naja nivea</i>	Till, 1957		Native species
	<i>Psammophis leightoni</i>	Till, 1957	As <i>Psammophis sibilans trinasalis</i>	Native species
	<i>Hemachatus haemachates</i>	Till, 1957		Native species
West Africa (country not stated)	Snakes <i>Boodon fuliginosus</i>	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	[<i>Condylura cristata</i>]	Micherdzinski, 1980		
	Snakes			
	<i>Heterodon platirhinos</i>	Thomasson & Blouin-Demers, 2015		Native species
USA (including Hawaii)	Lizards			
	<i>Uta stansburiana</i>	Goldberg & Bursley, 1991		Native species
	<i>Elgaria multicarinatus</i>	DeNardo & Wozniak, 1997; Wozniak & DeNardo, 2000		Native species
	<i>Tiliqua scincoides</i>	DeNardo & Wozniak, 1997; Wozniak & DeNardo, 2000		Non-native species
	Snakes			
	<i>Malayopython reticulatus</i>	André 1937	As <i>Python reticulatus</i>	Non-native species
	<i>Boa constrictor</i>	Radovsky 1971; DeNardo & Wozniak, 1997		Non-native species
	<i>Crotalus ruber</i>	Schroeder, 1934		Native species
	<i>Crotalus oreganus</i>	Schroeder, 1934	As <i>C. confluentus oreganus</i>	Native species
	<i>Masticophis flagellum</i>	Schroeder, 1934		Native species
	<i>Thamnophis sirtalis infernalis</i>	Schroeder, 1934		Native species
	<i>Thamnophis hammondi</i>	Schroeder, 1934	As <i>Thamnophis ordinoides hammondi</i>	Native species
	<i>Pituophis catenifer annectens</i>	Schroeder, 1934		Native species
	<i>Drymarchon couperi</i>	Reeves <i>et al.</i> , 2006		Native species
	<i>Antaresia maculosa</i>	Reeves <i>et al.</i> , 2006		Native species
Mexico	Lizards			
	<i>Iguana iguana</i>	Salazar, 2014		Native species
	Snakes			
	<i>Crotalus triseriatus</i>	Paredes-Leon <i>et al.</i> , 2008		Native species
	<i>Crotalus durissus</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Crotalus cerastes cercobombus</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Crotalus lepidus lepidus</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Crotalus atrox</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Crotalus ravus</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Pituophis deppiei deppiei</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Boa constrictor</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Gerrhonotus liocephalus</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Lampropeltis triangulum</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Barisia imbricate</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Barisia ciliaris</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Corytophanes cristatus</i>	Rodriguez & Lazcano, 1992		Native species
	<i>Laemantus serratus</i>	Fuantes-Gómez <i>et al.</i> , 2020		Native species
	<i>Python bivittatus</i>	Fuantes-Gómez <i>et al.</i> , 2020	As <i>Python molurus bivittatus</i>	Non-native species
	Turtles			
	<i>Staurotipus triporcatus</i>	Paredes-León <i>et al.</i> , 2008		Native species
	<i>Trachemys scripta elegans</i>	Paredes-León <i>et al.</i> , 2008		Native species
	<i>Trachemys venusta</i>	Paredes-León <i>et al.</i> , 2008		Native species
Panama	Snakes			
	<i>Boa constrictor</i>	Miranda <i>et al.</i> , 2017		Native species
	<i>Epicrates maurus</i>	Miranda <i>et al.</i> , 2017		Native species
	<i>Corallus ruschenbergerii</i>	Miranda <i>et al.</i> , 2017		Native species
	<i>Corallus caninus</i>	Miranda <i>et al.</i> , 2017		Native species
	<i>Python regius</i>	Miranda <i>et al.</i> , 2017		Non-native species
Nicaragua	Snakes			
	<i>Boa constrictor</i>	Rimbaud <i>et al.</i> , 2006		Non-native species
Antigua	Snakes			
	<i>Alsophis antiguae</i>	Daltry <i>et al.</i> , 2001		Native species
Brazil	[<i>Mesomys ecaudatus</i>]	Ferreira da Silva <i>et al.</i> , 2018		
	Lizards			
	<i>Eryalius iheringii</i>	Mendoza-Roldan <i>et al.</i> , 2020b		Native species
	<i>Pogona vitticeps</i>	Mendoza-Roldan <i>et al.</i> , 2020b		Non-native species
	Snakes			
	<i>Boa constrictor constrictor</i>	Barbosa <i>et al.</i> , 2006	As <i>Python reticulatus</i>	Native species
	<i>Malayopython reticulatus</i>	Fonseca, 1933; Micherdzinski, 1980		Non-native species
	<i>Corallus hortullana</i>	Mendoza-Roldan <i>et al.</i> , 2020b	As <i>Corallus hortullanus</i>	Native species
	<i>Crotalus durissus</i>	Mendoza-Roldan <i>et al.</i> , 2020b	As <i>Crotalus durissus terrificus</i>	Native species
	<i>Pantherophis guttatus</i>	Almeida Pereira <i>et al.</i> , 2019	As <i>Pantherophis guttata</i>	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; Zemskaia, 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			
	<i>Leiosaurus bellii</i>	Mauri, 1967	As <i>Ophiodes striatus</i>	Native species
	<i>Teiurus teyou</i>	Mauri, 1967		Native species
	<i>Ophiodes fragilis</i>	Mauri, 1967		Native species
	Snakes			
	<i>Epicrates cenchria crassus</i>	Mauri, 1967		Native species
	<i>Helicops leopardine</i>	Mauri, 1967		Native species
	<i>Chironius carinatus</i>	Mauri, 1967		Native species
	<i>Erythrolamprus poecilogyrus</i>	Mauri, 1967	As <i>Leimadophis poecilogyrus</i>	Native species
	<i>Xenodon merremii</i>	Mauri, 1967		Native species
	<i>Lystrophis dorbignyi</i>	Mauri, 1967		Native species
