



Research Article

PROGRESSION OF PARASITISM FROM PHORESIS IN MITES

***Harikaran Karunakaran and Selvamuthukumaran Thirunavukkarasu**

Department of Entomology, Faculty of Agriculture, Annamalai University, Annamalai Nagar-608002, Tamil Nadu.

Article History: Received 28th May 2023; Accepted 26th June 2023; Available online 31st August 2023

ABSTRACT

The mites are the smallest (less than a millimeter in length), the most diverse, and the most common of all arachnids. Mites are ubiquitous and inhabit all known terrestrial, marine, and freshwater habitats, including arctic and alpine extremes, tropical plains and desert barrens, and surface and mineral soils (Dunlop and Alberti, 2008). More than 55,000 species have been described up to date, accounting for 5% of all living species today. Mites are experts at transport with the aid of large animals, mostly insects. It is a temporary relationship called phoresy that allows the mites to exploit scarce resources. Phoresy in the subclass Acari includes insects that feed on carriers. Phoresy evolved from free-living ancestors. The primary waste material used by floating mites appears to be rotting logs. However, rapid changes in the later life stage allowed the development of short-term resources. Although phoresy is a form of social interaction, most interact with mites. These relationships can be very complex and context-specific, but they often use the vector's sources or descendants (Seeman and Walter, 2023). The switch from phoretic to parasitism seems popular, but the scientific evidence for a switch from phoretic to permanent parasitism seems to be lacking.

Keywords: Phoresy, Parasitism, Mites, Acari, Phoresy.

INTRODUCTION

Acarids include mites, the largest group of species of Arthropods, with identified and more than 48,000 species. This figure is misleading because it is estimated that only 5% to 10% of mite species are identified. Compared to other arthropod groups such as spiders and scorpions, mites are distinguished by their small size (adult is between 0.1 and 30 mm long) and their ecological diversity. Some mites are predators, like almost all other arachnids, but the mites may also feed on plants, fungi, or bacteria, or act as parasites or on other animals. Mites are one of the oldest groups of 4,444 arthropods from the Devonian period in the fossil record (O'Connor, 2009). Insects are the most diverse group of arthropods, and insect pests can account for more than half of all pests (Price, 1980). The ancient and diverse group of arachnids called mites (Acari) includes such well-known parasites as ticks, chiggers and Varroa mites. It is true that mites frequently occupy the parasitic niche as ectoparasites and, to a lesser extent, as endoparasites of invertebrates and vertebrates, although mite diversity is not as well documented as insect diversity. The basic concepts

of mite ecology and the diversity of parasites and the evolution of parasitism are well discussed here.

Ecology of mites

All over the world, there are mites where that offer a variety of food ecosystems. While most non-mite arachnid organisms are predators, mites have gone beyond this behavior to employ parasitism, phytophagy, fungiphagy, algae, detritus, and other feeding strategies. Although they eat a variety of materials, most mites, like their arthropod relatives, feed on liquid and must first dissolve the liquid substance in order to eat. As with all other arachnid groups, predation is considered an important eating strategy for mites. Predatory mites are found in all habitats and feed on a variety of organisms such as other mites, small hexapods such as collembola, and Symphyla, eggs of other arthropods, and nematodes. Throughout the history of mites, their feeding habits by parasitizing other animals have led to numerous changes, resulting in many morphological changes. Parasitic mites exist as ecto- and endoparasites of vertebrate and invertebrate hosts. Among invertebrates, the two branches are parasitized by mites,

*Corresponding Author: Harikaran Karunakaran, Research Scholar, Department of Entomology, Faculty of Agriculture, Annamalai University, Annamalai Nagar-608002, Tamil Nadu, Email: harikaran99kk@gmail.com.

mollusks and arthropods, while in vertebrates all taxa are parasitized, but birds and mammals are the main targets.

