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ON THE ORIGIN OF PARASITISM IN TROMBICULID MITES
(ACARIFORMES: TROMBICULIDAE)

BY Andrew B. SHATROV

SUMMARY: The original hypothesis is proposed that the parasitism of trombiculid mite larvae (Trombiculidae) is a rather young historical phenomenon which developed after the quiescent stages (calyptostases) had evolved in the ontogenesis of this group of trombidiform mites. The larvae being primarily predatory-entomophagous with biting-sucking mouthparts, they could easily pass to parasitism on vertebrate animals in pasture conditions, firstly on mammals, becoming primarily lymphophagous, and, due to wide polyphagy, they are similar to free-living blood-sucking insects, e.g. Diptera. The problem of specificity and specialization in trombiculid mites and other related groups is discussed.

For the origin of parasitism in any group animal, including trombiculid mites (Trombiculidae), two main conditions are indispensable. Firstly, in the pattern of individual development of the given group animal, there should be something that inevitably pre-determines and eases the transition to parasitism at definite stages of development at a definite historical period. Secondly, parasitism can successfully arise and develop only with some favourable morphological basis contributing to the fixing of newly arising relations of the representatives of the group with an environment. It may be also supposed that parasitism, in either form, basically serves only one main strategic aim of individual development and survival of organisms.

What takes place in this relation in trombiculid mites? First of all, from a consideration of the life cycle of trombiculids, it appears that the average time of their larval parasitism (3–5 days) takes less than 1% of the general (400–600 days) or, especially, maximum (more than 1000 days) duration of their whole life (SHATROV, 1993a, 1996). The greatest parts of the trombiculid life, most important in their reproductive strategy, are occupied by the active deutonymph and, especially, the adult, which live in rather conservative environments, such as soil and litter,
predominantly at a depth of 10–20 cm (DANIEL, 1961). Nevertheless, during a relatively short time spent feeding on vertebrate hosts, the small larvae (200–300 μm long on average) reach very large sizes (800–900 μm) and volumes that are comparable to those of the active post larval stages (length 1200 μm in deutonymph and 1600 μm in adults). They then drop from the host, returning to a natural environment, and start to moult. Despite the significant changes in body size and external morphology, the organization and differentiation of the internal organs during postembryonic development of mites do not depend on their larval parasitism. Indeed, there are no changes in the basic feeding behaviour in trombiculids, as it is observed, for instance, at the metamorphosis of insects (WHITTEN, 1968), or in their diet, in as much as protein—originally from an animal diet (BECKLEMI SchEV, 1970)—is invariably involved. Moreover, the adaptations of larvae to parasitism (SHATROV, 1983) are practically expressed only by general adaptations of the organism to extraoral digestion and to the assimilation of a protein meal.

The reasons for this situation are concealed in rather good preadaptations of the organ systems of this group of mites to realization of this type of feeding behaviour. The peculiar adaptations of larvae to biting the host and to piercing the skin (SHATROV, 1980, 1981, 1983, 1984) are developed mainly in terms of morphology, and within these preadaptations, which seem to be characteristic for all Parastenogona at all stages of their ontogenesis. It is important to note that, in conditions of well developed preadaptations, as well as of primitive organization of a digestive system, a transition to parasitism by a single stage at a time, as in trombiculids, or of all stages at once, is made rather easily and does not cause considerable structural transformations in the organism. Besides that, the initially biting-sucking mouthparts of trombiculids has predetermined their relatively easy transition to lymphophagy in the larval instar, with its rather minor subsequent adaptations, as is apparently the case of some insects and mites (BECKLEMI SchEV, 1970). Nevertheless, the effectiveness of larvae feeding during their parasitic habit is quite significant. Indeed, the simple figures demonstrate that the duration of larval feeding on the hosts, lasting typically 3–5 days, corresponds well with the total time (3.5 days) required by adult mites to eat the arthropod eggs which they consume during their whole life, assuming that during a lifetime of 500 days the mite consumes 2 eggs per day on average and takes 5 minutes to suck each one dry, these being the average parameters of feeding in culture (SHATROV, 1993a, 1996).

