

An Investigation into the Life-histories and
Ecology of the Hydracarina.

A Thesis Presented for the Degree of Doctor of
Philosophy in the Faculty of Science at the
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By

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Introduction

The Hydracarina form an abundant and most important element in fresh water habitats, reaching densities of over 20,000 per sq.metre in lakes and over 150,000 per sq.metre in rivers. Despite their abundance, a considerable literature throws very little light on their ecology or life-history, and in fact the full life-histories are known for less than 5% of the 3,000 known species.

The work described in this thesis was planned to provide qualitative and quantitative data on one aspect of the life-history, namely the parasitic larval phase, and it was decided to concentrate exclusively on this aspect without following up any of the other interesting lines of research which suggested themselves from time to time.

Nevertheless, as mites had to be closely observed both in the field and in the laboratory it was inevitable that other facts should come to light concerning their way of life and distribution, and these are also described either in the body of the thesis or in the appendices.

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General Account of Procedure.

The majority of the work required for this investigation has been laborious rather than technical, involving a great deal of straightforward collection and observation and a minimum of apparatus. The major part of the work was not concerned with distribution and did not therefore necessitate a precise analysis of the physical and chemical differences of the sites used. Chemical analyses of river waters were readily available from the River Boards and it was decided that apart from temperature, rate of flow, pH and measurements of area and depth, no further investigation of the physical factors should be carried out. In point of fact no significant differences were found which could explain anomalies in the distribution of the mite fauna. (see P.79). A brief account of the collecting techniques is given and, as very few workers have previously made any serious attempts to breed Hydracarina a rather fuller account of this part of the work is included. Breeding out is particularly important, as it is only in this way that the life histories can be fully determined.

1. Free living adults, nymphs and larvae.(a) Ponds, lakes and ditches.

Ponds were sampled by means of a fine nylon net fitted with a glass tube. The net mesh was fine enough to trap Protozoa and there was, therefore, very little possibility of mite stages escaping through it. Collections were made by allowing quantities of water from selected parts of the pond to filter through the net, and emptying the concentrate from the glass tube at the bottom of the net into a glass jar for transport back to the laboratory. No attempt was made to collect

2.

known quantities of pond water since it was quite obvious that mite density varied very greatly from one part of a pond to another, and the intention behind the research did not call for accurate estimates of the overall populations. The collected material was turned out into a white dish and visible mites removed with a fine pipette. The remaining material was washed through two sieves, of 1.18 and 3.54 meshes per mm. respectively and the contents of the sieves washed into petri dishes and examined under the low power binocular microscope. It was found convenient to put the petri dish into a white porcelain tray for this work and to illuminate it with the brightest available lamp. Small mites and especially the larvae show up well against a white background. They can be picked up readily as they move about over the fine sand which passes through the top sieve, and in this connection it is very desirable to do the sorting while the mites are still alive. Picking out dead mites from material which has been preserved is a much longer and more tedious process.

Female mites from these collections were isolated in small glass tubes on the sides of which they often laid their egg batches. The latter could be examined and counted by placing the tube under the binocular microscope.

(b) Flowing water.

Rivers were sampled by searching small boulders for visible mites and also by collecting bottom flora and sand over measured areas. The boulders were rolled over and the visible mites and their eggs picked off with a fine pipette, or else with a needle.

For the collection of measured areas of the substrate a cutting

3.

tin of approximately 25 sq.cms. area was used. The tin was placed in position and pressed down. All plants in the cutting area, together with a thin layer of the substrate were transferred to a bottle and the mites were later dislodged with a fine jet of water and washed through sieves as described above. The concentrate was then searched as already described. It was found that an ordinary domestic, steel pastry cutter made an excellent cutting tin and that on the calcareous rock of the Derbyshire rivers it could be pressed into the surface deposit and would bring out a wad of moss and calcareous crust which stopped water escaping, so that the whole wad could be most easily transferred to a bottle. In some Yorkshire rivers it was not possible to push the tin into the substrate in this way and, after the plant material had been cut through it was necessary to push a flat metal plate under the cutting tin before lifting. This could possibly lead to a small proportion of the material, together with some mites being lost, due to their being pushed away by the flat plate, but it was thought that this loss would not be significant. When the tin was being used to sample moss from small falls in fast flowing water it was not easy to effect the transfer without losing the sample. In this case it was found that it was easiest to have the receiving bottle in a sling so that both hands were left free for manipulating the sample.

2. Parasitic stages in Mussels.

Mussels to be examined for Unionicola spp were usually collected by hand and visually, but in deeper water were raked for with a very long handled rake. The mites were removed by dissection of the host. Stocks of mussels were kept until required in sand-filled flower pots

in an artificial pond. This ensured a reliable supply of mussels even when other sites were covered with ice. The flower pots made searching for the mussels unnecessary and the mussels survived under these conditions for at least the duration of the experiment, i.e. three years.

3. Other parasitic stages.

(a) Hemiptera.

(i) Gerrids.

Gerrids were caught by sweeping the water surface, particularly through reed patches, with a net and removing the insects into 1 cm. diameter tubes in which they could be examined immediately with a x 15 lens. This enabled counts of mites on the insects to be made with reference to the position of attachment. The ease with which larvae of Limnochares aquatica, L., are dislodged from the host, made examination in the field most desirable. Host species were also taken to the laboratory and studied under the low power binocular microscope after anaesthetisation. Very small larvae under the head of the host could not always be discerned with the hand lens through the glass of the tube, and for this reason the field counts will, in general, underestimate the degree of infection of the gerrids by an estimated 2%. The ease with which these mite larvae and those on some midges can be dislodged in the course of transport suggests yet another reason for the paucity of reported parasitism by water-mite larvae on insects.

(ii) Corixidae.

Corixids were caught from amongst vegetation and examined for mites under a hand lens and under the binocular microscope. Eylais spp

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nymphochrysalids were easily visible under the elytra using the hand lens, if they were engorged enough to raise the elytra, but could be found only with difficulty under the microscope if they were too small to do so. In autumn collections it was found necessary to open the wings of the corixids in order to look for the very small larvae present at this time of year.

(iii) Other aquatic Hemiptera

Notonecta glauca, L., Nepa cinerea, L., and Hydrometra stagnorum, L., were caught when seen and examined for mites. The numbers of these three species found during the survey were too low to give any very reliable results.

(b) Chironomid pupae.

Chironomid pupae were caught by netting and inspected under a lens. A count of mite larvae resting upon them was thus made in the field and a recount under the low power binocular microscope in the laboratory. Pupae were allowed to hatch under a bell jar and the number of parasitised adults compared with the number of pupae bearing mite larvae. Pupae not carrying mite larvae were used as possible hosts for tests on larvae hatched from eggs laid by mites in the laboratory.

Chironomid pupae were also collected on stones from river beds and allowed to hatch from a tank covered with nylon netting. They were not examined in the field as it was considered that this would involve too much disturbance of the pupae, since their cases would have to be separated from the rock in order for an examination to be carried out. The hatched midges were then examined for mites.

(c) Adult chironomids and other Diptera.

Adult midges and mosquitoes were collected in a large nylon net and 'pootered' into glass tubes. They were taken back to the laboratory, etherized, and examined under the microscope. It was found that by collecting the midges from swarms, a great deal of host sorting was obviated, as the swarms are nearly always of only one species. Large numbers of midges of a single species can thus be caught in a very short time. Unfortunately this method was not always possible and midges had also to be caught by sweeping through the vegetation with the net. The latter method produced a reasonable proportion of each sex, while the former tended to give a vast preponderance of males.

(d) Odonata nymphs were collected by sweeping with the pond net, and searching the material collected. Captured nymphs were examined under the microscope for mite larvae. They were kept in glass dishes in the laboratory and used for mite counts before and after emergence.

Unparasitised nymphs were used to test the host-finding abilities of Arrenurid larvae.

(e) Odonata imagines provided an excellent opportunity for close observation under field conditions of parasitism by water-mite larvae. They were caught in a nylon net and examined under a x 15 lens immediately. Mites in situ could be quite easily counted and the hosts were then confined in a large glass jar loosely packed with grass until counting for the site was finished. The hosts were then released apparently unharmed. This method made it possible to examine a large proportion of the local populations of the host species in the vicinities of isolated ponds, and to re-examine the same populations on several visits spread over several weeks, while avoiding the errors

which could be introduced by removing a significant proportion of the damsel-flies and also avoiding unnecessary destruction of the fauna.

Emergent Odonata adults were also examined, by the following method. After the nymph had left the water, the grass or reed stem on which it was resting was carefully cut with scissors and the nymph and its support could then be moved to a suitable position for examination. In this way the behaviour of the mites carried by the nymphs from the water could be carefully observed without interrupting the emergence of the host or causing it any damage. Great care was taken to handle only the support and it was found unnecessary to handle the insect at any time. After the host had been examined the reed was stood in a grass clump to enable the host to expand its wings and complete its metamorphosis.

(f) The fly, Weidemannia bistigmata, Curt., posed problems rather different from those associated with other insect hosts, owing to its habit of flying in close proximity to the water surface. After several unsuccessful attempts to catch it with a net sweeping low over the surface I found that it was possible to catch the insect by using a 'pooter' with a long mouth-piece. The mouth-piece was kept in the mouth, while the entry tube was brought near to the flies as they settled on rocks in the river. Sudden suction usually succeeded in trapping the fly. Considerable practice was necessary before this technique was mastered as it was all too easy to draw up water into the 'pooter' if the entry tube was placed too close to the stream. It was easier to catch the flies when they were congregating on the under-side of an overhanging part of a boulder, as they were easily disturbed by the 'pooter' if it cast any shadow on them. This method of collection

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was not nearly as convenient nor as certain as the metting of Chironomids or Odonata and as a result the number of the Empids examined was far less than for the other two groups.

Breeding methods for Water-mites.

As there was very little previous information on methods of breeding water-mites a considerable amount of time and thought had to be devoted to this aspect of the work, as it seemed most likely to provide fundamental evidence on the life-histories.

Females caught in spring and summer were isolated in small glass tubes provided with plant material and loose microscope cover slips. With the exception of Hydrachna spp females of pond dwelling mites laid their eggs either on the sides of the tubes, on the plants, or on the cover slips. Any situation on the glass was excellent for counting the eggs in the egg-masses, and for watching the development of the larvae within. Larvae bred from such eggs were used for host-preference experiments. Eggs found in the ponds were also isolated but their value was much less owing to the difficulty of accurately identifying the larvae which hatched from them.

The rheophilic mites present a much greater problem owing to their very small size and the fact that they produce only two to four eggs at a time, and that these are apparently laid singly amongst the leaves of aquatic mosses. It was found possible, however, to isolate ovigerous females of these very small species in petri dishes to which a small amount of moss had been added. This moss was searched, leaf by leaf, under the high power of the binocular microscope, to ensure that no mite eggs or other stages were present at the start of each experiment.

This proved to be a most tedious and time-consuming undertaking and any worker wishing to carry out such work on a large scale would be well advised to grow mite-free moss under controlled conditions for use in the work. On the other hand this work produced the hitherto unknown and quite unexpected larva of Aturus scaber, Kramer. The application of this method to the other rheophilic mites would settle the question of whether they also hatch from their eggs as larvae or emerge in the nymph stage, and would be a first step towards an understanding of various problems of their life history which are discussed later in this thesis.

If mite larvae found on insects are to be accurately identified to species they must be bred out to the adult stage. This involves taking them through two pupal stages as well as the nymph stage. Most of the parasitic larvae dealt with in this work were found on Diptera, and it was found that if parasitised hosts were enclosed in glass tubes in which there was a little water and a piece of reed, the mites were able to make their way down the reed into the water, and would usually pupate either on the bottom of the container or in the hollow end of the reed itself. After pupation they were transferred to small glass tubes to await emergence as nymphs.

Alternatively, if the host died and fell into the water, the mites were often able to make their way under the surface to pupate as before. It was found in some cases that if parasitised hosts were shaken in a little water, the majority of parasitic mite-larvae would make their way under the surface and pupate on the bottom. Nymphs which hatched from these nympho-chrysalids were offered Ostracods and Cladocera and

were fed on whichever of these they would eat until pupation to teleio-chrysalids took place. There was a very heavy mortality of nymphs especially in those which had to be kept over winter. The nymphs of river mites are believed to feed for the most part on insect larvae, and no way of providing these continuously was discovered. As a result no river mites were bred right through to adults.

It was found possible to keep the majority of still-water species in tubes containing 10 ml. of pond water, for from one to five months, and most of the river species survived for at least one month in petri dishes containing a little moss and sand.

It should be stressed that methods of breeding water-mites are far from being perfected and that the establishment of more or less fool-proof methods of taking the mites through to adulthood from their larval stages would be the most useful single aid to working out their complete life-histories. Indeed, as is argued later in this thesis, if valid generalisations about the life-histories of the water-mites are to be made, breeding-out techniques will have to be perfected and it is hoped that it will be possible to proceed with this line of research later.

Previous work on water-mite ecology and life histories.

The presence of larval and nymphochrysalis stages of water-mites on aquatic and aerial invertebrates has attracted the attention of many naturalists but as many of the early workers were not specialists, the mite stages were not always recognised as such and were often described as eggs.

The first published record appears to be that of Frisch, who in 1730 described "a little red water-spider" which fed on the newly hatched young of the "wasserlaus" when the latter were so small that "I could scarcely see them with my usual lens." Seven years later Boorhaave (1737) published manuscripts and drawings made by John Swammerdam, M.D., some sixty years previously. These described a water-scorpion "covered with a prodigious number of nits of different sorts and sizes" which, on dissection, proved to contain a little spider. He commented, "I cannot determine to what species of insect this is to be referred, or by what kind of creature it is thus deposited on the water-scorpion. Nevertheless..... it proves that there are in the nature of things eggs which acquire a sensible growth by an extraneous nourishment." Swammerdam himself seems to have had doubts, however, as he went on to state that he would not strenuously oppose anyone who wished to consider this a complete insect rather than an egg.

Linnaeus, 1761, described Acarus aquaticus (= Limnochares aquatica, L.) a free-living mite whose "eggs" were laid on Nepa.

C. de Geer, 1768, observed several water insects infested with the red, pear-shaped parasites noted by previous authors. These "eggs"

were described and figured, as well as the nymphs which emerged. This record is particularly interesting as it is the first example of an attempt being made, not to dissect and study the anatomy of the parasite, but to keep it and see what would emerge. This is the method which would appear to offer most hope of gaining any real knowledge of the life-histories of the Hydracarina, and one, indeed which has been followed during the work for the present thesis.

C.G. Bonz, 1783, described Acarus ypsilophorus (= Unionicola ypsilophora, Bonz) from Mytilus cygneus (= Anodonta cygnea, L.), and Unio pictorum, L.

Pfeiffer, 1821 - 25, gives a brief account of mites found in Anodonta cellensis. Eggs and larvae were also found and isolated mites moved awkwardly, but when the host mussel was added to the dish the mites rapidly found their way into it.

Audouin, 1822, described under the name of Achlysia dytisci, a "new genus of tracheate, six-legged Arachnid" two parasites found on the body of Dytiscus marginalis, L., from the forest of Fontainbleu in June, 1819. They measured 6 mm. by $3\frac{1}{2}$ mm., and were of a yellow-orange colour. Audouin dissected the specimens but was unable to find any internal organs, while externally he recognised "un soucoir" and six legs.

Duges, 1834, described the parasitism of Limnochares aquatica, L., on Gerris lacustris, L., and referred Audouin's species to Hydrachna geographica, Müller, and H. globosa, De Geer. He studied the latter species under aquarium conditions and described the egg-laying in the leaves of Potamogeton, the resulting larvae and their metamorphosis.

Girod, 1889 studied the anatomy of Atax ypsilophorus (= Unionicola ypsilophora, Bonz) parasite of Anodonta spp., and Atax bonzi (= Unionicola bonzi, Claparede) parasite of Unio spp.

The references given so far have been of isolated observations on single mites, mostly made by naturalists in the course of other work. In 1880, however, Neumann published a monograph on the Swedish water-mites and also a short paper on the development of the Hydracarina the same year. These were followed during the next twenty years by an increasing number of large works, mostly taxonomic in content, culminating in Piersig's "Deutschlands Hydrachniden" (1897-1900) which summarises most of the knowledge of the Hydracarina up to that time. In this work there are descriptions and figures of sixteen larvae, together with what appear to be the first records of mite larvae metamorphosing to nymphs without any parasitic stage intervening.

Fearnside, 1900, and Chatterjee, 1901, appear to have been the first of a number of authors about this time to observe water-mite larvae attached to mosquitoes. Both were primarily interested in the hosts and the mites were not identified. Gros, 1904, made observations on larvae parasitic on Anopheles maculipennis, Meigen, (Insecta, Diptera) and his description led Motas, 1928, to conclude that the mite concerned was probably Hydrodroma despiciens, Müller. The fact that 174 years elapsed between the first paper on parasitic stages of water mites on aquatic insects and the first published account of larvae of the group of Dipteran hosts is of the greatest possible significance. It illustrates quite clearly how much less obvious and how much better concealed the Dipteran parasites are than those which attack aquatic insects, and will be dealt with fully in the discussion later in this

thesis.

After 1890 an increasing number of papers on the Hydracarina appeared, covering a great many aspects of their biology and for this reason it will be clearer if the references relevant to this thesis are given under particular subject headings rather than in chronological order.

(a) Pairing.

Koenike, 1891, described pairing in Piona fuscata, (= P. nodata, Müller) and observed the spermatophores, which on breaking allow the sperms to escape. The chitinous spicules on the sperms, described by Koenike, may, according to Viets, 1923, tear the spermatophores so that the contents are thus able to enter the female genital orifice. Viets also described the pairing of Pionopsis lutescens Hermann, which, he says, is like that of Piona, and has described that of Typhis ornatus, Koch. Viets observed that the packet of spermatophores, together with their spicules were enveloped in a gelatinous covering which was associated with a structure which resembled a "bolster". He gives a microphotograph of the end of a copulatory leg of Piona longicornis, Müller, in which the spicules are shown hanging with the sharp end downwards, and also the "bolster".

Motas, 1928, describes the spermatophores of Piona nodata, Müller, in which the packet of 6 - 8 spermatophores carried by the male is also covered by a gelatinous substance the bundle of spicules being connected with a brown fibrous ring which passes between the claws on the third feet, holding the ends of the legs together. The pyriform spermatophores are $57\mu \times 25\mu$, and their contents are granular each spermatophore

phore connecting with a coiled tube.

The beginning of pairing has been seen by Walter, 1922, and by Motas, 1928, in Forelia cetrata, Koenike, but neither author has seen the actual act of fertilisation. The copulation of Feltria georgei, Piersig (= P. setigera, Koenike) has been described by Motas, 1928, as similar to an account given by Thor, 1901, for Kongsbergia materna, Thor. In these species the male siezes the female with his palpi, the fifth segments lodging in the antero-lateral depression of her body. The male then grasps the female firmly with his first two pairs of legs just in front of her fourth pair which are thus immobilised. According to Motas the male then rubbed the female genital orifice backwards and forwards with his third legs, which are provided with three strong spines. Similar movements were made by the male fourth legs although they were not in contact with the female. Motas watched this action for over two hours but at last saw the pair separate before the male had extruded his spermatophores and assumed that the latter are normally transferred by the third legs. Thor, on the other hand, after observing movements of the male fourth legs towards the female genital orifice concluded that these legs fulfilled a dual role of excitation and fertilisation and that the hairs on these legs carried the spermatophores.

The pairing of Brachypoda versicolor, Mtiller, has also been described by Motas, 1928, and during pairing the terminal joint of the male fourth leg makes a right angle with the preceding joint, reminding Motas of an adjustable spanner, by means of which the male grips the female with the third and fourth pairs of legs on either side. The

male is in an almost vertical position, the first two pairs of legs waving feebly; the third legs, forming a ring in front of the female, carry the spermatophores while the fourth legs grip her firmly round the middle of the body. The anterior extremity of the female is engaged in the posterior ventral cavity of the male. The female lies passively, legs outstretched, palpi under the genital opening of the male for the duration of pairing, all the efforts of the male tending to bring together the posterior end of the female and the packet of spermatophores carried by his own third legs. The male does not succeed at once, and the body of the female rises and falls repeatedly until the male succeeds in leaving his spermatophores at the entrance of the female genital slit..

Uchida, 1932, has pointed out that the pairing patterns of water-mites can be placed in four different categories according to the relative positions assumed by the pair, as follows:-

(i) The male comes in front of the female, the posterior dorsal part of the male connecting with the posterior ventral part of the female by means of the petiole or sticky glands in Arrenurus spp. or the fourth pair of legs in Aturus spp. He called this the "Arrenurus" type of pairing and it has been described for various Arrenurus spp by Motas, 1928, and for three Arrenurus spp and for Aturus scaber, Kramer, by Lundblad, 1929.

(ii) The male and female come together at right angles, the ventral surfaces opposing one another, and the anterior end of the female meeting the posterior end of the male. The female is held by the fourth legs of the male. This is called the Piona conglobata, Koch

type and has been described by Piersig, 1900, Motas, 1928 and Viets, 1914. It includes P.nodata, Müller, Pionopsis lutescens, Hermann, and Brachypoda versicolor, Müller.

(iii) The male siezes the female by the anterior dorsal surface with his palpi. This is known as the Feltria setigera, Koenike type and was described by Motas, 1928.

(iv) The ventral surfaces are opposed, the male gripping the female by her anterior ventral surface with his palpi and legs so that the genital openings of the pair come into opposition. This, Uchida called the Midea type and it has been described by Lundblad, 1929, for Midea orbiculata, Walter, and by Motas, 1928, for Eorelia cetrata, Koenike.

(b) Egg-laying.

No records have been found concerning the time elapsing between pairing and egg-laying, but Stout, 1953 b., states that a female of Piona novae-zealandiae, Stout, (= P.uncata exigua, Viets) isolated for a month laid fertile eggs.

Sokolow, 1924 and 1925, has provided the two main pieces of work on egg-laying and spawn of water-mites, the term "spawn" being used by Sokolow and many other continental workers to include the eggs together with the egg coverings. He publishes a table giving egg numbers per batch, egg diameters, the time taken to hatch for 37 species, and for 19 of these gives a definite 'spawning-time'. For purposes of comparison he includes figures of egg-diameters from Piersig, 1901, and gives a key for the spawn of 32 species.

Viets, 1936, also gives a key to the spawn.

Motas, 1928, published a table giving the egg-numbers, size and ratio of the length of egg to length of female body for 30 species. Extracts from these tables are given later in the thesis in table (ix) and the correlation between this ratio and the development of the larval stages of the mites is discussed there. The duration of embryonic life is given as 14 - 42 days, varying with species and probably with temperature. The latter point has been examined experimentally with over-wintering eggs of Protzia eximia Protz, and the results of these experiments are given on P. 78. Imamura, 1951, has described two species which spend 11 and 9 days respectively in the egg stage, so that Motas' lower limit can be reduced still further, while Zschokke and Steinmann are quoted by Soar and Williamson, 1925, as saying that mites from mountain streams are not prolific in eggs and that such eggs are large and have a long embryonic period.

The possibility has been put forward by Wesenberg-Lund, 1918, and others that some mites may over-winter as eggs, and this is, of course, well established for species of Unioncola parasitic in fresh-water mussels. It has also been proved in the course of the present work for Protzia eximia, Protz.

The egg-laying process has been described for a few species. Thon, 1901, for example, saw a female of an Eylais species lay her egg masses and then cover them with an excretion from the apex of the capitulum. Wesenberg-Lund, 1918, observed the egg-laying of a Hydrachna spp where a slit cut in plant tissue by the mandibles was enlarged into a cavity by the rostrum, and the eggs, after deposition at the entrance of this cavity, were pushed into it by the rostrum.

Stout, 1953 b., describes the egg-laying of Hydrachna maramauensis, Stout, in the longitudinal galleries (aerenchyma) of a Potamogeton stem. The mite held the stem with its legs and pierced it with its mandibles pushing the whole rostrum down into the stem. The mite then held the plant with its palpi and laid its eggs in two rows in the mine so formed. Stout says that Anacharis cannot be used by the mite as the stem has no longitudinal galleries.

(c) Larval life.

Although water-mite larvae have been collected or reared from eggs by many investigators and there are descriptions for quite a large number, including systematic keys by Viets, 1936 and Sparing, 1959, it is still extremely difficult to find much information on their modes of life up to the time that the nympho-chrysalis is formed. Soar, 1906, wrote, "There are sixty known genera of water-mites and of these we do not have any definite information on the early stages for more than six." Viets, 1936, was able to give hosts for species belonging to nine genera, while Sparing, 1959, gives hosts for species of twenty-three genera out of 262 genera now known. It is significant that the proportion of genera for which this information is available has actually fallen since Soar's day.

Sparing, 1959, distinguishes four larval groupings,

(i) Development of two generations with two egg-laying seasons.

Eggs are laid in water-plants and the larvae are parasitic on insects with aquatic adults. When the nymphs leave the hosts they are little smaller than the adults, which are comparatively short-lived. Overwintering is in the parasitic nympho-chrysalis stage on the hosts, or

else as eggs.

(ii) Two generations and two egg-laying times with the larvae parasitic in sponges, and the eggs laid in the host tissues. When the nymph leaves the host it is large compared to that of other species. Pupation of the nymph takes place in the host tissues after the mite's return on completion of the free-living stage and there is over-wintering as adult.

(ii.b) Often more than one generation. Egg-laying takes place throughout the winter, the eggs being laid in the host tissues. The hosts are fresh-water mussels. Pupation of the larvae and nymphs takes place in the host tissues and over-wintering is either as adult or egg.

(iii) Egg laying on stones or water plants denotes larvae parasitic on insects with aerial adults. The fully grown and ready to pupate larvae or the nympho-chrysalids but not the nymphs proper drop off the hosts. The nymphs are proportionately small on emergence, in isolated cases even as small as the larvae. Pupation of the nymphs takes place on water-plants and over-wintering is in general as adults or nymphs or in both stages.

(iv) Egg-laying period may extend a short or long time. Eggs and are laid on water-plants/in isolated species the larvae are not released from the spawn. The larvae are not parasitic and the nymphs are, as a result, very small, the whole growth taking place in the free-living stages. Pupation of the nymphs takes place on plants and over-wintering is as adults or nymphs.

Sparing points out that mite larvae are not, as Piersig thought,

parasitic mainly on insects that are aquatic as adults, but that most species seem to favour insects with aerial adults. Her suggestion that larvae parasitic on aquatic adult insects belong to the genera Hydrachna, Eylais and Limnochares, however, seems to be an oversimplification of a very complicated state of affairs.

Several attempts have been made by various authors to fit the parasitism of water-mite larvae into some sort of orderly system but even with the present limited knowledge of hosts it becomes obvious that any such scheme is bound to have many exceptions. Unfortunately the natural desire for order has led some authors to reject perfectly valid observations where these did not conform to some pre-conceived pattern. For example, Killington and Bathe, 1947 b., recorded various damselflies attacked by larvae of Limnochares aquatica, L., and pointed out that Munchberg, had dismissed previous reports of this mite attacking the Odonata. In the pond where this was observed there was a one hundred per cent infestation of Gerrids by these mite-larvae and this may have given rise to the transfer of some of the mites to the Damselflies as hosts. Similarly, although in the genus Arrenurus, the subgenus Arrenurus s.str., has been found to infest Odonata, while the other three sub-genera are found on Diptera, Nematocera as well, this division cannot be accepted exclusively without rejecting several authentic observations. Motas, 1928, described an Arrenurus larva parasitic on Hydrophilus spp. (Insecta, Coleoptera) and Uchida, 1932, found many larvae of an Arrenurus spp which were found to be exclusively parasitic on Hydrophilus larvae. These parasites doubled their size in three days and left the host after four or five days, forming their

nympho-chrysalids on the bottom of the aquarium. Uchida was unable to rear them further but, apart from the fact that this is the only paper describing beetle larvae as hosts for larval water-mites, it also illustrates the shortness of the parasitic stage, which is a major source of difficulty in dealing with the life histories of the *Hydracarina*. Soar, 1901, found two *Arrenurus* larvae attached to a young fish. This also is a unique record and it appears likely that in this case the relationship cannot be a normal one for with the widespread interest in fish in all their stages, there would surely have been more records than one if they were commonly used as hosts by mite larvae.

