Ornithodorus
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Argasids have soft leathery bodies lacking a dorsal scutum and the capitulum is covered by the body. They are transient feeders on mammals and birds and have multi-host life-cycles, spending the majority of time hiding in cracks/crevices in the surrounding environment, especially nests and dens. Infestations by sand tampans (*Ornithodorus* spp.) occur on a wide range of mammalian hosts; some species causing allergy, toxicosis and paralysis as well as transmitting viral, bacterial and protozoal diseases.

Classification:

Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class:	Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass:	Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder:	Parasitiformes (ticks and some mites, with posterior stigmata)
Order:	Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family:	Argasidae (soft ticks, lack dorsal scutum, capitulum covered by body, hide in cracks/crevices)
Genus:	*Ornithodorus* (parasitic on skin of mammals)
Species:	various species cause anaemia and toxicosis in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and tarsi I each bearing a complex sensory pit (Haller's organ). They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 tick species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	Capitulum				Idiosoma				Usual no. of hosts
	location	basis capitulum	mouth-parts	palps	integument	festoons	eyes	male ventral plates	
Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Argasidae contains 5 subfamilies (Antricolinae, Argasinae, Nothoaspisinae, Ornithodorinae, Otobinae) which vary in morphology, biology, host range and specificity. Members of the subfamily Ornithodorinae have flat discoid bodies with a roughened mamillated integument but lacking distinct lateral margins. Two genera (*Alectorobius* and *Ornithodorus*) have been described as haematophagous ectoparasites on mammalian and avian hosts around the world. Members of the genus *Ornithodorus* (syn. *Ornithodoros*) are often nidicolous with 2 nymphal stages and adult ticks feeding on animals inhabiting nests, roosts, burrows and dens (larval stages develop within eggs and do not feed). Around 120 *Ornithodorus* spp. have been described from domestic and wild animals, sometimes in association with skin lesions and blood loss. Several species have been allocated to 7 subgenera (*O.* (*Alectorobius*), *O.* (*Alveonasus*), *O.* (*Ornithodorus*), *O.* (*Pavlovskyella*), *O.* (*Proknekalia*), *O.* (*Reticulinasus*), and *O.* (*Subparmatus*)), but the majority remain unplaced. In the few species whose life-cycles are known, the ticks appear to have a reasonably broad host specificity with nymphs and adults feeding intermittently on a small range of sympatric host species, often those sharing sandy habitats (hence the common name for many species as 'sand tampans'). Several species have also been shown to be efficient vectors for the transmission of viral and bacterial infectious diseases in livestock, especially relapsing fevers, Q fever and swine fever.

***Ornithodorus* species**	**Hosts**	**Clinical signs**	**Distribution**
O. acinus (syn. *Argas*)	host unknown, collected from caves		Africa
O. (*Pavlovskyella*) *alactagalis*	Carnivora: canid (fox), mustelid (European badger); Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: cricetid (European hamster, dwarf hamster, water vole), dipodid (small five-toed jerboa), murid (house mouse, jird, fat sand rat); Primates: hominid (human); Galliformes: phasianid (chicken); Sauria (unspecified lizard); Anura: bufonid (European green toad, burrow)	(vector for spirochaetosis, relapsing fever borreliosis)	Europe
O. (*Alectorobius*) *amblus* (syn. *Argas*)	Charadriiformes: larid (Inca tern); Pelecaniformes: pelecanid (Peruvian brown pelican); Sphenisciformes: spheniscid (Humboldt penguin); Suliformes: phalacrocoracid (red-legged cormorant, Guanay cormorant), sulid (Peruvian booby, blue-footed booby); Primates: hominid (human)	inflammation, pruritus	South America
O. anduzei	host unknown, collected from bat cave		South America
O. antiquus	fossil (amber)		Central America
O. apertus	Artiodactyla: suid (warthog, burrows); Rodentia: hystricid (porcupines, burrows)		Africa
O. aquilae	Accipitriformes: accipitrid (golden eagle, ferruginous hawk); Falconiformes: falconid (prairie falcon, American kestrel)		North America

O. arenicolous	Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: ctenodactylid (common gundi), murid (fat sand rat, Shaw's jird, lesser Egyptian gerbil); Sauria: agamid (Egyptian spiny-tailed lizard), varanid (unspecified monitor lizard)		Egypt
O. (*Pavlovskyella*) *asperus* (syn. *O. verrucosus*)	Rodentia: murid (great gerbil, red-tailed gerbil); Carnivora: canid (wolf, jackal, fox), mustelid (badger); Primates: hominid (human); Bucerotiformes: upupid (hoopoe); Coraciiformes: coraciid (roller); Galliformes: phasianid (chicken); Passeriformes: sturnid (starling); Testudines: testudinid (unspecified tortoise); Sauria: agamid (agama); Serpentes: colubrid (grass snake), viperid (blunt-nosed viper)	(vector for borreliosis)	Central Asia
O. atacamensis	Sauria: liolaemid (tree iguana), teiid (dwarf tegu)		South America
O. azteci	Chiroptera: emballonurid (lesser dog-like bat), mystacinid (short-tailed bat), noctilionid (lesser bulldog bat), phyllostomid (Aztec fruit-eating bat, Cuban fruit-eating bat, Jamaican fruit-eating bat, Waterhouse's leaf-nosed bat, Tome's sword-nosed bat, common vampire bat)		Central America
O. batuensis	Chiroptera: hipposiderid (diadem leaf-nosed bat), pteropodid (cave nectar bat, dusky fruit bat, western naked-backed fruit bat, Sulawesi rousette, Geoffroy's rousette, Leschenault's rousette, Lucas's short-nosed fruit bat), vespertilionid (narrow-winged pipistrelle, Temminck's bat)		South-East Asia
O. brasiliensis (mouro tick)	Artiodactyla: tayassuid (collared peccary); Carnivora: canid (dog), mephitid (Molina's hog-nosed skunk); Cingulata: dasypodid (southern long-nosed armadillo); Primates: hominid (human)	irritation, lesions, toxicosis	South America
O. brodyi	Chiroptera: emballonurid (proboscis bat), mormoopid (Parnell's mustached bat), phyllostomid (great fruit-eating bat, Aztec fruit-eating bat, Jamaican fruit-eating bat, big-eared woolly bat, Seba's short-tailed bat, Sowell's short-tailed bat, fringe-lipped bat, common vampire bat), vespertilionid (black myotis)		Central America
O. (*Alveonasus*) *buettikeri*	hosts unknown		Oman
O. (*Alectorobius*) *camicasi*	Chiroptera: pteropodid (Egyptian fruit bat)		Africa
O. (*Alveonasus*) *canestrinii* (syn. *Argas*)	Artiodactyla: bovid (sheep, goat, cattle, gazelle); Rodentia: caviid (guinea pig), murid (great gerbil); Galliformes: phasianid (chukar partridge)		Central Asia
O. (*Alectorobius*) *capensis* (seabird soft tick)	Anseriformes: anatid (duck); Charadriiformes: alcid (ancient murrelet), larid (western gull, silver gull, red-billed gull, black-tailed gull, kelp gull, Hermann's gull, common tern, sooty tern, spectacled tern, roseate tern, white tern, sandwich tern, greater crested tern, royal tern, common noddy, black noddy, brown noddy, blue noddy, lesser noddy), scolopacid (spotted sandpiper, ruddy turnstone); Galliformes: phasianid (chicken); Gruiformes: rallid (spotless crake); Pelecaniformes: pelecanid (brown pelican), threskiornithid (roseate spoonbill); Phaethontiformes: phaethontid (red-tailed tropicbird); Procellariiformes: diomedeid (black-footed albatross, Laysan albatross), hydrobatid (Markham's storm petrel), oceanitid (Polynesian storm petrel), procellariid (black-winged petrel, Bonnin petrel, Bulwer's petrel, Kermadec petrel, Phoenix petrel, little shearwater, streaked shearwater, wedge-tailed shearwater, Christmas shearwater); Strigiformes: strigid (burrowing owl); Suliformes: fregatid (lesser frigatebird, great frigatebird), phalacrocoracid (spotted shag, European shag, Brandt's cormorant), sulid (brown booby, masked booby, red-footed booby, Australasian gannet); Sphenisciformes: spheniscid (little penguin, Jackass penguin, African penguin); Lagomorpha: leporid (rabbit); Primates: hominid (human); Sauria: iguanid (marine iguana); Testudines: cheloniid (green sea turtle)	irritation (vector for Soldado virus, possibly West Nile virus, rickettsioses, Q fever)	Australia