More than 60 families of Acaridae harbor parasitic species of other diseases. Most of these parasites can be attributed to the independence of the parasite. Many species live in the skin (such as fur and feather), where they feed on blood with special piercing mouths or on horny objects or, less specifically, on sebaceous gland secretions with the mouth. Others colonize the respiratory and auditory tracts as well as other openings such as the cloaca. In ticks and parasites, Mesostigmata blood feeding seems to be the norm, animals often spend their time away from their hosts, in contact with food only. Since most of these animals spend most of their lives away from their carriers, there are some adaptations suitable for their carriers, but there are many oral adaptations (Figure 1). Ticks are the mites that attract the most attention of scientists because of their blood-sucking habits and their ability to transmit many diseases. Ticks carry more pathogens than any other bloodsucking arthropod, including many protozoa, bacteria, viruses and fungi (Nicholson *et al.*, 2009). The tick has a highly modified mouth, dorsal-shaped teeth for attaching the tick to the tissues of the host in the abdominal cavity, and modified chelicerae for cutting flesh. Conversely, parasitic mites will be more concentrated in sebum and keratinous secretions, and most species will require individuals from vertebrate hosts. Parasitic mites, unlike most Mesostigmata, have developed many adaptations or remain in the host. Exaggerated legs and claws, grooved sternum and leg patterns to "pinch" vertebrate hairs, disc-shaped suction cups to attach to the host, and changing body shape at hair follicles are a few of these patterns. For example (Nicholson *et al.*, 2009). There is no need to continue with specific diseases because many types of pests live under the skin, in the nose, or in other body openings or quills.

Evolution of parasitism from phoresy

Phoresy is a phenomenon in which organisms are transported from another species to a new location or food source with no other benefit (other than distribution) to the carrier. Phoresy is believed to be a step in the parasitism of many mite colonies (Kho, 1975; O'Connor, 1982; Athias-Binche, 1991, 1995; Houck and O'Connor, 1991).

Examples

According to (Cure, 1975), the *Blattisocius* genus is a good example of phoresy induced by parasitism. *B. dentriticus* and *B. keegani* have been found in many plant and animal species, including moth tympanic crypts, and are representatives of the ancestral records of the genus. Female mites of *Blattisocius tarsalis* fly over moths and feed on many moth eggs. While they occasionally feed on their planktonic hosts, female mites usually do not. Both nymphs and adults of *B. patagiorum* feed on moths and drink hemolymph. According to research, they can only mature and reproduce by feeding on hemolymph.

RESULTS AND DISCUSSION

The Astigmata, a group known to use swimming for other animals, is one of the best studies of swimming for parasitism. Many astigmata have specialized swimming archaia called heteromorphs (Houck & O'Connor, 1991), especially for swimming. Fixed, dysfunctional foregut with extensive sclerosis. Deutonymphs swim among insects of the genus *Chilocorus* (Coccinellidae) and free-living prey on insects of all members of the genus *Hemisarcoptes* (Hemisarcoptidae). Later nymphs of *Hemisarcoptes cooremani* have been shown to grow when attached to their diving host *Chilocorus cacti* (Houck & O'Connor, 1990). The swimming period has been shown to last between 5 and 21 days; without it, the mites do not molt and do not die. According to radiological studies (Houck & Cohen, 1995), *H. cooremani* obtains material from insects. (Houck and Lindley, 1993) showed that the foregut of the mite is a material without an oral cavity, but presenting a midgut that is open to sucking. These mites feed by their hosts through the anus.

Fain and Bafort, 1967 noted bloating in the last aquatic nymphs of *Hypodectes propus*, and indeed this gutless, mouthless stage appears to be responsible for all food intake throughout life. (Okamoto *et al.*, 1991) also found post-nymph swelling and increased growth of *Lardoglyphus kono* after diving and attachment to bark beetles. All of these examples may represent changes in the overall interference system. The only phylogenetic study examining parasites focusing on Psoroptidia (Klimov and O'Connor, 2013). These mites require persistent infection in animals and birds and exhibit host specificity (Klimov & O'Connor, 2013). Many ecological groups are found in Psoroptidia, including respiratory endoparasites, feather mites, outer hair and fur mites, epidermal mites, and skin-burrowing mites. Hair mites and feather mites are collectively known as this group, while dust mites have historically been considered the most important members of Psoroptidia. Interestingly, (Klimov and O'Connor, 2013) conclude that parasitism first appeared in Psoroptidia, while dust mites (Pyroglyphidae) are the more common members of this group, suggesting a transition from parasitism to free-living. The analysis is based on data from 315 taxa and 6164 nucleotides. Many believe (Futuyma & Moreno, 1988; Agnarsson *et al.*, 2006; Cruickshank and Patterson, 2006; Goldberg & Igic, 2008), compulsive parasitism is irreversible; However, when you look at the morphology of Psoroptidia, you rarely see nutritional changes that will facilitate this transition. Extensive sampling has been done among parasites of the mite tree of life, and a combination of physical assessments can be used to document evolution.