Among the *Pionidae*, Uchida, 1932, found larvae of *Piona carnea*, Koch, *P. obturbans*, Piersig, and *Typhis ornatus*, Koch, attached exclusively to the pupae of *Chironomus thummi*, Kieffer. One pupa was parasitised by as many as two hundred of the mites. The larvae of the chironomid were not attacked "probably on account of their rapid movement". At the death of the host Uchida saw the larvae change hosts and surmised that they may do so several times before reaching the nympho-chrysalis stage. *Piona coccinea*, Koch, and *P. conglobata*, Koch are both reported as parasitic on chironomids by Sparing, 1959, and Motas, 1928 found larvae of *Piona disparilis*, Koenike on females of *Cricotopus biformis*, Edwards (Diptera, Nematocera) at the time of egg laying. The mites were attached by their palpi but when the hosts died the mite larvae made their way to the egg rafts and then entered the nympho-chrysalis stage. He used these observations to cast doubt on the records of Piersig, 1900, who had stated that parasitism in *Piona rotunda*, Kramer and

P.fuscata, (= P.nodata, Müller) was suppressed and that the larvae underwent metamorphosis to nymphs without any attachment to a host. Motas suggested that the fleeting nature of the parasitism had misled the earlier worker. However Stout, 1953, b., described the species Piona novae-zealandiae, Stout, (= P.uncata exigua, Viets) which when isolated in a container "from which all visible life had been carefully removed" produced nymphs in a week or ten days. Cook reported (1956) that in the case of an unidentified Forelia spp, nymphs hatched from the eggs thus cutting out the larval stage altogether, and Lundblad, 1927, reported the same for Pionacercus leuckarti, Piersig. Similar abbreviated life-histories have been observed in other families for Brachypoda versicolor, Müller, (Piersig, 1900), Limnesia undulata, Müller, (Neumann, 1880) and L.connata, Koenike. (Piersig, 1900). Robert M. Crowell, 1960 reports that in Thyas stolli, Koenike, one female laid approximately 190 eggs in 6 batches. The average diameter of these eggs was .142 mm., and they hatched in three weeks after deposition to give larvae. A group of morphologically indistinguishable females laid batches of from 2 to 6 eggs, with an average of four eggs per female and an average diameter of .24 mm. These large eggs hatched 7 days after laying producing not larvae but nymphs. He found larvae of T.stolli Koenike on two mosquitoes of the genus Aedes. This is the only known observation by a single worker of both life-history types in a single mite species, and offers a perfect explanation of the anomalies which worried Motas and others.

In the Unioncolidae there is a greater knowledge of the hosts than in any other family because, as many of the adult mites are found in the mantle cavities of fresh-water mussels the host can be identified

at the same time that the mite is discovered. Some members of the family have not been found in association with molluscs however, and nothing whatever is known of their life-histories. Unioncola crassipes, Müller is an exception as the adults and larvae are found in the tissues of fresh-water sponges, but the British species Unioncola figularis, Koch although widely distributed appears to be free-living as adult while its larva is so-far unknown. Unioncola aculeata, Koenike is reported by Mitchell, 1955, as being free-living in all its active stages and merely entering the mussels for its resting stages, including egg-laying, and although Mitchell summarises our knowledge of mites which parasitise mussels, like many other workers who have studied the subject he can give no information on the larval life.

Welsh, 1930 onwards, examined the reactions to light of certain Unioncola spp larvae and found that they are positively phototaxic when they have been separated from the host for 24 hours, but that they show a sudden and distinct reversal of this phototaxism when material from the host tissues is added to their container. My own attempts to repeat Welsh's experiment have met with no success, the mite larvae remaining positively phototaxic even in the presence of mantle tissue. However, the reaction observed by Welsh, if it is in fact the normal reaction of the larvae, would explain how the larvae find their way back into their hosts after their free-living phase.

Very few records exist of the actual attachment of the larvae to their hosts. Wesenburg-Lund, 1918, observed Hydrachna williamsoni (= H. processifera, Koenike) larvae swim around at great speed and refuse to attach to Naucoris spp, Nepa spp, Notonecta glauca, L.,

Corixa spp or to the smaller Dytiscidae, but readily attack Dytiscus marginalis, L., (Insecta Coleoptera) covering the host so closely that "the chitin was totally concealed". Imamura, 1950, describing the life-history of Partnunia uchidai, Imamura, says that the larvae occasionally jump 2-3 cm., above the water, a feat also described by Lundblad for Thyas barbiger, Viets. It seems reasonable to assume that since P. uchidai parasitises six species of stone-fly imagines this leaping is concerned with attaining its place on its host. My own observations on this habit in the larvae of Protzia eximia, Protz are described on P.66.

According to Efford, 1960, some larvae wait in the pupal cases of Chironomids until the adults emerge and are thus able to board the imago as it leaves the water. Soar and Williamson quote Taylor as having shown that the larvae found on the pupae of Orthocladus rivulorum, (Diptera Nematocera) accompany the pupae to the surface and pass from the pupa to the imago at the moment of emergence. Efford also found larvae of Feltria minuta, Koenike, one attached to Protonemura mayeri, Pictet, nymph, and thirty-four, together with one Lebertia spp larva on a single Caddis fly larva. Whether these can be supposed to have been awaiting the metamorphosis of a possible host is by no means certain, as in the first place, this is only the third record of water-mites associated with the Trichoptera and no records have been found at all of parasitic larvae attached to caddis-fly adults. However during the present work the larvae of Protzia eximia Protz have been in fact found to parasitise a Caddis fly. (see P. 66).

Killington and Bathe, 1947, a., state that Krendowsky, 1878, was

the first to record the passage of larval water-mites from the skins of nymphal dragon-flies on to the adults, a happening which was also observed by Dr. Ris, quoted by F.W. & H. Campion, 1909. On the other hand, Tillyard, 1917, thought the mites were not parasites and suggested that the female probably laid her eggs or viviparous young on the dragon-flies at the time of their emergence from the water. The fact that such an opinion should still have been held so recently shows once more how little real information was available on the habits of water-mite larvae.

Twinn, 1939, states that Simuliid cocoons often contained fixed to the abdomen of the pupa within, about fifteen small mite larvae, and although no damage by them has been proved, it was noted that where the mite larvae were larger than usual the abdomens of the Simuliids were often devoid of contents. This appeared to suggest that the mites were feeding on the abdominal contents of the Simuliids. It was further noted that species whose cocoons were open-ended were affected in this way while those species with sealed ends to their cocoons were not.

Davies, 1959, reported that larval mites clinging to the pupal cases of Simuliids easily transferred themselves to the adult insects at the time of emergence. Newly hatched flies had ten to thirty-two mite larvae on them, whereas a day or two later this number had been reduced to from one to three mite larvae. He concluded that there was a large larval mortality amongst the mites as a result of falling off the hosts. Davies also counted hosts and mites and found infestations varying from 0 to 16% of male flies infected, and from 0 to 86% of

female flies infected. On one batch of females he found 14,434 mite larvae on 3,088 flies. Mite larvae doubled their size while on the hosts and left the flies as they were egg-laying. Davies thought that the mite larvae were pulled off the host by sticking to the egg masses and were later washed free from the latter.

Mitchell, 1959 and 1961, described experiments on Arrenurus spp in which the hosts were dipped under water. In some cases although no movement was ever noticed in dry larvae while attached to the hosts, as soon as they were wetted, fully engorged larvae became active, moving the legs with increasing power until the mouth parts became free from the host integument. Mites thus activated were able to swim away when the host was dipped in the water. One species, although becoming active on damping required external pressure to remove them from the hosts, but Mitchell points out that the hosts of this species oviposit by flying low over the water and striking the surface with the tip of the abdomen. Other mite species show no reaction to damping but left the host if it was kept in water for 24 hours. Mitchell noted a strong connection between the habits of the hosts and the sites on the hosts selected by the mite larvae, parasites of the Coenagrionidae, which submerge completely when ovipositing tending to be on the thorax and legs of the host, while those on Libellulidae, which dip only the tip of the abdomen into the water, are found on the last few abdominal segments. Mites which showed no wetting reaction were mostly on the host thorax. Mitchell concludes that site selection is more important than host specificity. He also points out that there seems to be no sex selection by the parasitic and that in the case of those which re-enter the water actively this may result in the loss of those which

attach to male hosts.

The whole question of site selection on the host and of losses due to attachment to male hosts is dealt with in the discussion later in the thesis.

Marshall and Staley, 1929, 1930 and 1930.b., have dealt with the reactions of host mosquitoes to the bites of larval water-mites. This reaction takes the form of a tubular process from the host integument, and was also noted by Ian-Chou Feng, 1933, who describes the finding of Anopheles hyrcanus var sinensis infested with as many as thirty to forty mite larvae. These were greenish in colour and were attached by their mouth parts most frequently to the sides of the abdomen or to the underside of the thorax. He was unable to identify the mites but adds that the hosts seemed to suffer no harm, being as active as unparasitised mosquitoes.

Uchida and Miyazaki, 1935, however state that Anopheline mosquitoes parasitised by an Arrenurus spp were unable to take a blood meal, and as this is an essential in the breeding pattern of the female mosquito, there must be a critical inhibition of its breeding cycle.

Brumpt, 1929, observed Dytiscus marginalis, L., parasitised by larvae of Hydrachna processifera, Koenike, and noted that intense infestation can lead to the death of the host, a factor also noted by Wesenburg-Lund, 1918. Brumpt also quotes Ulmer, 1912 as having found insects in Baltic amber parasitised by water-mite larvae, showing that this relationship was already in being in the Oligocene.

Crisp, 1959, studied the effects of parasitic mite on egg production in Corixa scotti, D + S (Insecta, Hemiptera), in some lakes in Ireland.

He found that in twenty parasitised females the percentages bearing fully developed eggs was only 5 ± 4.8 compared to 89 ± 7.4 in unparasitised females, and that the number of eggs were $.15 \pm 1.63$ in unparasitised females. He concluded that the presence of the mites lowered the fecundity of the hosts. Crisp's findings will be discussed later in this thesis but the most remarkable feature of his paper is the fact that it appears to be the only recorded attempt by any worker to examine numerically the effect which mite larvae have on their hosts.

(d) Nymphochrysalids.

The formation of the nymphochrysalis in many species has been described by numerous authors. Sparing, 1959, points out that this stage in Hydrachna spp and Eylais spp is spent on the host and that this is associated with the habit of over-wintering in the parasitic stage. In other genera the nymphochrysalis is formed after the larva has left the host, and has been described by Uchida, 1932, and many others. Unfortunately Imamura appears to use the term "nymphochrysalis" to denote the larval stage on its insect host and this tends to be rather misleading. Mitchell, 1959, gives the time spent by various Arrenurus species in this stage as varying from two days up to two weeks, and this agrees with figures given by other authors for mites not over-wintering on their hosts. The time elapsing between the larvae leaving the host and the formation of the nymphochrysalis is from one to six days.

(e) Nymphs.

Nymphs of many species have been described and a key to some 65 species is given by Viets, 1936. The nymphs appear to lead a life

very similar to that of the adults, being mostly predatory on small aquatic Arthropods. Arrenurid nymphs are said by Mitchell, 1959, and others to feed chiefly on Ostracods. Nymphs of Unionicolidae are usually parasitic in the same mussels as the adults, but the nymph of Unionicola crassipes, Muller, leaves the host sponge and nothing is known of its behaviour until it returns for its pupation in the host tissues.

(f) Teleiochrysalis.

The formation of the teleiochrysalis has been described by Motas, 1928, and others. The nymph usually attaches itself to a plant by its palpi and the adult forms within the old nymphal integument. The usual duration of this stage is about one to two weeks.

(g) Adults.

The adults of most known species are free-living. Exceptions are the Unionicolidae which include many parasites of fresh-water mussels, as well as U. crassipes, Müller which is parasitic in fresh-water sponges, as is Torrenticola spongicola, Viets, according to Arndt and Viets, 1937. The same authors mention one species Parasitalbia sumatrensis, Viets, which is parasitic in its adult stage on an Ephemerid larva. André and Lamy, 1930, report the finding of a Hygrobatid mite, Pontarachna punctulum, Philippi, in Oysters in the Bay of Naples and quote van Beneden as having found Hydrachnids in both marine mussels and oysters. Von Ihring, 1890, found Unionicola ampullariae, Koenike in a South American Ampullaria spp (Mollusca, Gastropoda) and Annadale, 1921, observed a very small mite in the gill filaments of Paludina lecythis, Benson. In recent years Motas and Imamura have described

many mites from Europe and Japan respectively, obtained from underground waters in caves and deep wells. These include members of seventeen families and seven of the ten super-families of the Hydracarina. No records have been found of the way of life, food or development of any of these troglobiontic mites.

It is generally accepted that mites of still waters feed chiefly on small crustacea, especially Ostracods, Copepods and Cladocera. Mites of flowing waters eat chiefly chironomid larvae, young Ephemerids and Crustacea. Motas, 1928, described the feeding of three Hygrobates spp on Baetis larvae, and of Sperchon denticulatus, Koenike, on chironomid larvae. He had also seen larvae of Piona disparilis, Koenike attacking and eating the chironomid Gricotopus biformis, Edwards, twice its own size. An interesting point about this observation is that this chironomid is also the host of the mite larva in its parasitic stage. The connection between the Hydracarina and the chironomidae appears repeatedly in the literature and is discussed in the appropriate part of this thesis. Motas also reported Arrenurus spp as feeding freely on Ostracods opening up the shells with their palpi. He saw A.cuspidator, Müller, A.bruzellii, Koenike and A.maculator, Müller feeding on much bigger Cypris virens, Jurine, which they attacked by seizing an antenna, which was pierced with the mandibles so that the victim's juices could be extracted.

Uchida, 1922, saw Arrenurus spp feeding on Nematodes and, 1932, described in detail the feeding of Acercus ornatus (= Typhis ornatus) Koch, on daphnids. These were seized with all eight legs and weighed to the bottom. The prey was then held with the palpi and carried to

the wall of the aquarium or to a water-plant, when it was pierced with the mandibles and its fluids sucked up. "The mite holds its prey with its palpi, using the first three pairs of legs to support itself while the fourth pair are lifted at an angle of 45° to the horizontal and quiver from time to time convulsively." Uchida also reported Hydrodroma despiciens, Müller and Hydryphantes dispar, Schaub, as eating dead insects but never attacking living Arthropods. They, however, as well as Typhis ornatus, Koch, were attacked and eaten by Limnesia fulgida, Koch, which also fed on Chironomid larvae and Asellus if injured. The latter were frequently surrounded and attacked by several of the mites.

Mitchell, 1957, has reviewed the phylogeny of the group in the light of present knowledge of the life histories. He cites the "standard" life-history of parasitic larva giving rise to free-living nymphs and adults as "Larval level I" and from this, Level IIA with an extension of the association with the host and Level IIB with its suppression are derived. He argues that Level IIIA the mussel parasites with free-living larvae, as well as the exceptional case of Parasitalbia sumatrensis, Viets, with a parasitic adult and other stages unknown, must be examples of secondary parasitism derived from Level IIB, and that the abbreviated life-histories which exclude parasitism in the larval stage altogether must be derived from that level also. He adds that the latter life-history is common to many still water forms and is "probably typical of most rheophilic species and has evolved many times," and that the eggs of Sperchonidae, Axonopsidae and Torrenticolidae are extremely large and few in number

which is considered presumptive evidence that the young emerge in an advanced stage, the nymph. This will be discussed in detail later in the thesis, where it will be shown that Mitchell's view is hardly tenable, but is included here to complete this review.

The situation at the commencement of this work is that information on the Hydracarina is scattered throughout a large and diffuse literature, the major part of which is concerned with the taxonomy of the group. The life histories are known for less than 5% of the described species despite the interesting aspects of this life-history and its obvious importance in the proper understanding of the ecology of the mites. Although there are many papers describing the finding of larvae on Arthropods, a large proportion of these records come from workers whose main concern was the host and who were often unable to identify the mites. Only three papers have been found in which any attempt is made to put the host-parasite relationship on a numerical basis, and even in one of these the mite species is not identified. Furthermore very little attempt has been made to devise experimental investigation of the methods by which parasitism is achieved, or of the host-specificity of the mite larvae.

One of the major problems connected with the Hydracarina lies in the fact that, with mite densities reported of up to twenty thousand per sq. metre in some waters, and with the accepted normal life-history including a larva which is parasitic on Arthropods, the number of reports of infected hosts seems far too small. Where a flood of literature might well be expected there is, in fact, hardly a trickle and this is one of the aspects of the subject dealt with in this thesis.

It should not be forgotten, however, as can be confirmed from a consideration of previous work, that there are other very critical stages in the life-histories of water-mites which could also greatly affect their ecology. The number of eggs laid by the females, the longevity of the larvae before their attachment to a host, the mortality rate amongst the two chrysalis stages and in the nymphs themselves, and the ability of the mites to migrate from one pond to another or from one river system to another, are all aspects which must be of the greatest importance to the survival of every species, and which have been given due consideration in the present work.

It is apparent, therefore, from an examination of the previous work that there are certain conspicuous gaps in the available knowledge of the Hydracarina, and that these point to lines of enquiry which would be likely to repay investigation. The work developed in this thesis was planned to supply some of this missing information and in this way to lead to a better understanding of the biology of the group.

Life Histories and the Parasitism of the Larvae on
Insect and other Hosts.

It has been shown by many workers that the majority of those water-mites for which the complete life-history is known follow a complicated life-history which includes three active stages, each of which is preceded by an inactive stage. During the inactive stages metamorphosis takes place within a membrane to which the general term 'apoderma' is given, but which takes the specialised name corresponding to the names of the metamorphosing phase, as used by Kramer. The whole general life-history is summarised by Soar and Williamson (1925) as follows.

Inactive stage	Metamorphosis as	Within Apoderma named	Which ruptures to release
1. Egg	2. Schadonophan	3. Schadonoderma	4. Larva
5. Nympho-chrysalis	6. Nymphophan	7. Nymphoderma	8. Nymph
9. Teleio-chrysalis	10. Teleiophan	11. Teleioderma	12. Imago

Some American workers use the term Imago-chrysalis for 9. Normally the larva or both the larva and the nymphochrysalis are parasitic on an insect host.

For convenience this will be referred to as the "standard" life history and known life histories where either the larvae develop quickly without parasitism or where the whole larval stage is suppressed and the nymph hatches from the egg will be referred to as the "abbreviated" life history.

Mite densities of 20,000 per sq.metre have been recorded by American workers and this, together with the "standard" life history including a larva parasitic on insects, would lead to the expectation of large numbers of reports of insects bearing such parasites. A thorough survey of the literature however, shows that this is not, in fact, the case, and that there are far fewer such reports than would be reasonably expected. It was considered probable that there were two main alternatives to be investigated. First that the "standard" life-history may not be as wide-spread as was thought, and that far more species may follow the "abbreviated" life histories than previous workers had realised, and secondly that there may in fact be more insects parasitised than the literature would seem to indicate. In the latter event it was borne in mind that mite larvae are small, are often attached to their hosts with their mouth-parts embedded in the host's arthrodial membranes so that the anterior part of the mite is hidden by the skeletal plates of the host, and that if they happened to be the same colour as their hosts they would be very difficult to see and could well have been overlooked by previous workers because of their inconspicuousness. In addition the time they spend on the hosts may be comparatively short so that they may not be on the host at the time the latter is examined. In order to test these two alternatives it was decided to examine as many prospective hosts as possible and to spread these examinations throughout the whole year, and also, in order to ensure that the larvae should not be overlooked to examine the hosts while anaesthetised under the low-power binocular microscope. This, of course, made it impossible to do this work in the field, but this

handicap had to be accepted if the results were to be reliable.

An examination of those water-mite life-histories which are already fully known shows that they can be roughly divided into four categories which are, for convenience dealt with separately. These are -

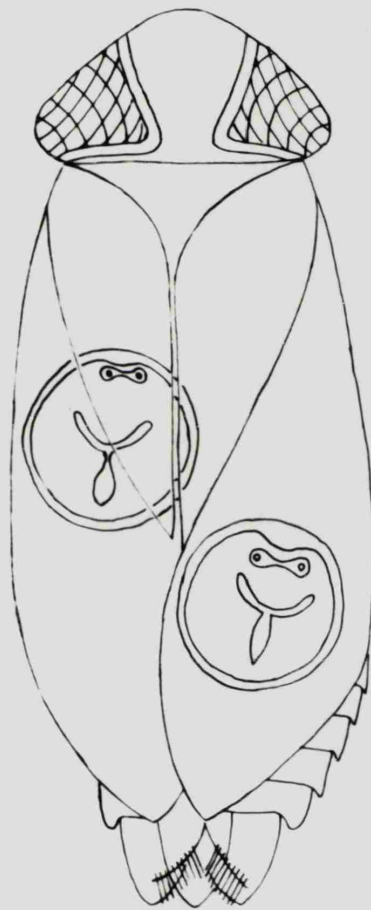
1. Those mites which infect insects with aquatic imagines, often spending the winter in the nympho-chrysalis stage on the host.
2. Those which infect insects with aerial imagines, on which their parasitism is often extremely brief.
3. Those with "abbreviated" life-histories.
4. The species of the genus Unionicola some of which are parasitic as adults in fresh-water Mussels and Sponges and others of which are free-living or have life-histories so far unknown.

Category 1.

Mites infecting insects with aquatic imagines.

Over a period of four years insects having aquatic imagines were collected in as large numbers as were available at all times of the year and were searched for mite larvae. Parasitism by water-mites on the Hemiptera seemed to agree with the results of previous workers. Larvae of the mite, Limnochares aquatica. L., were found during the summer on Gerris lacustris, L., and nympho-chrysalids of the genera Eylais, Latraille and Hydrachna, Müller, during the winter on Corixa spp and on Notonecta glauca, L., respectively. Other Hemiptera were found in small numbers but no mites were recorded from them, while during the period under survey the number of Coleoptera was low and no mite stages

Fig (i)



**Nymphochrysalids
of
Eylais bisinuosa
under the wings of
Cymatia coleoptrata.**

were found on them at all. Notonecta glauca, L., was found infected with Hydrachna spp nympho-chrysalids from sites, 2,3,4,5, and from Saddington reservoir, Leicester. The specimens from sites 2 and 5 were kept in an aquarium until the nymphs separated from their hosts and later emerged as adults. They were then identified as Hydrachna leegei, Koenike.

Cymatia coleoptrata, Fabr., infected with Eylais bisinuosa, Piersig, were collected from site 4. The mites were in the nympho-chrysalis stage and were attached under the wings of the host. (See fig.1). In cases where the parasites were small they could not be seen without moving the wings of the host, but where larger individuals were concerned their size caused them to project towards the posterior end of the host and they were then easily visible. As many as four mites were found on one host and out of 31 hosts 23 were infected with a total of 29 mites between them. In the majority of specimens the mite was approaching half the length of the host. Species of Corixa from sites 2,3 and 7 were examined but carried no mites. It is extremely difficult to collect Corixids during the winter, and collections were mostly made during early spring and summer. Unfortunately this may be expected to miss the parasitic phase of water-mites on these insects. Attempts to find mite stages on Corixids in the autumn ought on theoretical grounds to be successful, but in practice have not proved to be so. The mite larvae are very tiny when they hatch from the eggs and the hosts need to be immobilised so that search can be carried out under the wings. Furthermore the number of Corixids in the ponds tends to be very large at this time of year and this may account for the lack of observed

parasitism.

Gerris lacustris, L., were collected and examined from sites 2,3,4,5,7,8 and 9 as listed in table (i). In 1960 no parasitism was seen except from site 4 and in this site the insects were infested with larvae of Limnochares aquaticus, L., a well-known parasite of this host. The mite was not found in any of the other sites in this year. As numerical data concerning this parasitism does not appear in the literature, however, the full figures for both 1960 and 1962 are given in tables (ii) and (iii). It will be seen that in 1960 the numbers were at a maximum in July and thereafter declined steadily as regards the proportion of hosts attacked, the number of mites per host and the maximum number on a single host, and in the proportion attached to the thorax. Another interesting point is that in this year, although exhaustive searches were carried out, no parasitised Gerrids were found in site 5, although the two sites are separated by a mere 12 metres of roadway and have been so isolated for not more than ten years. In 1962 the figures show that the Gerrids from both sites were heavily infected. It seems likely that prior to 1960 some change in conditions had affected the mite population in site 5 and that they had not been re-established by that year. The most likely factor could well have been the drought of 1959 which may have reduced or eliminated the mite population in this site, while the Gerrids could have re-established themselves by flying in after the drought ended, and after any parasitic mite larvae had left their hosts.

Table (iv) gives the measurements of the larvae of Limnochares aquatica, L., found on a single host. It will be noted that the mites

Table (i).

COLLECTIONS OF Gerris lacustris, L., FROM VARIOUS SITES.

Date.	Site.	No. of hosts collected	No. of mite larvae
1.6.60	4	28	0
8.6.60	4	13	0
20.7.60	4	33	95
20.7.60	2	10	0
20.7.60	5	40	0
25.7.60	7	28	0
25.7.60	8	25	0
25.7.60	9	32	0
3.8.60	4	48	65
3.8.60	5	44	0
5.8.60	4	20	12
5.8.60	5	23	0
10.8.60	4	30	2
19.8.60	Clea Lakes, Co.Down	30	0
21.8.60	Pools on R.Deer, Wigtown	21	0
23.6.62	4	29	112
23.6.62	5	38	114
21.7.62	4	31	266
21.7.62	5	27	311

The mite larvae were all of the species Limnochares aquatica, L., and this mite has been found in sites 4 and 5 only.

41.

Table (i)a.

COLLECTIONS OF G.lacustris, L., FROM AN ARTIFICIAL POND AT ARNOLD.

Date	No. of hosts collected	No. of mite larvae
1.7.61	50	0
4.7.62	47	0
3.7.63	44	0
10.7.64	102	0

30 Gerrids with 350 mite larvae were added to this pond in July, 1960.

No adult Limnochares aquatica, L., have ever been found in this pond.

Table (ii).

DETAILS OF Limnochares aquatica, L., LARVAE, PARASITISINGGerris lacustris, L., AT SITES 4 AND 5 IN 1960.

Date.	1 June	8 June	20 July	3 Aug.	5 Aug.	10 Sept.
Site no.	4	4	4	4	4	4
No. of hosts	28	13	33	48	20	30
No. infested	0	0	29	32	9	1
Situation of mite larvae on hosts						
Head	0	0	27	34	6	2
Thorax	0	0	68	18	2	0
Abdomen	0	0	0	11	4	0
Legs	0	0	0	2	0	0
Total	0	0	95	65	12	2
Av. mites per infested host	0	0	3.3	2.2	1.3	2
% hosts infested	0	0	88	67	45	3
Site no.	5	5	5	5	5	5
No. of hosts	27	22	31	36	17	19
No. infested	0	0	0	0	0	0

43.

Table (iii).

DETAILS OF Limnochares aquatica, L., LARVAE PARASITISING
Gerris lacustris, L., AT SITES 4 AND 5 IN 1962.

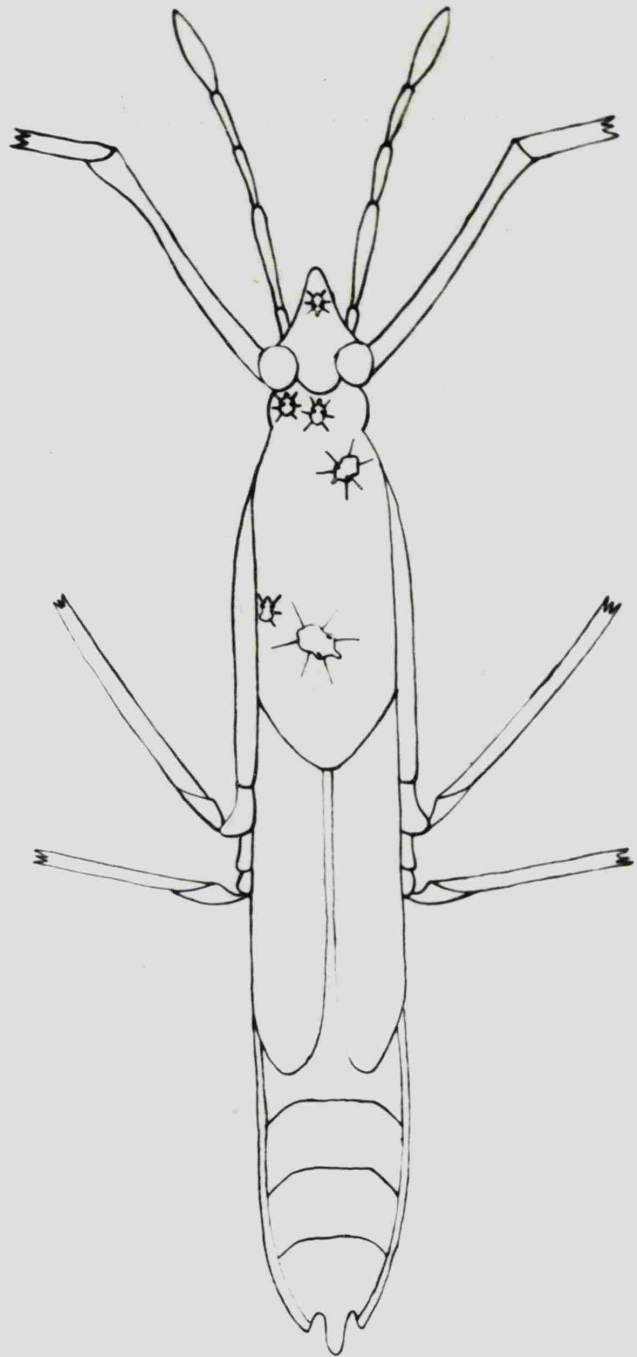
Date	23 June		21 July	
Site no.	4	5	4	5
No. of hosts	29	38	31	27
No. infested	26	27	30	27
Situation of mite larvae on hosts				
Head	54	56	63	87
Thorax	31	35	119	132
Abdomen	23	23	82	90
Legs	4	0	2	2
Total	112	114	266	311
Av. mites per infested host	4.3	4.2	8.8	11.5
% hosts infested	89.6	71	96.8	100

Table (iv).