What is the objective reason for such a concentrated and effective feeding, which only possible through parasitism? Reasons for the origin of parasitism in trombiculid mites and, consequently, for its role and value in their life strategy, are to be thought in particular features of individual development of mites, which would have required and made indispensable their transition to a new feeding specialisation. It is clear, that in a free-living, non-parasitic way of life, the hungry larvae would have to feed for the same amount of time and as often as the adult mites, in order to achieve the sizes of the fed larvae. This would greatly lengthen the duration of the life cycle, defeating the achievement of a mature condition. Given the relatively low reproductive potential of trombiculid mites (200–300 eggs per female), it would reduce their survival rate and could prove fatal for their existence. Simultaneously rich in yolk and small-sized, as in many other arachnids, the eggs of trombiculid mites are not only reservoir of nutrient materials, but also the structural basis determining an extra-genetic regulation of the early developmental steps (RAFF, KAUFMAN, 1986). This has predetermined the apparently fast embryonization of the first larval instar in evolution, which transforms into a quiescent non-feeding and non-motive prelarva with a so-called lecithophagous aphagia (GRANDJEAN, 1938a, b; ROBAUX, 1970, 1974; CONNEAU, 1974, 1976; SHATROV, 1998; etc.), as well as the appearance of a small-sized heteromorphic second larval instar, or active larva as such. However, reserve nutrient materials in an egg only suffice for the structural formation of an organism of a hungry larva, in which, contrary to all other instars, the midgut has a clear epithelium of the walls and the cuticle shows strongly expressed ridges of the external layers (SHATROV, 1993b). The heteromorphism of the larva and the ridges of its cuticle is the only possible form of an organism of the early stage in trombiculid mite development with small-sized eggs, compared with the
adult mites. Any other form of an organism, for example with flat sclerites, would result in another scheme of development with several larval moults, which would be extremely disadvantageous. Indeed, for the successful reproduction of a mite population, a large survival rate of the pre-imaginal, first of all larval, stage is apparently indispensable, together with fastest development from a newly hatched individual to the size and organisation of a mature adult organism. Reaching this final result seems to be possible in two ways: by repeated predatory feeding of all stages of development, including larvae, which appears to have been natural for this branch of Actinopodida and, apparently, took place in the early stages of the evolution of the group; or by formation of more effective way of feeding at any one stage of development within the available preadaptations. The first way, as has already been mentioned, is apparently non-effective and has not become fixed in evolution. As is obviously seen, steady co-adaptations with arthropods as hosts, which would result in the formation of parasitic systems, have not developed for some reason in the larvae of trombiculid mites, contrary to the systematically close trombidiids and water mites. This problem appears to have been solved by means of their larvae attacking vertebrate animals in pasture conditions and the subsequent gradual adaptation of larvae to prolonged feeding with the simultaneous development of the stylostome, so characteristic for trombiculid larvae (Höffpily & Schumacher, 1961, 1962; Hase et al., 1978; Shatrov, 1980), whereas the other related groups successfully exploit arthropods as their hosts. That is why, among problems of relations of trombiculids with vertebrate animals, the problem of the origin of parasitism in this group of arachnids is of great interest for comparative and evolutionary parasitology. However, among the vast variety of publications on trombiculid mites, this problem has only been briefly discussed in few articles (Ewing, 1944, 1949; Audy, 1951, 1961; Wharton & Fuller, 1952; Muliarskaya, 1969). Becklemischev (1970) has also considered this problem in his articles on ecological parasitology. At the same time, both in general and in part, this problem is extremely poorly understood and remains unresolved. Opposing opinions have been expressed about whether the primary parasitism of trombiculid larvae was on vertebrates (Ewing, 1949) or arthropods (Audy, 1961; Muliarskaya, 1969; Becklemischev, 1970). As can be seen, the latter point of view is more widespread among acarologists than the former. However, the complete absence of paleontological data allows a developmental history of this group of mites to be only presumptively considered, based on general principles of paleogeography (Wharton & Fuller, 1952) and comparative anatomy. New ways need to be looked for to solve such a problem. In the present context, it is extremely important to point out two circumstances. Firstly, as we know, in the life cycle of trombiculid mites three quiescent instars (stages) are expressed: prelarva, proto — and tritonymph, and secondly, apparent host-parasite specificity is totally lacking in the parasitizing larvae. As has been noted, although there are considerable differences in sensitivity among a preferable circle of the potential hosts to different trombiculid species, practically any terrestrial vertebrate can serve as the host almost for any species of trombiculid larva (Wharton & Fuller, 1952). Based on the assumption that the larval parasitism never spreads to the imaginal phase, and that the original transition to parasitism can be realised only in actively feeding phases of the arthropod life cycle (Becklemischev, 1970), it is possible to explain the larval phase parasitism of trombiculid mites only by the pattern of their ontogenesis. Thus, during the formation of their parasitism, the heteromorphism of larvae already existed, and the quiescent instars in their ontogenesis had already been formed. The presence of the quiescent and hence non-parasitic prelarva supports this assumption, indicating that parasitism became established after its morphological reduction in the evolutionary history of the group. From this it can be supposed that parasitism in trombiculid mites is a relatively young historical phenomenon and arose after the development of quiescent instars in their ontogenesis. In the available classifications of parasitism of terrestrial arthropods on vertebrate animals (Becklemischev, 1970; Nelson et al., 1975; Balashov, 1982), the factor of their ontogenesis, as a historically conditioned character of the development of a given group of parasitic organisms, remains, unfortunately, beyond the considerations. Concerning this problem, the solution of which
requires detailed investigations of developmental processes in the different groups of parasitic arthropods, two main aspects may be noted, namely the influence of ontogenesis on parasitism and the influence of parasitism on ontogenesis. On the one hand, in the majority of parasitic groups the individual development depends on parasitism and develops in tight connection with it (e.g. in ixodid ticks). On the other hand, as, for example, in trombiculid mites and perhaps in other Parasitengona, parasitism is only superimposed on the prepared form of an ontogenesis and does not transform it significantly. In this case, therefore, the nature of the individual development has obvious priority over the larval phase parasitism. Much longer feeding periods of larvae of the genus Hannemannia, immersed in tissues of the amphibian host (Ewing, 1926; Hyland, 1950, 1961), let alone the parasites of the genus Vatacarus in the respiratory tracts of reptiles (Audy et al., 1972; Vercammen-Grandjean, 1972), are, apparently, examples of a considerably tighter interaction in a parasite-host system than that seen in the case of ectoparasitic larvae. This kind of relationship in some groups of trombiculid mites inevitably leads to transformation of an available type of ontogenesis and life scheme of these parasites as a whole, leading, ultimately, to whole life-cycle endoparasitism, i.e. to a change in the type of parasitism. This type of development of the host-parasite interactions, deviating from the main type, is doubtless secondary and later in terms of evolution, despite the old age of the hosts of these mites (reptiles and amphibians), in comparison with mammals. As has already been noted (Mitchell, 1970), extremely important factors for understanding the morphology and evolution of mites of the cohort Parasitengona are the positional relationship and principles of organisation of the organs which have not been supplied with an effective circulatory system, which is, particularly in trombiculid mites, almost completely absent. The extra-oral digestion, which is the most typical physiological feature of these arachnids, results in an apparent simplification of organization of their alimentary system and can be considered as one of the morphophysiological reasons for the origin of parasitism. The development of parasitism is also extremely simplified due to the special morphofunctional organization of the bite-sucking mouthparts with a soft-skinned apical part of the hypostome, capable of forming a sucker (Shatrov, 1981), as well as biochemical properties of a salivary secretion, apparently preadapted to effective hydrolytic decomposition of proteins (Mitchell, 1970) through the process of extra-oral digestion. Therefore, it has been recognized, that the evolution of the digestive system as such is, as a whole, the main factor in the evolution of this and many closely related groups of trombidiform mites (Mitchell, 1970). Thus, the capability of larvae of some trombiculid species to attack and successfully feed not only on vertebrates, but also on arthropods (Ewing, 1949; Audy, 1950; Wharton & Fuller, 1952), as is characteristic for closely related trombiculids and water mites, demonstrates a general adaptive potential of all these groups and their similar morphofunctional preadaptations, each of them realised by means of particular and fine morphological and ecological properties. Concerning the ecological reasons of the origin of parasitism