The multi-species phylogenetic hypothesis for parasitic mites was proposed by (Klompen *et al.*, 2007) and (Dowling and O'Connor, 2010) demonstrated a good understanding of parasitism. The super family Dermanssoidea, detailed below, consists mostly of different organisms, but elsewhere in the tree, there are other independent organisms, including the most famous group, the tick. Ticks share an ancestor with free-living sea cucumbers, but the transition from free-living to free-living

is unknown. Ticks are divided into three families: Argasidae, Ixodidae, and Nuttalliellidae. Argasidae is a group of monophyletic mites known as soft ticks. Argasids have multiple nymphal stages (2-8), all feeding many times in a short period. Mating usually takes place outside the host and may occur several times, with the female laying several eggs. Argasids are usually nidicolous and all stages feed on the nest owner. The genus *Argas* and *Carios* mainly feed on bats and birds, while *Ornithodoros* feeds on mammals, birds and reptiles. The genus *Otobius* is very unique, having only two stages of feeding, the nymph and non-feeding adult and is usually found in the ear canal of large mammals. Ixodidae is a monophyletic group of Ixodidae. Ixodes have only one nymphal stage, and each stage (larva, nymph, adult) feeds only once in a long period. Mating usually takes place in the host and the female lays eggs before she dies. Individuals are occasionally found in burrows, but are often found in open environments searching for hosts. Each life stage usually feeds on different hosts (for example, larvae feed on mice or birds, nymphs feed on wolves or rabbits, adults feed on and befriend deer). This group is divided into five families, each with 12 known members (Barker & Murrell, 2004). It is usually found in the ear canal of large mammals.

The most unusual tick family is the monotypic Nuttalliellidae, which is thought to be a link between Amphipods and Pansauridae due to their lizard-like and lizard-like features. *Nuttalliella namaqua* (Bedford, 1931), is the only known species with only 18 females and three female nymphs. They have been found in rocks of Namaqualand, Cape Province, South Africa (Bedford, 1931) and cracks in large rocks in Tanzania (Keirans *et al.*, 1976). Individual males have been isolated from the mud burrows of otic rats, a mammal, and two swallows (Hoogstraal, 1985), but the primary host of the fruit is unknown. Because ticks are found on rocks and rocky outcrops, rock dens, *Procapra capensis* or rock house lizards are considered the main source of the mites. According to (Hoogstraal, 1985), live females and nymphs do not contribute to any of the bird or animal specimens commonly used for post-tick. Nothing is known about the biology of this family. Except for Dermanyssina and Ixodida, only four families have vertebrate species. These families are not necessarily related, but what they all have in common is that most animals in the group live independently or with arthropods such as Arthropods, psalids or centipedes on fallen leaves or rotting trees. All of these parasites feed on snakes or skin and share a common habitat with arthropods. Diplogyniidae (*Ophiocelaeno*), Heterozetoniidae (*Amheterozetoni*), Paramesitidae (*Ophiomesit*), and Schizogyniidae (*Indogynium*) are four parasitic families that emerged from the transition from arthropods to vertebrates.