MEASUREMENTS OF 18 LARVAE OF Limnochares aquatica, L.,
 FOUND ON THE DORSAL SURFACE OF A SINGLE SPECIMEN OF
Gerris lacustris, L., TO DEMONSTRATE THE CONSIDERABLE
 RANGE IN SIZE OF THE PARASITES.

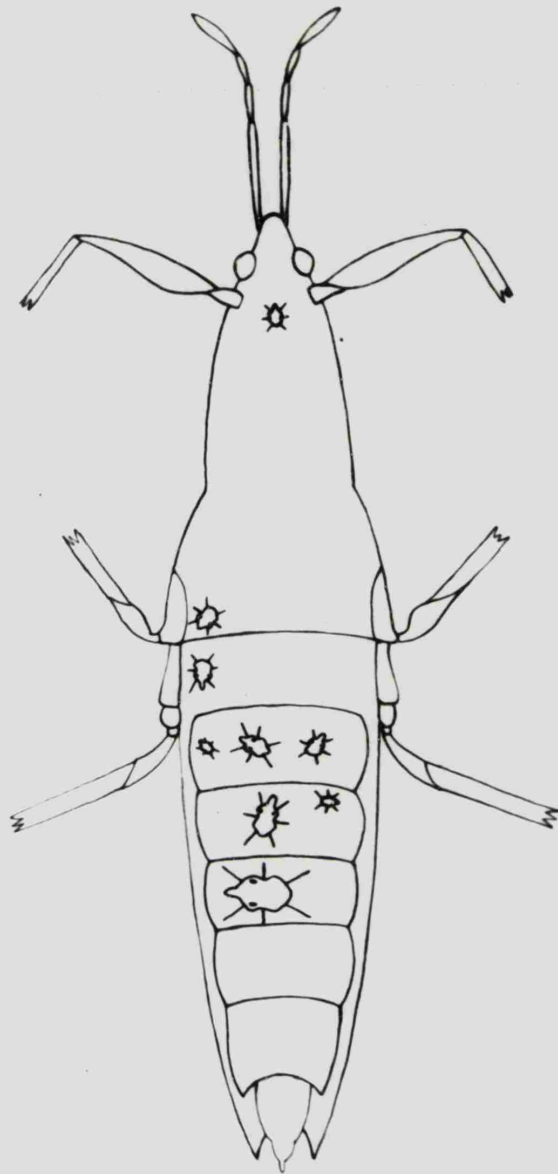
Mite No.	Position on Host.	Length mm.	Breadth mm.
1	head	.435	.277
2	head	.375	.262
3	head	.326	.211
4	head	.180	.164
5	head	.440	.295
6	extreme anterior prothorax	.230	.164
7	extreme anterior prothorax	.295	.195
8	prothorax	.295	.195
9	metathorax	.392	.260
10	metathorax	.342	.245
11	mesothorax	.277	.180
12	mesothorax	.245	.164
13	mesothorax	.425	.295
14	mesothorax	.410	.262
15	mesothorax	.360	.245
16	first abdominal segment	.342	.245
17	second abdominal segment	.180	.164
18	second abdominal segment	.277	.180

Fig (ii)



**Gerrid with larvae
of *L.aquatica*.**

Fig (iii)



**Ventral view of
Gerrid with larvae
of
Limnochares aquatica.**

vary in size over a considerable range which can be taken as evidence that they have been on the host for different periods of time, and that, therefore, they do not depend on any particular event such as metamorphosis in the life of the host as is the case for mite larvae found on midges and dragon-flies. The ability to board the host at any time is no doubt dependent on the fact that the larvae run actively on the surface of the water. A typical distribution of mite larvae on a gerrid is illustrated in figures (ii) and (iii). Limnochares aquatica, L., was not found in any sites other than these two and attempts to introduce it into an artificial pond at Arnold were unsuccessful. Infected Gerrids were released into this pond on each of three separate occasions but the mites did not become established although the hosts did so. 89 Gerrids and 350 mite larvae were involved in these attempts, but annual sampling at the time when parasitism is at its height in the original sites failed to reveal any parasitic larvae from the artificial pond. The results of these samples are given in table (i)a. Individual adult mites of this species survived in the laboratory for as long as six months in about 200 m.l. of canal water and died, only when the container was accidentally allowed to dry up.

Nepa cinerea, L., Ranatra linearis, L., and Hydrometra stagnorum, L., were examined from several sites but the number of insects found was insufficient for negative evidence of this sort to be really significant. The results of these counts are given in table (v), and the difficulty of dealing with "nil returns" from prospective hosts is discussed on p.95.

Table (v).

LIST OF MISCELLANEOUS INSECTS EXAMINED FOR PARASITIC WATER-MITES.

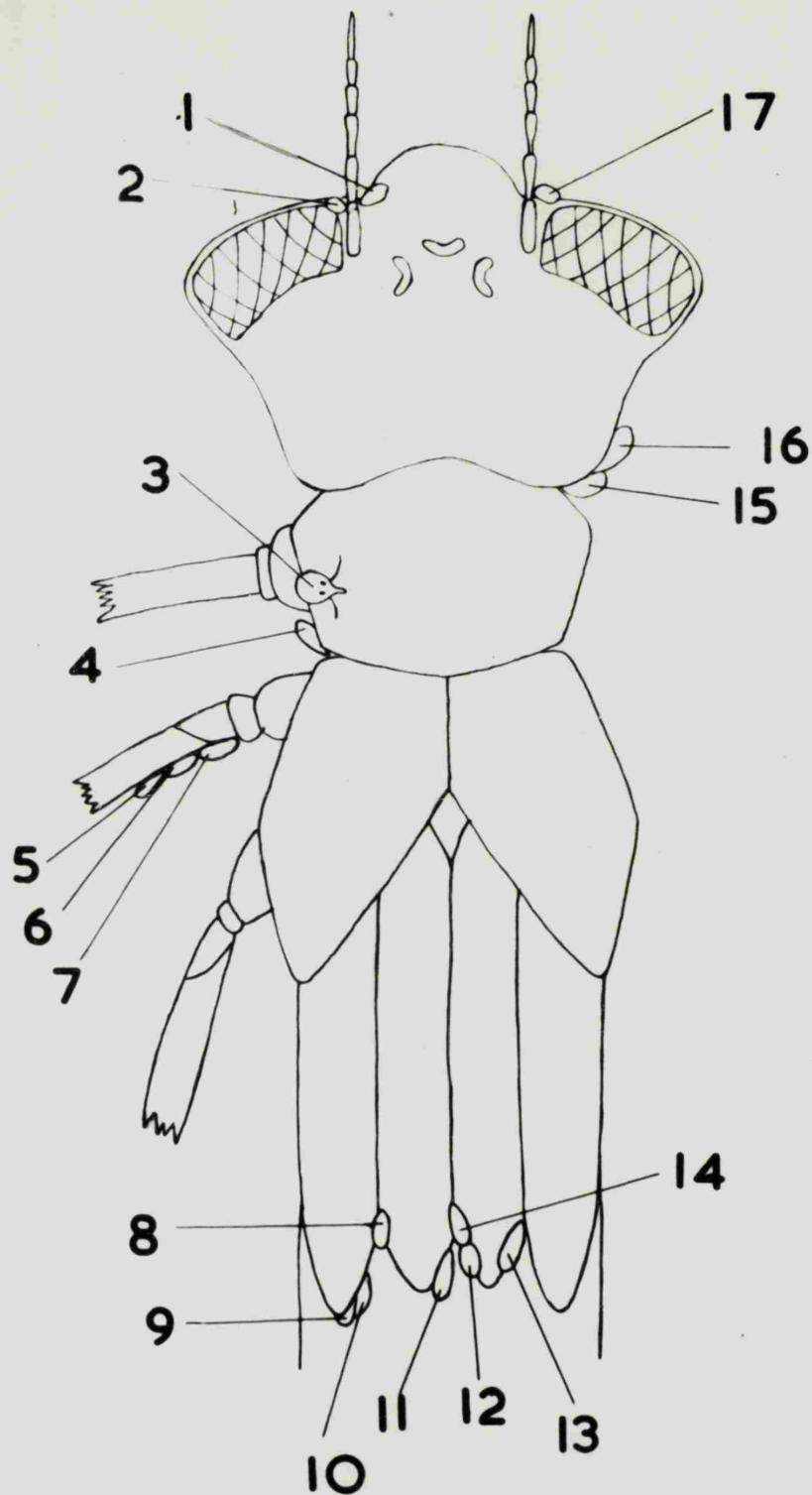
Date	Species	Site no.	Hosts examined	Hosts infected	Total mites
Hemiptera					
28.5.60	<i>Corixa</i> species	7	72	0	0
1.6.60	<i>Notecta glauca</i> , L.	9	16	0	0
8.6.60	<i>Ranatra linearis</i> , L.	9	3	0	0
	<i>Nepa cinerea</i> , L.	2	4	0	0
17.8.60	<i>Notonecta glauca</i> , L.	Irish peat pool	12	0	0
19.8.60	<i>Hydrometra stagnorum</i> , L.	Clea lake	30	0	0
	<i>Notonecta glauca</i> , L.	Clea lake	32	1	5
1.1.61	<i>Notonecta glauca</i> , L.	3	4	2	15
23.6.61	<i>Notonecta glauca</i> , L.	7	25	0	0
5.8.61	<i>Corixa</i> species	7	32	0	0
10.9.61	<i>Corixa</i> species	2	12	0	0
10.3.62	<i>Cymatia coleoptrata</i> , Fab.	4	31	23	29
25.3.62	<i>Cymatia coleoptrata</i> , Fab.	4	22	15	25
21.9.64	<i>Cymatia coleoptrata</i> , Fab.	4	22	5	6
Ephemeroptera					
28.5.60	Nymphs	5	30	0	0
	Nymphs	7	10	0	0
1.6.60	Nymphs	9	12	0	0
2.6.63	Adults	12	250	0	0
14.8.64	Adults	12	962	0	0

Table (v) continued.

Date	Species	Site no.	Hosts examined	Hosts infected	Total mites
Coleoptera					
17.8.60	Hydrophilus species	Peat pool	20	0	0
23.6.62	Gyrinus species	4	24	0	0
21.7.62	Gyrinus species	4	28	0	0
Neuroptera					
5.8.61	Larvae	7	22	0	0
Plecoptera					
7.6.63	Adults	12	26	0	0
13.7.63	Adults	12	30	0	0
Trichoptera					
6.6.63	Adults	11	81	0	0
15.5.64	Adult females	12	22	9	14
Diptera					
5.8.61	Chironomid larvae	7	17	0	0
8.5.63	Chironomid pupae	2	113	0	0

See also table (vii).

Fig(iv)



**Nymph of *Coenagrion*
showing positions of
Arrenurus larvae.**

Category 2.

Insects with aquatic immature stages and aerial imagines.

Of the insects which have aquatic immature stages and aerial adults the Ephemeroptera do not appear to be attacked at all by mite-larvae, probably on account of the interruption caused by their final moult and their short aerial life, while the Plecoptera are known to be attacked by one genus, Partnunia, which has no known British species. Specimens from these two insect orders, together with Trichoptera and Hymenoptera were examined during the course of this work, but except for one unidentified species of Trichoptera, none were found bearing mites. Results of these collections are included in table (v). The two orders Odonata and Diptera have been widely reported as hosts of Hydracarina and it appeared necessary to examine these two groups as fully as possible.

Adult mites were collected from site 6 and batches of eggs were laid by females of Arrenurus buccinator, Müller, a week later. These eggs hatched in four weeks and a well-developed nymph of Coenagrion puella, L., (Insecta, Odonata, Zygoptera) was added to a dish containing 30 of the mite larvae. The following day this nymph was examined and it was found that all 30 mite larvae were attached to it as shown in fig. (iv). The positions of the mite larvae on the nymph were as follows:- caudal lamellae, 1; wing cases, 8; first left leg, 1; second left leg, 5; prothorax, 2; suture between head and prothorax, 1; head, 4; mask, 1; and ventral part of the thorax, 7. The average length of these larvae was .165 mm. and they were still occupying the same positions one week and two weeks later. Measurements on the second occasion showed that the average length was still .165 mm., so

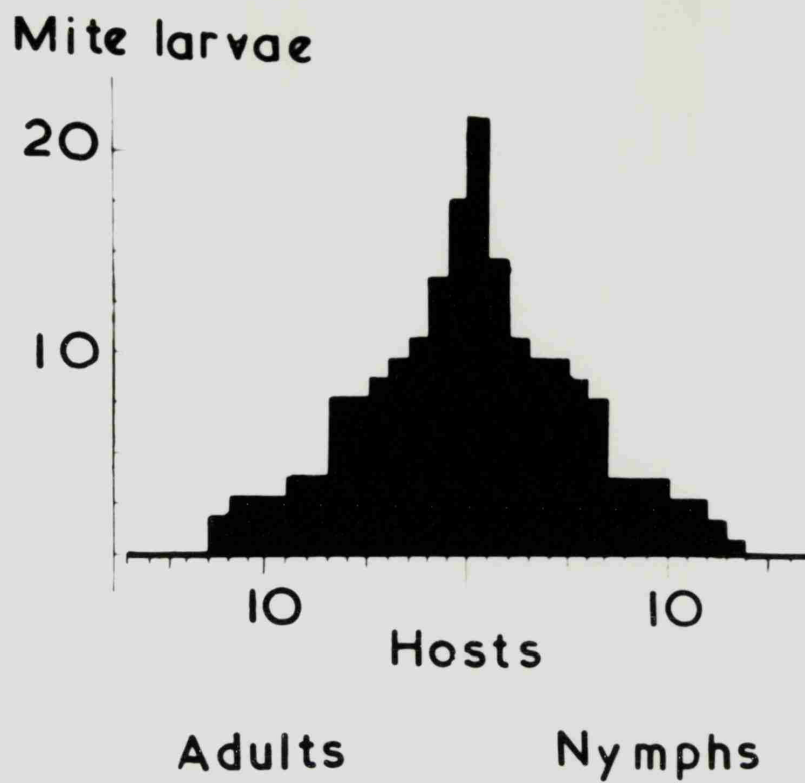


Fig (v)

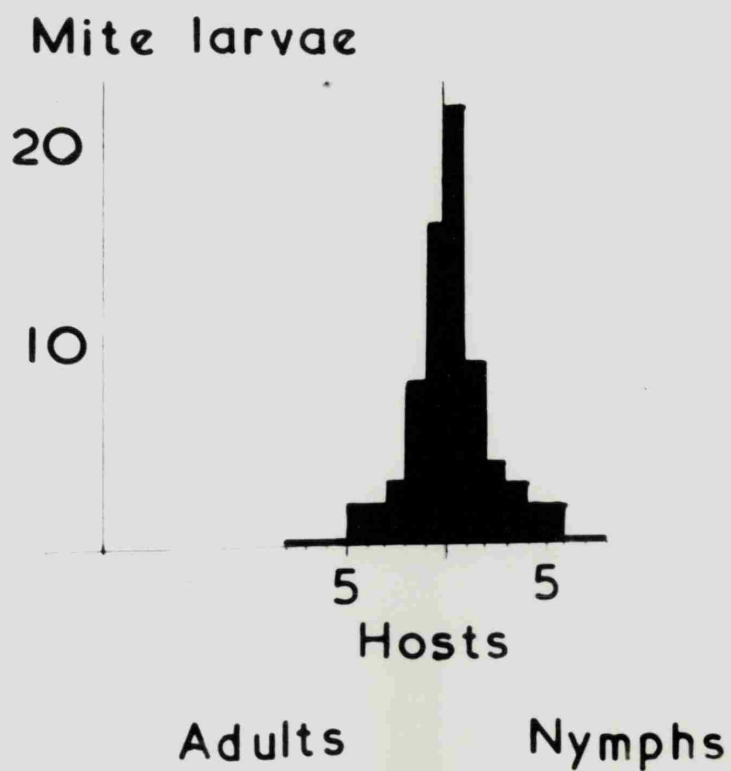


Fig (vi)

that there was evidence for thinking that no growth had taken place.

A series of nymph collections was made from sites 6 and 8 the results of which are given in table (vi) and show a steady increase in the proportion of hosts attacked up to the middle of May. On 13.5.61 there was a strong emergence of Zygopteran adults and these were examined for parasites. There seems to be no correlation between the average of 17 mite larvae per adult host with the average of 2.5 mite larvae per nymph, but it was thought that the mite larvae may have the ability to distinguish between nymphs in the last nymphal instar and younger nymphs, so that many of them may mount their hosts quite near to the time of its emergence.

This possibility was checked by experiments on 18 Zygopteran nymphs in the laboratory. Larvae of Arrenurus buccinator, Müller, were kept with nymphs of Coenagrion puella, L., and after twenty-four hours the nymphs were examined and the mite larvae on them counted. As can be seen from fig. (v) and from fig. (vi), which refers to a further 6 nymphs kept separately, in each experiment the number of mites found on individual Zygopteran nymphs correspond so closely with the numbers found on individual adults after emergence that this correspondence is unlikely to be accidental and it can be reasonably assumed that the initial contact between larva and host takes place on the last instar host nymph so that the mite larva is carried through the surface film by the host when it leaves the water immediately before metamorphosis.

Further evidence on this point was obtained by watching the emergence of the Zygopteran adults. Two emergent damselflies were seen to have mite larvae already in position on the ventral plates of

Table (vi).

FIELD COLLECTIONS OF DAMSEL-FLIES.

	Nymphs				
Date, May 1960.	3rd	13th	20th	23rd	26th
Number	30	27	33		18
No. infested	1	15	19		8
No. of mite larvae	2	65	80		20
Mites per infested host	2	4.3	4.2		2.5
% hosts infested	3	56	57		44

	Emergent adults			
Number	38	25	15	16
No. infested	38	25	15	16
No. of mite larvae	646	419	408	564
Mites per infested host	17	16.8	27	35
% hosts infested	100	100	100	100

	Flying adults			
Number	33	12	52	45
No. infested	33	12	47	34
No. of mite larvae	300	72	609	417
Mites per infested host	9.3	6	13	12.3

the thorax before the abdomen had been withdrawn from the exuvia and this suggested that if an emergence was watched from its commencement it would be possible to see exactly how the mite larvae behaved. Attempts to do this in the laboratory were not successful but eventually the process was observed under field conditions. A nymph was seen leaving the water and kept under close observation until the emergence of the adult started. The grass stem on which it was resting was then cut and removed from the water and the subsequent events watched under a x 15 lens. Mite larvae were already moving up the thorax and wings of the nymphal skin and were wandering over the head and thorax of the emerging adult. By the time the wings were freed from the exuvia, 14 mite larvae had already made their way onto the imago and 10 of these were already in position on the ventral plates of the thorax. The other 4 were on the dorsal part of the thorax, while 3 still remained on the exuvia, two of them being still quiescent on the wing tips. One of the latter started to move rapidly over the exuvia and just succeeded in reaching the last abdominal segment of the adult as it was extracted. One mite larva was left stranded on the exuvial wing tip although it had started moving just before the adult damselfly had fully emerged.

A second nymph was found at a slightly earlier stage and larval mites were wandering all over the exuvia when it was first examined. Twelve of these were still on the nymphal skin when the adult wings were freed and again one larva was left behind when emergence was completed. The mites appeared to be set in motion by the swelling movements of the host and were actively moving about for the most part before the exuvia actually split. The initial migration of the mite larvae seemed always

to be upwards so that most of them walked up over the head of the host on their way to the ventral plates of the thorax. Occasionally a mite larva found itself on the head of the exuvia instead of on that of the emergent adult and in this case it invariably wandered down to the abdomen before starting again in an upward direction . The fate of larvae left behind on the exuvia was not observed but it is assumed that they would be able to return to the water to seek another host. The mite larvae live for at least four weeks in the laboratory so that there seems no reason why they should not be able to do this unless the return passage through the surface film is difficult for them.

On each occasion in early May when it was possible to observe Coenagrion puella, L., and Pyrrhosoma nymphula, Sultz, emerging in fair numbers 100% infestation by mite larvae was found and by 25th May a second, larger, Arrenurus spp was competing for the same hosts. The two species did not appear to have any influence on each other and individual hosts often carried large mixed populations of the two. The site of infection was the same for both species, between the legs on the ventral plates of the thorax. The average number of mite larvae per host on emerging Zygopterans on four occasions were 17, 16.8, 27 and 35, while on Damsel-flies caught on the wing on the same dates the averages were 9.3, 6, 13 and 12.3 larvae per infested host, respectively. This suggests a considerable loss of larvae during the parasitic stage. The significance of this reduction in numbers in connection with the numbers of eggs laid is discussed on p.97.

Measurements of larvae showed that there was no measurable growth during two weeks of waiting on the host nymph, while measurements at

the time of emergence of the host and on hosts which were pairing showed an average tenfold increase in the volume of the mite larvae.

These observations appear to show that the mite larvae find last-instar Zygopteran nymphs and remain on them without feeding to await their metamorphosis at which time a transfer is achieved and a "feeding" attachment to the host is brought about. During this parasitic attachment there appears to be a considerable reduction in the numbers of mite-larvae which are able to maintain their positions on the host and a considerable increase in the individual bulk of those which do manage to do so.

As no emergent damselflies were found without mite larvae no attempt was made to measure the effect they might have on the egg-production of the host. In view of the wide-spread nature and abundance of the host, however, it seems that the effect of the mites upon it, even in such large numbers, cannot be very serious. This aspect of the parasitism of water-mite larvae is discussed on p. 107.

Insects which have aquatic juvenile stages and aerial adults form a very large component of the aquatic fauna and in numbers of individuals the Diptera must be amongst the most plentiful of these. Dipteran imagines were collected from the sites used in this work and as it was found that considerable numbers were parasitised by water-mite larvae and that in addition nearly all samples showed at least a small degree of parasitic infection it was decided to make further collections from places not included in the main body of the work in order to establish as far as possible the true position of these insects as hosts of water-mites. The results of these collections are given in table (vii).

Table vii. (part 1)

COLLECTIONS OF DIPTERA, NEMATOCERA FROM VARIOUS SITES.

- a) Anopheles claviger, Meigen parasitised by Arrenurus medio-rotundatus,
Thor, larvae.

Date	Site	No. of Hosts	No. Parasitised	Total mites	% Hosts affected	Av. mites per host parasitised
10.9.62	10	139	6	16	4.3	2.67
24.9.62	10	83	9	9	11	1.00
9.9.63	10	37	19	46	52	2.40
9.10.63	10	18	2	2	11	1.00
19.5.64	10	105	0	0	-	-
17.9.63	17	12	7	13	58	1.86

- b) Chironomus (Polypedilum) nubeculosus, Meigen, parasitised by
Hygrobates longipalpis, Hermann, larvae from a lake at Inver,
Donegal.

30.8.63	-	51	19	85	58	4.5
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- c) Endochironomus dispar, Meigen parasitised by a Typhis spp.
larvae from a ditch at Southwold, Suffolk.

26.8.62	-	22	7	11	32	1.57
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Table vii. (part 1, continued)

d) Chironomus dorsalis, Meigen parasitised by Piona variabilis, Koch,
P.conglobata, Koch, P.spp., Hygrobates longipalpis, Hermann,
Unionicola intermedia, Koenike, and Typhis spp.

Date	Site	No.of Hosts	No. Parasitised	Total mites	% Hosts affected	Av.mites per host parasitised
29. 8.62	11	137	44	107	32	2.4
2. 9.62	11	58	12	225	20.5	2.1
7. 9.62	11	74	9	17	12.2	1.9
14. 9.62	11	64	17	37	26.5	2.2
22. 9.62	11	148	15	24	10.1	1.6
29. 9.62	10	243	38	93	15	2.4
6.10.62	10	121	20	38	16.5	1.9
6.10.62	11	47	9	16	19.2	1.8
20.10.62	10	62	2	2	3.2	1.0
15. 9.63	11	154	2	2	1.3	1.0
1. 6.64	11	340	23	37	6.8	1.6

e) Brillia modesta, Meigen parasitised by Atractides spp. (probably
A.spinipes) larvae.

20.10.63	12	250	54	80	21.6	1.5
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f) Black midge carrying red mite, probably Hydrodroma despiciens,
Müller, on the extreme anterior part of the thorax.

13. 8.62	5	681	16	18	2.35	1.13
1. 9.62	5	156	3	3	1.9	1.0

Table vii. (part 1, continued)

g) Chironomus plumosus, L., and Camptochironomus tentans, parasitised by Piona uncata, Koenike, Hygrobates spp., Unionicola intermedia, Koenike, U.spp., (probably U.aculeata, Koenike) and Typhis spp.
Female midges.

Date	Site	No. of Hosts	No. Parasitised	Total mites	% Hosts affected	Av. mites per host parasitised
4. 9.62	1	39	21	141	54	6.7
7. 9.62	1	22	12	118	54.5	9.8
6.10.62	1	6	3	21	50	7.0
6. 9.63	1	29	22	112	76	3.8
Male midges.						
4. 9.62	1	5	2	13	40	6.5
7. 9.62	1	11	9	60	82	6.7
6. 9.63	1	10	8	71	80	8.8

The same two hosts with U.intermedia, Koenike and U.spp. only.

Female midges

15. 8.64	1	26	18	77	69	4.2
20. 8.64	1	29	22	112	76	5.1

Male midges

17. 8.64	1	17	16	250	94	15.6
20. 8.64	1	10	8	71	80	9.8

h) Small black Chironomus spp parasitised by Pionopsis lutescens, Hermann.

10. 9.62	10	17	5	23	29	4.6
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i) Small black Chironomus spp with Piona variabilis, Koch and P.species.

29. 9.62	11	936	16	17	1.74	1.1
6.10.62	11	261	3	4	1.15	1.3

54 (c)

Table vii (part 1, continued)

j) Cricotopus trifasciatus, Panzer parasitised by an unidentified mite larva.

Date	Site	No. of Hosts	No. Parasitised	Total mites	% Hosts affected	Av. mites per host parasitised
13. 8.64	16	96	26	49	51	1.9
27. 6.64	16	13	6	6	46	1.0
13. 9.64	16	67	13	45	19	3.5

k) Dixa aestivalis, Meigen, parasitised by an Arrenurus spp.

13. 8.63	16	10	1	2	10	2.0
15. 8.63	12	22	3	5	14	1.7

l) Small green midge parasitised by a Hygrobates spp. Loch Lomond, Scotland.

25. 8.63		65	1	1	1.5	1.0
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(part 2)

COLLECTIONS OF DIPTERA, BRACHYCERA, FROM VARIOUS SITES.

a) Weidemannia bistigmata, Curtis, parasitised by larvae of Protzia eximia, Protz.

15. 5.64	12	33	14	48	42.4	3.4
30. 5.64	12	37	17	33	45.9	1.9
15. 5.64	13	20	14	22	70	1.6
29. 8.64	12	24	15	23	62.5	1.5

b) Unidentified Empids.

2. 6.63	R. Wharf	250	0	0	0	0
30. 5.64	12	117	0	0	0	0

In the river Greet, in June and July, 1961 most of the stones on the bottom were well covered with a variety of pupal cases belonging to Chironomids, Simuliids and Trichoptera. Careful search revealed that amongst these cases were many batches of Hydracarine eggs as well as adults of Hygrobates fluviatilis, Strom, Sperchon denticulatus, Koenike, S. clupiefer, Piersig, and Lebertia spp. Sperchon denticulatus, Koenike, females were isolated and laid eggs which hatched on 1.6.61. Small stones bearing pupal cases of the insects were searched to ensure that no mite stages were present and then added to the aquarium containing these larvae. The tank was covered with a nylon net and the emerging insects transferred to glass tubes for examination. During two weeks 20 Chironomids, 2 Simuliids, 10 Trichopterans and 2 Hymenopterans emerged from the water and of these 10 of the Chironomids bore 27 mite larvae between them. 26 of these were Sperchon denticulatus, Koenike, but one was a Hygrobates spp larva which must have been missed in the preparatory search. This larva was placed ventrally on the abdomen of the host. The Sperchon larvae were nearly all placed laterally on the anterior part of the thorax of their hosts, though two were found on the head and one on the abdomen of the hosts.