O. (*Alectorobius*) *casebeeri*	Rodentia: cricetid (big-eared climbing rat, Stirton's deer mouse)		Central America
O. carvernicolous	Chiroptera: phyllostomid (pale spear-nosed bat, fringe-lipped bat, greater round-eared bat, Pallas's long-tongued bat, Seba's short-tailed bat, Geoffroy's tailless bat, flat-faced fruit-eating bat)		South America
O. cerradoensis	Rodentia: caviid (Brazilian guinea pig), echimyid (punare)		South America
O. (*Alectorobius*) *cheikhi*	Charadriiformes: larid (tern nesting sites)		North Africa
O. (*Alectorobius*) *chironectes*	Didelphimorphia: didelphid (water opossum); Rodentia: cricetid (hispid cotton rat)		Central America
O. (*Reticulinasus*) *chiropterphila*	Chiroptera: rhinolophid (rufous horseshoe bat)		India
O. cholodkovskyi	Chiroptera: rhinolophid (greater horseshoe bat); Rodentia: murid (unspecified rodent burrows)		Central Asia
O. (*Alectorobius*) *clarki*	Chiroptera: mormoopid (big naked-backed bat, Davy's naked-backed bat)		Central America
O. (*Alectorobius*) *collocaliae*	Apodiformes: apodid (cave swiftlet)		Indonesia
O. compactus	Testudines: testudinid (leopard tortoise, geometric tortoise, angulate tortoise, serrated tortoise, tent tortoise, Greek tortoise, great padloper, speckled padloper)		Africa
O. concanensis	Chiroptera: molossid (Mexican free-tailed bat), vespertilionid (big brown bat, tricolored bat, cave myotis, Townsend's big-eared bat); Accipitriformes: accipitrid (golden eagle, red-tailed hawk); Falconiformes: falconid (prairie falcon); Passeriformes: hirundinid (cave swallow, cliff swallow)		North America
O. (*Alectorobius*) *coniceps*	Anseriformes: anatid (ruddy shelduck, common scoter); Apodiformes: apodid (house swift); Charadriiformes: larid (Pallas's gull, common tern, sandwich tern, roseate tern); Columbiformes: columbid (domestic pigeon, wood pigeon, African rock pigeon, rock dove); Galliformes: phasianid (chicken); Passeriformes: hirundinid (swallow, crag martin), passerid (house sparrow, rock sparrow); Pelecaniformes: pelecanid (Dalmatian pelican); Suliformes: phalacrocoracid (great cormorant); Artiodactyla: bovid (sheep); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), murid (mouse); Chiroptera: vespertilionid (Kuhl's pipistrelle); Primates: hominid (human)	irritation (vector for avian spirochaetosis, Baku virus, possibly West Nile virus)	Mediterranean
O. coprophilus (now *Antricola*)	Chiroptera: phyllostomid (Waterhouse's leaf-nosed bat) plus several collections from bat guano		North America
O. (Ornamentum) coriaceus (pajaroello tick)	Artiodactyla: bovid (cattle, sheep), cervid (white-tailed deer, black-tailed deer, mule deer); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: cricetid (deermouse), murid (mouse, rat), sciurid (squirrel, chipmunk); Primates: (unspecified monkey), hominid (human); Galliformes: phasianid (chicken); Passeriformes: hirundinid (cliff swallow)	painful bite, irritation [plus vector for African swine fever, epizootic bovine abortion)]	Americas
O. cyclurae	Sauria: iguanid (Cuban rock iguana)		Cuba
O. darwini	Sauria: iguanid (marine iguana, Galapagos land iguana)		Galapagos Islands
O. davisi	Rodentia: cricetid (yellowish rice rat)		South America
O. (*Alveonasus*) *delanoei* (syn. *Argas*)	Rodentia: caviid (guinea pig), hystricid (crested porcupine); Eulipotyphla: erinaceid (long-eared hedgehog)		Central Asia
O. (Alectorobius) denmarki	Charadriiformes: larid (common noddy, brown noddy, black tern, sooty tern, unspecified gull nests); Suliformes: sulid (brown booby)		North America
O. dugesi	Rodentia: cricetid (white-throated woodrat, nest); Artiodactyla: suid (pig); Chiroptera (unspecified bat); Primates: hominid (human)	(vector for African swine fever)	Americas
O. dunni	Chiroptera: noctilionid (lesser bulldog bat); Rodentia: caviid (guinea pig), murid (white rat)		Central America