Parasitism in Mesostigmata has always been considered limited to the Dermanyssoidea super family, except for the mention of Ixodida (ticks) and a few rare species associated with skins and snakes. With a life history that includes free-living, soil-dwelling animals, arthropod predators in vertebrate and invertebrate nests or colonies,

facultative and obligate vertebrate parasites, breathing and hearing mammals of birds, and frogs, dermatomites have impressive ecological amplitude. Impressive morphological adaptations can be found in this group. Until recently (Dowling and O'Connor, 2010), the only hypothesis of the endoparasitic evolution of Dermanyssoidea was not based on experimental research or even on morphological isomorphism (Evans, 1955; Radovsky, 1969, 1985). Therefore, species that parasitize vertebrates are often grouped into Dermanyssoidea, and most of them have been separated into families due to major morphological changes or host rarity. (Evans, 1955) said that all disease groups descended from predatory ancestors, based on the theory that predatory dermozoans can feed on their hosts and use blood for food, but not all are parasites due to lack of time.

According to Evans theory, the mites first adapted to parasitism and only needed a host to eat. (Radovsky, 1969, 1985), on the other hand, argued that animals living in vertebrate burrows evolved from free-living ancestors and that contact with hosts eventually led to genetic diversity and the evolution of species. (Dowling and O'Connor, 2010) conducted the first study to examine parasitic evolution within a phylogenetic framework. Eight of the 15 recognized families were included in their analysis and suggested at least six different vertebrate parasite origins within Dermanyssoidea (rare, mostly monotypic and host family-specific but present). The second analysis (Dowling & O'Connor, 2010), which excludes two parasitic families Spinturnicidae and Spelaorhynchidae from the superfamily, looks at the relationships of Dermanyssina and suggests relationships with Eviphidoidea. These two analyses showed that the hypothesis that most species belong to Dermanyssoidea as they are parasitic is correct, although there is no morphological evidence to support this relationship. While there is no character to support a relationship with Eviphidoidea, there is also no character to support that the two extracted families of Dermanyssoidea parasitize on bats. Dermanyssoidea also offers a singular opportunity to study the evolution of parasites because of the diversity of Dermanyssoidea represented among mammals and parasites. There are different ecological relationships even within individual genera like *Androlaelaps* and *Haemogamasus*. The *Androlaelaps* depending on the variety of their vertebrate hosts and are widely distributed. In a laboratory setting, (Reytlat, 1965) compared the feeding habits of four *Androlaelaps* species (*A. fahrenheiti*, *A. longipes*, *A. casalis*, and *A. semidesertus*). The ability of the mites released in the laboratory to feed on blood, arthropods or a mixed diet, as well as take food from their hosts, has been used to determine the level of parasite adaptations. *A. longipes* and *A. casalis* produce the same number of offspring when fed blood or arthropods, but both species produce the most offspring when fed mixed milk. The diet of arthropods alone does not allow *A. fahrenheiti* and *A. semidesertus* to reproduce by demonstrating their dependence on the host. All four animals have normal chelicerae toothed chelicerae that can form wounds that cause mice to bleed. According to (Reytlat, 1965) and (Radovsky, 1985), *A. fahrenheiti* mainly feeds on other small arthropods, including dried blood, scratches and open

wounds. Additionally, *Haemogamasus* exhibits a wide variety of nutritional ecologies, from carnivores to blood cells (Radovsky, 1985). The only non-parasitic species is *Haemogamasus pontiger* (Evans & Till, 1966), which is usually found on barn floors and debris from barns. (Furman, 1959a) reported that, unlike *A. fahrenheiti*, none of the *H. pontiger* species in one experiment fed on dried blood; instead, 63% of them fed on the blood flowing from their rodent hosts. According to (Hughes, 1961), *H. pontiger* is a predator and carnivore that does not require a host because it only requires rice seeds as food to sustain its life.