One midge bearing two mite larvae was placed in a small tube for further examination and some thirty hours after the emergence of the host one of the mite larvae was accidentally knocked off the host. It ran actively across the desk and did not appear to be impeded either by the polished surface of the wood or by the rough surface of a blotting pad. It has been assumed by various previous workers that if the host midges died and did not fall into water any mite larvae they bore would

be lost. The fact that detached larvae are capable of considerable running activity suggests that this may be a false appraisal of the situation and that at the very least mite larvae would be able to make their way from vegetation rooted in the water and even possibly from the stream banks themselves back into the water. The host concerned above died two days later and was allowed to fall into water. The remaining mite larva left the host, passed down through the surface film and swam about until it came across a midge pupa, on which it was still waiting a week later. Unfortunately this midge failed to emerge and both midge and mite larva died. This appears to support Uchida (1932) who suggested that mite larvae may change hosts if the first host died.

The passage of the second larva back through the surface film demonstrates an ability which seems to vary between individual mites, even of the same species. When infected midges are put into water the insects float until decomposition takes place. The body surface of the insects appears to be unwettable. Mite larvae on the insects sometimes remain attached to the host and die, and sometimes pass down into the water and form nympho-chrysalids. I have been unable to determine the precise reasons for these differences in ability to pass from the host into the water, but it has been found that if the midges are in contact with plant material having stems passing down through the surface then the number of mite larvae stranded in the surface film becomes practically nil.

In July and August, 1962 numerous pupae of the midge Anatopynia varia, Fabricius, were collected from sites 8 and 9 and it was found

that approximately 70% of the midge pupae were carrying mite larvae. The greatest number of larvae found on one pupa was 6. Adult midges were difficult to obtain at these sites but of the few which were caught, 4 carried single mite larvae attached to the anterior part of the thorax and one bore 26 mite larvae arranged round the same area in such a way that the midge appeared to be wearing a red collar. The mass of parasites in this case made the midge top-heavy so that it frequently fell forward onto its head. It appeared to have no difficulty in flying however. This midge was placed in a boiling tube together with a piece of rush and a little water, and after three days the midge had died and fallen into the water and 9 nympho-chrysalids were found at the bottom of the rush stem. Nymphs which hatched from these were identified as an Arrenurus spp but although they lived for some time feeding on a diet of Ostracods, they all died before undergoing further metamorphosis. Other Arrenurus nymphs which have been bred out from their hosts have often behaved in this way, and those which have been successfully bred through to imagines have had to be kept over-winter. In view of the large proportion of nymphs which are found in the early spring it may well be that in this genus most individuals usually over-winter in the nymphal stage. As there are no satisfactory keys to species level for the nymphs of the Hydracarina, the difficulty of breeding out the animals from the larval stage on the hosts right through to the adult stage is still the major barrier to a fuller knowledge of their life-histories.

Midge pupae bearing mite larvae were put into suitable containers in the laboratory and covered with bell jars, in an attempt to correlate

the pupal infestation with the parasitism of the adult host. In the most successful of these experiments 8 pupae, 6 of which bore 10 mite larvae between produced on emergence 4 adults bearing 1 mite larvae each. Examination of the exuviae revealed that one had 2 mite larvae wandering about inside it, one had a mite larva apparently attached to the dorsal abdominal segments, while 3 mite larvae were observed to be swimming freely in the water.

Unparasitised midge pupae were added to this water and within five minutes one of these was carrying a mite larva. Within half an hour all 6 mite larvae had settled on midge pupae.

Similarly 2 mite larvae from site 9 were enclosed in a petri dish with one Chaoborus spp and one other midge species pupae. After one hour it was seen that neither of the midge pupae bore mite larvae although the latter had several times landed on the two pupae and walked about on them for a few seconds before disembarking and swimming away. One midge pupa of the known host species, Anatopynia varia, Fabricius, was then added to the water and within half an hour both larvae were established on it and were still in position six hours later. On hatching next day this midge carried two attached mite larvae.

Again 20 mite larvae from site 9 were added to a dish containing a large number of Culex pipiens, L., pupae. Observations at hourly intervals showed no attachment in six hours and within two days all 43 mosquitoes had emerged but none of them carried mite larvae. These observations appear to show a decided degree of host selection in the larvae of this Arrenurus spp. The pupae involved were all much the same size and showed a similar degree of activity. There can be little

doubt however that the mite larvae can distinguish between the different pupae used in the tests and that they show a very marked preference for that of Anotopynia varia, Fabricius.

In every case the mite larvae were attached to the host midge at the extreme anterior end of the thorax and this position was unchanged even when the individual host was considerably overloaded and the remainder of its body unoccupied. No members of the host species were found bearing any other water-mite larvae, nor were these larvae found on any other host species. It is concluded that this mite is confined to this position when on this particular host species.

Large numbers of Chironomids were collected from sites, 1, 2, 5, 10, 11 and 16 and, in order to introduce the greatest variety of mites and hosts into consideration, collections were also made from other places not otherwise investigated in the course of this work. Infestations varied from about 2% on a midge species from site 5, up to a maximum of 82% with an average of 6.7 mites per host from site 1. This great variation in numbers of mites per host and of hosts infested is probably connected with the species of mite and host, rather than with some peculiarity of the site concerned. From Chironomus plumosus, L. caught frequently at sites 1 and 2 many nymphs were obtained and one of these finally emerged on 3rd February, after living in a small bottle in the laboratory since the previous August. It was identified as a male of Piona uncata, Koenike. The full life history of this mite was not previously known but is now available from material from site 2 and is given on p. of the appendix to this thesis. A most interesting point arising in this connection is that the life

history discovered for the mite from this site is entirely different from that observed by Stout, (1953, b) for the New Zealand form, Piona uncata exigua, Viets, which was found to have an "abbreviated" life-history, developing from larvae to nymph without any recourse to parasitism. This matter is made more explicable by Robert M. Crowell's observations on Thyas stolli, Koenike, and is dealt with fully in the discussion, on p. 86.

Mites removed from their hosts were identified as far as possible from the key in Sparing (1959) and from the Chironomids at site 1 mites of the genera Piona, Typhis and Hygrobates were obtained. In several cases these three genera were competing for space on the same individual midge. In this event there appeared to be a segregation of the parasites, Piona spp occupying the posterior end of the abdomen, Hygrobates spp the anterior part of the abdomen and Typhis spp the legs. Where Piona spp were the only mites present they usually occupied the anterior ventral part of the abdomen. This suggests that Hygrobates spp are able to take precedence over Piona spp for this site on the host.

Pionopsis lutescens, Hermann, was found on a Hydrobaenus (Orthocladius) spp., from site 1. The mite was hidden away in the hollow formed by the posterior part of the thorax and the ventral anterior part of the abdomen, and was hard to see even under the binocular microscope. Out of 210 midges examined from a swarm, only 5 were infected and the position of the mite was the same in each case.

Parasitism by more than one mite species on a single host individual was not observed on hosts from any other still-water sites during the survey but it was noted from two river sites. In material

from the river Greet, Spechon denticulatus, Koenike larvae were found anteriorly on the thorax of a midge which also harboured a Hygrobates spp larva ventrally on its abdomen.

At Linton in Yorkshire an emergence trap covering 0.2 sq. metre was set up in shallow running water under a bridge. In 24 hours 60 Chironomids, 2 Simuliids and 1 Trichopteran emerged and of the Chironomids 21 were parasitised with a total of 31 mite larvae. These were identified as belonging to the genera Spechon, Hygrobates or Atractides, and Lebertia. There was no obvious sign that one part of the host was more subject to attack than another and where Spechon spp and Hygrobates spp were found on the same host there were three of the former and two of the latter clustered around the anterior part of the thorax of the host. The parasitised Chironomids belonged to two genera, Chironomus and Hydrobaenus, (Orthocladus). Midges caught by sweeping with the net in the area of the same bridge showed approximately 50% infestation by mite larvae of the same genera.

Chironomus dorsalis, Meigen was collected on many occasions from sites 10 and 11. It was consistently attacked by a Typhis spp which was sited invariably on the abdomen. Unlike the mite larvae from sites 1 and 2 it was distributed along the whole length of the abdomen without any signs of obvious concentration at either end. The rate of parasitism varied from 32% down to 10% with a maximum of 9 mite larvae on one midge and an overall average of just under one mite per midge examined.

Anopheles claviger, Meigen, from site 10 was found to be supporting a 5 to 11% infestation by larvae of Arrenurus medio-rotundatus, Thor.

The mite larvae were attached to the abdomen of the host and were not observed in any other position. These mite larvae were easily dislodged and on falling into water were able to pass down reed stems and form nympho-chrysalids. The presence of the plant stem seemed important to the larvae in their passage through the surface film, as two larvae which fell into water without any plant material present became trapped in the surface film and were still held fast some twenty four hours later. When these were pushed through the film they were able to undergo metamorphosis in the normal way. The nympho-chrysalids obtained from these larvae were transferred to 10 m.l. glass bottles and kept throughout the winter. The nymphs emerged in one to three weeks and were fed on Ostracods. In five to six months those which survived formed their teleiochrysalids and adults emerged ten to twelve days later. The adults were left for a few days to allow the caudae of the males to fully develop and were then identified. It has been noticed that mite larvae trapped in the surface film can often be enabled to pass downwards by gentle shaking of the container. It is quite likely therefore that under normal field conditions the ripple action of the water may result in a much less serious barrier to their passage than does the still surface of a laboratory vessel.

It was noted that these mite larvae were often dislodged from the host mosquitoes while in the glass tube being transported to the laboratory. It was thought that this might be a reaction to humidity such as Mitchell (1959) reported for several Arrenurus spp parasitic on Odonata. Fresh specimens of the infected host were therefore carefully held in forceps and dipped swiftly into water, just brushing the

surface with the host's abdomen. This treatment did not dislodge the mites but it was seen that they immediately became active, and mostly fell from the host a few seconds later. The same test was applied to Chironomus plumosus, L., bearing larvae of Piona uncata, Koenike, with precisely similar results. Not all the mite larvae reacted in this way however, and with heavily parasitised hosts there were usually some which failed to leave the host at all, even if it was left on the surface of the water. It seems likely that there is some minimum degree of engorgement necessary before mite larvae will react in the above manner. Mitchell (1959) showed that for some Arrenurus spp there appears to be an optimum state of engorgement as far as this reaction is concerned and that when this is exceeded the mite larvae will not become dislodged in this way either. I did not find any signs of this with either of the mite larvae used, but it may occur more frequently with parasites on the longer-living Odonata than with those on the mosquitoes and midges.

It was also noticed that when the hosts were transported under overcrowded conditions, those which were parasitised suffered by comparison with their unaffected companions. Thus 58 specimens of Chironomus dorsalis, Meigen, were confined in a glass tube for transport, and on reaching the laboratory it was found that out of 12 which were carrying mite larvae, 11 had died in transit. The 46 remaining unparasitised midges and one of the parasitised midges were still alive. This suggests that, at least under unfavourable conditions, the presence of mite larvae may be a grave disadvantage to their hosts. Evidence on this point in the literature is somewhat contradictory, and the matter

is discussed on p. 107.

At site 17, in addition to the mosquitoes mentioned above, Chironomids of at least three species, as well as Dixa spp., were caught and examined. The Chironomids showed 6%, 8% and 17% infestation respectively and of 12 specimens of Dixa aestivalis, Meigen, three were parasitised by an Arrenurus spp. This is the first known record of Dixa spp. as a host for the Hydracarina.

On 20th October, 250 specimens of the Chironomid Brillia modesta, Meigen, were collected from over the river Dove. On laboratory examination it was found that 54 of these were parasitised with a total of eighty mite larvae. Some of the midges were enclosed with water and plant material and the mite larvae were successfully taken through to the nymphal stage when they were identified as an Atractides spp. Two species referable to this genus are found in the Dove, A. spinipes, Koch which is extremely common and A. octoporus, Piersig which is comparatively scarce. As no descriptions of the larva of the latter species appear in the literature it is not possible to state which of the two species is involved.

In view of the consistency of the observations given above it may be of interest to refer to two other collections made much further afield. In August 1962 at Southwold in Essex 22 midges were collected, representing the bulk of a small swarm, flying among reeds in a marshy area. Of these 7 bore 11 mite larvae between them and the other 15 were free of mites. The mite larvae were all on the abdomens of the hosts and were grey and not easy to see. One of these larvae was measured at .262 mm. long on 25.8.62 and .295 mm. long on 27.8.62, an

increase in length of $12\frac{1}{2}\%$. As the midge died it was dropped into a tube of water. The mite left the midge within half an hour and swam about. A nympho-chrysalis was formed the following day. Larvae from these hosts were identified as Typhis spp.

A collection of the midge Chironomus (Polypedilum) nebeculosus, Meigen from Inver in Donegal, Ireland, yielded 51 midges of which 29 bore between them 85 mite larvae. The largest number of parasites on one host was seven. Most of the mite larvae were placed centrally on the abdomens of the hosts, and left the latter when they fell into water in a boiling tube. Nympho-chrysalids were formed immediately and the mites eventually identified as Hygrobatas longipalpis, Hermann, the life history of which has been previously described in Japan by Imamura (1954).

In all the above mentioned cases the mites on a single host have been at the same stage of development and of approximately the same size, and this is taken as evidence that they have gained access to the host at the same time. It is thought probable that this access is gained at least in the majority of cases at the time of the host's metamorphosis and that the initial contact with the host is made by the mite larva with the host pupa, as described on p.57 for Anatopynia varia, Fabricius, and an Arrenurus spp. This of course is similar to the method by which mite larvae parasitise Odonatan adults but is in direct contrast to the infestation of Gerrids by Limnochares aquaticus, L., or of Corixids by Eylais spp. It is interesting to find, therefore, that the larvae of Protzia eximia, Protz, obtain their position on their Dipteran hosts in a manner similar to that of the mites which parasitise the Hemiptera. The larvae of P.eximia, Protz have been reared in the laboratory from

eggs collected in the Dove and have been seen to run on the surface of the water, and at certain times to jump from the surface. Larvae confined in a small glass tube were seen jumping in this way distances measured at up to 2 cm. from the water surface, and at one time the jumping was so vigorous that the water in the tube actually appeared to be effervescing. The significance of this behaviour was not known at the time although it was assumed to be connected with the attainment of the position of the larvae on the host. It was found in a series of experiments described on p. 78 that eggs of P.eximia, Protz laid during the winter hatch when the temperature rises to a point somewhere above 5.5 C., and for this reason it was decided to make field observations in the spring with a view to studying more of the behaviour of the larvae. In late spring it was found that larvae were actively running over the surfaces of boulders projecting out of the water, and it was noticed that when these larvae were walked over either by an unidentified Caddis fly, the females of which were egg-laying amongst the wet mosses on the surface of the boulders or on the fly Weidemannia bistigmata, Curt., which was using the same boulders as a resting place, that the mite larva apparently vanished and on closer observation it was seen that under these circumstances the larva jumped from the surface of the stone, thus gaining a position on the undersurface of the host. Counts were carried out on this fly and it was found on the first occasion that of 33 of the flies 14 bore 48 mite larvae between them while 19 were without parasites, while on a second occasion 36 hosts bore 64 mite larvae between them, with a maximum of 12 on one host, and 20 were without mites. Of the Caddis flies 22 were caught,

of which 19 bore 14 mites between them. Where several mite larvae were found on the same host it was found that they often varied considerably in size, showing that they had not all been on the host for the same length of time.

The observations summarised above, together with the other results listed in table (vii), do much to strengthen the impression that the Diptera are of much greater importance in the lives of the Hydracarina than was previously thought, and that if more prospective hosts were caught and carefully examined more mite life histories would be unveiled.

Category 3.

Mites having "abbreviated" life-histories.

Nothing in the above work has thrown any light on the possibility that rheophilic mites may have a life-history which involves a direct development from egg to nymph as suggested by Mitchell (1957) and other authors. It seemed desirable to clear up this point if possible and to this end 12 females of Aturus scaber, Kramer, were isolated in a petri dish together with a little moss which had been carefully examined under the microscope, leaf by leaf, to make sure it contained no animal life, including eggs. Similarly 4 females and two males of Kongsbergia materna, Thor and 5 females of Aturus crinitus, Thor were also isolated.

These three petri dishes were set up on 1.3.64 and on 31.3.64 a single egg was found in the first dish, stuck to a moss leaf. A larva hatched from this on 3.5.64 and the same day eight other larvae hatched out in the same dish. This larva is described and figured in the

taxonomic section of this work. This most unexpected discovery was followed two weeks later by the hatching of two larvae of Kongsbergia materna, Thor. No larvae were obtained from the third dish. Larvae identical with those of A. scaber, Kramer, have also been collected from moss in the river Dove. Some of these larvae lived for three weeks after hatching, but none changed to nympho-chrysalids and this may mean that they, in fact, have an as yet unknown parasitic stage.

It was also felt that an examination of the distribution of some of the rheophilic species might help to throw some light on their probable life-history patterns and to this end moss samples were taken from as many rivers as could be visited, and the mites from them identified. These records, together with as many previous records as could be found, were plotted on a map of Britain and it was found that of the Aturidae treated in this manner, Aturus scaber, Kramer and Kongsbergia materna, Thor were both common and widespread, while A. crinitus, Thor, A. brachypus, Viets, A. intermedius, Protz and K. largiollii, Maglio, all appear to be confined to very small areas of the country. The possible reasons for these restricted distributions are treated more fully in the discussion on p. 111.

Although the theory that those mites with very low egg-production were unlikely to lead parasitic lives seemed most plausible, the possibility that it would be disproved made it desirable to have available figures comparing the relative densities of mites and insect larvae in the rheophilic habitat. Mite densities vary greatly over the surface of a river, and it was decided to confine actual counts to areas covered with moss, where mite densities were greatest and

sampling methods least complex. It was found that moss samples of standard size could be quite easily cut with a domestic pastry cutter made of steel. This could be pushed into the moss, and in calcareous waters such as the Dove a portion of the calcareous layer on the rock would be dislodged acting as a water seal. The whole wad could then be transferred into a bottle and removed to the laboratory. Mites and insects were then sieved from the moss and counted. A tin with an area of approximately 25 sq.cms. was used and the results are given in table (viii). Mite densities were found ranging from 20,000 per sq. metre up to 250,000 per sq. metre, while the density of insect larvae varied up to over 1 million per sq. metre. In general the figures demonstrated that the number and density of insects was quite sufficient to support the very large mite population whether its habit was predatory or parasitic, and that in the latter case there ought to be no difficulty in finding hosts. This work, in fact, did little to help elucidate the life-histories, but did at least provide some interesting information on the size of the mite population in the moss fauna.

No cases of "abbreviated" life-histories were actually demonstrated.

Category 4.

The species of the genus *Unionicola*.

The situation regarding mites of the family Unionicolidae is quite distinct from that of mites in other families. In species for which the life-history is known the adults and nymphs are usually parasitic in fresh-water mussels or sponges while the larvae are thought to

Table (viii).

COUNTS OF MITES AND INSECT LARVAE FROM MOSS SAMPLES.

Site	Area surveyed sq.cms.	Mites counted	Density Mites per s.mtr.	Insects counted	Density Insects per s.mtr.
R.Ure,Hawes	31.3	479	153,000	1,126	360,000
R.Nidd	31.3	43	14,000	763	244,000
Dove,Mapleton	31.3	96	31,000	3,242	1,035,000
Dove,Stepping stones	31.3	247	79,000	384	122,000
do.	31.3	186	59,000	312	100,000
Dove,Ilam	23.8	a 198	83,000	1,782	748,000
Dove,Ilam	23.8	b 99	42,000	507	213,000
Dove,Ilam	23.8	c 94	40,000	500	210,000
Dove,Ilam	23.8	d 173	73,000	301	126,000
Dove,Ilam	23.8	e 115	48,000	172	72,000

a,b,c were taken at 2 metre intervals across a fall, each sample being taken 10 cms. above the fall face.

d and e were taken immediately below b and c respectively, 10 cms. below the line of the fall.

be free-living. Unionicola intermedia, Koenike was found in the mussel Anodonta anatina, L., from a variety of sites. Adults, nymphs and developing eggs were present all the year round, but the proportion of eggs was greatest during early winter, showing this to be the main egg-laying period. Of the adults females usually out-numbered males by at least two to one, and during the winter months nymphs were considerably more frequent than adults. The number of eggs varied from 800 to 4,000 per mussel. Teleiochrysalids were found on only one occasion, April, 1960, when 212 were found, loosely attached to the gills of the host near to the exhalent siphon. Larvae were obtained outside the host in January, 1962, in an aquarium tank in which mussels from a stream at Tollerton had been placed a week earlier. It was thought that the hatching of these larvae had been brought about due to the rise in temperature when the mussels were brought indoors from the cold stream, but similar results were not obtained with mussels from Rufford lake in November or December, 1962, nor from Tollerton in January or February in either of the next two years. In consideration of the above facts, it may be that the hatching of the eggs was coincidental to the moving of the hosts into warmer conditions rather than a result thereof.

During collections from site 1, between the gravel pits and the Trent, large numbers of Chironomus plumosus, L., were caught, parasitised by Piona uncata, Koenike, a Typhis spp., and an unidentified mite larvae. The latter was often present in very large numbers and in August 1964, 82 midges were examined, bearing between them 510 of these larvae. Some of these parasitised midges were preserved but the majority were

released in a large aquarium tank in which was 2 cms. of water, together with a number of flower pots containing water-mint in flower and reeds. The tank was covered with nylon mesh. Within four days all the midges had died and fallen into the water or become trapped in the plant material, and a very large number of mite larvae were seen swimming about in the tank.

Contrary to previous experience, however, none of these larvae passed into the nymph-chrysalis stage, and all had died within ten days of the commencement of the experiment. It was at first thought likely that the larvae concerned were too young to undergo metamorphosis, but when a second collection of chironomids was released into a similar tank and the larvae behaved similarly, this atypical result prompted me to make a further careful examination of the preserved material, and it eventually became apparent that these larvae were, in fact, identical with larvae of Unionicola intermedia, Koenike, present in the mantle tissue of Anodonta anatina, L., from a number of sites.

The larval behaviour of this mite and of other Unionicola species has been completely unknown previously, and it has always been assumed that since the adults and nymphs are parasitic in mussels, the larval stage would prove to be a brief, free-living, dispersal stage, serving merely to spread the infection to other nearby hosts.

It is unfortunate that this mite was not previously identified as it would have been interesting to provide the larvae with their Lamelli-branch host and demonstrate the formation of the nympho-chrysalids therein. This will, of course have to be done at the next opportunity, but the extreme importance of the present observation merits immediate

description, and will be discussed later in the thesis.

U.ypsilophora, Bonz were obtained from Anodonta cygnea, L., in Lakes at Newstead Abbey. Adults were present in small numbers throughout the year but eggs were absent from specimens examined during late March and April. Larvae were not found at any time.

U.crassipes, Müller, adults were collected from sites 5, 8, 10 and 18. This mite is described as parasitic on fresh-water sponges and the finding of eggs, larvae and adults in the tissues of sponges is described by many authors. In site 5 however no sponges have been found in four years of careful searching and the mites have all been found either in the vicinity of willow roots or amongst Chara spp., at the bottom of the pond. It seems that this species must, in fact, be able to live on some other food source apart from its known parasitic existence on fresh-water sponges. In this connection Halbert (1909) described a small-sized form which he named U.rivularis Halbert, which he states is non-parasitic. The mites from site 5 were of normal size, averaging 1.2 mm. in body length.

U.aculeata, Koenike, has been found in gravel pits at Beeston and from the canal at Market Harborough, at both sites in the mussel Anodonta anatina, L., in association with U.intermedia, Koenike. Mitchell (1955) states that this mite spends its quiescent stages in the mussel and that the adults and nymphs both leave the mussel immediately after hatching from their respective chrysalid stages. The finding of both adults and nymphs in mussels during June and again in early August seems to show that in this country and in this host the mites spend more time in the mussel than did those examined by Mitchell

in America.

U.figularis, Koch, has been found in three ponds in Essex and from a peat cutting in Northern Ireland. It does not appear in the area mainly under survey for this work, but is included here for the sake of completeness. In one of the Essex ponds the adults can be found at any time of the year, though most common in the spring. This pond dried up except for an area of about 2 sq. metres in the drought of 1957 and close inspection of the bottom yielded no signs whatever of Lamellibranch molluscs and it can be said with considerable assurance that Anodonta spp and Unio spp are indeed absent. Several nymphs of this mite were obtained in August 1962, while a year previously several larvae were captured which according to Sparing's key should belong to this genus. Examination of Gastropod molluscs from this pond has not yielded any signs that these animals may be used as hosts and it appears probable that this mite has a life history which will prove very different from that of any previously described member of the genus. The ability of the mites to colonize a flooded peat cutting and to repopulate the Essex pond so rapidly after the 1957 drought also supports this point of view.

Additional and miscellaneous observations.

The previously described observations have all had a direct bearing on the life-history patterns and development of the Hydracarina and are therefore of primary importance to this thesis and form the main evidence on which the discussion is based. It is apparent, however, that the egg-production of these mites is likely to be a pointer to their probable way of life and as counts were made of eggs laid by a

number of species during the course of the investigation, a table of these egg counts is included in that part of the discussion to which it bears most relevance. (p.92) where the correlation between egg-numbers and parasitic or other habit is discussed.

Furthermore, during the course of this work, as a result of very careful observation of water-mites both under their natural conditions and in the laboratory, certain observations were made not directly connected with the work in hand, but nevertheless of some interest. Moreover since similar observations have not been reported by previous workers and may be of help to future students of the group they are added here.

1). Predators.

Hydra spp are well known predators of fresh-water plankton. It was found that when water-mites are released into a tank containing Hydra spp that they are apparently immune from capture. The mites Limnesia fulgida, Koch, Eylais extendens, Müller and Hydrodroma despiciens, Müller, were seen to come into contact with the tentacles of Hydra spp on many occasions and invariably they were released after a few seconds of struggle. On no occasion was a mite seen to be engulfed. Sometimes the mite would remain still, surrounded by the tentacles, for a considerable time, but in the end would always struggle again and get free. No successful predation on water-mites was, in fact, observed.

One case of non-predatory action fatal to a water-mite was observed in the river Nidd, in Yorkshire. A large stone was found on which about 150 batches of Chironomid eggs were deposited. Embedded

in two of these egg masses were two Protzia eximia, Protz. It was assumed that the slow-moving mites had been on the stone when the eggs were laid and had been trapped when the masses were laid on top of them. Both were dead.

2) Feeding.

Many species have been seen feeding on Cladocera and on Ostracods, and these observations have merely confirmed the previous records of many authors.

One most interesting observation was made on the mite Hydrodroma despiciens, Müller from a ditch in Leicestershire. A single mite of this species was left in a small dish in which were some Chironomid egg masses. It was noticed that as the mite walked about over one of the egg masses the eggs in the mass disappeared one by one. Examination under the microscope disclosed that the mite was probing in the gelatinous matrix with its mandibles and was extracting the contents of each egg which it found. This mite is reported by Wesenberg-Lund (1918) as a parasite in its larval stage in adult Chironomids but this is believed to be the first observation of predation by an adult water-mite on eggs of the same group. This opens up a possible line for conjecture on the origin of the parasitic habit of the larvae.

3) Formation of chrysalis stages.

In all the species investigated the nympho-chrysalis has been formed by the larva, either unattached to anything, lying freely on the bottom of the container, or else the larvae have first made their way into the pith of reeds or other plants provided. Arrenurus spp nympho-chrysalids have been obtained from the mud at the bottom of

ponds. Nympho-chrysalids of Eylais spp and Hydrachna spp were found on their hosts, attached by the larval mouth parts.

Teleiochrysalids were seen either lying loosely on the bottoms of glass containers, or amongst moss roots from various rivers, or attached to algal threads or to other plants by the nymphal palpi.

4) Longevity.

It is not at all easy to devise means of measuring the exact life spans of very small animals, and previous authors have made estimates varying from a few weeks to about three years. There may of course be considerable variation in the life spans of different species. Observations during the present work have not helped much in this respect, but the following points are worth noting.

Eggs have taken times varying from 14-40 days to hatch, and larvae have lived from three days up to as long as forty-two days. Adults have lived in the laboratory for up to six months in the case of Limnochares aquatica, L., although during this time their container dried up three times so that there was no free water, although the algal mass was still damp.

A female of Limnesia fulgida, Koch was accidentally left in about 1 m.l. of water in a small tube, and when rediscovered three months later was still swimming busily about. During this time it had no visible food matter in its container which was in the dark the whole time.

A colony of Neumania spinipes, Müller, from a pond in Yorkshire was maintained from June 1963 until February 1965 in an aquarium. The water level was maintained with tap water and in addition to the mites

the tank contained a quantity of a filamentous alga and a strong Ostracod population. The original collection included Piona variabilis, Koch, Hydrochreutes krameri, Piersig, and Arrenurus albator, Müller, and one female of the latter species was also present in September 1964. It is probable that this was developed from one of the Arrenurus nymphs in the original culture. There were, however no Neumania nymphs present and the adults at the end of the experiment must have either lived for 20 months in captivity or have developed in the culture without a parasitic phase.

5) Effect of temperature on hatching of over-wintering eggs of Protzia eximia, Protz.