	<i>Lystrophis semicinctus</i>	Mauri, 1967		Native species
	<i>Dipsas turgida</i>	Mauri, 1967	As <i>Sibynomorphus turgidus</i>	Native species
	<i>Imantodes cenchoa</i>	Mauri, 1967		Native species
	<i>Leptodeira annulata annulata</i>	Mauri, 1967		Native species
	<i>Clelia clelia</i>	Mauri, 1967	As <i>Pseudoboa cloelia</i>	Native species
	<i>Oxyrhopus rhombifer</i>	Mauri, 1967	As <i>Pseudoboa rhombifera</i>	Native species
	<i>Tomodon dorsatus</i>	Mauri, 1967		Native species
	<i>Tachymenis ocellata</i>	Mauri, 1967	As <i>Tomodon ocellatus</i>	Native species
	<i>Philodryas baroni</i>	Mauri, 1967		Native species
	<i>Philodryas patagoniensis</i>	Mauri, 1967	As <i>Philodryas schotti</i>	Native species
	<i>Erhythrolamptus aesculapii</i>	Mauri, 1967		Native species
	<i>Micrurus frontalis</i>	Mauri, 1967		Native species
	<i>Micrurus lemniscatus</i>	Mauri, 1967		Native species
	<i>Bothrops alternata</i>	Mauri, 1967		Native species
	<i>Bothrops ammodythoides</i>	Mauri, 1967		Native species
	<i>Bothrops jararacussu</i>	Mauri, 1967		Native species
	<i>Bothrops neuwiedii meridionalis</i>	Mauri, 1967		Native species
	<i>Crotalus terrificus terrificus</i>	Mauri, 1967		Native species
Australia and Oceania				
Australia	Lizards			
	<i>Amphibolurus muricatus</i>	Domrow, 1988		Native species
	<i>Carlia longipes</i>	Domrow, 1988		Native species
	<i>Chlamydosaurus kingie</i>	Domrow, 1988		Native species
	<i>Lacerta viridis</i>	Domrow, 1988		Non-native species
	<i>Tiliqua rugosa</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Tiliqua scincoides</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	Snakes			
	<i>Acanthophis antarcticus</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Antaresia children</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Aspidites ramsayi</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Hoplocephalus bitorquatus</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Hoplocephalus stephensii</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Liasis fuscus</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Morelia viridis</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Morelia spilota metcalfei</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Notechis scutatus</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Pseudechis porphyriacus</i>	Norval <i>et al.</i> , 2020, 2021		Native species
	<i>Pseudonaja textilis</i>	Norval <i>et al.</i> , 2020, 2021		Non-native species
	<i>Python bivittatus</i>	Norval <i>et al.</i> , 2020, 2021	As <i>Python molurus bivittatus</i>	Native species
<i>Tropidechis carinatus</i>	Norval <i>et al.</i> , 2020, 2021		Native species	
New Zealand	Lizards			
	<i>Tiliqua scincoides</i>	Heath, 1986		Non-native species
Country not stated	Lizards			
	<i>Sceloporus graciosus graciosus</i>	Radford, 1950		
	Snakes			
<i>Hierophis viridiflavus</i>	Radford, 1950	As <i>Coluber viridiflavus viridiflavus</i>		

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			
		<i>Echis carinatus</i>	Zemskaya, 1951		Non-native species
Undated	Moscow Zoo	Snakes			
		<i>Macrovipera lebetinus</i>	Bregetova, 1956	As <i>Vipera lebetina</i>	Native species
		<i>Platiceps karelini</i>		As <i>Coluber karelini</i>	Non-native species
1954–1955	Damchik section, Astrakhan’ Nature Reserve, Astrakhan’ oblast’ (Lower Volga region)	Snakes			
1959–1960		<i>Natrix natrix</i>	Markov <i>et al.</i> , 1964		Native species
		<i>Natrix tessellata</i>			Native species
		<i>Elaphe dione</i>			Native species
1973–1976	Manure pile, Cherniy Mys settlement, Kolyvan’ district, Novosibirsk oblast’ (Western Siberia)	Snakes			
		<i>Natrix natrix</i>	Belova & Grigoriev, 1981		Native species
2005	Bogdinsk-Baskunchak Nature Reserve, Astrakhan’ oblast’ (Lower Volga region)	Snakes			
		<i>Dolichophis caspius</i>	Bakiev, 2007		Native species
23–30 August 2008	South-Eastern part of Novosibirsk oblast’ (Western Siberia)	Snakes			
		<i>Gloydus halys</i>	Simonov & Zinchenko, 2010		Native species
Undated	Moscow Zoo	Snakes			
		<i>Simalia boeleni</i>	Vasiliev & Balakina, undated	As <i>Morelia boeleni</i>	Non-native species
April 2009	Moscow	Lizards			
		<i>Darevskia brauneri</i>	this paper, new record		Native species
		<i>Ophisops elegans</i>	this paper, new record		Native species
		Snakes			
		<i>Python regius</i>			Non-native species
		<i>Telescopus fallax</i>	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 20° C to 30° 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 gallotocolus* 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*, *Leptodeira*, 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 crocodylians, 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 crocodylian.

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-Gómez *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 temperature optimum (Mendyk, 2015). Maslova & Dochevov (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. saurorum* (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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