O. dusbabeki	Chiroptera: molossid (velvety free-tailed bat, black mastiff bat, Pallas's mastiff bat), noctilionid (greater bulldog bat), phyllostomid (Jamaican fruit bat), vespertilionid (big brown bat)		Cuba
O. (Alectorobius) dyeri	Chiroptera: emballonurid (gray sac-winged bat, lesser dog-like bat), mormoopid (Parnell's moustached bat), phyllostomid (fringe-lipped bat, lesser long-nosed bat, Waterhouse's leaf-nosed bat, California leaf-nosed bat, Cozumelan golden bat), vespertilionid (fish-eating bat)		Americas
O. eboris (syn. *Argas*)	Rodentia: hystricid (porcupine, burrow)		Africa
O. echimys	Rodentia: echimyid (speckled spiny tree-rat)		South America
O. (Alectorobius) elongatus	host unknown, recovered from crate		Central America
O. eptesicus	Chiroptera: vespertilionid (Argentine brown bat)		South America
O. eremicus	Rodentia: cricetid (deer mouse)		North America
O. (*Pavlovskyella*) *erraticus* (species complex incl. *O. costalis, kairouanensis, marocanus, merionesi, normandi, occidentalis, rupestris, sonrai, Argas erraticus*) (European soft tick, sand tampan)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig, boar); Carnivora: canid (Egyptian red fox); Eulipotyphla: erinaceid (long-eared hedgehog), soricid (African giant shrew); Rodentia: cricetid (golden hamster), hystricid (crested porcupine), murid (house mouse, common spiny mouse, fat sand rat, African grass rat, black rat, pleasant gerbil, pygmy gerbil, slender gerbil, Cheesman's gerbil, Harwood's gerbil, Sundevall's jird, Shaw's jird), nesomyid (Gambian pouched rat), sciurid (striped ground squirrel, burrow); Chiroptera (unspecified bat); Primates: hominid (human); Sauria: agamid (Egyptian spiny-tail lizard), scincid (common skink), varanid (Nile monitor); Serpentes: viperid (puff adder); Anura: bufonid (western leopard toad, Berber toad, African toad, European green toad); Passeriformes: acrocephalid (tree warbler), muscicapid (unspecified chat); Strigiformes: strigid (burrowing owl, little owl)	irritation (vector for Q fever, borreliosis (tick-borne relapsing fever) and African swine fever)	Europe, Africa, Middle East
O. faccinii	Anura: bufonid (ornate forest toad), cycloramphid (rock river frog)		South America
O. (*Reticulinasus*) *faini*	Chiroptera: pteropodid (Egyptian fruit bat, Leschenault's rousette)		Africa
O. foleyi (syn. *Argas*)	Artiodactyla: bovid (zebu, goat), camelid (dromedary); Primates: hominid (human)		Africa
O. (Alectorobius) fonsecai	Chiroptera: emballonurid (lesser dog-like bat), phyllostomid (Seba's short-tailed bat, fringe-lipped bat, common vampire bat)		South America
O. (Alectorobius) furcosus	Artiodactyla: suid (pig); Rodentia: caviid (guinea pig), murid (rat); Lagomorpha: leporid (rabbit); Primates: hominid (human); Columbiformes: columbid (pigeon)	(possible vector for borreliosis and Mexican spotted fever)	South America
O. galapagensis	Sauria: iguanid (marine iguana), tropidurid (Galapagos lava lizard); Passeriformes: thraupid (small ground finch)		Galapagos Islands
O. graingeri	Chiroptera: megadermatid (vampire bat), nycterid (Egyptian slit-faced bat), rhinolophid (horseshoe bat); Rodentia: hystricid (porcupine); Primates: hominid (human)		Africa
O. (Alectorobius) grenieri	Rodentia: nesomyid (Malagasy giant rat, burrow)		Madagascar
O. guaporensis	host unknown, collected from bat roosts		South America
O. (*Ornamentum*) *gurneyi* (syn. *Argas*) (kangaroo soft tick)	Diprotodontia: macropodid (red kangaroo, eastern grey kangaroo, common wallaroo); Rodentia: murid (rat, mouse); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Sauria: agamid (bearded dragon), scincid (sleepy lizard)	irritation (vector for Q fever)	Australia
O. (Alectorobius) hadiae	Chiroptera: pteropodid (Geoffroy's rousette, greenish naked-backed fruit bat, lesser short-nosed fruit bat)		Indonesia
O. hasei (syn. *Argas*)	Chiroptera: emballonurid (sac-winged bat), molossid (velvety free-tailed bat, black mastiff bat, dwarf dog-faced bat, Mato		South America

	Grosso dog-faced bat), mormoopid (ghost-faced bat, Davy's naked-backed bat), noctilionid (lesser bulldog bat, greater bulldog bat), phyllostomid (flat-faced fruit-eating bat, stripe-headed round-eared bat, pygmy round-eared bat, little yellow-shouldered bat, Salvin's big-eyed bat, great fruit-eating bat, dwarf little fruit bat, Antillean fruit-eating bat, Jamaican fruit bat, Miller's long-tongued bat, greater spear-nosed bat, Orinoco sword-nosed bat, striped hairy-nosed bat, brown tent-making bat, fringe-lipped bat, common vampire bat), vespertilionid (black myotis, cave myotis, solver-tipped myotis, Thomas's big-eared brown bat, tiny yellow bat); Rodentia: cricetid (northern grass mouse)		
O. hermsi (sand tampan)	Rodentia: cricetid (eastern deer mouse), murid (canyon mouse, bushy-tailed wood rat, desert wood rat), sciurid (western chipmunk, American red squirrel, golden-mantled ground squirrel, tree squirrel); Chiroptera: vespertilionid (mouse-eared bat); Primates: hominid (human); Passeriformes: turdid (bluebird), tyrannid (Say's phoebe); Piciformes: picid (unspecified woodpecker)	irritation (vector for borreliosis (relapsing fever) and African swine fever)	North America
O. (*Ornithodorus*) *huajianensis*	Rodentia: sciurid (Tarbagan marmot)		China
O. (*Ornithodorus*) *indica*	Artiodactyla: cervid (Indian muntjac)		India
O. jerseyi	fossil (amber)		Central America
O. (Alectorobius) jul	host unknown, collected from bat cave		South America
O. (Alectorobius) kelleyi	Chiroptera: molossid (Mexican free-tailed bat), vespertilionid (big brown bat, little brown bat, pallid bat, tricolored bat, canyon bat, eastern small-footed myotis, western small-footed myotis, California myotis, Rafinesque's big-eared bat); Rodentia: caviid (guinea pig), murid (white rat); Primates: hominid (human)		North America
O. (Alectorobius) knoxjonesi	Chiroptera: emballonurid (gray sac-winged bat)		Central America
O. (*Alectorobius*) *kohlsi* (syn. O. *boliviensis*)	Chiroptera: molossid (velvety free-tailed bat, Sinaloan mastiff bat), vespertilionid (black myotis); Primates: hominid (human)		South America
O. lahillei	Sauria: teiid (dwarf tegu); Serpentes: colubrid (Chilean green racer)		South America
O. (*Alectorobius*) *lahorensis* (syn. *Argas*) (sand tampan)	Artiodactyla: bovid (sheep, argali, goat, Afghan urial, cattle), camelid (camel); Perissodactyla: equid (horse, donkey); Rodentia: caviid (guinea pig), murid (mouse); Lagomorpha: leporid (European hare); Carnivora: canid (dog); Primates: hominid (human); Galliformes: phasianid (chicken) (2-host cycle)	irritation, anaemia, toxicosis, paralysis (vector for brucellosis, Q fever, tularemia, anaplasmosis, piroplasmosis, Persian relapsing fever)	Eurasia
O. (*Pavlovskyella*) *macmillani*	Diprotodontia: phalangerid (common brushtail possum); Psittaciformes: cacatuid (galah); Strigiformes: strigid (southern boobook owl, morepork)		Australia
O. (*Reticulinasus*) *madagascariensis*	Chiroptera: pteropodid (cave-inhabiting fruit bats)		Madagascar
O. (*Subparmatus*) *marinkellei*	Chiroptera: mormoopid (big naked-backed bat, Wagner's mustached bat, Parnell's mustached bat)		South America
O. (*Alectorobius*) *maritimus*	Charadriiformes: alcid (common murre, razor-billed auk), larid (common tern, roseate tern, sandwich tern, herring gull, yellow-legged gull, black-legged kittiwake); Pelecaniformes: ardeid (little egret); Suliformes: phalacrocoracid (great cormorant, European shag); Primates: hominid (human)	irritation, weight loss, reduced growth (vector for Soldado virus)	Europe
O. (*Alectorobius*) *marmosae*	Didelphimorphia: didelphid (Robinson's mouse opossum); Rodentia: cricetid (climbing mouse)		South America
O. (Alectorobius) microlophi	Sauria: tropidurid (four-banded Pacific iguana, Atacamen Pacific iguana)		South America