Several batches of eggs of Protzia eximia, Protz were collected from crevices in boulders in the river Dove on 8.2.64 and divided into three groups each of which was placed with river water in a small glass tube. One of these tubes was left at room temperature in the laboratory while the other two were placed in a refrigerator at 5.5°C. On 19.2.64 it was seen that the eggs in the laboratory had undergone development to the "schadonophon" stage, where the developing larva can be easily seen within the egg membrane, and the shell of the egg has separated into two halves to allow stretching of the embryo. The other two groups of eggs showed no change. The batch at room temperature hatched from 26.2.64 until 3.3.64 and the larvae lived about three weeks.

On 3.3.64 a second batch was removed from the refrigerator and allowed to rise to room temperature. These reached the "schadonophon" stage by 14.3.64 and hatched about 21.3.64. The third batch were now placed in the laboratory and behaved similarly, hatching after a further

three weeks.

This seems conclusive evidence that the hatching of these eggs is controlled by water-temperature. In the river Dove the temperature rises to about 10°C in late spring and the critical temperature for hatching must lie between these limits, i.e. 5.5° and 10°C.

6). Chemical analyses of water.

Chemical analyses of the river waters were readily available from the Annual Report of the Trent River Board, and these were referred to from time to time. Nothing in the reports threw any light, however, on the restricted distribution of Aturus crinitus, Thor, and the following extracts will demonstrate the chemical similarity of the rivers examined.

River	Position	Nitrogen			Cl.	CaCO ₃	pH	Oxygen
		NH ₄	NO ₂	NO ₃				
Dove	Mapleton	.05	.003	1.8	14	178	7.9	6.3
Dove	Hartington	.1	.02	1.5	13	163	7.7	6.3
Manifold	Ilam	.1	.003	1.5	15	150	7.4	7.2
Derwent	Cromford	.1	.01	1.9	19	139	7.9	9.1

(All chemicals in parts per million)

There appears to be no explanation from these figures as to why A. crinitus, Thor. should be found at Mapleton but not up river as far as Hartington, nor yet in the Manifold. Nor do they throw any light on the fact that Torrenticola amplexus, Koenike, is found at Cromford but not at any of the other sites.

List of Main Sites Worked.

1. Gravel pits, flooded, beside the Trent.
2. Large shallow lake overgrown with reeds. Depth 2' average.
3. Disused canal. Stretches of up to 200 metres still water-filled.
4. Disused canal. Broken into 100 metre sections by concrete walls.
5. do.
6. Small road-side pond. 10 metres radius, 2 metres maximum depth.
7. Small road-side ponds, separated by 1 metre ditch.
8. Road-side pond. 20 metres x 10 metres. Maximum depth 5 metres.
9. Pond in field. 10 metres diameter, 1.5 metres maximum depth.
10. Lake at Clumber Park. 5 Kmetre. long, 40 metres wide.
11. Large Lake. Approximately 200 metres diameter. Depth unknown, but very shallow near margins. Bottom mud and gravel.
12. Trout stream.
13. Trout stream.
14. Torrent with boulder bottom.
15. River below small weir. Boulder bottom with mosses.
16. Trout stream and trout breeding ponds.
17. Stream leaving spring in field.
18. Trout stream with hard rock bottom with some loose stones.

Sites by numbers.

- Site 1. Beeston gravel pits.
- Site 2. Trent Lane Lake.
- Site 3. Nottingham Canal, Bramcote.
- Site 4. Canal at West Bridgford.
- Site 5. Canal at West Bridgford, section 2.
- Site 6. Fosse Way, I.
- Site 7. Fosse Way, II.
- Site 8. Widmerpool, I.
- Site 9. Widmerpool, II.
- Site 10. Clumber Park.
- Site 11. Rufford Lake.
- Site 12. River Dove at Ilam.
- Site 13. River Dove at Mapleton.
- Site 14. River Manifold at Ilam.
- Site 15. River Derwent at Chatsworth.
- Site 16. River Wyeat 3 ponds.
- Site 17. 3-ponds helocrene.
- Site 18. River Greet at Kirklington.

Plate 1.

Rufford Lake. Site 11.

Habitat of Chironomus dorsalis Meigen and other midges parasitised by Piona variabilis, Koch, P. conglobata, Koch, P. species, Typhis species, Hygrobates longipalpis, Hermann, Unionicola intermedia, Koenike, and Pionopsis lutescens, Koch.

Widmerpool 2. Site 9.

Habitat of Arrenurus buccinator, Müller, A. maculator, Müller, Limnesia fulgida, Koch, Hygrobates longipalpis, Hermann, Hydryphantes ruber, De Geer, Piona nodata, Müller, P. carnea, Koch P. conglobata Koch, Pionopsis lutescens, Koch, Typhis ornatus, Koch, and Eylais hamata, Koenike.

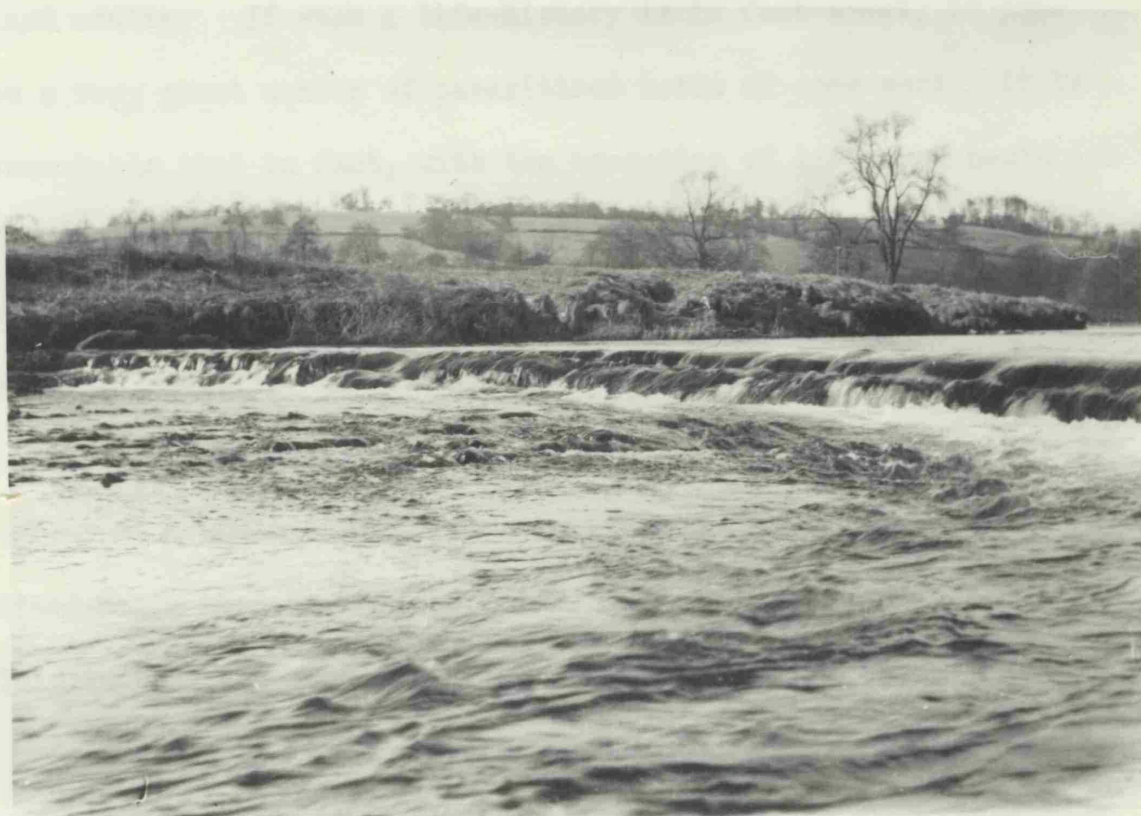


Plate 2.

River Dove at Mapleton. Site 13.

Two views showing typical step formation. Mites are found in great abundance on the mosses growing on the rock faces of the small falls.

The stones in the foreground of the upper picture and to the left below the fall in the lower picture, are the resting places of the fly Weidemannia bistigmata, Curtis, and of an unidentified Caddis fly. It is from these stones that the larvae of Protzia eximia Protz jump up onto their hosts.



Discussion.

1) The nature and prevalence of the "standard" Life-history.

As was pointed out in the introduction, previous work on the Hydracarina has produced descriptions of over 3,000 species in the adult stage, together with descriptions of considerable numbers of nymphs larvae and eggs. Nevertheless the number of complete life-histories known is less than 200 and of these more than half are in the single genus Arrenurus. As the amount of literature on the water-mites has grown, the vast increase in taxonomic material has served to deepen the problems posed by our serious lack of understanding of the life histories. Mitchell (1957) reviewed the known life-histories with regard to their relevance to the phylogeny of the group and agreed with the previous workers that the primitive life-history included a parasitic larva and free-living nymphs and adults. If such a life-history is in fact usual, it presupposes a very great number of parasitised hosts of some sort. It is quite remarkable that in fact, with the exception of Arrenurus hosts are known for less than 100 species. The literature includes many references to larvae and nympho-chrysalids found on a variety of insects, and of various stages parasitic in molluscs, but with mite densities of 20,000 per sq. metre in some localities and in view of the cosmopolitan nature of the group as a whole it would be reasonable to expect far more parasitised hosts than have in fact been forthcoming.

This lack of observed parasitism may be explained in several ways and it was in order to throw a little more light on this subject that the present investigation started. In the first place there have been

recorded by several authors a small group of mites which follow an abbreviated life history either hatching from the egg directly as nymphs or entering the nympho-chrysalis stage without any parasitism as larvae. A list of these mites together with authors is given in table (ix). From this table it can be seen that these species are distributed in four super-families and five families in each of which are known parasitic members. In addition published figures of egg numbers and sizes, particularly in proportion to the size of the adult female have led to the conclusion that there are more mites which may also follow this shortened pattern. Extracts are given from these published figures in table (x) together with my own measurements. From these tables the following species can be seen to produce very large eggs in very small numbers, with a ratio of 3.5 : 1 or less for body length of female to egg length. Pionacercus uncinatus, Koenike, Brachypoda versicolor, Müller, Aturus crinitus, Thor, A. asserculatus, Walter, A. scaber, Kramer, A. elongatus, Walter, A. intermedius, Protz, Kongsbergia materna, Thor, K. largiollii Maglio, K. walteri, Metas, Atractides nodipalpis, Thor, Oxus ovalis, Müller, Ljania bipapillata, Thor, Feltria romijni, Besseling, and F. minuta, Koenike.

Two of these, Brachypoda versicolor, Müller and Pionacercus leuckarti, Piersig, have already been observed (Lundblad, 1927) to hatch from their eggs as nymphs, without any larval stage intervening, and Mitchell (1954) points out that gravid females of the genus Aturus often contain a single egg, half the length of the body and that it seems quite likely that more of these species will be found to follow a shortened life-history similar to the two described by Lundblad. Mitchell (1957) goes so far as to say that this pattern may be typical of rheophilic types, and remarks that

Table ix.

LIST OF SPECIES DEVELOPING TO NYMPH WITHOUT ANY PARASITIC STAGE.

Species	Hatched as.	Author.
Super-family HYDRYPHANTAE.		
Family: Thyasidae.		
<u>Thyas stolli</u> , Koenike.	larva	Crowell, 1960
Super-family LEBERTIAE.		
Family: Lebertiidae.		
<u>Lebertia stigmatifera</u> , Thor.	larva	Lundblad, 1924
Super-family PIONAE.		
Family: Limnesiidae.		
<u>Limnesia undulata</u> , Müller.	nymph	Piersig, 1900
<u>L. connata</u> , Koenike.	nymph	Piersig, 1900
Family: Pionidae.		
<u>Piona nodata</u> , Müller.	larva	Piersig, 1900
<u>P. rotunda</u> , Kramer.	larva	Piersig, 1900
<u>P. uncata exigua</u> , Viets.	larva	Stout, 1953.b.
<u>Pionacercus leuckarti</u> , Piersig.	nymph	Lundblad, 1927
<u>Forelia species</u> .	nymph	Cook, 1955
Super-family AXONOPSAE.		
Family: Axonopsidae.		
<u>Brachypoda versicolor</u> , Piersig.	nymph	Piersig, 1900

Table x.

Extracts from egg-laying data tables. Mites showing very low ratio
body length : egg length.

Species	No. of eggs	Body length	Egg length	Ratio.
1. After Motas, 1928				
<u>Pionacercus uncinatus</u> , Koenike.	1 - 3	.505	.135	3.5 : 1
<u>Brachypoda versicolor</u> , Müller.	1	.500	.150	3.3 : 1
<u>Aturus elongatus</u> , Walter.	1 - 2	.320	.150	2.1 : 1
<u>A. asserculatus</u> , Walter.	1 - 2	.377	.150	2.5 : 1
<u>A. scaber, rotundus</u> , Romijn.	2 - 3	.421	.156	2.6 : 1
<u>Kongsbergia materna</u> , Thor.	1 - 2	.390	.145	2.6 : 1
<u>K. largiollii</u> , Maglio.	1 - 2	.280	.135	2.8 : 1
<u>K. walteri</u> , Motas.	1	.366	.140	2.6 : 1
2. After Sokolow, 1925				
<u>Atractides nodipalpis</u> , Thor.	6 - 12	.600	.200	3.0 : 1
<u>Oxus ovalis</u> , Müller.	6	1.000	.225	4.4 : 1
3. After Cook, 1955				
<u>Forelia</u> spp.	5 - 8	.560	.140	4.0 : 1
4. Jones.				
<u>Aturus scaber</u> , Kramer.	1 - 4	.468	.164	2.9 : 1
<u>A. crinitus</u> , Thor.	1 - 2	.410	.197	2.0 : 1
<u>Kongsbergia materna</u> , Thor.	1 - 2	.369	.136	2.7 : 1
<u>Ljania bipapillata</u> , Thor.	2 - 4	.355	.176	2.7 : 1
<u>Feltria romijni</u> , Besseling	2 - 4	.376	.171	2.2 : 1

"Eggs of Sperchonidae, Axonopsidae and Torrenticolidae are extremely large in size and small in number. This is considered presumptive evidence that the young emerge in an advanced stage, the nymph".

Attractive though Mitchell's assumptions may be, however, they have not been borne out by the observed facts. The seven species of the genus Sperchon, for which life-histories are fully known all have larvae parasitic on Diptera, while the Torrenticola spp for which information is available is parasitic in sponges. Sperchon denticulatus, Koenike, from the river Greet was found to be parasitic on at least four species of midge, and larvae of this genus have also been found from midges collected over the river Dove and from Linton Beck, Yorkshire. Information is available on the habits of only three members of the Axonopsidae and of these, Ljania bipapillata, Thor, is reported by Efford (1960) as parasitic in its larval stage on 4 species of Chironomid, Brachypoda versicolor, Müller does in fact hatch from the egg as a nymph and Parasitalbia sumatrensis, Viets is peculiar in that it is parasitic as an adult on an Ephemerid larva and nothing whatever is known of its development.

An interesting point in this connection arises from a paper by Robert M. Crowell (1960) who reports that the American mite Thyas stolli, Koenike lays eggs of two different sizes producing offspring with very different life-histories. A female laid egg masses totalling about 190 eggs in all, with an average diameter of .142 mm. while another group of females deposited egg masses varying from 2 to 6 eggs each with an average of four eggs per female, affixed to Sphagnum leaves, and having an average diameter of .24 mm. The eggs of the first female

hatched to larvae about 15 - 21 days after deposition, while the larger eggs of the other group hatched to nymphs only 7 days after laying. The adults laying these two sorts of eggs were morphologically indistinguishable and Crowell was able to offer no explanation of this particular phenomenon. He found larvae identical with laboratory hatched larvae of Thyas stolli, Koenike on Aedes vexans, Meigen and on another Aedes spp. It seems certain here that the same species of mite is laying two sorts of egg, one of which gives rise to parasitic larvae while the other gives rise directly to nymphs. This compares with the work of Stout, (1953.b) who found that the larvae of a subspecies of Piona uncata, Koenike, P.uncata exigua, Viets, when isolated in a dish from which all visible life had been removed developed into nymphs in 10-12 days. In my own collections from sites 1 and 2, the British specimens of P.uncata, Koenike, have been shown to give rise to larvae which are parasitic on Chironomus plumosus, L. and other Chironomus spp., and which have a development time of about 30 - 50 days from egg hatching to the emergence of the nymph. Limnesia undulata, Muller has also been shown by various authors to have both a direct and a parasitic development, though no one author appears to have observed both phenomena. This may, indeed, explain the anomalies in past records where disputes have arisen over observations of larval hatches which have apparently contradicted the observations of previous workers who had observed direct hatching of the nymphs from eggs of the same species.

The most noteworthy feature of these direct developments, whether the nymph hatches from the egg or is formed after a short free-living larval life, is the extreme shortness of the time required from egg

laying to nymphal emergence compared with the mites following a parasitic life-history. Thus in the case of Thyas stelli, Koenike the time taken for the parasitic development is 21 days plus probably at least 10 days from larval hatch to nymphal emergence, making at least 31 days compared to 7 for the direct development to nymph, and in Piona uncata, Koenike it is 30 - 50 days compared to 10 - 12 days for the non-parasitic development. There may be some pattern involved in this alternative type of egg and the quickly developing egg giving rise rapidly to nymph may well be the equivalent of the rapid developmental stages in other Arthropods such as Aphids and Cladocera. It is of course purely a matter of conjecture as to how the difference is brought about but analogy with other Arthropod groups suggests that the nymph-producing eggs might conceivably be parthenogenetic in origin. Some slight support for this theory is provided by the fact that one of the females of P.uncata exigua, Viets studies by Stout, laid its eggs after being isolated for a month. It is true that parthenogenesis has not been demonstrated in the Hydracarina, but in many of the rheophilic mites particularly, the proportion of males to females is very low indeed and this type of development does at least offer a feasible explanation of the ability of some species to maintain themselves with an apparently inadequate egg production.

The very real difficulties which arise in connection with the egg production numbers of some of the water-mites is well illustrated by Efford's work on Feltria romijni, Besseling, and its host, Tanytarsus (Stempellina) flavidula, Edwards, (Diptera, Nematocera), in a stream in Oxfordshire. Despite his close observation of this species over a period

of fourteen months there are still important gaps in our knowledge of its life history which make it impossible to understand for instance how it manages to maintain itself. Efford produces evidence and argument to show that the mite has a life-span not exceeding one year, with a single main breeding season. Eggs develop slowly in the females over winter, reaching a peak of just over two per female in May. A similar peak in August was put down to females which had over-wintered as nymphs. Efford suggests that there is a 50% mortality of larvae which attach to male hosts as these do not return to the water, and a further mortality, not estimated, due to rain, spiders and other extraneous factors destroying the hosts. The next greatest mortality, he claims, occurs to the young adults between October and December and amounts to at least 50% and affects both sexes alike. Since the number of eggs laid must be sufficient to replace both sexes of the parent generation and also to provide for all losses before maturity the minimum number of eggs laid by each female to maintain the population would have to be rather more than eight, in order to stand the two consecutive 50% reductions, or at least four times the observed number. It follows therefore that there must be some supplementary method of reproduction giving at the very least a fourfold increase in numbers annually, in addition to the main egg production which Efford has described. Although nymphs are observed throughout the year, Efford concluded from his analyses that there was a steady increase in their size, and that therefore these do not represent more than one generation of nymphs.

As has been already mentioned, mite larvae detached from the host are often capable of running about even on a completely dry surface such

as blotting paper, and Efford may therefore be mistaken in thinking that parasitism on the male host must inevitably mean the death of the mite larva. Provided the host dies somewhere near the water the mite larvae may find their way back to it. Despite this there is still a major discrepancy between the reproductive powers which he observed and those which are needed to maintain the population at a steady level. A possible clue to this puzzle is to be found in the observations of Piersig (1900), Stout (1953,b) and above all of Crowell (1960) of the direct development of Piona rotunda, Kramer, Piona uncata exigua, Viets, and Thyas stolli, Koenike from egg laying to nymphs in 12, 10 and 7 days respectively. Since Efford sampled his stream by means of core samples taken in the first four days of every month, the elapse of three and a half weeks between successive samples could possibly have been enough to permit an unobserved increase in number. Furthermore, Crowell has now established that it is possible for a particular species of mite to lay eggs which develop directly to nymphs as well as eggs which produce larvae in the normal way, and it is at least a tenable theory that Feltria romijni, Besseling, may do likewise. Efford also found two females in late summer bearing eleven eggs each. Although this represents much greater individual egg production, the fact that Efford found only two such females makes it appear unlikely that this could be of any very great significance in the general life history of the species. In fact despite Efford's careful and accurate study he was unable to offer any satisfactory explanation as to how the species is able to maintain itself with such low reproductive powers.

During my own observations in the rivers Dove, Manifold and

Derwent during the months of December, January and February at water temperatures of from 4°C down to 1°C I have found large numbers of larvae swimming amongst the moss. Counts have revealed densities of up to 900 larvae per sq. metre of moss and diligent search has failed to find any parasitised insects or other hosts, except for a single Chironomid pupa bearing a single Hygrobatid larvae from the Wye, a tributary of the Derwent. In the laboratory these larvae are very prone to become trapped in the surface film, especially during the sieving process, and attempts to rear them further have all been unsuccessful. It seems possible, as Mitchell suggested, that these may have a non-parasitic development. The majority of these 'winter' larvae belong to the family Hygrobatidae.

On the other hand, eggs of Protzia eximia, Protz are commonly found in red masses on the undersides of boulders and amongst the moss samples. These eggs hatch out about three weeks after being brought into the laboratory and, as explained on page 78, it was shown that this is almost certainly due to the rise in temperature involved. It has also been shown on p.66 that the larvae of this mite are parasitic on the fly Wiedemannia bistignata, Curtis during the spring and summer, and it can be assumed, therefore, that the postponement of hatching until a temperature of about 5.5°C is reached helps to ensure that the larvae shall be active at the time when the host is available.

The presence of Aturid mites in the rivers throughout the year, together with the difficulties involved in identifying particular individual mites, has precluded any possibility of measuring their individual life spans, and it is quite possible that they live for more

than one egg-laying season.

Collections of Chironomids from the vicinity of many rivers and streams from early spring to late autumn produced many examples of parasitism by mite larvae. Larvae of the genera Hygrobates and Atractides were found from early spring to October on midges flying over the river Dove, and in June and July over Linton beck in Yorkshire. Larvae were found in samples from the Dove all through the winter. Larvae of Sperchon spp were found on Chironomids from Linton beck and Sperchon denticulatus, Koenike, larvae, were found to be parasitic on Chironomids in June and July in samples from the river Greet. Larvae of Lebertia spp were found on midges from the emergence trap at Linton and also in moss samples from the Dove during the winter.

The situation with the rheophilic mites which have been examined can therefore be summed up as follows:

no cases of nymphs hatching from the eggs have been observed, and even in those groups which produce the smallest numbers of eggs, the larvae appear to resort to parasitism. In the case of Aturus scaber, Kramer, the lack of development of the larvae after hatching and their death about three weeks later points to the conclusion that they also lead a parasitic life. Crowell's work on Thyas stolli, Koenike, demonstrates that an individual species of mite may have more than one life-history pattern, and shows the need for close observation throughout the year under conditions which would minimise the chances of unobserved nymphal hatches. The present work has cleared up, satisfactorily, the position of Protzia eximia, Protz, and the observed presence of Hygrobatid larvae on almost all midge swarms examined from April to October supplies

sufficient evidence to explain the presence and maintenance of the large populations of mites of this family found in the rivers. The family Aturidae and the genera Sperchon, Lebertia and more particularly Feltria and Ljanina still pose many problems.

The Hydracarina which live in still waters usually lay more eggs than the rheophilic species listed in table (x) and examples showing previously published figures and my own records are given in table (xi). The problem with these is not, therefore, to explain how the mites manage to maintain themselves with a low egg production, but, on the contrary, to explain why so many larvae have not attracted a great deal more attention from zoologists when in their parasitic stages. It would be reasonable to expect that if most mites lead a parasitic larval life, then very large numbers of parasitised insects would have been observed. The number of such hosts reported is certainly less than would be necessary to support such a view of the life-histories and it is worth considering possible reasons for this state of affairs.

There are many reports in the literature of the large nympho-chrysalids of Eylais and Hydrachna spp. as these are usually bright red in colour and this, together with their large size, makes them conspicuous. Furthermore they are most frequently found on Coleoptera and Hemiptera, both of which were well-worked groups even in the early days of descriptive zoology. Life-histories published for instance by Viets, Munchberg, Imamura and Sparing however, point to the Diptera (Nematocera) as being the most common hosts of water-mite larvae, and it is noticeable that most of the reports of mites on these hosts have been made concerning hosts of economic importance such as the mosquitoes

Table (xi)

Egg-laying table for mites living in slow-moving waters, or in ponds and lakes.

1. After Motas 1928. Body lengths from Soar and Williamson.

Species	Egg no.	Length	Body lengths	Ratio
<u>Eylais hamata</u> , Koenike.	several 100s	.150	4.5	30 : 1
<u>Limnochares aquatica</u> , L.	100	.180	4.0	22 : 1
<u>Hydryphantes ruber</u> , Geer.	50-180	.135	2.0	15 : 1
<u>Hydrodroma despiciens</u> , Müller.	40-210	.160	2.0	12 : 1
<u>Limnesia maculata</u> , Müller.	25-30	.190	2.0	10.5 : 1
<u>L. fulgida</u> , Koch.	31-44	.200	2.0	10 : 1
<u>Neumania vernalis</u> , Müller.	22	.160	1.3	8 : 1
<u>Typhis latipes</u> , Müller.	26	.150	1.0	7 : 1
<u>Pionopsis lutescens</u> , Hermann.	54-76	.175	2.0	11 : 1

2. Jones.

<u>Eylais hamata</u> , Koenike.	2,224	.140	4.5	31 : 1
<u>Hydryphantes ruber</u> , Geer.	2,126	.135	2.2	15 : 1
<u>Limnesia fulgida</u> , Koch.	200	.190	2.1	11 : 1
<u>Piona carnea</u> , Koch.	14	.230	2.5	11 : 1
<u>P. conglobata</u> , Koch.	32	.180	1.0	5.5 : 1
<u>P. nodata</u> , Müller.	41	.197	1.9	11 : 1
<u>P. uncata</u> , Koenike.	124	.230	1.8	8 : 1
<u>Pionopsis lutescens</u> , Hermann.	39	.186	1.9	10 : 1
<u>Arrenurus buccinator</u> , Müller.	28	.190	1.2	6.5 : 1
<u>A. maculator</u> , Müller.	24	.200	1.2	6 : 1

which act as vectors for diseases of Man. Many of the reports have been made by workers interested in the hosts alone, and often little has been done to identify the mites or ascertain the frequency with which the hosts are infected. There have, however, been 48 mite species reported to parasitise Diptera (47 Nematocera, 1 Brachycera). So many of the above-mentioned reports have accrued accidentally as a result of mite larvae being found during research involving the hosts that it appeared imperative to catch and examine large numbers of possible hosts if a realistic appraisal of the degree of parasitism were to be made. During the present work, therefore, large numbers of Chironomids, mosquitoes and other insects were caught and examined and two points at once became apparent. In the first instance the mites were often extremely difficult to see even under the binocular microscope, and could, therefore, have been very easily overlooked. Although some midges bore mite-larvae quite conspicuously on the thorax or abdomen it should be realised that when the parasitic larvae first attach themselves to the hosts they are very small, and since they become fixed at the inter-segmental membranes with their heads often pushed right into the soft joint, only a very small proportion of the mite's abdomen may be visible. As the mite feeds it becomes engorged and will become more easily visible but the probability is that it remains attached to the host for very few days and that examination of the hosts, unless carried out at very frequent intervals are liable to miss the parasitic stages altogether. Under crowded conditions, and also when the mites are well engorged, mite-larvae are very easily dislodged from their hosts and if the latter are taken any distance before examination

they may well have lost their parasites. Furthermore mites were frequently found attached singly to the host in the hollow formed by the posterior part of the thorax and the ventral part of the first abdominal segment. In this position the mite, usually of a similar colour to the host, was almost invisible except at particular angles. In order to be able to count the numbers of hosts affected, the hosts had to be moved about so that the light fell directly into this hollow.

The second point of interest here is that, although in some cases swarms of midges were examined in which over 50% of the individuals were carrying parasitic mite larvae, in many other cases, particularly with the smaller host species, the infections were of the order of 2% and on several occasions over 200 midges were examined before one was seen to be infected. Thus a large number of midges could be examined without revealing the fact that they were infected with parasitic mite larvae. As the figures in table (vii) show, a very high proportion of the midge swarms examined showed some proportion of parasitism by larval water-mites and it must be concluded from this that the importance of the Diptera (Nematocera) in the general pattern of mite life-histories is even greater than previously published accounts would have suggested.

On two occasions Arrenurid mite larvae were found as parasites on Dixa aestivalis, Meigen. These are the only two known records of parasitism by water-mites on the Dixidae and this addition of yet another Nematoceran family to the list of host insects strengthens still more the conviction that this division of the Diptera is of primary importance in the life-history of the Hydracarina.