The liponissoides group of hemophilic bacteria consists of various species. This group is distinguished by modified, elongated, edentulous chelicerae that pierce rather than rip apart the skin of the host (Radovsky, 1985). *H. liponysoides* does not kill arthropods in the laboratory; it only reluctantly and negatively eats white blood cells (Radovsky, 1960). These animals also eat adults and small rodents, which suck the skin and cause bleeding. *Liponysoides* species can also overeat, which is the practice of eating more than usual at one time (Radovsky, 1985). A strong indication that the ability to feed from the host and reproduce by relying on blood is the main feature of this disease is the transmission of two separate strains from the host to the parasite of the species. This evolution could begin with free feeding in vertebrate nests. The opportunity for co-ownership is provided by the ancestral active predation of small arthropods in the vertebrate nest, while the pre-adaptation that allows the mites to colonize the disease niche is their ability to use many nutrients for growth and development. Although these two species have an opportunity to examine the transition from mammals to organisms within a genus, no phylogenetic studies have included a sample size large enough to identify changes in evolutionary context. History of parasitic behavior: They are not early stages of parasitic or non-parasitic organisms and, as mentioned earlier, this lifestyle has evolved many times over. The time of the first evolution of the host would be limited by the origin of the disease infecting arthropods or vertebrates. Therefore, there is much debate as to which vertebrate was the first host of the tick, leading to various dates for the origin of the tick from the Devonian to the Cretaceous. Since the majority of fossilized parasitic organisms are restricted to amber beds starting in the Middle Cretaceous, the fossil record of mites and ticks is largely useless in this regard. Unknown early date or power is still on. Data from the host's fossil record or a molecular clock can also frequently be used as a substitute. For instance, the monotypic family Manitherionyssidae, which is currently restricted to pangolins, has no fossil evidence of mesostigmatids. These unusual animals split from their sister groups in the late Cretaceous slightly earlier than previously believed, according to molecular evidence (Meredith *et al.*, 2009). The fossil record dates back to the Eocene. Use this information to also limit the mite's origin. This line of thinking is flawed because it implies that the

early parasites used the same strategy that they are using now. Compared to the current parasite's fossil record, biogeographic and/or fossil calibration (if any) may provide a better measure of parasite abundance, as described in Fertility (De Baets *et al.*, 2015). Furthermore, we cannot ignore previous host changes (Poulin, 2011) or the use of extinct populations. Consider the bird tick (Argasidae: Argasinae), which (Mans *et al.*, 2012) suggest diverged from other Argasid subfamilies (parent species, Ornithodorinae) during the Triassic era. This, it seems, predates the oldest extant birds. According to research by (Chitimia Dobler *et al.*, 2018), the estimated separation of prostatic ticks (Ixodes) and all other hard ticks (Metastratiata) in the family Ixodidae is consistent with the end-Permian mass extinction event. The vertebrate fauna was significantly altered by this occurrence. (Chitimia-Dobler *et al.*, 2018) claim that Ixodes are typically found in animals found that cynodonts, which later gave rise to mammals during the Triassic period, were associated with prostate (Ixodes) ticks.

CONCLUSION

I have provided a thorough explanation of the origin and evolution of parasitism in acari in relation to their niche in this review. It is evident that mites have frequently taken advantage of the parasitic niche by living on both invertebrates and vertebrates as ectoparasites and, to a lesser extent, endoparasites. Given that we may have only identified a small portion of the mite diversity; there are probably still a large number of unusual and peculiar parasitic connections hidden from view.

ACKNOWLEDGMENT

The authors express sincere thanks to the Head of the Department of Entomology, Faculty of Agriculture, Annamalai University, Annamalai Nagar, Tamil Nadu for the facilities provided to carry out this research work.

REFERENCES

- Agnarsson, I., Avilés, L., Coddington, J. A., & Maddison, W. P. (2006). Sociality in threaded spiders: repeated origins of an evolutionary dead end. *Evolution*, 60(11), 2342-2351.
- Athias-Binche, F. (1991). *Evolutionary ecology of dispersal in mites*. In: Dusbabek, F. & Bukva, V. (Eds.), *Modern Acarology 1*. Prague: SPB Academic, pp. 27-41.
- Athias-Binche, F. (1995). Phenotypic plasticity, polymorphisms in variable environments and some evolutionary consequences in phoretic mites (Acarina): a review. *Ecologie*, 26(4), 225.
- Barker, S. C., & Murrell, A. (2004). Systematics and evolution of ticks with a list of valid genus and species names. *Parasitology*, 129(S1), S15-S36.