O. mimon	Chiroptera: phyllostomid (striped hairy-nosed bat), vespertilionid (big-eared brown bat, Brazilian brown bat, Argentine brown bat, diminutive serotine); Didelphimorphia: didelphid (white-eared opossum, agile gracile opossum, Paraguayan fat-tailed mouse opossum); Rodentia: cricetid (small-footed bristly mouse); Primates: hominid (human); Passeriformes: dendrocolaptid (straight-belled woodcreeper, narrow-billed woodcreeper, buff-throated woodcreeper), thraupid (grey-headed tanager)		South America
O. montensis	Anura: bufonid (terrestrial toad)		South America
O. (*Subparmatus*) *mormoops*	Chiroptera: mormoopid (leaf-chinned bat), phyllostomid (Waterhouse's leaf-nosed bat)		Central America
O. moubata (syn. *Argas*) (sand tampan, eyeless tampan, hut tampan, African tampan)	Artiodactyla: bovid (cattle, sheep, goat, Lichtenstein's hartebeest, waterbuck), giraffid (giraffe), suid (pig, common warthog, desert warthog); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), hystricid (Cape porcupine), murid (mouse), nesomyid (Gambian pouched rat); Tubulidentata: orycteropodid (aardvark); Pholidota: manid (ground pangolin); Carnivora: canid (dog), felid (cat, lion); Chiroptera: pteropodid (straw-coloured fruit bat); Primates: cercopithecid (guenon), hominid (human); Galliformes: phasianid (chicken, turkey); Sauria: chamaeleonid (chameleon), gekkonid (tropical house gecko), gerrhosaurid (black-lined plated lizard); Serpentes: viperid (puff adder, rhombic night adder, blunt-nosed viper); Testudines: testudinid (greater padloper, serrated tortoise, tent tortoise)	irritation (vector for borreliosis (African relapsing fever), aegyptianellosis, spirochaetosis, trypanosomes, African swine fever, Q fever)	Africa, Middle East
O. (*Alectorobius*) *muesebecki*	Suliformes: sulid (masked booby); Primates: hominid (human)		Africa
O. (Alectorobius) multisetosus	Chiroptera: pteropodid (bare-backed fruit bat, greenish naked-backed fruit bat)		Indonesia, New Guinea
O. (Alectorobius) natalinus	Chiroptera: natalid (Gervais's funnel-eared bat)		Cuba
O. nicollei	Carnivora: canid (dog, coyote); Rodentia: cricetid (Allen's wood rat, swamp rat), sciurid (squirrel); Primates: hominid (human); Serpentes: viperid (sidewinder, Florida diamond-back rattlesnake)		Mexico
O. normandi	Rodentia: murid (Shaw's jird, rat); Primates: hominid (human)	(vector for borreliosis)	South America
O. octodontus	Rodentia: octodontid (common degu)		South America
O. (Alectorobius) papuensis	Chiroptera: pteropodid (bare-backed fruit bat, greenish naked-backed fruit bat, common tube-nosed fruit bat, cave nectar bat)		Indonesia
O. parkeri (syn. *O. wheeleri*) (sand tampan)	Rodentia: cricetid (deer mouse, southern grasshopper mouse, pack rat, sagebrush vole), heteromyid (chisel-toothed kangaroo rat), mustelid (weasel), sciurid (white-faced prairie dog, marmot, golden-mantled ground squirrel, California ground squirrel, Columbian ground squirrel, Richardson's ground squirrel, least chipmunk); Lagomorpha: leporid (cottontail, black-tailed jackrabbit, hare); Carnivora: canid (kit fox), mustelid (weasel); Primates: hominid (human); Strigiformes: strigid (burrowing owl); Testudines: testudinid (desert tortoise)	irritation, allergic reactions [plus vectors for borreliosis (relapsing fever), Rocky Mountain spotted fever, African swine fever]	Africa, Europe, North America
O. (*Alveonasus*) *peringueyi*	Passeriformes: hirundinid (cliff swallow)		Africa
O. (*Alveonasus*) *peusi*	Passeriformes: hirundinid (red-rumped swallow), sittid (western rock nuthatch)		Africa
O. (Alectorobius) peruvianus	Chiroptera: molossid (velvety free-tailed bat), phyllostomid (long-tongued bat, common vampire bat)		South America
O. (Alectorobius) piriformis	Chiroptera: miniopterid (common bentwing bat), pteropodid (Leschenault's rousette)		India
O. porcinus (syn. *O. moubata*	Artiodactyla: bovid (cattle, zebu), suid (pig, bushpig, warthog); Rodentia: hystricid (porcupine); Tubulidentata:	irritation [plus vectors for	Africa, Europe