in trombiculid larvae, there are obvious contradictions in their interpretation, as suggested by Becklemischev (1970). On the one hand, trombiculids are trapping entomophagous with biting-sucking mouthparts, while on the other, their transition to parasitism on mammals is realised not from a free way of life, but from a type of parasitism on insects. Such a case of the origin of parasitism of a slowly motile stage in pasture conditions is an unusual example among terrestrial arthropods, therefore Becklemischev considered it as an exception of the general rule, but imaginary, owing to primary parasitism of trombiculids on arthropods. Apparently, he blended two groups—Trombiidiidae and Trombiculidae—as their systematic and classification were badly understood in his time. However, from the position of Becklemischev (1970) it remains unclear how trombiculid larvae, for the second time, shifted from parasitism on insects to attacking vertebrates in pasture. It is probable, therefore, that the assumption of the exception attack of slowly crawling larvae in a pasture conditions of vertebrate animals is not imaginary, but true exception from the general rule. Originally, vertebrate animals, most likely mammals, simply "collected" naturally predatory larvae, and those, in turn, tried to attach and feed. Feeding, exceeding in duration a one-time
ingestion of a portion of a feeding substratum, resulted only through the adaptation of larvae with short mouthparts to penetration through a dense layer of an epidermis of the potential host-vertebrate animal and the achievement of a layer of a connective tissue, provided through the formation of a particular feeding tube-stylostome. Such an explanation of the origin of parasitic relationships of trombiculids on vertebrate animals corresponds rather better to the assumption of BECKLEMISHEV (1970) about the transition and adaptation of arthropods with biting-sucking mouthparts to parasitism and hematophagy in pasture conditions (e.g. as in diptera), than to his own opinion about primary parasitism of trombiculids on arthropods. As a whole, the two branches—Trombidiidae and Trombiculidae—cannot be blended, and it also appears impossible to derive on group from the other. As has been already supposed, the trombidiids, are a more structurally advanced evolutionarily young group, than trombiculids (FEIDER, 1959), which belong the most generalised Actinedida (EWING, 1949). Consequently, as it may be thought, their parasitism on arthropods is a later phenomenon than parasitism of trombiculid larvae on vertebrates. Apparently, these processes completely independent of each other. In any event, the trombidiid larvae possess much more specialized and modified mouthparts and body setae than these of trombiculids (Ewing, 1949). Evolution of these two groups of trombidiiform mites in the direction of larval phase parasitism on different types of hosts (originally vertebrates and arthropods) has occurred, apparently, in different ways and probably had somewhat different particular morphological and ecological bases. The uniform, originally animal (protein) diet (BECKLEMISHEV, 1970) in both cases facilitated the transition to parasitism. Corresponding to BECKLEMISHEV (1970), the nature of the extracted food does not vary in forms initially with biting-sucking mouthparts, which at once become hematophages. Therefore, further morphological adaptations, in particular changes of mouthparts, are quite minor. In the case of trombiculid mites, the lymph and tissue fluids are the main feeding substratum, apparently, successfully substitutes for blood, and this types of feeding appears quite sufficient, being superimposed on primitively organized alimentary system. Thus, the larvae of trombiculid mites, originally being of entomophagous predators with the biting-sucking mouthparts in pasture conditions, easily passed to parasitism on vertebrates and become primary lymphophagous, directly realising one of the routes of arthropod transition to parasitism proposed by BECKLEMISHEV (1970). In this instance, the potential victims or hosts of trombiculid larvae appear to be a wide range of vertebrate animals, which can come into intimate contact with them (WHARTON & FULLER, 1952; TRAUB & WISEMAN, 1974). Such a means of obtaining nutritional materials inevitably resulted in the formation of tighter and continuous connections with animals, i.e. a step-by-step transition from a free carnivorous life to obligate larval parasitism is realized. Concerning dermal reactions, it has been shown that, independently of the kinds of the host-animal and the species of trombiculid larvae, a similar histopathological reaction of the host tissue is observed in general (HOEPLI & SCHUMACHER, 1962; NELSON et al., 1977). Nevertheless, it has also been proposed that the nature of reactions in the host skin at the place of larval attachment depends mainly on the host species (WILLIAMS, 1946) and serves as an indication of the novelty of a host for trombiculid larvae (AUDY, 1951). On this bases it has been concluded that trombiculids causing strong local reactions (trombidiosis or scratch-itch), were originally parasites