- Bedford, G. A. H. (1931). Nuttalliella namaqua, a new genus and species of tick. *Parasitology*, 23(2), 230-232.
- Chitimia-Dobler, L., Pfeffer, T., & Dunlop, J. A. (2018). Haemaphysalis cretacea a nymph of a new species of hard tick in Burmese amber. *Parasitology*, 145(11), 1440-1451.
- Cruickshank, R. H., & Paterson, A. M. (2006). The great escape: do parasites break Dollo's law?. *Trends in Parasitology*, 22(11), 509-515.
- De Baets, K., Dentzien-Dias, P., Upeniece, I., Verneau, O., & Donoghue, P. C. (2015). Constraining the deep origin of parasitic flatworms and host-interactions with fossil evidence. *Advances in Parasitology*, 90, 93-135.
- Dowling, A. P., & O Connor, B. M. (2010). Phylogeny of Dermanyssoidea (Acari: Parasitiformes) suggests multiple origins of parasitism. *Acarologia*, 50(1), 113-129.
- Dowling, A. P., & OConnor, B. M. (2010). Phylogenetic relationships within the suborder Dermanyssina (Acari: Parasitiformes) and a test of dermanyssoid monophyly. *International Journal of Acarology*, 36(4), 299-312.
- Dunlop, J. A., & Alberti, G. (2008). The affinities of mites and ticks: a review. *Journal of Zoological Systematics and Evolutionary Research*, 46(1), 1-18.
- Evans, G. O. (1966). Studies on the British Dermanyssidae (Acari: Mesostigmata). Part II Classification. *Bulletin of the British Museum (Natural History) Zoology*, 14, 107-370.
- Evans, G. O. (1955). A review of the laelaptid paraphages of the Myriapoda with descriptions of three new species (Acarina: Laelaptidae). *Parasitology*, 45(3-4), 352-368.
- Fain, A., & Bafort, J. (1967). Cycle évolutif et morphologie de Hypodectes (Hypodectoides) propus (Nitzsch) acarien nidicole a deutonymphe parasite tissulaire des pigeons. *Bulletins de l'Académie Royale de Belgique*, 53(1), 501-533.
- Furman, D. P. (1959). Feeding habits of symbiotic mesostigmatid mites of mammals in relation to pathogen-vector potentials. *American Journal of Tropical Medicine and Hygiene*, 8(1).
- Furman, D. P. (1959). Observations on the biology and morphology of *Haemogamasus ambulans* (Thorell)(Acarina: Haemogamasidae). *The Journal of Parasitology*, 45(3), 274-280.
- Furman, D. P. (1968). Effects of the microclimate on parasitic nest mites of the dusky footed wood rat, *Neotoma fuscipes* Baird. *Journal of Medical Entomology*, 5(2), 160-168.
- Furman, D. P. (1979) Specificity, adaptation and parallel evolution in the endoparasitic Mesostigmata of mammals. *Recent Advances in Acarology*, 2, 329-337.
- Futuyma, D. J., & Moreno, G. (1988). The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, 19(1), 207-233.
- Goldberg, E. E., & Igić, B. (2008). On phylogenetic tests of irreversible evolution. *Evolution*, 62(11), 2727-2741.
- Hoogstraal, H. (1985) Argasid and nuttalliellid ticks as parasites and vectors. *Advances in Parasitology*, 24: 135-238.
- Houck, M. A., & Cohen, A. C. (1995). The potential role of phoresy in the evolution of parasitism: radiolabelling (tritium) evidence from an astigmatid mite. *Experimental & Applied Acarology*, 19, 677-694.
- Houck, M. A., & Lindley, V. A. (1993). Microwave-primer technique for microscopic studies that involve arthropods. *American Entomologist*, 39(2), 117-119.
- Houck, M. A., & O Connor, B. M. (1990). Ontogeny and life history of *Hemisarcoptes cooremani* (Acari: Hemisarcoptidae). *Annals of the Entomological Society of America*, 83(5), 869-886.
- Houck, M. A., & OConnor, B. M. (1991). Ecological and evolutionary significance of phoresy in the Astigmata. *Annual Review of Entomology*, 36(1), 611-636.
- Keirans, J. E., Clifford, C. M., Hoogstraal, H., & Easton, E. R. (1976). Discovery of Nuttalliella namaqua Bedford (Acarina: Ixodoidea: Nuttalliellidae) in Tanzania and redescription of the female based on scanning electron microscopy. *Annals of the Entomological Society of America*, 69(5), 926-932.
- Klimov, P. B., & OConnor, B. (2013). Is permanent parasitism reversible? Critical evidence from early evolution of house dust mites. *Systematic Biology*, 62(3), 411-423.
- Klompen, H., Lekveishvili, M., & Black IV, W. C. (2007). Phylogeny of parasitiform mites (Acari) based on rRNA. *Molecular phylogenetics and evolution*, 43(3): 936-951.
- Mans, B. J., de Klerk, D., Pienaar, R., de Castro, M. H., & Latif, A. A. (2012). The mitochondrial genomes of Nuttalliella namaqua (Ixodoidea: Nuttalliellidae) and Argas africanus (Ixodoidea: Argasidae): estimation of divergence dates for the major tick lineages and reconstruction of ancestral blood-feeding characters. *PLoS One*, 7(11): e49461.
- Meredith, R. W., Gatesy, J., Murphy, W. J., Ryder, O. A., & Springer, M. S. (2009). Molecular decay of the tooth gene enamelin (ENAM) mirrors the loss of enamel in the fossil record of placental mammals. *PLoS Genetics*, 5(9): e1000634.
- Nelzina, E. N., & Danilova, G. M. (1956). Materials on the biology of mites of the family Haemogamasidae (Gamasoidea, Parasitiformes). 1. Nutrition of *Haemogamasus citelli* Breg. and *H. nidi Mich.* *Meditinskaya Parazitol*, 25, 352-358.
- Nicholson, W. L., Sonenshine, D. E., Lane, R. S. & Uilenberg, G. (2009). Ticks (Ixodida). In Mullen, G. R. & Durden, L. A. (eds), *Medical and Veterinary Entomology*, 2nd edn. London: Elsevier
- OConnor, B. M. (1982). Evolutionary ecology of astigmatid mites. *Annual Review of Entomology*, 27(1), 385-409.
- OConnor, B. M. (2009). Mites. In *Encyclopedia of Insects*, Academic Press, pp. 643-649
- Okamoto, M., Matsumoto, K., & Shirasaka, R. (1991). Studies on the attaching behavior of the Lardoglyphus