porcinus) (incl. subspp. *avivora, domestica, porcinus*) (eyed tampan)	orycteropodid (aardvark); Pholidota: manid (ground pangolin); Carnivora: canid (dog), felid (cat); Primates: hominid (human); Galliformes: phasianid (chicken)	African swine fever]	
O. (Alectorobius) procaviae	Hyracoidea: procaviid (rock hyrax)		Middle-East
O. (Alectorobius) pteropteryx	Chiroptera: emballonurid (lesser dog-like bat)		South America
O. puertoricensis	Rodentia: cricetid (swamp rat), echimyid (Guyenne spiny rat), murid (brown rat, black rat); Lagomorpha: leporid (forest cottontail); Carnivora: felid (cat), herpestid (mongoose); Primates: hominid (human): Galliformes: phasianid (chicken); Strigiformes: strigid (burrowing owl)		Central America
O. quilinensis	Rodentia: cricteid (central leaf-eared mouse)		South America
O. (*Reticulinasus*) *rennellensis*	Chiroptera: pteropodid (Solomon's naked-backed fruit bat)		Solomon Islands, New Guinea
O. rietcorreai	Rodentia: caviid (rock cavy)		South America
O. (*Alectorobius*) *rioplatensis*	Carnivora: mephitid (Molina's hog-nosed skunk); Rodentia: caviid (cavy), cricteid (naked-soled conyrat, rice rat); Sauria: liolaemid (James's tree iguana, high mountain lizard), phyllodactylid (Uruguay marked gecko)		South America
O. (*Alectorobius*) *rondoniensis*	Chiroptera (unspecified bat, caves)		South America
O. (*Alectorobius*) *rossi*	Chiroptera: phyllostomid (greater long-nosed bat, California leaf-nosed bat, Waterhouse's leaf-nosed bat, yellow-shouldered bat, long-tongued bat), vespertilionid (big brown bat, canyon bat)		North America
O. rostratus (syn. *O. nattereri*)	Artiodactyla: bovid (cattle, goat), suid (pig), tayassuid (peccary); Rodentia: murid (mouse); Lagomorpha: leporid (rabbit); Carnivora: canid (dog); Primates: hominid (human)	pruritus (vector for rickettsiosis and possibly Q fever)	South America
O. rudis (syn. *O. venezuelensis*) (sand tampan)	Rodentia: dasyproctid (agouti), murid (mouse, rat); Primates: hominid (human); Galliformes: phasianid (chicken) and other unspecified bird nests	irritation (vector for borreliosis (relapsing fever))	Americas
O. salahi	Chiroptera: pteropodid (Egyptian rousette)		Egypt
O. saraivai	Anura: cycloramphid (Boraceia button frog)		South America
O. savignyi (syn. *Argas, A. schinzii, O. morbillosus, pavimentosus*) (sand tampan, eyed tampan)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel), cervid (deer), giraffid (giraffe), suid (pig); Perissodactyla: equid (horse), rhinocerotid (rhinoceros); Carnivora: canid (dog), felid (lion); Primates: cercopithecid (crab-eating macaque), hominid (human); Galliformes: phasianid (chicken, turkey)	irritation, allergic reactions, toxicosis, paralysis (vector for Alkhurma haemorrhagic fever)	Africa, Middle East, India
O. (Alectorobius) sawaii	Procellariiformes: procellariid (streaked shearwater)		Japan
O. (Alectorobius) setosus	Chiroptera: molossid (broad-eared bat), mormoopid (Parnell's mustached bat, Wagner's mustached bat)		Americas
O. (*Reticulinasus*) *solomonis*	Chiroptera: pteropodid (unspecified flying fox, cave)		Solomon Islands
O. (Alectorobius) sparnus (syn. *Otobius*)	Rodentia: cricetid (desert woodrat, bushy-tailed woodrat, eastern deer mouse, canyon mouse, pinyon mouse, northern grasshopper mouse), heteromyid (long-tailed pocket mouse); Artiodactyla: cervid (unspecified deer)		North America
O. (*Alectorobius*) *spheniscus*	Sphenisciformes: spheniscid (Humboldt penguin); Primates: hominid (human)		South America
O. (Alectorobius) stageri	Chiroptera: molossid (Mexican free-tailed bat), vespertilionid (cave myotis, pallid bat); Primates: hominid (human)		Americas
O. steini (syn. *Argas*, *Carios*)	Chiroptera: pteropodid (cave nectar bat, Sulawesi rousette, Geoffroy's rousette, Leschenault's rousette, western naked-backed fruit bat, dusky fruit bat)		Asia

O. tabajara	Rodentia: caviid (rock cavy)		South America
O. (*Alectorobius*) *tadaridae*	Chiroptera: molossid (free-tailed bat)		Cuba
O. (*Alectorobius*) *talaje* (syn. *Argas, A. coniceps)*	Artiodactyla: bovid (cattle), camelid (llama, guanaco), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Rodentia: caviid (Spix's yellow-toothed cavy, rock cavy), cricetid (hispid cotton rat, Brazilian pygmy rice rat, terraced rice rat, Amazon marsh rat, white-throated woodrat, eastern woodrat, Southern Plains woodrat, pack rat, vesper mouse, cane mouse), echimyid (common punare, white-spined Atlantic spiny rat, Ihering's Atlantic spiny rat), heteromyid (Ord's kangaroo rat, desert kangaroo rat, hispid pocket mouse), murid (brown rat, black rat, mouse), nesomyid (Gambian pouched rat), sciurid (California ground squirrel, Mexican ground squirrel, round-tailed ground squirrel); Didelphimorphia: didelphid (southern opossum, white-eared opossum, gray short-tailed opossum); Carnivora: canid (dog), felid (cat); Chiroptera: vespertilionid (tropical big-eared brown bat, brown long-eared bat); Primates: atelid (mantled howler monkey), cebid (Colombian white-faced capuchin, squirrel monkey), cercopithecid (rhesus macaque), hominid (human); Charadriiformes: larid (brown noddy, sooty tern, Pallas's gull); Galliformes: phasianid (chicken); Passeriformes: furnariid (plain thornbird); Pelecaniformes: pelecanid (Dalmatian pelican); Sphenisciformes: spheniscid (little penguin, African penguin); Strigiformes: strigid (burrowing owl); Suliformes: phalacrocoracid (great cormorant), sulid (blue-footed booby); Sauria: lacertid (unspecified lizard); Serpentes: boid (boa, rainbow boa), pythonid (reticulated python)	(vector for borreliosis)	Americas
O. tartakovskyi	Rodentia: cricetid (hamster, Afghan vole), dipodid (small five-toed jerboa, northern three-toed jerboa, Bobrinski's jerboa, Severtzov's jerboa), hystricid (crested porcupine), murid (great gerbil, red-tailed gerbil, Libyan jird, Persian jird, Tamarisk jird, midday jird, short-tailed bandicoot rat), sciurid (yellow ground squirrel, red-cheeked ground squirrel, long-clawed ground squirrel); Eulipotyphla: erinaceid (long-eared hedgehog); Lagomorpha: ochotonid (Afghan pika); Carnivora: canid (red fox, jackal), mustelid (steppe polecat, marbled polecat, least weasel); Primates: hominid (human); Anseriformes: anatid (common shelduck); Passeriformes: passerid (house sparrow); Strigiformes: strigid (little owl); Testudines: testudinid (Mediterranean tortoise, Russian tortoise, steppe turtle); Anura: bufonid (European green toad); Sauria: agamid (steppe agama), anguid (European glass lizard), gekkonid (frog-eyed gecko), lacertid (reticulate racerunner), varanid (desert monitor); Serpentes: boid (dwarf sand boa), viperid (Halys pit viper)	(vector for borreliosis)	Russia
O. (*Pavlovskyella*) *tholozani* (syn. *O. crassi, p*apillipes, *Argas*) (sand tampan)	Artiodactyla: bovid (cattle, zebu, sheep, goat), camelid (Bactrian camel); Eulipotyphla: erinaceid (hedgehog); Rodentia: caviid (guinea pig), cricetid (golden hamster), hystricid (crested porcupine), murid (fat sand rat, great gerbil, Libyan jird, spiny mouse); Lagomorpha: leporid (rabbit); Carnivora: canid (dog, jackal, fox), mustelid (European badger); Chiroptera: rhinopomatid (mouse-tailed bat); Primates: hominid (human) and unspecified monkey; Columbiformes: columbid (rock pigeon), Galliformes: phasianid (chicken); Sauria: gekkonid (unspecified gecko)	irritation [plus vector for Persian relapsing fever, possibly Q fever, borreliosis, West Nile virus, Karshi virus, Kyasanur forest disease virus]	Africa, Eurasia
O. (*Alectorobius*) *tiptoni*	Chiroptera: noctilionid (greater bulldog bat)		South America
O. transversus	Testudines: testudinid (Galapagos giant tortoise)		Galapagos Islands
O. (*Alectorobius*)	Artiodactyla: bovid (cattle, sheep), camelid (llama, guanaco),	irritation, toxicosis,	North America