not of mammals, but of birds or even reptiles. Nevertheless, the particular organization of a feeding tube, or stylostome (HASÉ et al., 1978) is a characteristic feature for practically every trombiculid species (HASÉ et al., 1978; SMATROV, 1980, 1987), which obviously indicates a specific type of this implement of larvae which does not strictly depend on the host species. The initially pastoral nature of attack on animals predetermines the absence of an evident host-parasite specificity in trombiculids (BECKLEMISHEV, 1970), providing additional evidence of the historical youth of parasitism in their larvae. As a whole, the specificity is a composite multifactorial phenomenon, originating in the historical development of a given group, and in the most general case reflects the degree of a parasite presence on a definite host species. The specificity can be expressed both in the context of the concomitant evolution of a parasite and a host (phylogenetic spe-
specificity), and in the context of co-adaptation between the partners in conditions of similar ecological niches (ecological specificity) (Balashov, 1982), as well as by the number of hosts used (narrow and broad specificity). The problem of specificity in trombiculid mites is rather complex and has not yet been completely clarified, but merits brief consideration within the context of the problem of the origin of parasitism. So, examples of specificity of trombiculid larvae to different classes of terrestrial vertebrates, considered by Mouliarskaya (1969), are only particular cases of adaptation of larvae in connection with their definite localization on the hosts and have no general value. If the trombiculid larvae originally parasitized arthropods (Audy, 1961; Becklemishev, 1970), and the more ancient classes of terrestrial vertebrates corresponded more specialized genera of trombiculids (Mouliarskaya, 1969), the inevitable specificity arising in this case (Ewing, 1949) would not allow them to pass from the representatives of one class or even higher group of the hosts to another, as it does not take place, for example, in the same trombidiids. Actually, a tight host-parasite specificity in trombiculid larvae is not apparently presented, but what is really presented is the only preferred, due to compatible habitat, circle of the potential hosts. The latter has allowed trombiculid larvae to use as a source of food broad range of vertebrate animals at once, and under the appropriate conditions, has allowed the representatives of more ancient subfamily Leeuwenhoekiinae also to use insects (Ewing, 1949; Audy, 1950). According to the pronounced point of view, the larvae of trombiculid mites did not pass step-by-step from the representatives of one group of the hosts to the representatives of other groups, but due to morphological preadaptations have passed at once to parasitism on all classes of terrestrial vertebrates, mainly mammals. The subsequent morphological specialization has been developing very poorly and is expressed as a whole extremely gently, whereas the specificity is not expressed not only at generic and familiar level, but also at a level of higher taxa of the host-animals. The latter is just characteristic mainly for constant and all-life parasites (Kennedy, 1978; Balashov, 1982) and implies not only co-adaptation of members in a host-parasite system, but also co-evolution of groups of parasites and hosts of close systematic ranks, that is not obviously present in trombiculid mites. It appears, in this consideration, that only stylostome is a single and unique feature determining an extremely broad specialization of trombiculid larvae, and also trombidiids and water mites (Åbro, 1979, 1982, 1984, 1988) to parasitizing not only on vertebrate animals, but also on arthropods. If the larvae of trombidiids and water mites by virtue of still unknown eco-physiological conditions have initiated to parasitism on arthropods, for trombiculid larvae insects are, apparently, only the random hosts. It is clear from the above mentioned postulate, that stylostome serves as a universal device greatly adapting for obtaining of a feeding materials in a number of closely related groups of trombidiform mites during feeding of their larval instar on the broad rank of zoological objects. At the same time, stylostome is though to define in every case also the specificity of host-parasite interaction, i.e. general, but quite particular for each group, eco-physiological relations in a host-parasite system. Therefore, it is relevant in this sense to unite some related groups of trombidiform mites in an extra-systematic eco-physiological group of parasitic arachnids, forming stylostome during feeding. Concerning trombiculid mites it is more pertinently to speak about a biotopical specialization, instead of about ecological specificity, implying not specificity in the parasite-host system owing to co-adaptation in conditions of similar ecological niches (Kennedy, 1978), but only preferred for the given species a definite kind of biotope, and only thereby a definite circle of the possible hosts, which in this case would be as the main ones (Traub & Wiseman, 1974). So, these authors suppose, that the greatest fauna of trombiculids are in these animal species, which are more or less frequently located in a direct contact to soil (ground). Adapting of definite species of parasites to definite species of hosts can be limited by a number of factors, for example ecological, and in this case a kind of ecological specificity will appear to be received. It is legitimate to suppose, that the specificity as such is an absolute preference of the definite hosts by a given parasite and is developed on the basis of eco-physiological and morphological features during historical development, that as a matter of fact corresponds to phylogenetic specificity. Apparently, there