- konoï (Acari, Lardoglyphidae) hypopus and its molting into the tritonymph. *Medical Entomology and Zoology*, 42(3), 219-228.
- Poulin R (2011). Evolutionary ecology of parasites. Princeton University Press, Princeton. 360p.
- Price, P. W. (1980). Evolutionary Biology of Parasites. Princeton, NJ: Princeton University Press. 256p.
- Radovsky, F. J. (1969) Adaptive radiation in the parasitic Mesostigmata. *Acarologia*, 11(3), 450-483.
- Radovsky, F. J. (1985). Evolution of mammalian mesostigmatid mites. *Coevolution of Parasitic Arthropods and Mammals*, 441-504.
- Reytblat, A. G. (1965). Biology of the gamasid mite *Haemolaelaps semidesertus* Breg. (Gamasoidea, Parasitiformes). *Zoologicheskii Zhurnal*, 44, 863-870.
- Seeman, O. D., & Walter, D. E. (2023). Phoresy and mites: More than just a free ride. *Annual Review of Entomology*, 68, 69-88.
- Treat, A. E. (1975). Mites of Moths and Butterflies. New York: Cornell University Press.
- Williams, G. L., Smiley, R. L., & Redington, B. C. (1978). A taxonomic study of the genus *Haemogamasus* in North America, with descriptions of two new species (Acari: Mesostigmata, Laelaptidae). *International Journal of Acarology*, 4(3), 235-273.