It is generally accepted that there is in all animals a definite correlation between the number of offspring produced and the normal expectation which each of these offspring has of reaching maturity. An examination of the numbers of eggs laid by different species of water-mites could, therefore, be expected to give some indication of the likelihood of the species having a parasitic larval stage, and of the difficulty such a larva might be expected to have in finding and attaching itself to a host. It was in accordance with this tenet that Mitchell (1957) concluded that the rheophilic mites with very low apparent egg numbers would probably prove to have an 'abbreviated' development. The fact that in the majority of cases where their life-histories have since been worked out they have, in fact, proved to be parasitic requires some explanation. These mites have been shown to parasitise as larvae various Chironomids, and their very low egg production is apparently compensated for by the fact that they live in a habitat where prospective hosts are present in enormous numbers and in very dense concentrations. In the Dove, midge larvae were counted in several moss samples and figures of up to one million per sq. metre of moss were obtained. This enormous density of prospective hosts in the micro-habitat where the mites themselves are found remove the difficulties usually associated with a parasitic way of life, and it can be appreciated that an egg number lower than that normally expected with parasitic animals might well be sufficient in these cases. The 'expectation of life' of a parasite must, in fact, depend to a very great extent on the availability of its host and on theoretical grounds alone we would expect a lower reproductive rate in a parasite with a

super-abundant host than in one whose host is not so readily available. The figures available for the water-mites appear to be entirely in support of this principle.

In general the ability of any mite species to maintain itself through a parasitic phase will depend on a combination of four factors; a) the number of larvae produced by each female; b) the longevity of the larvae from the time of hatching to the time at which they would die if unsuccessful in attaching to a host; i.e. their "host-searching" time; c) the degree of host-availability; and d) the ability of the larvae to regain the water at the end of their parasitic phase, which in turn would be dependent on the habits of the hosts. Of these factors it is unlikely that (d) will vary very much as all known water-mite hosts are animals which either live entirely in water or which spend the majority of their time over or near the water. Since mite egg-numbers are known to vary from 1 per female to at least 2,224 per female the assignment of an arbitrary factor for (d) is unlikely to invalidate any subsequent argument, and if (a) and (b) are known it should be possible to make valuable deductions about the probable hosts. The degree of host-availability will itself depend to a great extent on the actual methods by which the larvae contact their hosts, and obtain their attachment to them. Larvae of the genus Hydrachna are believed by Mitchell to be evolved independently from other water-mites and certainly differ from them in larval form and behaviour. The mouth-parts of these larvae are huge, often making up half the bulk of the animal. The larvae swim actively after their hosts and attain their position thereon without ever passing through the surface film. Since

they parasitise insects such as beetles and water-bugs which are almost completely aquatic many of these mite larvae never leave the water at all, and all stages of their life histories are spent beneath the surface.

The remaining larvae can be conveniently divided into three categories: (i) those which break through the surface film under their own power and run actively over the water surface; (ii) those which swim actively in order to find their hosts and are carried through the surface film by the latter as they leave the water immediately prior to metamorphosis and (iii) the members of the family Unionicolidae whose adults are parasitic in the mantle cavities of Lamellibranch or Gastropod Molluscs and whose larvae have been assumed by previous workers to be a free-living dispersal stage.

(i) Larvae which run on the surface of the water belong to the Super-families Limnocharae and Hydrophantae and are capable of passing through the surface film by their own efforts. I have found that when surface running larvae of Eylais spp are shaken vigorously so that they become wetted and pass down into the water they recover and regain the surface film in less than three hours. Mitchell (1957) states that aerial larvae run on the surface and, with the exception of Eylais spp "attack the aerial adults of aquatic insects". He goes on to say that Eylais larvae attack the adults of Haliplids and Corixids and remain in the plastron of air under the wings throughout their feeding stages, and form their nympho-chrysalids in this position on the hosts so that the larvae do not return through the surface film, although the nymphs do so after emergence from the nympho-chrysalis. He claims that most

members of this group are Dipteran parasites and locate the host pupae and cluster around the breathing horns until emergence of the host imago, when they climb onto the host and dig in the mouth parts before the host chitin has had time to harden. In point of fact hosts have been proved for only 24 species out of approximately 360 species having this type of larva, and of these two are parasitic on Plecoptera, 4 on Hemiptera, one on Diptera and Hemiptera, one on Hemiptera and Coleoptera, one on Hymenoptera, 3 on Coleoptera and one on Odonata. The other 11 are indeed parasitic on Diptera but it hardly seems that enough information is available to make any sort of generalisation profitable or that the present figures point to a majority dependence on the Diptera. The two species of Partnunia for which information is available are both parasitic on Plecoptera and P. uchidai. Imamura attains its position on the host by jumping as much as 2 cm. from the water surface. Thyas larvae have been observed to jump in this way also, and it has been surmised that this habit is associated with the attainment of their position on their Dipteran hosts. As described on p.66, I have observed in the field the method by which Protzia eximia, Protz, larvae attain their position on their insect hosts by jumping from the surface of boulders, on to the undersides of insects which walk over them. The mechanism of this response to the nearness of the host is not certainly known but Hughes, (1959) states that according to Lees (1948.a) Ixodes ricinus, reacts to mechanical stimulation or shading, such as would be caused by the approach of the host animal, by climbing onto and clinging to anything that brushes against it. Similar reactions are brought about by the smell of animal hair

accompanied by a rise in temperature. Olfactory receptors and temperature receptors are recognised in this species and it seems likely that the reaction of Protzia eximia, Protz to its insect hosts is probably a response to light or chemical stimuli or both.

Larvae in category (i) usually lay large numbers of eggs, varying from 200 up to over 2,000 per female. Thus two females of Eylais hamata, Koenike were observed to lay 4448 eggs between them, and the obvious conclusion to be drawn from this very large egg number is that the hazards faced by the young stages must be considerable and that only a very small proportion must reach adulthood. The larvae live for less than a week in the absence of a host, and parasitise Corixids and Beetles which they presumably have to catch while the hosts surface for air. The larvae are able to run rapidly over the water-surface and it would seem that a fast moving mite larva ought to have little trouble in catching a stationary Corixid. The density of the hosts in the ponds and canals is probably a limiting factor here, however, and large numbers of larvae are probably needed to compensate for a comparatively low host density and also for the fact that the hosts tend to remain inactive during inclement weather. The low 'searching-time' available to the larvae may result in heavy losses when the weather is not conducive to host activity.

(ii) Those larvae which swim actively and which are, in general, longer lived than the surface runners usually seem to find their hosts in the water when the latter are in their immature stages, remaining with the prospective host until it completes its metamorphosis when a feeding attachment to the adult is achieved. The larvae live from three to

six weeks after hatching from their eggs so that the 'searching-time' available to them is considerable. This group includes the known parasites amongst the rheophilic mites, which mostly lay very small numbers of eggs as well as the bulk of the 'pond' mites which lay from 20 - 50 eggs on average. Presumably the former make up to some extent for their very low egg numbers by parasitising the super-abundant insect fauna of the rivers. The problem of finding a host becomes trivial for an animal which parasitises insects whose pupal cases cover large areas of river bed and whose larvae have up to three weeks 'searching-time'.

That category (ii) larvae enjoy a considerably better expectation of life than the surface runners can be seen by a comparison of mites having similar hosts. Thus Hydryphantes ruber, Geer given by Viets (1936) as a parasite of Culex, has a larva which runs actively on the water surface. A female of this species laid 2228 eggs as compared to an average of 30 to 35 for those Arrenurus species which parasitise the same or related hosts. This offers confirmation of the benefits to the mites of finding their hosts in the pupal stage and awaiting their metamorphosis rather than finding them on the water surface at the actual time of metamorphosis. The time spent by a mosquito at the surface on emergence is extremely brief and this, coupled with the comparatively short larval life of the mite must make this type of host - parasite contact very problematical. The fact that H. ruber, Geer lays fifty times the number of eggs laid by the other mosquito parasites offers a fair judgement of the unsatisfactory nature of its host-finding methods compared to theirs.

(iii) The Unionicolidae.

The family Unionicolidae have always been separated from the remaining water-mite families due to the fact that their adults and nymphs are, for the most part, parasitic in the mantle cavities of Fresh-water mussels. It has been generally assumed that the larvae of these mussel-parasites have been free-living, and have left their hosts for a comparatively short time, acting as a means of dispersal. There have been, however, no previous records of larvae of the genus Unionicola caught in the field outside the hosts. Mitchell, 1957 deduced that the parasitism of this genus was secondary and assumed that they had evolved from ancestors which had developed an "abbreviated" life-history.

During the course of the present investigation, however, it has been demonstrated that in fact the larvae of Unionicola intermedia, Koenike, and another Unionicola species, probably U.aculeata, Koenike, are parasitic on the midge Chironomus plumosus, L., during August and September. It has also been pointed out on p.74 that a third species, U.figularis, Koch, may also prove to have a parasitic larva.

In the circumstances it appears that the larvae of this genus behave in a way precisely similar to the remainder of the Super-family Pionae, and that the parasitism of the adults can be looked upon as a comparatively minor adaptation. As Mitchell has pointed out, U.aculeata Koenike, uses the molluscs only as shelters for the pupal stages, and the parasitism of the other members of the genus is likely to be merely an extension of this habit.

This discovery, in fact, makes the whole position of the Unioni-

colidae much easier to understand. They have, previously, appeared to be quite atypical in their life-histories of the super-family into which both the adults and larvae belong on grounds of morphology. Of the thirty other species of the Pionae whose life histories are known, 29, belonging to 4 of the six other families are parasitic as larvae on Diptera, Nematocera, or have abbreviated life-histories, while one is marine and parasitic on Ostrea.

As it is also known from Crowell, 1960 that the same mite species can have parasitic and abbreviated life histories, the apparent anomalies of the life-histories of this super-family now appear to be resolved. This most important discovery, leading to a simplification of the position of the Unionicolidae restores the two species concerned to category (ii) as far as their larval behaviour is concerned and it will be most surprising if, in view of the similarity in egg numbers and host-searching time of the Unionicolidae with the other mites in that category further research does not show other members of the family to have similar larval behaviour.

It is highly probable that in the life of an individual mite the detachment from the host and the subsequent return through the surface film is of at least as great importance as the attachment to the host. Detachment may be achieved at the time the host is egg-laying or when it dies and falls into the water. Several authors have drawn attention to the fact that the males of many known hosts may not in fact return to the water at all and the future of mites attached to them must be problematical.

Mitchell has carried out tests with Arrenurus major, Marshall

and its host Ischnura verticalis, Say. Fully engorged larvae become active a few seconds after being damped, the legs moving in such a way as to relax the grip of the mouth parts on the host. Mites thus activated can detach themselves from the host and swim away if it is dipped in water. The time during which the larvae can leave the host is, however, limited and if they fail to leave during this time they become further engorged and will not then leave unless the host is kept in water. Mitchell found that some species had larvae which would become activated in this way and would leave the host quite readily when it was submerged, while others would leave the host only if it was immersed in water for some time. It seems from this that in some species the normal time for leaving the host is when it dips under the water at egg-laying, while for other species the normal time of leaving is after the host has died and fallen into the water. My own experiments, carried out with Chironomids bearing mite larvae showed similar results to those which Mitchell obtained. The midges were activated by damping and were easily dislodged thereafter. When fairly large numbers of hosts were confined in an enclosed space, it was found that the respiratory moisture was sufficient to bring about the dissociation of the mite from its host. This made it necessary to take a large number of tubes on collections so that the hosts would not be over-crowded. Arrenurus spp seem more prone to become detached from their host mosquitoes than Piona spp do from their host midges. It was found that mite larvae are able to make their way easily back down through the surface film after leaving the host especially if there is any plant material available for them to walk down. In this

connection it was of interest to note that larvae which were not engorged became entrapped in the surface film much more often than did engorged larvae. If the larvae were so engorged as to be almost spherical in shape they seemed to pass through the film without the slightest trouble even in the complete absence of plant material and with the surface quite still. Agitation of the surface appeared to simplify the passage for less engorged larvae. Under field conditions it is unlikely that either there would be no plant stems available or that the surface would be completely calm and this problem of entrapment in the surface film may be purely a laboratory phenomenon.

2) Effect of Parasitic water-mites on their hosts.

There is very little evidence of the effects that parasitic larvae have on their hosts. Isolated papers have dealt with some effects and Marshall and Staley (1929, 1930 and 1930.b) reported on the production of a tubular process at the site of the insertion of the mouth parts of Arrenurid mites into the host mosquitoes. Apart from this physical reaction locally there was no suggestion that the mite adversely affected the reproductive capacity or viability of the host. Lang-fou Cheng (1933) found mosquitoes bearing as many as 40 mite larvae each. He claimed that these mosquitoes were as active as unparasitised specimens. Uchida and Miyazaki (1935) on the contrary state that Anopheles females parasitised by water-mite larvae could not be persuaded to bite, and since a blood meal is essential to these insects before their eggs are laid, this must provide a serious interruption to the life-cycle of the hosts. The belief that the presence

of water-mite larvae must be harmful to the hosts also led to attempts to control malaria in parts of Italy by the introduction of Arrenurid mites known to parasitise Anopheline mosquitoes. Unfortunately no conclusions on the efficacy of this step were drawn owing to the subsequent draining of the marshes. Wesenberg-Lund (1918) studied the effect of Hydrachnid larvae on Dytiscus marginalis, L., and of Eylais larvae on Cymatia coleoptrata, Fabricius. On the former host, mite larvae reared in the aquarium covered the whole ventral surface of the hosts, all of which died, probably, according to the author, as a result of the large number of parasites. The conditions of this experiment, providing a small number of hosts for a very large number of mite larvae in a restricted volume of water may well be far removed from the conditions which may be expected in the field, and from this point of view it cannot be considered to give very reliable evidence of the normal effect of the mite larvae on this host. In the second case the bugs were obtained in the wild, and were parasitised by one mite each. The latter were large compared to the hosts however, and Wesenberg-Lund reports that the bugs were "annoyed" by the parasites which were attached under the wing cases and which upset the hydrostatic and respiratory efficiency of the plastron of air.

Twinn (1939) reported that damage to the nymphal abdomens of some Simuliids is associated with the presence thereon of mite larvae. Crisp (1959) studied the effect on egg production of Corixa scotti, D. & S. of parasitic water-mite larvae. He found that parasitised females contained an average of 5 ± 4.8 fully developed eggs, compared with 89 ± 7.4 in unparasitised females, and concludes that the presence

of the mites reduces the fecundity of the host. Unfortunately Crisp did not identify the mites even to genus, but argued that as "all the mites identified from Corixids have belonged to the genus Hydrachna" and that the only representative of this genus in the lake concerned was H.cruenta, Müller, "it is probable that the ecto-parasites on C.scotti, D. & S. belong to this species". In point of fact several species of the genus Eylais are well known to be parasitic on Corixids and in any event, the knowledge of parasitism in the group is so slight that this sort of deduction is not valid. As Crisp's paper seems to provide the only published attempt to measure statistically the effect of mite larvae on the reproductive powers of their hosts it would be regrettable if the faulty argument as to the mite concerned were allowed to obscure the importance of the statistical conclusions.

Numerous authors have pointed out that many Odonata show 100% infestation with larval water-mites at least up to the time at which they lay their eggs. It has even been suggested that the presence or absence of parasitic mites can be used as an accurate assessment of the age of the Dragonflies. In my own work I found 100% infections by Arrenurid mites on Coenagrion puella, L., and Pyrrhosoma nymphula, Sultzer, at the time of the emergence of the damselflies and it is probable taking into consideration the extent of this parasitism varying from 17 to 35 mite parvae per host, that very little harm is done to the hosts by the mites. On the other hand my measurements showed that the mite larvae increased to eight times their original volume while attached to their hosts, and this growth is presumably at the expense of the host. This appears likely, therefore, to be a

long-established parasitic relationship in which the host has become adjusted to the presence of the mites and is not seriously inconvenienced by them.

On one occasion when 58 specimens of Chironomus dorsalis, Meigen were transported back to the laboratory in a glass tube, those which were parasitised showed considerably less viability than their unparasitised companions. Eleven out of twelve which bore larvae of a Typhis spp died before reaching the laboratory, whereas none of the 46 unparasitised Chironomids had done so. The suggestion is obvious that under these unfavourable conditions the presence of parasitic mite larvae adversely affects the host midges. On the other hand, parasitised midges have frequently laid egg masses which appear normal, and there is little evidence to suggest that in this case either, parasitism is particularly disadvantageous to the host. A single specimen of Anatopynia varia, Fabricius, was caught, bearing 36 mite larvae of an Arrenurus spp round the junction of the head and thorax. The mass of parasites was such that the midge was unable to balance itself when at rest and kept falling forward onto its head. It was able to fly normally, however, and may not have been as greatly inconvenienced as a superficial appraisal of its circumstances might suggest.

As can be seen, the evidence regarding the effects which parasitic water-mite larvae may have upon their hosts is by no means conclusive, and is in some instances quite contradictory.

Water mites are known as parasites of insects as far back as the Oligocene period, and it is quite likely that a relationship of such

long standing may have reached a state of balance where the host has evolved a reproduction rate sufficient to counteract any adverse effects of the parasites.

3) Distribution and its relationship to life-histories.

Very little is known about the methods of dispersal of the water-mites. It is easy to understand how the mites of flowing water can disperse themselves in a down-stream direction but far less easy to understand how they can make any progress against currents which are much faster than their own maximum swimming speeds. Equally, it is difficult to explain how still-water mites could disperse themselves from one pond to another. In the "standard" life history, however, there is a ready-made answer for those mites which follow it. Parasitism on flying insects gives the parasite an excellent means of dispersal while it is in its parasitic stage.

The possibility of using an examination of distributions as a "research tool" for deducing information on the probable life-histories depends on a sufficiently accurate knowledge of such distributions together with the realisation that arguments based upon them can be used in one direction only. For instance we can argue that a mite having a world wide distribution, together with a wide distribution locally in those countries where it is found must have a very successful method of dispersal, and is therefore likely to be parasitic on flying insects. However it does not follow that the reverse is true. A mite having very restricted and local distribution may be dependent on some factor in the micro-habitat which is itself not widespread, or

may be host-specific on a scarce and poorly distributed host.

The only work dealing with the distribution of the British water-mites is Soar and Williamson's "British Hydracarina" (1925-1929). This gives distribution records for all the species described, but an examination of these shows that they are more nearly the distribution records of the collectors than those of the mites. In point of fact few areas in the British Isles have been thoroughly worked for this group and the only parts of the country where it can be said with any confidence that something approaching a complete mite fauna list can be made up are the areas surrounding the Fresh Water Biological Association's Laboratory, Windermere and the Flatford Mill area. The areas immediately surrounding the other Field Centres have also presumably been well worked over, but in the absence of specialists it is doubtful if all species found have been identified and in any case no records appear to have been published. In Ireland the area around Dublin was studied by Halbert for many years and records for this area are probably almost complete also. For many parts of the country no records exist at all however, and, for example, Professor Carr in his Fauna of Nottinghamshire (1916) and supplement (1935) points out that there are no records of water-mites for the county and appeals for young zoologists to take an interest in the group. Soar and Williamson give only five records for Derbyshire despite the fact that a rich mite fauna exists in the rivers of that county.

In these circumstances it was felt that some benefit might be derived from an examination of the distribution of one particular family of mites and it was decided that the Aturidae would be a suitable family

with which to deal. The considerations leading to this conclusion were as follows:-

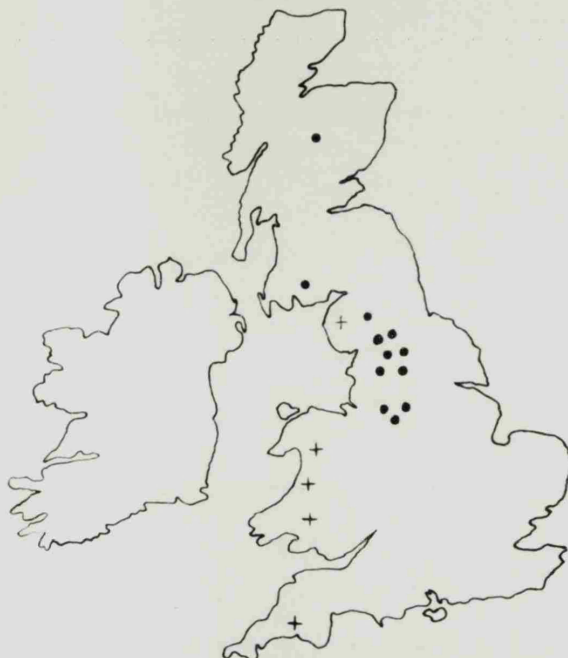
- a) There were only five members of the family previously recorded from these islands (I have added one more). It seemed possible to deal with the whole group, therefore, without selection.
- b) The species reported from this country have widespread distributions elsewhere in the world (see table) and very sparse and erratic known distributions within the British Isles.

World Distribution

	Scandinavia	Western Europe	Central Europe	Eastern Europe	Balkans	Italy
<i>Aturus scaber</i> , Kramer.	+	+	+	+	+	-
<i>A. crinitus</i> , Thor.	+	+	+	+	+	+
<i>A. brachypus</i> , Viets.	-	-	-	-	+	-
<i>A. intermedius</i> , Protz.	-	+	+	+	+	-
<i>Kongsbergia materna</i> , Thor.	+	+	+	+	+	-
<i>K. largaiollii</i> , Maglio.	-	+	+	-	-	+

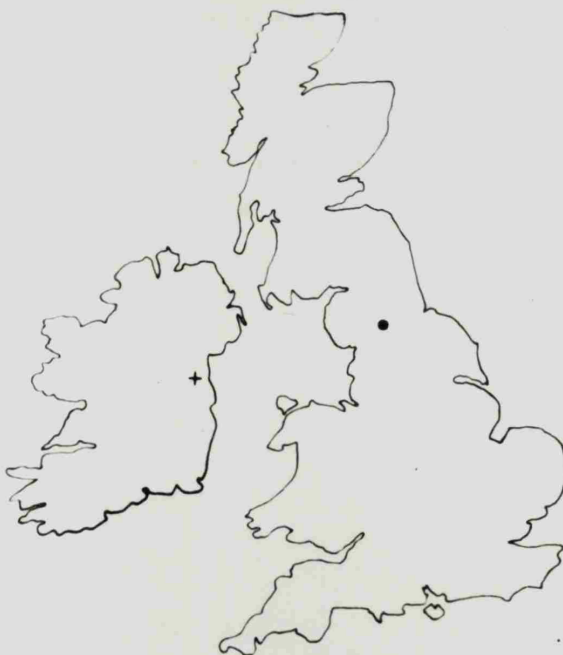
The British distribution is shown in the maps, from which it can be seen that *A. scaber*, Kramer, is wide-spread and common throughout Great Britain, although it appears to be absent from East Anglia. *A. brachypus*, Viets has been found in the Lake District only (Geldhill), although a doubtful record from Eire also exists. This record was queried by Viets (1956). Geldhill (personal communication) collected seven specimens in 1959 and five in 1960 from a small stream, in collections which totalled over 3,000 mites in all. It is possible

Map(i)



Aturus scaber Kr. &
Kongsbergia materna Th.

Map (ii)



Aturus intermedius Pr.

- Jones
- + Other workers

Map (iii)



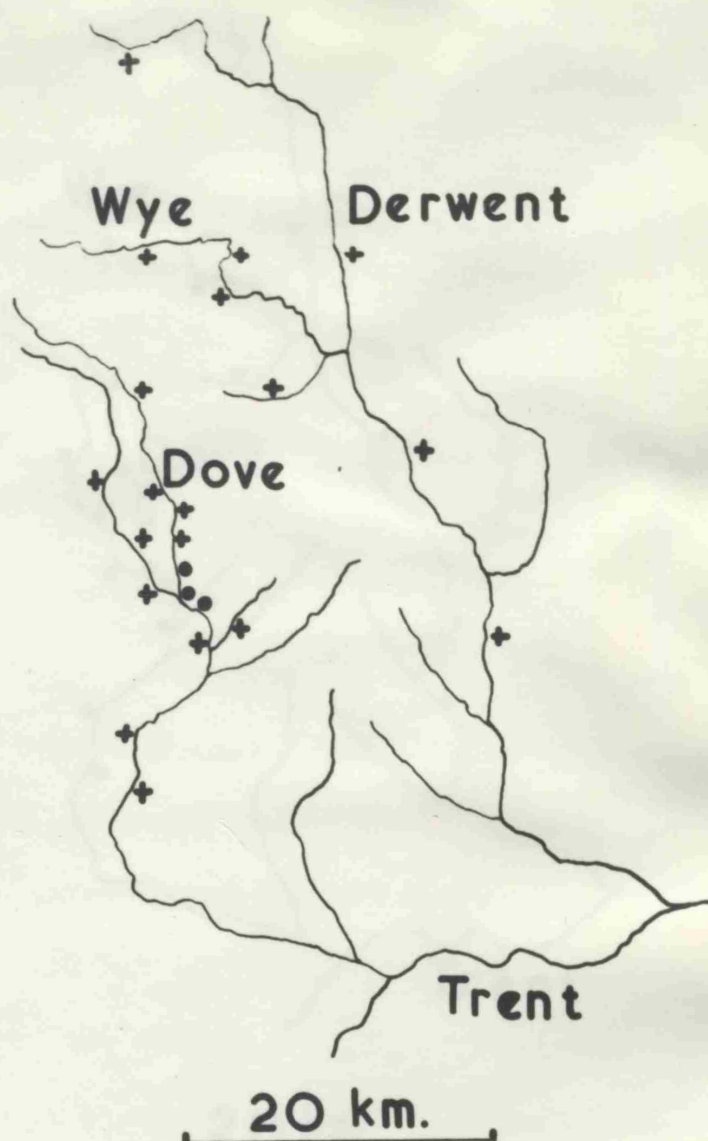
**A. brachypus V. &
K. largiollii Maglio**

Map (iv)



Aturus crinitus Thor.

- Jones
- + Other workers

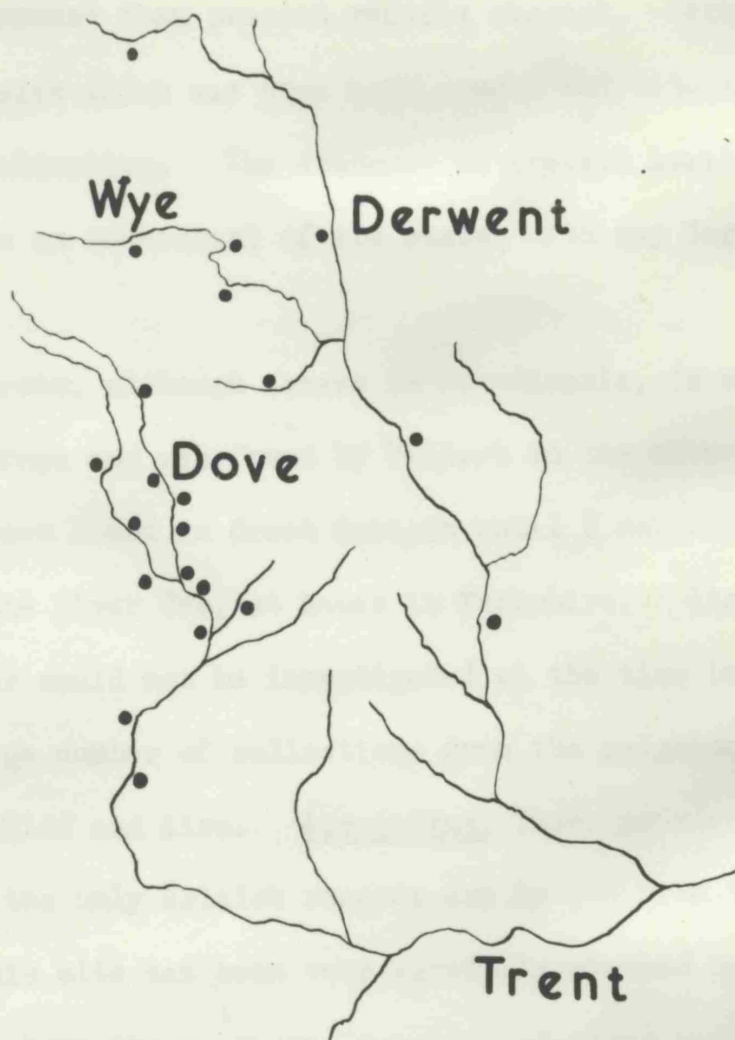


Peak District rivers

Aturus crinitus Thor

- mite found

+ mite not found



20 km

Peak District
rivers

• *Aturus scaber* Kramer &
Kongsbergia materna Thor

that this may be an example of a comparatively rare mite, which may prove to be more wide-spread than present reports suggest. Alternatively it may be a species which was once more common and wide-spread and which is near to extinction. The evidence at present available is insufficient to make an assessment of its status with any degree of certainty.