turicata (syn. *Argas, O. americanus, venezuelensis*) (sand tampan, relapsing fever tick)	cervid (deer), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Eulipotyphla: talpid (mole); Rodentia: cricetid (pack rat, Southern Plains woodrat, northern grasshopper mouse), geomyid (tuza), heteromyid (kangaroo rat), murid (rat), sciurid (Fisher ground squirrel, California ground squirrel, spotted ground squirrel, thirteen-lined ground squirrel, black-tailed prairie dog); Lagomorpha: leporid (rabbit, black-tailed jackrabbit, desert cottontail); Primates: hominid (human); Strigiformes: strigid (burrowing owl); Testudines: testudinid (gopher tortoise, desert tortoise, yellow-marginated tortoise), emydid (western box turtle), Anura: ranid (gopher frog); Serpentes: viperid (unspecified rattlesnake)	allergies [plus vectors for Q fever, borreliosis (relapsing fever), and African swine fever]	
O. (Alectorobius) tuttlei	Rodentia: dasyproctid (agouti); Perissodactyla: tapirid (South American tapir)		South America
O. (*Proknekalia*) *vansomereni* (syn. *Argas*)	Passeriformes: hirundinid (lesser striped swallow, red-rumped swallow), muscicapid (mocking cliff chat)		Africa
O. viguerasi	Chiroptera: mormoopid (Peter's ghost-faced bat, Davy's naked-backed bat, sooty mustached bat, Parnell's mustached bat), phyllostomid (Cuban fruit-eating bat, Cuban flower bat)		Cuba
O. xerophylus	Rodentia: cricetid (central leaf-eared mouse)		South America
O. yumatensis	Chiroptera: phyllostomid (great fruit-eating bat, Aztec fruit-eating bat, Jamaican fruit bat, Waterhouse's leaf-nosed bat, common vampire bat), vespertilionid (cave myotis, southern myotis, Yuma myotis, tricolored bat, Mexican big-eared bat, Rafinesque's big-eared bat, Townsend's big-eared bat); Primates: hominid (human)		North America
O. (*Alectorobius*) *yunkeri*	Charadriiformes: larid (spectacled tern); Procellariiformes: diomedeid (waved albatross); Sphenisciformes: spheniscid (Galapagos penguin); Suliformes: phalacrocoracid (flightless cormorant), sulid (blue-footed booby); Sauria: iguanid (marine iguana, beach); Carnivora: otariid (Galapagos sea lion, beach)		Galapagos Islands
O. zumpti	Carnivora: herpestid (yellow mongoose); Rodentia murid (four-striped grass mouse, rock rat, Saunder's vlei rat, Indian gerbil)		Africa

Parasite morphology: Sand tampans, *Ornithodorus* spp., form 4 different types of morphological stages during their development: eggs; larvae; nymphs; and adults. Eggs are oval-spherical measuring around 0.5 mm long and are surrounded by a translucent brown-red waxy layer. Larvae have subglobular bodies measuring 0.5-0.9 mm in length and they are covered by a tan-brown smooth cuticle. They have 6 pale tan-coloured legs attached to the anterior half of the body and protruding beyond the lateral margins. They have anterior mouthparts that also project beyond the body margin. Larvae lack respiratory stigmata and tracheae as respiration and water regulation occurs through the tegument. Nymphs have ovate-ellipsoidal dorsoventrally-flattened bodies when unfed, but become swollen and subglobular when engorged. *Ornithodorus* spp. have 4-7 nymphal instars growing up to 3-7 mm long depending on the species. They are usually tan-dark brown in colour and sometimes have dark irregular patterns. The cuticle appears rough in texture due to the presence of numerous small tubercles or mammillae (rounded bumps), sometimes with tiny reticulated folds. Nymphs have a pair of respiratory stigmata often surrounded by circular-oval plates and they typically have 8 long thin tan legs projecting beyond the anterior lateral margins of the body. The heads of early nymphal instars, particularly unfed stages, may be visible in dorsal view, but those of mature and engorged instars are usually located underneath the idiosoma and are not seen dorsally. Adult ticks have sac-like globular bodies that appear partially flattened when unfed but become dorsally convex when engorged. They typically have rounded or pyriform profiles, but the dorsal and ventral surfaces meet without forming a lateral margin or suture (whereas a suture is present in *Argas* spp.). They range in size from 4-15 mm long and are covered by unsclerotized leathery cuticles with wrinkled roughened surfaces due to the presence of numerous small rounded raised areas (mammillae), sometimes with fine irregular folds (in contrast, ixodid ticks have sclerotized dorsal plates). Adults may be grey, tan, orange, dark brown and even light red in colour, many pale species often turning blue to dark red after feeding. Most species are inornate but several species are ornate and have areas with pale reticulated cuticular patterns. All ticks have 2 main tagma, the head (capitulum) and the body (idiosoma). In argasids, the capitulum is hidden in a ventral depression (camerostome) underneath the anterior idiosoma and is not visible in dorsal view (whereas that of ixodid ticks projects forwards and is visible dorsally). It lacks porose areas which are present on the dorsal surfaces of ixodid females. The capitulum consists of the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma (feeding structure comprising 2 palps, 2 chelicerae and toothed hypostome). The mouthparts are small relative to body size but are well adapted for piercing skin and sucking blood. The sensory palps move