can be only represented a physiological preference by definite groups of trombiculids of definite groups of hosts with respect to obtaining of appropriate food during parasitizing, i.e. some kind of physiological specificity (SASA, 1961), which, in turn, is determined by both phylogenetic and environmental factors. Concerning historical aspect of a problem, it is necessary to note, that the direct paleontologic data on trombiculid mites are absent. According to Vainshtein (1978), the fossils of trombidiform mites (water forms) are known since mean Jurassic, and in the upper Cretaceous (in mineral resins) the great many of nowadays dwelling families of terrestrial mites is already revealed. However, the originating and following radiation of different groups of trombiculid mites and, furthermore, development of their phase larval parasitism, seem to have taken place not earlier paleogene, already after differentiation of their ontogenesis into quiescent and active stages, as is mentioned above. At the same historical period the development of placental mammals is proceeded as well. As it has been supposed, the local biotopical distribution of those or diverse species of trombiculid mites is determined by nature of a way of their life and requirements of free-living stages, whereas their geographical distribution in many respects depends on an spreading of larvae by their hosts during the time of parasitizing (Wharton, 1946). Thus, the primary hosts of trombiculid larvae were mammals, which were attacked by larvae in conditions of a pasture. Just at the process of parasitism on mammals trombiculids have formed so characteristic for them stylostome. On birds, reptiles and amphibious larvae have begun to attack already later, and in these cases the deviations from normal course of parasitism and ontogenesis are possible (Hyland, 1950, 1961; Audy et al., 1972). The feeding on insects, as was already mentioned, has in many respects random nature. If trombiculids have mastered for parasitism practically all classes of vertebrate animals, besides fishes, trombidiids and water-mites specialised in parasitism extremely on arthropods. All these groups, probably, were originally isolated from one another due to morphological reasons, but also due to ecological ones. At the same time, the general morphophysiologic preadaptation, basis of the whole branch of trombidiform mites leads to convergent features of parasitism in a number of their families. In any of these groups the transition to parasitism were irreversible and considerably increased both their competitive strength and morphologic and physiologic stability. Probably, it explains well the morphologic conservatism of free-living deutonymphs and adult mites, and, on the other hand, extremely diversity of this family with an invariable general plan of the inner organisation. Diagnostic signs of larvae distinguishing subfamilies in Trombiculidae do not concern adaptive structures nor assisting in parasitism of their representatives. It may be supposed that specific differentiation is irrelevant to parasitism in most cases and is provoked by a complex of other factors. This problem is still badly investigated. The evolution of any separately taken sign, for example of tarsal setae complex (Vercammen-Grandjean et al., 1973), does not reflect the evolution of the whole group, as it would be desirable to see it to the authors, i.e. the progressive changes of a level of its organization. At the same time, the propulsions of these transformations in tarsal setae complex remain uncleared. It may be concluded that the larvae of trombiculid mites are most probably primary parasites of mammals, whereas the remaining classes of terrestrial vertebrate animals as well as birds are their secondary and evolutionary (historically) later hosts. At the same time, correlated evolution of trombiculids and vertebrates is not apparently observed: that is mainly defined by the capability of larvae to obtain appropriate food (nutrition) during a rather short period with the help of universal stylostome, while the whole remaining ontogenesis proceeds outside of the host in a natural environment. Therefore, the life cycle pattern is thought to predominate over the host-parasite relationships in this group of trombidiform mites. This investigation is supported by grant N 00-04-48885 from the Russian Foundation for Fundamental Researches.

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