A.intermedius, Protz, although absent in Scandinavia, is wide-spread elsewhere in Europe and was found by Halbert in the river Liffey in Eire, but had not been found in Great Britain until I collected several specimens in the river Ure, at Hawes in Yorkshire. Its distribution in that river could not be investigated at the time but it was not found in a large number of collections from the neighbouring rivers Wharfe, Swale, Nidd and Aire. A.crinitus, Thor. is also found throughout Europe but the only British records are my own from the Dove. The distribution of this mite has been very carefully checked by collections made throughout the year over a period of three years and it appears to be confined to a stretch of about 5 kilometres between the lower end of Dovedale and the village of Mapleton. This stretch of river consists of a series of level reaches separated by small falls of up to 1 metre in height, which are formed by rock formations stretching across the stream. Between these successive falls the water may be shallow, running over a rock or boulder bottom, or may be up to 2.5 metres in depth, running over sand, in which various aquatic plants are rooted. This formation continues upstream for several kilometres but A.crinitus, Thor, which is found on the mosses growing on the steps has not been found above the stepping stones fall,

some 800 metres above the road at Ilam, nor has it been found in the Manifold which enters the Dove at Ilam, and which has no similar step formation, although the same mosses are growing on the boulders which cover much of the bottom.

A discontinuous distribution of this sort suggests either a recent arrival which has not yet spread far from its point of introduction, a well established species which has become restricted to a particularly favourable habitat, or a species which is confined to a precise area where some peculiar conditions pertain, essential to its well-being. Angelier (1954) points out that A. crinitus, Thor. is absent from Corsica and suggests that this is due to the high summer temperatures reaching 20 C in most rivers and 25 C in some. A. crinitus, Thor. is given by Viets, (1940) as a glacial relict species and this is the most likely explanation of its presence and very local distribution in Derbyshire. It is unlikely to be a recent introduction in the process of spreading from its place of origin as in this case it could be expected to be found in the Manifold, which joins the Dove in the middle of the "Aturus crinitus" range, and in any case it seems unlikely that a mite widespread on the continent would 'jump' directly to Derbyshire. Its very restricted range in the Dove is probably due to conditions of its micro-habitat, as it is common in those parts of the river where it is found, yet does not spread upstream into Dovedale, nor downstream below Mapleton, nor yet into the Manifold. The absence of the step formation may explain its absence from the latter two, but its absence from the falls in the Dale is puzzling. The mite survives in the laboratory in petri dishes for at least three months

even though the room temperature varies between 15° and 27°C.

Investigation of the step area and of the river bed immediately above the step at "stepping-stones" fall, showed a remarkable difference in the mite fauna, both as regards numbers of individuals and of species identified. The results of one such comparative collection follows. The amounts of moss from the step and of Ranunculus aquaticus from 1.5 metres above the step were cut from measured areas and transferred in bottles to the laboratory before being sieved and the mites sorted and counted.

Species	Moss on step		1.5 metres above	
	Adult	Nymph	Adult	Nymph
<i>Sperchon setiger</i> , Thor.	2	16	14	17
<i>Atractides spinipes</i> , Koch.	2	6	7	25
<i>A. octoporus</i> , Piersig.	-	2		
<i>Ljania bipapillata</i> , Thor.	3	-		
<i>Kongsbergia maternia</i> , Thor.	24	20		
<i>Feltria romijni</i> , Besseling.	51	-		
<i>Aturus</i> spp.	44	-		
<i>Protzia eximia</i> , Protz.	-	2		
<i>Lebertia</i> spp 1.			1	
<i>Lebertia</i> spp 2.	18	-		
<i>Atractides</i> spp larvae.		3		

The two Aturus spp females were not separated for this investigation.

It can be seen that, whereas the larger mites are fairly evenly distributed, the members of the family Aturidae appear to be confined to the mossy area. The complete absence of Aturus spp from an area a mere 1.5

metres upstream from a step on the moss of which they were common suggests that a moss free stretch of river could possibly act as a barrier to the spread of the animal upstream. This may, indeed explain the absence of A.crinitus, Thor, in Dovedale itself, as there is a stepless stretch of about 800 metres of fairly deep water immediately above its highest known habitat.

In so far as the distribution can be used as a pointer to life-history patterns, then, it seems likely that of the six members of the family Aturidae found in this country, A.scaber, Kramer, and K.materna, Thor, being both widespread and common, both within this country and in Europe, might therefore be expected to have good means of dispersal, and can reasonably be concluded to lead a parasitic life. This is confirmed to some extent in the case of A.scaber, Kramer by the fact that the eggs hatch to larvae, which died after three weeks under laboratory conditions without further metamorphosis. The evidence in the other three cases is not such as to make any firm conclusions profitable, but their peculiar and restricted distributions would be much less surprising if they were found to have a direct development or to be parasitic on a non-flying host.

4. The connection between larval life and taxonomy.

Sparing pointed out that the morphology of water-mite larvae could be used to correct errors in the assessment of the taxonomic positions of the adults. Similarly it might be possible to resolve difficulties in the classification of the group by reference to the life-history patterns of the larvae.

In point of fact a review of the larval habits reveals that the accepted classification is in accord with what is known of the larval life. Thus it can be seen from the table of known hosts that the Hydrachnae are in a group of their own, having swimming larvae which parasitise Hemiptera and Coleoptera. Hydrovolziae and Limnocharae have running larvae which find their hosts either on the water surface or on damp substrates at the waters edge. They parasitise a variety of insects including Hemiptera Coleoptera, Trichoptera and Plecoptera as well as Diptera, but have never been observed to attack the Nematocera. Limnochara aquatica, L. will attack Odonata if its normal hosts (Gerrids) are not sufficiently plentiful. The Hydryphantae are the last super-family with surface running larvae but 10 of those species whose life histories are known parasitise Diptera, Nematocera, and one each Hymenoptera, Odonata and Plecoptera. Larvae of one species have been found in the mantle cavities of Gastropod molluscs, but no attachment to the tissues was reported and this may be an accidental association, as the same species is a known parasite of Culex spp. Thyas stolli, Koenike is the only species in this super-family reported to have an abbreviated life-history. The Lebertiae, with the exception of Torrenticola spongicola, Viets, are parasitic on Diptera, Nematocera, but in this super-family are also the members of the genus Pontarachna, which are marine, and in the case of P. punctulum, Philippi, found in Oysters, and Unionicola species, and two closely related genera, which are found in Lamellibranch or Gastropod molluscs but whose larvae have also in two cases been shown to parasitise Diptera.

Of the super-families Axonopsae, Mideopsae and Krendowskiae, the

life histories of only three species are known and no conclusions can be drawn.

In the Arrenuridae life histories are known for 44 species and of these, those in the sub-genera Arrenurus and Megaluracarus, parasitise Odonata and Diptera, Nematocera, while the other two sub-genera are known to parasitise the Diptera but have not, so far been reported from other insect orders.

In classifying animals which have several stages to their life-histories, it is always a difficult problem to know how much weight to give to any particular stage. A recent paper by Sneath and Sokel, "Numerical Taxonomy" suggests a new approach to this problem. These authors programme a computer to analyse measurements of large numbers of features in animals under review. As many as 50 different features can be used, and the result is produced as a "dendrogram", the root of which gives the more similar species while the fingers give the more diverse species. It would be a major undertaking to deal with even the more controversial members of the Hydracarina in this way, but the method is mentioned as a possible way of solving some of the outstanding taxonomic problems in this group.

5. Recapitulation of main points.

Information on the life-histories of the Hydracarina may be obtained either by direct or indirect methods. The former involve collecting parasitised hosts and breeding out the mites until they reach a stage of their development wherein it is possible to identify them or starting from eggs laid by captive and isolated females and

supplying these with suitable host material so that their host selection can be observed. Both these approaches involve considerable difficulty but have, during the present study yielded a fair return in terms of information. Indirect methods of investigation are intuitive and cannot therefore give as certain results as the direct methods, but deductions from distribution, longevity of the larval stage in the absence of a host, and the numbers of eggs produced by each female not only indicate the most profitable lines for further direct research but also provide valid material from which unknown life-history patterns can be forecast.

Both methods point unmistakably to the great importance of the Diptera, Nematocera, as hosts of the water-mites, and of the benefits associated with the larval habits of making contact with the host in the water as distinct from on the surface thereof.

The position of the Unionicolidae has been considerably clarified by the discovery of larval parasitism in members of this group well known as Mussel parasites in their nymphal and adult stages and it is no longer necessary to look upon this family as having evolved separately from the rest of the super-family Pionae.

A continuation of this research ought to include host preference tests on Unionicola larvae after their parasitic stage, as this would be complementary to Mitchell's work on host specificity in this genus, and could be expected to settle finally the position of the Gastropods as possible hosts for the genus.

Methods for breeding out mite larvae to adults need to be perfected, and this would be of particular use with the rheophilic species with

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which I have had no success at all in this direction.

Life histories are known in full for well under 5% of the described species, and none at all for the many species found in underground waters. There is, therefore no lack of opportunity for further work on the natural history of the group.

Summary

1. There is a great lack of knowledge on the life histories and larval behaviour of the Hydracarina. This investigation has attempted to provide additional information and in order to do this a very large number of aquatic and semi-aquatic animals have been collected, anaesthetised and examined.

This work has led to the conclusions that

a) Parasitism by mite larvae on insects is much more frequent than the literature would suggest,

b) That while few aquatic invertebrates escape altogether, the Diptera are of primary importance as hosts, and that

c) Because of the great numbers and concentrations in which their larvae are found in practically all fresh-water habitats, the Nematocera are almost certainly the most important host group for the British water mites.

2. Parasitism by the larvae of two species of the genus Unionicola on Chironomids is observed for the first time. This genus, previously looked upon as being parasitic in fresh-water mussels in its nymphal and adult stages but free-living as larvae is thus shown to be much more similar in its life-history pattern to the remainder of the superfamily Pionae than had hitherto appeared to be the case.

3) Descriptions and drawings of the larvae and full parasitic life-histories are given for Piona uncata uncata, Koenike and Protzia eximia, Protz.

4. The Hitherto unknown larva of Aturus scaber, Kramer was bred under

laboratory conditions and later found in moss from the river Dove, and is figured and described.

5. Parasitism by mite larvae of the genus Arrenurus on insects of the Dixidae (Diptera) is reported for the first time.

6. Parasitism by mite larvae on adult Caddis flies, (Trichoptera) is described for the first time, the species concerned being Protzia eximia, Protz.

7. The transfer of 'jumping' larvae from damp substrates onto their hosts has been observed, and previous conjectures as to the usefulness of this habit to the larvae confirmed. It has been seen that this habit enables the larvae to gain a position on Empids resting on boulders in the river Dove and on Caddis fly adults which were egg-laying on the mosses on these boulders.

8. Hosts are given for the first time for Hydrachna leegei, Koenike, Eylais bisinuosa, Koenike, Piona variabilis, Koch, Arrenurus medio-rotundatus, Thor, Unionicola intermedia, Koenike, larvae and the larvae of another Unionicola spp. probably U. aculeata, Koenike. The parasitism of Arrenurus buccinator, Müller and A. maculator, Muller on Odonata Zygoptera, and of Piona conglobata, Koch, Pionopsis lutescens, Hermann, Hygrobates longipalpis, Hermann, and Sperchon denticulatus, Koenike, on Chironomids has been confirmed and the hosts listed.

9. Confirmatory observations are reported of the transfer in the field of Arrenurid larvae from the nymphs to the adults of their Zygopteran hosts.

10. A complete, up-to-date table of the known hosts of water-mites, together with information as to which species and genera have so far

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unknown life-histories has been compiled as a result of careful
sifting through the past literature coupled with my own observations.

Appendix A.

Life History and larva of Protzia eximia, Protz.

The eggs of this species are found throughout the winter in crevices of boulders in fast flowing rivers such as the Dove and Manifold. The eggs hatch in the laboratory when the temperature is raised above 5.5°C and it is probable that water temperature is the controlling factor in the wild.

The larvae run actively on the water surface and are found in large numbers on the moss on boulders which protrude from the water. It was found that the larvae jump from the water surface or from the moss onto passing flies of the species Weidemannia bistigmata, Curtis, and an unidentified Caddis fly, and adopt a parasitic attachment to their hosts. Parasitised hosts were found in considerable numbers from early May until September. This can be taken as evidence of a second egg-laying period, as it is unlikely that larvae of the winter eggs would be hatching so late in the summer.

The larva has not been previously described in the literature and a description therefore follows.

Measurements. *M.*

	1	2	3	4
Length	251	240	290	290
Breadth	128	120	120	128
Capitulum	51	68	51	51
Palpi	86	102	86	86
1st leg	308	376	360	308
2nd leg	290	290	308	290
3rd leg	326	376	342	326

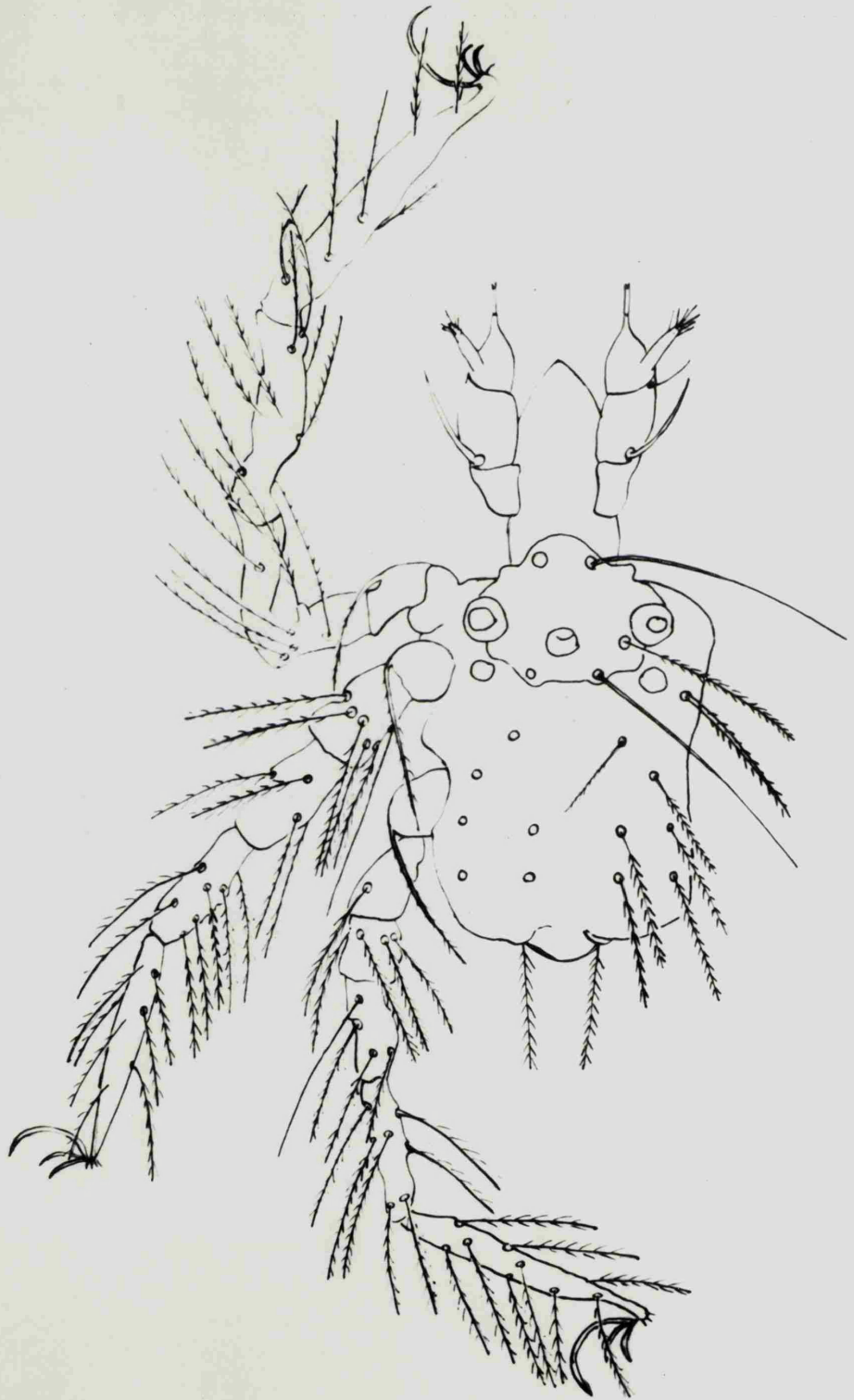
On the anterior part of the dorsum is a not-very-well defined plate bearing the median eye and three pairs of long bristles, the middle pair of which are pectinate. The paired eyes are large and close to the edge of this plate. The rear eye of each pair does not appear pigmented. There are seven pairs of pectinate bristles behind the plate, an inner two pairs and an outer four pairs, with a single pair on rounded protuberances at the extreme posterior end of the larva.

The legs are long, and bear large numbers of long pectinate bristles. The rear side of segment 2 of the second leg, and the proximal dorsal part of segment 4 of the third leg each bear a simple bristle.

The claws consist of one very large median claw with two smaller claws, one on either side of it.

The palpi bear a strong curved spine on P.II, and a bristled protuberance on P.III. There are only 4 apparent segments.

Protzia eximia Protz



Larva

Dorsal surface

125.

Appendix B.

Larva of Aturus scaber, Kramer.

The larvae are found in moss samples from rivers during the summer months.

The larva is oval in outline with a distinct invagination in the posterior end, reaching further forwards than the rear edges of either the dorsal or ventral plates. The excretory field is without a plate, and two pairs of long spines lie close to the excretory pore. A single bristle is inserted on the ventral armour close to the more posterior of these. The posterior bristles are very long and inserted on two protuberances similar to those of Hygrobates spp. Palp segment III bears a powerful curved spine. P.IV end in a strong almost straight claw and bears two bristles. P.V. is very small and bears a short curved spine.

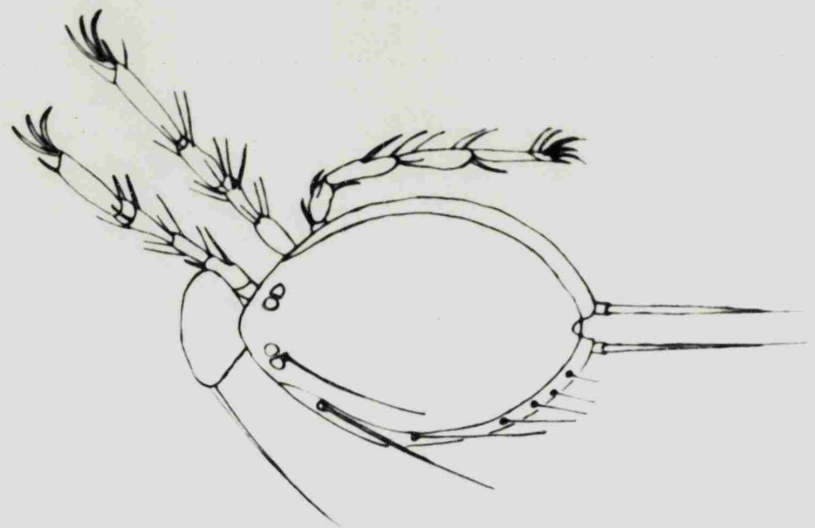
The anterior dorsal bristles are very long, the one inserted against the eyes reaching $55\frac{1}{4}$ and the one at the anterior part of the body off the dorsal shield reaching $61\frac{1}{4}$.

The suture between the second and third epimera is plainly visible as far as the rearmost point of the first epimeron and is almost parallel to the body axis. The bristle on the third epimeron is inserted some distance from the suture.

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Aturus scaber, Kramer, Larva.

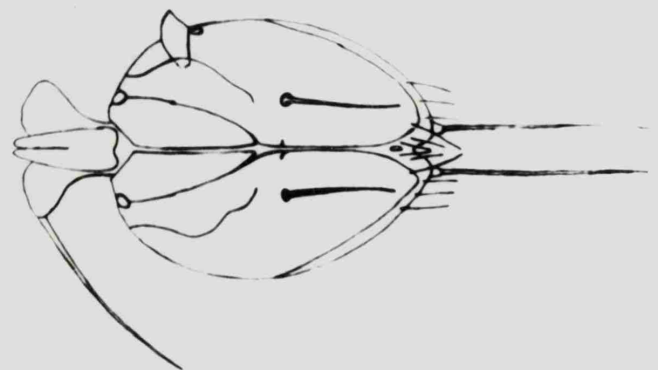
	1	2	3
Length of body	232 μ .	223 μ .	223 μ .
Capitulum	53	53	53
Posterior bristles	116	107	107
Breadth	137	137	142
1st leg	142	137	142
2nd leg	142	137	144
3rd leg	160	142	160



Aturus scaber Kramer

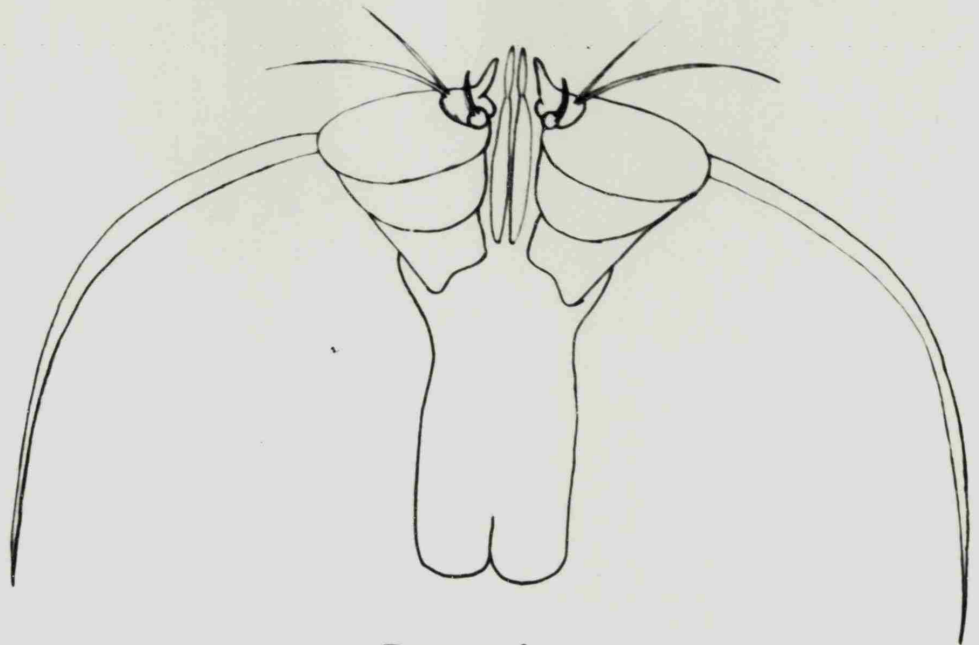
larva

Dorsal surface



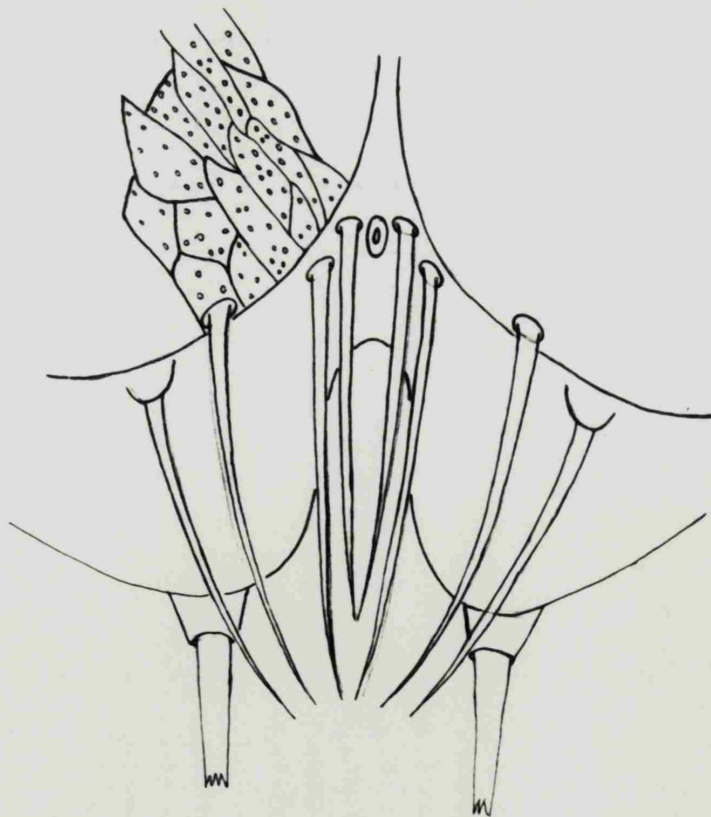
Ventral surface

Aturus scaber Kr. larva



Palpi

Excretory field



Appendix C.

Piona uncata, Koenike

This mite has been commonly found in sites 1 and 2 and is one of the first mites to appear in numbers after the winter. Fully developed gravid females are found in fair numbers, often swimming in open water, especially where there is rich plankton. In the laboratory they catch and eat Cladocera and this seems to be their main diet. The earliest record obtained for them in these sites was March 1, 1960, but they are usually common by early April and remain so until about the beginning of June. Eggs are laid in the laboratory almost always within a week of capture of the females, but it is almost certain that the normal period of oviposition in the field is early May. This is based on the fact that females can be caught in the field up to the first half of May full of eggs, showing that egg laying has not taken place. The rise of temperature in the laboratory probably promotes early egg laying.

The eggs are laid in a long string, which may contain from 6 to 40 eggs. Each egg is enclosed in its own compartment but before the larvae hatch the inner walls appear to break down and the larvae often find their way into other sections of the string before making their way to the outside. The strings found in the wild are usually attached to algal threads or to pond weeds. In the laboratories they are frequently laid on the glass sides of a specimen tube. Larvae hatch in two to three weeks and will live in the laboratory for four to six weeks. As the larvae have been found on hosts in late August and early September, it is possible that some mites may over-winter as

nymphs and require some time before mating and egg-laying so that their eggs form a late batch of larvae. This is likely as males seem to make their appearance in the open water rather later than the females, about the end of April, or beginning of May.

The larvae are found on Chironomous plumosus, L. and other Chironomus spp. Nympho-chrysalids are formed in the laboratory at the bases of rushes. The larvae will often travel into the pith at the cut end of the stem a distance of 5 mm. before pupating. The nymph hatches within three weeks and under laboratory conditions may live for three months before forming the teleiochrysalis. Under field conditions this would lead into the winter and would presumably give rise to the late mites mentioned above. Nymphs have not in fact been found in the spring in the wild, so that the teleiochrysalis may be formed during the winter.

It seems probable that this mite has only one generation per year, and normally hibernates as adult or possibly nymph and teleiochrysalis. An isolated female laid 124 eggs in seven strings and this number would seem quite sufficient to support the parasitism involved in its life history.

The larva.

The larva is similar except in size to that of P.coccinea. The P.IV bears two bristles approximately half the length of the long bristle on P.III.

E.I. comes to a sharp point reaching past the insertion of the palpi.

The suture between E.II and E.III is almost equidistant between

the rear edge of E.I. and the bristle on P.III. The excretory plate is roughly triangular with well rounded angles. It is rather longer than broad. The rear edge of E.III deviates round the bristle.

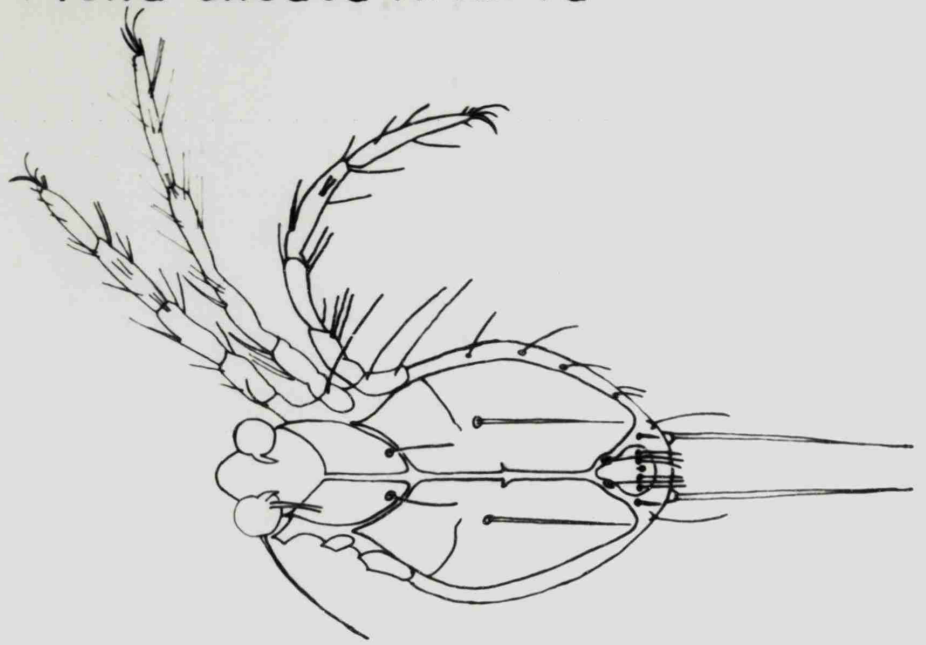
Measurements. 4.