laterally and do not enter the skin when feeding (ticks lack antennae). Each palp has 4 segments of equal length (unlike ixodids where they are not equal), although the last segment may appear slightly smaller as it is located in a recess in segment 3 and fitted with small setae. The specialized chelicerae are used for cutting the skin of the host enabling soft ticks to reach down to dermal capillaries. The chelicerae have 2 segments and are tubular with long curved shafts in spinose sheaths, ending in 2 cutting digits with recurved teeth. They have a horizontal cutting action, ripping and tearing flesh to form a small pool of blood. The hypostome is then inserted into the blood pool to facilitate feeding as well as anchoring the tick to the host. The hypostome is an extension of the basis capitulum and is dentate with backward-facing teeth. The alimentary tract consists of an anterior buccal canal (formed dorsally by the chelicerae and ventrally by the hypostome), paired salivary glands (like clusters of grapes), muscular pharynx (with pharyngeal valve), tubular oesophagus, large saccular midgut (stomach or ventriculus) with several pairs of branched diverticula (caeca) with excretory elements (Malpighian tubules and coxal glands) with a short tube leading to the vesicular rectal sac (analogue of hindgut in ticks) and subterminal ventral anus. The idiosoma lacks hard sclerotized plates (only present on ixodids) and consists of an anterior podosoma (with legs and genital pore) and a posterior opisthosoma (area behind coxae bearing spiracles and anus). Argasids have small respiratory spiracular plates (stigmata) located between coxae III and IV (whereas ixodids have large spiracular plates behind coxae IV). Most species lack eyes, but a few species have simple eyes located laterally in supracoxal folds (e.g. *O. savignyi* and *O. coriaceus*). The podosoma bears 8 long slender legs, each with 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) often bearing distinct humps and all ending in a pair of claws without pad-like pulvilli (present in ixodids). The coxae lack spur-like projections (present in ixodids) and the dorsal tarsus I has a unique sensory apparatus (Haller's organ) with an anterior pit and posterior capsule (used for odor, temperature, light and mechanical sensation). Argasids generally show limited sexual dimorphism, although females are able to engorge to several times the size of males and they have wider genital apertures. Females have a single saccular ovary (grape-like when gravid) with paired tubular oviducts (with distal ampulla) leading to a common uterus (with associated accessory glands) opening to the vagina (with cervical and vestibular regions). The cervical region acts as a receptaculum seminis and the vestibular vagina actively prolapses during oviposition. The genital aperture consists of a transverse slit (wider than long) surrounded by a prominent fold and connected to special Gene's organs which produce waxy egg coatings during oviposition. Males have 2 testes connected by tubular vas efferentia to a common vas deferens with a large multilobed accessory gland leading to the ejaculatory duct. The genital aperture is circular to crescent-shaped without an apron and without external genitalia. Males produce spermatophores (packets of spermatids) which are grasped by his chelicerae and placed under the genital operculum of females.

Site of infection: Nymphs, adults and sometimes larvae of *Ornithodorus* spp. are ectoparasitic on a range of vertebrate hosts, including mammals (belonging to 60 families in 14 orders, including ungulates, marsupials, small herbivores, carnivores, bats, rodents, primates), birds (belonging to 11 passeriform and 27 non-passeriform families in 18 orders, including seabirds, shorebirds, waterbirds, fowl, birds of prey), reptiles (13 lizard families, 4 snake families, 3 tortoise families) and amphibians (3 frog/toad families). The parasites crawl onto hosts to feed on blood and then drop off into the surrounding environment, many species burrowing into sandy soil and others being nidicolous (dwelling in nest/burrows). Ticks have often been found feeding on hosts in sites that are difficult to groom (such as the head, neck and belly) but they may also occur more widespread on other body regions (legs, shoulders, flanks and under the wings of birds).

Pathogenesis: Sand tampans are haematophagous and use their piercing/sucking mouthparts to cut the skin of the host and suck blood from pools of blood forming in the dermis (process known as telmophagy). Even though ticks feed transiently and feeding times are short (around 30 minutes), their bites can be painful and cause considerable irritation with tissue trauma, inflammation (erythema, oedema), pruritus, and occasional focal haemorrhages and necrosis. During feeding, ticks inject saliva containing various vasoactive compounds with cytolytic, anticoagulant, vasodilatory, and vascular permeability activities, and the saliva of some species is also thought to contain analgesic compounds. Individual hosts may develop allergic or hypersensitivity reactions to salivary compounds, which exacerbates skin lesions and exaggerates host responses. Some species (e.g. *O. savignyi* and *O. lahorensis*) may even cause signs of paralysis in domestic livestock, not from any neurotoxic components in saliva but from toxicosis reactions involving rashes, tracheopharyngeal compression and muscle weakness. Infested animals may suffer severe biting stress, particularly tethered or housed animals. They may attempt to groom affected areas by licking, preening, biting or scratching, sometimes leading to self-trauma which can lead to open wounds susceptible to secondary bacterial infections. Heavy infestations may also cause significant blood loss manifest as anaemia, which can sometimes be fatal. Domestic livestock may not feed efficiently with consequential meat and/or milk production losses. The ticks may also act as efficient vectors (biological and/or mechanical) for the transmission of infectious diseases caused by arboviruses (including African swine fever virus), bacteria (various *Borrelia* spp. causing relapsing fever, *Brucella* spp. causing brucellosis, *Coxiella* sp. causing Q fever, *Francisella* sp. causing tularaemia, *Pajaroellobacter* sp. causing epizootic bovine abortion) and haemoprotozoans (*Theileria* spp. causing piroplasmosis).

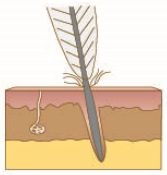
Developmental cycle and mode of transmission: Like all ticks, *Ornithodorus* spp. undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult through several nymphal stages to form adults. They have multi-host life-cycles as the feeding stages are transient ectoparasites that suck blood from a succession of hosts and rest in the surrounding environment between feeds. Gravid female ticks lay eggs in small batches in sandy soil or sheltered spaces in host nests or burrows. Depending on environmental conditions, the eggs hatch in 7-30 days (longer in drier conditions) releasing small 6-legged larvae.

There is only one larval stage which is quite hardy and may survive for months in the environment. Studies on different tick species vary in whether the larvae feed or not: those of most species (e.g. *O. moubata*) are thought not to feed before moulting; while those of several species (e.g. *O. turicata*) have been observed to feed rapidly (15-30 minutes) before dropping off and moulting; and those of a few species (e.g. *O. puertoricensis*) have been found to feed for extended periods (several days) before detaching and moulting. Larvae moult to form 8-legged nymphs which develop through 4-7 instars (whereas ixodid ticks only form one nymphal instar). Nymphs may survive for weeks without feeding but each instar requires a bloodmeal before dropping off the host to moult to the next stage. The final nymphal instars moult to form adult ticks, which may also survive for weeks in the environment before locating hosts on which to feed. Both males and females feed on blood, typically rapidly (minutes to hours) and periodically for their whole lifespans, although intervals between bloodmeals may be months. Adults are extremely hardy and may survive even in harsh conditions up to 5-7 years without feeding. Mature ticks do not mate on hosts, and argasids may mate multiple times (whereas ixodids usually only mate once). Females undergo multiple gonotrophic cycles and lay small batches (15-130) of eggs after feeding, producing several hundred to over one thousand eggs in their lifetimes. Many *Ornithodorus* spp. are nidicolous and inhabit protected niches in nests (in cliffs, burrows, on the ground and some in trees) or in caves, dens, hides and habitual resting places. Some are endophilic and may infest indoor spaces in barns, stables, houses and even crevices in stone and clay walls and fences. Other species burrow into litter and loose soil frequented by hosts, often sandy resting places under shady trees or rock overhangs. A few species (e.g. *O. savignyi*) are hunter ticks and actively seek hosts by scuttling along ground when stimulated by host vibrations, heat or odours (including pheromones produced by resident ticks). A couple of species that parasitize livestock (*O savignyi* and *O coriaceus*) are also unique in that they have simple eyes and rest near ground level in shaded areas where animals rest and sleep. Most species are nocturnal feeders on hosts in tropical and subtropical regions, including steppes, semideserts and regions with long dry seasons.

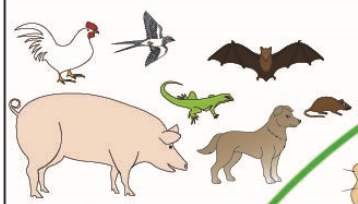
Differential diagnosis: Infestations may be indicated on clinical grounds by the occurrence of painful and pruritic skin lesions sometimes associated with anaemia. However, a variety of other aetiological agents may cause similar disease syndromes, including other arthropods, infectious micro-organisms and some other pathologies (especially inflammatory and allergic conditions). Diagnoses are generally made by the direct observation of tick stages biting hosts, even though such stages are often transient feeders. Ticks are best identified by microscopic examination of specimens collected from the host plumage or pelage. More recently, molecular biological techniques have been used to identify and characterize species following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal DNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal DNA, cytochrome c oxidase subunit I) gene sequences.

Treatment and control: Opportunistic or incidental infestations detected on individual hosts may be treated by physically removing ticks using fine surgical instruments (tweezers, forceps) or special removal devices (twists, loops/lassos, tick keys or V-shaped tools). Ticks should be removed gently without crushing to avoid squeezing saliva and gut contents back into wounds, and without tearing to avoid leaving fragments embedded in wounds causing inflammatory reactions. Some clinicians have reported moderate successes removing ticks using chemical sprays (freezing agents or pyrethroid acaricides), but traditional folklore remedies using stringent or volatile chemicals applied to the backs of ticks may do more harm than good as distressed or dying ticks may regurgitate or release toxic or pro-inflammatory materials. Individual hosts may require supportive chemotherapies to combat pain, pruritus, inflammation and possible secondary bacterial infections. Livestock and companion animals are more usually treated using a range of acaricidal chemicals, including arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT, lindane), organophosphates (dioxathion, fenchlorphos), organophosphonates (chlorfenvinphos, dichlorvos, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, cythioate, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazole (fipronil), chloronicotinyl (imidacloprid), isoxazolines (afoxolaner, fluralaner), natural products (rotenone) and some insect growth regulators or chitin synthesis inhibitors (methoprene, pyriproxyfen). Treatments may be applied topically or systemically via a range of modalities, including emulsions, sprays, showers, dips, footbaths, dusts, powders, drenches, injections, pour-ons, spot-ons, impregnated collars or tags, medicated supplementary feeds, or using self-treatment devices (bait boxes, rubbing posts or rollers, and treated nesting materials). Regrettably, there are growing reports of tick populations developing resistance to various arsenic compounds, organochlorines, organophosphates, pyrethroids and formamidines, so it is recommended that acaricides be used strategically (only when needed) and in cyclic rotation to avoid further resistance problems. Animals often require periodic re-treatment as ticks can survive in the surrounding environment for long periods. Some formulations with long-lasting residual activity have also been used against resting stages in local environments, notably around households, farms, military bases, and recreational areas. Various preventive measures may also be adopted to break transmission cycles by enhanced health surveillance (screening programmes, quarantine, culling), grazing management (avoid overstocking, pasture rotation, pasture spelling/resting, clearing vegetation (cut, slash, burn, plough), stabling), and wildlife management (exclusion of reservoir hosts by barriers, trapping or hunting, vermin control, diversion of habitual migration routes, and encouraging grooming species such as oxpeckers).

Ornithodorus

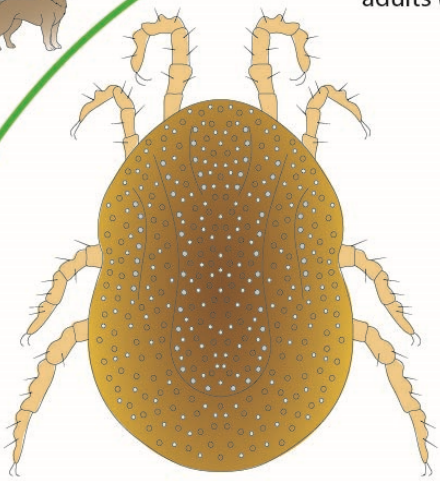


skin
(blood loss,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)

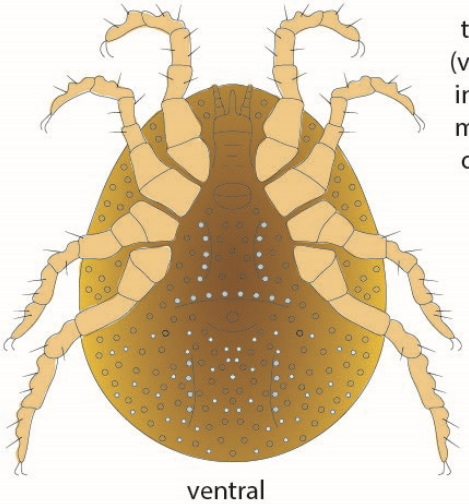


Hosts
(birds, mammals,
reptiles)

adults (~ 10 mm)



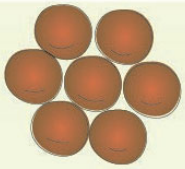
dorsal



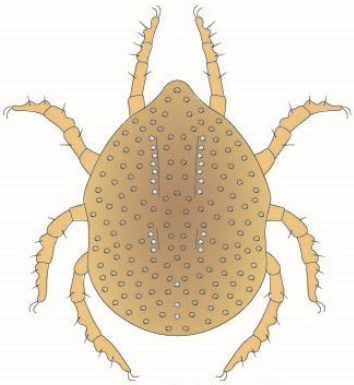
ventral

eggs laid in
soil/nests/burrows

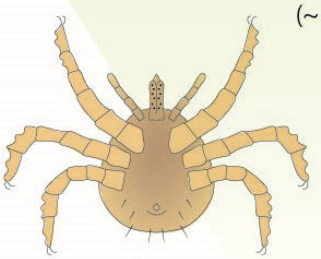
N+A are transient ectoparasites
emerging to feed on host blood



eggs
(~ 0.5 mm)



nymph (dorsal)
(~ 6 mm)
[4-7 instars]



larva
(ventral)
(~ 0.8 mm)

hatch

L of some species feed,
those of others do not

most species are
nidiculous or reside
in sandy soil

Ornithodorus spp. have multi-host cycles where
nymphs (N) and adults (A), sometimes larvae (L)
occur on a succession of individual hosts

Ornithodorus adult dorsal

Ornithodorus adult ventral