Length	393	393	427	402
Breadth	222	193	222	222
Capitulum	119	119	131	119
Posterior bristle	154	131	154	154
1st leg	291	291	308	308
2nd leg	342	324	342	324
3rd leg	324	359	359	350

Excretory plate.

Length	47	47	52	47
Breadth	40	40	44	40

Piona uncata K. larva



Ventral surface

Excretory field

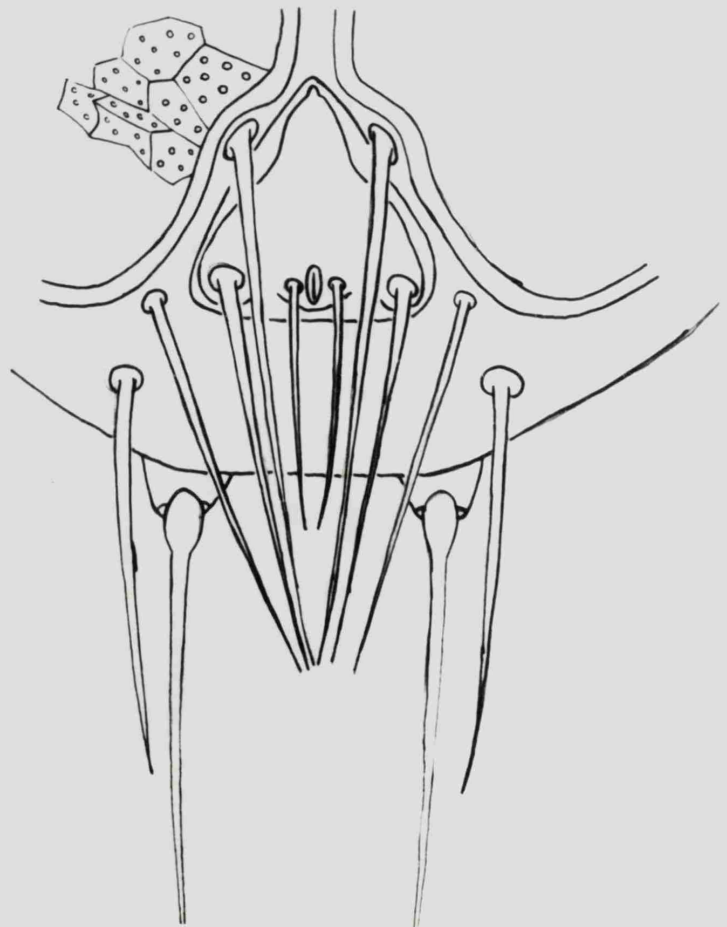


Plate 3.

Top. Larvae of Unionicola species, (probably U. aculeata,
Koenike.) on leg of Chironomus plumosus, L.

Bottom. Larvae of Unionicola intermedia, Koenike, on
anterior ventral part of the abdomen of a
female of Chironomus plumosus, L.



Plate 4.

Top. Typhis species larvae on the abdomen of a
chironomid from Clumber Park, Site 10.

Bottom. Enlargement of central portion of above.

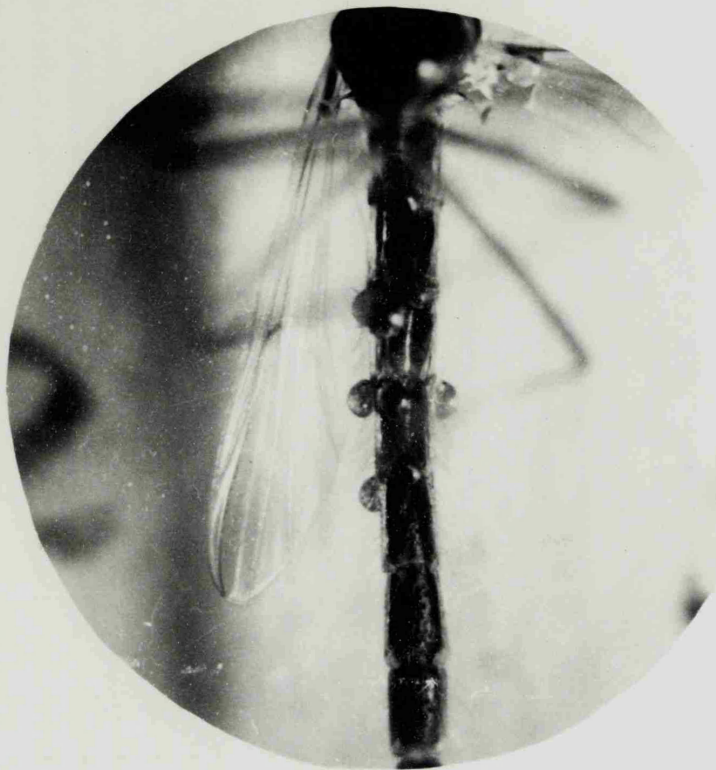


Plate 5.

Larvae of Arrenurus buccinator, Müller and another
Arrenurus species on the thorax of the Damsel Fly,
Coenagrion puella, L. from site 7.

Top. Enlargement x 10.

Bottom. Enlargement x 20.



Plate 6.

Top. Larva of Aturus scaber, Kramer, ventral surface.

x 250.

Bottom. Larva of Protzia eximia , Protz, dorsal surface.

x 225.

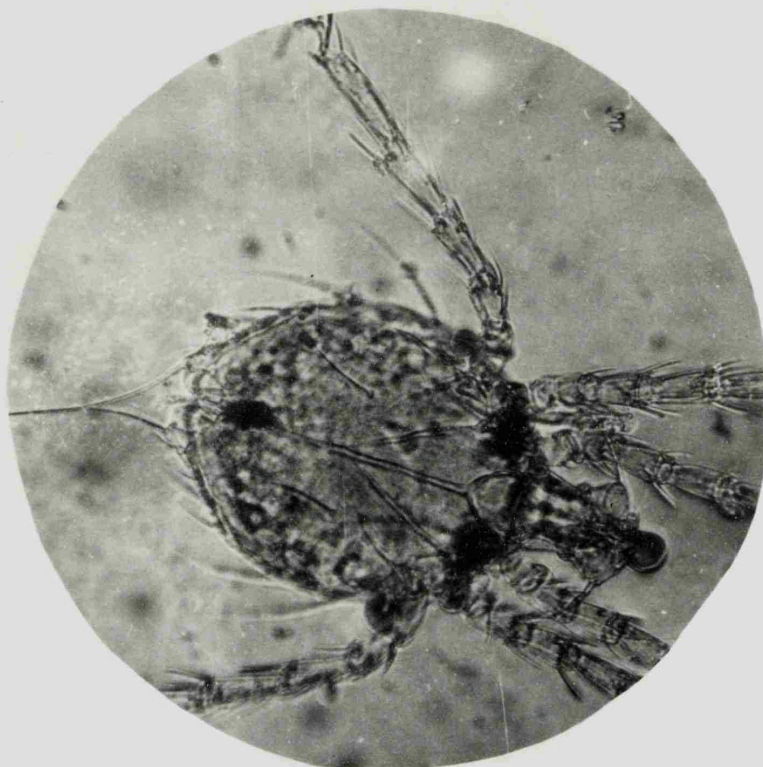


Table of Known hosts of Water-Mites.

One of the major difficulties involved in a study of Water-mite life histories lies in the very scattered nature of the literature. Previous records involving the life-histories of individual mites can be found only by reference to a large number of separate papers, involving a great deal of research for comparatively little information.

It is for this reason that I have collected together all the information which I found in the literature, as well as my own records and have included them here in one comprehensive table. It also appeared that this table would be of much greater value if it included details of those families, genera and species for which there is as yet no information available.

The scheme of Classification followed is that used in Viets (1956) with the addition of new species described by various authors since that date.

The earliest known Author is given in each case together with the date of publication. My own records are given as "Jones" without a date.

TABLE OF KNOWN HOSTS OF WATER-MITES.

Mite classification	Host	Author	Host classification
1. Super - family HYDROVOLZIAE. Viets.			
Hydrovolziidae, Thor.			
Hydrovolzia, Thor.			
H. gerhardi, Mitchell.	Microvelia americana, Uhler.	Mitchell, 1954	Ins. Hem.
H. 12 species.	No information.		
2 genera, 6 species.	No information.		
2. Super - family HYDRACHNAE. Part Müller, Viets 1931.			
Hydrachnidae, Leach.			
Hydrachna, Müller.	Corixinae.	Sparing, 1959	Ins. Hem.
H. cruenta, Müller.	Dorsal on Dytiscs.	Wesenberg - Lund, 1918	Ins. Col.
H. geographica, Müller.	Nepa. Ranatra.	Wesenberg - Lund, 1918	Ins. Hem.
H. globosa, De Geer.	Dytiscidae.	Viets, 1936	Ins. Col.
	Cymatia. Notonecta.	Viets, 1936	Ins. Hem.
H. magniscutata, Marshall.	Notonecta undulata, Ranatra spp.		
	Arctocorixa, spp.	Crowell, 1960	Ins. Hem.
H. maramauensis, Stout.	Anisops wakefieldi.		
	Arctocorixa arguta.		
H. processifera, Koenike.	Dytiscus marginalis, L.	Stout, 1953, b.	Ins. Hem.
H. uniscutata, Thor.	Dytiscs.	Wesenberg - Lund, 1918	Ins. Col.
H. leegei, Koenike.	Notonecta glauca, L.	Wesenberg - Lund, 1918	Ins. Col.
H. 91 species.	No information.	Jones	Ins. Hem.
1 genus, 1 species.	No information.		

3. Super - family LIMNOCHARAE. Viets.

Limnocharidae, Grube.

Limnochares, Latreille.

L.aquatica, L.

Gerrids.	Duges, 1834	Ins. Hem.
Veliids & Hydrometrids.	Sparing, 1959	Ins. Hem.
Aquarius palludum & Limnophorus rufoscutellatus.	Imamura, 1953	Ins. Hem.
Zygoptera imagines.	Killington & Bathe, 1947.b	Ins. Ode.
Gerris lacustris, L.	Jones.	Ins. Hem.

L.4 species.

3 genera, 12 species.

Eylaidae, Leach.

Eylais, Latreille.

E.bisinuosa, Koenike.

E.extendens, Muller.

E.discreta, Koenike.

E.hamata, Koenike.

Cymatia coleoptrata.Fab.	Jones.	Ins. Hem.
Corixinae.	Sparing, 1959	Ins. Hem.
Corixinae.	Sparing, 1959	Ins. Hem.
Cymatia.	Viets, 1936	Ins. Hem.

Dytiscus, Colembetes, Gyrinids.

Hydrophilus, Rantus, Ilybius.

Hyphodrus, Graphoderes.

Gills of fishes.

Dytiscs & Gyrinids.

Dytiscs & Gyrinids.

Dytiscs & Gyrinids.

Anisops waikfieldi.

Viets, 1936	Ins. Col.
Viets, 1936	Cho. Pis.
Piatkov, 1915	Ins. Col.
Piatkov, 1915	Ins. Col.
Piatkov, 1915	Ins. Col.
Stout, 1953.a	Ins. Hem.

E.infundibulifera, Koenike.

E.mutilla, Koenike.

E.setosa, Koenike.

E.waikewai, Stout.

E. spp.	Corixa spp. nymph.	Jones	Ins. Hem.
E. 150 species.	No information.		
1 genus, 1 species	No information.		
Piersigiidae, Wolcott.	No information.		
1 genus, 4 species.	No information.		
Protziidae, Viets.			
Protzia, Piersig.			
P. eximia, Protz.	Weidemannia bistigmata Curtis.	Jones.	Ins. Dip.
P. 18 species.	Unidentified Trichopteran.	Jones.	Ins. Tri.
1 genus, 17 species.	No information.		
Partnunia, Piersig.	No information.		
P. steinmanni, Walter.	Plecoptera.	Munchberg, 1954	Ins. Ple.
P. uchidai, Imamura.	6 species Plecoptera imagines.	Imamura, 1957	Ins. Ple.
5 genera, 16 species.	No information.		
4. Super - family, HYDRYPHANTAE, Viets.	No information.		
3 families, 4 genera, 11 species.	No information.		
Thyasidae, Thor.	No information.		
2 genera, 3 species.	No information.		
Thyasides, Lundblad.	Aedes lutescens	Lundblad, 1927	Ins. Dip.
T. dentata, Thor.			
Panisopsis, Viets.	Dipteran imagines.	Walter, 1915	Ins. Dip.
P. curvifrons, Walter.			

P. new species.	Apterous stoneflies	Womersley, 1953	Ins. Fle.
P.4 species	No information.		
3 genera, 3 species.	No information.		
Thyopsis, Piersig.			
T.cancellata, Protz.	Various tipulids.	Munchberg, 1935	Ins. Dip.
T.1 species.	No information.		
Thyas, Koch.			
T.barbigera, Viets.	Tipulids.	Munchberg, 1935, 36, 56	Ins. Dip.
T.spp. (probably T.pachystoma, Piersig).	Tipulids	Munchberg, 1935, 36, 56	Ins. Dip.
T.stolli, Koenike.	(1) Aedes vexans & Aedes spp.	Crowell, 1960	Ins. Dip.
T.stolli, Koenike.	(2) Hatched as nymphs.	Crowell, 1960	none
T. 13 species.	No information.		
1 genus, 1 spp.	No information.		
Trichothyas, Viets.			
T.muscicola, Mitchell.	Limonia humidicola O.S.	Mitchell, 1953	Ins. Dip.
T.10 species.	No information.		
9 genera, 12 species.	No information.		
Paniscus, Koenike.			
P.michaeli, Koenike.	Gyrocompa ubiginosa, Hal.	Lundblad, 1927	Ins. Hym.
P.4 species.	No information.		
8 genera, 8 species.	No information.		
1 family, 1 genus, 1 species.	No information.		
Hydryphantidae, Thor.			
Hydryphantes, Koch.			
H.ruber, De Geer.	Culex.	Viets, 1936	Ins. Dip.
	Paludina.	Thor, 1899	Mol. Gas.

H. dispar, Von Schaub.	Ephydrinae.	Soar, 1906	Ins. Dip.
H. 37 species.	No information.		
Georgella, Koenike.			
G. helvatica, Haller.	Ischnura, Agrion.	Munchberg, 1935-6	Ins. Ode.
G. 7 species.	No information.		
2 genera, 4 species.	No information.		
Hydrodromidae, Viets.			
Hydrodroma, Koch.			
H. despicens, Müller.	Chironomids, Corethra.	Wesenberg - Lund, 1918	Ins. Dip.
H. 10 species.	No information.		
3 genera, 10 species.	No information.		
5. Super - family LEBERTIAE, Viets.			
6 families, 33 genera, 113 species.	No information.		
Sperchonidae, Thor.			
Sperchon, Kramer.			
S. brevirostris, Koenike.	Orthocladius sordidellus, Zetterstadt.	Thiennemann, 1908	Ins. Dip.
S. denticulatus, Koenike.	Chironomids.	Sparing, 1959	Ins. Dip.
	4 spp. Chironomids.	Jones.	Ins. Dip.
S. setiger, Thor.	Pupa of Melusina (Simulium) ornata.	Besseling, 1939	Ins. Dip.
S. squamosus, Kramer.	Orthocladius sordidellus, Zetterstadt.	Viets, 1936	Ins. Dip.
S. glandulosus, Koenike.	4 spp. Chironomids.	Efford, 1960	Ins. Dip.
S. longissimus, Viets.	Orthocladius (Stempellina) flavidula, Edwards.	Efford, 1960	Ins. Dip.
S. jasperensis, Marshall.	Simulium spp.	Davies, 1959	Ins. Dip.
S. spp.	Chironomids.	Jones.	Ins. Dip.

S.64 species.	No information.			
3 genera, 6 species.	No information.			
Lebertiidae, Thor.				
Lebertia, Neuman.				
L.stigmatifera, Thor.	Direct development without parasitism.	Lundblad, 1924		none
L.glabra, Thor.	2 spp. Chironomids.	Efford, 1960		Ins. Dip.
L.spp.	Chironomids	Sparing, 1960		Ins. Dip.
L.spp.	Chironomids.	Jones.		Ins. Dip.
L.204 species.	No information.			
1 family, 4 genera, 56 species.	No information.			
Torrenticolidae, Piersig.				
Torrenticola, Piersig.				
T.spongicola, Viets.	Sponges.	Arndt & Viets, 1937		Porifera.
T.132 spp.	No information.			
4 genera, 9 species.	No information.			
1 family, 4 genera, 9 species.	No information.			
6. Super - family PIONAE, Viets.				
Pontarachnidae, Thor.				
Pontarachna, Philippi.				
P.punctulum, Philippi.	Ostrea.	André & Lamy, 1930		Mol. Lam.
P.8 species.	No information.			
1 genus, 6 species.	No information.			

Limnésiidae, Thor.			
4 genera, 4 species.	No information.		
Limnesia, Koch.			
L. connata, Koenike.	Hatched as nymph.	Piersig, 1900	None
L. undulata, Müller.	Hatched as nymph.	Piersig, 1900 and others.	None
	Tanytarsus decorus, Johannsen.	Crowell, 1960	Ins. Dip.
L. fulgida, Koch.	Chironomids.	Sparing, 1959	Ins. Dip.
	Water-beetle larvae.	Wesenberg-Lund, 1918	Ins. Col.
L. maculata, Müller.	Chironomids.	Sparing, 1959	Ins. Dip.
L. 107 spp.	No information.		
8 genera, 21 species.	No information.		
2 families, 2 genera, 8 species.	No information.		
Hygrobatidae, Koch.			
8 genera, 16 species.	No information.		
Hygrobates, Koch.			
H. foreli, Lebert.	Chironomids.	Lundblad, 1927	Ins. Dip.
H. longipalpis, Hermann.	Corethra, Chironomids.	Munchberg, 1935	Ins. Dip.
	Various Chironomids.	Jones.	Ins. Dip.
H. 75 species.	No information.		
19 genera, 48 species.	No information.		
Atractides, Koch.			
A. nodipalpis, Thor.	8 spp. Chironomids.	Efford, 1960	Ins. Dip.
	Midge imagines.	Imamura, 1953	Ins. Dip.
A. spp. (probably A. spinipes)	Various Chironomids.	Jones.	Ins. Dip.
A. 145 species.	No information.		

4 genera, 4 species.	No information.		
Unionicolidae, Oudemans.			
1 genus, 11 species.	No information.		
Unionicola, Haldeman.			
U. aculeata, Koenike.	Not parasitic, but resting stages. found in mussels.	Mitchell, 1955	None
U. aculeata, Koenike.	Campeloma lecisium Say.	Chandler, 1934	Mol. Gas.
U. abnormipes, Wolcott.	Anodonta anatina, L.	Jones.	Mol. Lam.
U. arcuata, Wolcott.	Lampsillis siliquoides.	Mitchell, 1955	Mol. Lam.
U. bonzi, Claparede.	Lampsillis siliquoides.	Mitchell, 1955	Mol. Lam.
U. cirrosa, Koenike.	Unio douglassiae nipponensis.	Imamura, 1953	Mol. Lam.
U. ampullariae, Koenike.	Unio nepeanensis.	Koenike.	Mol. Lam.
U. diversipes, Viets.	Ampullaria.	Andre & Lamy, 1930	Mol. Gas.
U. crassipes, Müller.	Naiades.	Viets, 1926	Mol. Lam.
U. fissipes, Koenike.	F.W. Sponges.	Arndt & Viets, 1927	Porifera
U. formosa, Dana & Whelpley.	Anodonta latimarginata.	Andre & Lamy, 1930	Mol. Lam.
U. fassulata, Koenike.	4 Anodonta species.	Mitchell, 1957	Mol. Lam.
U. intermedia, Koenike.	Lampsillis siliquoides.	Mitchell, 1955	Mol. Lam.
Adults & Nymphs.	Anodonta anatina, L.	Mitchell, 1955	Mol. Lam.
Larvae	Anodonta anatina, L.	Jones.	Mol. Lam.
U. japonensis, Viets.	Various Chironomids.	Jones.	Ins. Dip.
U. parasitica, Uchida & Imamura.	Viviparous malleatus.	Imamura, 1953	Mol. Gas.
U. perforatus, Koenike.	Anodonta beringiana.	Imamura, 1954	Mol. Lam.
	Anodonta latimarginata.	Andre & Lamy, 1930	Mol. Lam.

<i>U. procurvipes</i> , Koenike.	<i>Anodonta gigantea</i> .	André & Lamy, 1930	Mol. Lam.
<i>U. rugosa</i> , Koenike.	<i>Anodonta latimarginata</i> .	André & Lamy, 1930	Mol. Lam.
<i>U. uchidai</i> , Imamura.	Fresh-water mussels.	Imamura, 1953 & 1954	Mol. Lam.
<i>U. serrata</i> , Wolcott.	<i>Lampsyllis siliquoides</i> .	Mitchell, 1955	Mol. Lam.
<i>U. ypsilophora</i> , Bonz.	<i>Anodonta cygnea</i> , L.	Mitchell, 1955	Mol. Lam.
	<i>Anodonta cygnea</i> , L.	Jones.	Mol. Lam.
<i>U. spp.</i> larva. probably <i>U. aculeata</i> , Koenike.	Various Chironomids	Jones.	Ins. Dip.
<i>U. 71</i> species.	No information.		
<i>Polyatácides</i> , Lundblad.			
<i>P. promineus</i> , Koenike.	Fresh-water mussels.	Lundblad, 1937	Mol. Lam.
<i>Atacella</i> , Lundblad.			
<i>A. schubarti</i> , Viets.	<i>Diplodon delodontus expansus</i> , Kuster.	Viets, 1954	Mol. Lam.
<i>A. clathrata</i> .	Fresh-water mussels.	Lundblad, 1937	Mol. Lam.
<i>A. 3</i> species.	No information.		
<i>Najadicola</i> , Piersig.			
<i>N. ingenus</i> , Koenike.	3 genera of mussels.	Mitchell, 1955	Mol. Lam.
1 genus, 1 spp.	No information.		
<i>Neumania</i> , Lebert.			
<i>N. deltooides</i> , Piersig.	Chironomids.		
<i>N. uchidai</i> , Imamura.	Midges.	Sparing, 1959	Ins. Dip.
<i>N. 86</i> species.	No information.	Imamura.	Ins. Dip.
9 genera, 93 species.	No information.		
<i>Huitfeldtia</i> , Thor.			
<i>H. rectipes</i> , Thor.	Chironomids.	Munchberg, 1935	Ins. Dip.
<i>Feltriidae</i> , Thor.			

Feltria, Koenike.	Chironomids.	Vitzhum, 1941	Ins. Dip.
F.setigera, (?) Koenike.	Tanytarsus (Stempellina) flavidula,		
F.romijni, Besseling.	Edwards.		
F.minuta, Koenike.	Several spp Chironomids.	Efford, 1960	Ins. Dip.
F.40 species.	No information.	Efford, 1960	Ins. Dip.
2 genera, 3 species.	No information.		
Pionidae, Thor.	No information.		
2 genera, 4 species.			
Typhis, Koch.			
T.ornatus, Koch.	Chironomus thummi (Pupae).	Uchida, 1932	Ins. Dip.
T.species.	Various Chironomids.	Jones.	Ins. Dip.
T.15 species.	No information.		
1 genus, 1 species.	No information.		
Pionopsis, Piersig.			
P.lutescens, Hermann.	Chironomids.	Sparing, 1960	Ins. Dip.
P.3 species.	No information.		
Pionacercus, Piersig.			
P.leuckarti, Piersig.			
P.6 species.	No information.		None
Piona, Koch.			
P.carnea, Koch.	Chironomus thummi (Pupa).	Uchida, 1932	Ins. Dip.
P.coccinea, Koch.	Chironomids.	Sparing, 1959	Ins. Dip.
P.conglobata, Koch.	Chironomids.	Sparing, 1959	Ins. Dip.
	C.dorsalis, Meigen.	Jones.	Ins. Dip.

P. disparilis, Koenike.	Cricotopus spp.	Motas, 1928.	Ins. Dip.
P. linguaplax, Crowell.	Polypedilum spp.	Crowell, 1953.	Ins. Dip.
P. nodata, Müller.	Direct development.	Piersig, 1900.	None.
P. reighardi, Wolcott.	Tendipes decrus, Johannsen.	Crowell, 1960.	Ins. Dip.
P. rotunda, Kramer.	Direct development.	Piersig, 1900.	None.
P. uncata uncata, Koenike.	Chironomus plumosus, L. and other Chironomids.	Jones.	Ins. Dip.
P. uncata exigua, Viets.	Direct development.	Stout, 1953.	None.
P. variabilis, Koch.	Chironomids.	Jones.	Ins. Dip.
P. species.	Chironomids.	Jones.	Ins. Dip.
P. 114 species.	No information.		
Forelia, Haller.			
F. species.	Nymph hatched from eggs.	Cook, 1956.	None.
F. 16 species.	No information.		
1 genus, 2 species.	No information.		
7. Super-family, AXONOPSÆ, Viets.			
Axonopsidae, Viets.			
11 genera, 30 species.	No information.		
Brachypoda, Lebert.			
B. versicolor, Müller.	Hatches as nymph.	Piersig, 1900.	None.
B. 8 species.	No information.		
2 genera, 39 species.	No information.		
Ljania, Thor.			
L. bipapillata, Thor.	4 species Chironomids.		Ins. Dip.
L. 3 species.	No information.		
13 genera, 43 species.	No information.	Efford, 1960.	

Parasitabilia, Viets.				
P.sumatrensis, Viets.	As adult, on Ephemerid larvae.	Viets, 1935		Ins. Eph.
Aturidae, Thor.				
5 genera, 130 species.	No information.			
8. Super-family MIDEOPSALAE, Viets.				
8 families, 12 genera, 72 species.	No information.			
9. Super-family, KRENDOWSKIAE, Viets.				
4 families, 14 genera, 50 species.	No information.			
10. Super-family ARRENURAE, Oudemans.				
Arrenuridae, Thor.				
11 genera, 28 species.	No information.			
Arrenurus, Dugés.				
Sub-genus Arrenurus, s.str., Dugés.				
A.abbreviator, Berlese.	Libellulidae.	Munchberg, 1935		Ins. Odo.
A.affinis, Koenike.	Libellulidae.	Munchberg, 1935		Ins. Odo.
A.agrionicolus, Uchida.	Agrionidae.	Imamura, 1958		Ins. Odo.
A.americanus major, Marshall.	Ischnura verticalis, Say.	Munchberg, 1951		Ins. Odo.
A.batillifer, Koenike.	Libellulidae.	Munchberg, 1935		Ins. Odo.
A.bicuspidator, Berlese.	Libellulidae.	Munchberg, 1935		Ins. Odo.
A.bleptopetiolatus, Cook.	Epiciridulia princeps, Hagen.	Mitchell, 1959		Ins. Odo.
A.bruzelii, Koenike.	Libellulidae.	Munchberg, 1935		Ins. Odo.
A.claviger, Koenike.	Libellulidae.	Munchberg, 1935		Ins. Odo.

<i>A. compactilis</i> , Marshall.	<i>Enallagma ebrium</i> , Hagen.	Mitchell, 1959	Ins. Odo.
<i>A. compactus</i> , Piersig.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. crenatus</i> , Koenike.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. crassidaudatus</i> , Kramer.	<i>Corethra cristallina</i> , Degeer.	Munchberg, 1935.a.	Ins. Dip.
<i>A. cuspidator</i> , Müller.	<i>Anopheles maculipennis</i> , Meigen.	Munchberg, 1958	Ins. Dip.
<i>A. cuspidifer</i> , Piersig.	Libellulidae.	Munchberg.	Ins. Dip.
<i>A. daisetsuensis</i> , Imamura.	Libellulidae.	Munchberg, 1935	Ins. Odo.
	<i>Aeschna nigroflava</i> ,		
	<i>Enallagma deserti</i> .	Imamura, 1954	Ins. Odo.
<i>A. fimbriatus</i> , Koenike	<i>Anopheles maculipennis</i> , Meigen, <i>Theobaldia annulata</i> .	Munchberg, 1936	Ins. Dip.
<i>A. fissicornis</i> , Marshall	Libellulidae	Mitchell, 1959	Ins. Odo.
<i>A. latus</i> , Barrois & Moniez.	<i>Anopheles maculipennis</i> , Meigen.	Munchberg, 1938	Ins. Dip.
<i>A. leuckarti</i> , Piersig.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. maculator</i> , Müller	Libellulidae.	Munchberg, 1935	Ins. Odo.
	Various <i>Zygoptera</i> .	Jones.	Ins. Odo.
<i>A. neumani</i> , Piersig.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. ornatus</i> , George.	<i>Zygoptera</i> .	Killington & Bathe, 1947.a.	Ins. Odo.
<i>A. planus</i> , Marshall.	<i>Anisoptera & Zygoptera</i> .	Munchberg, 1952	Ins. Odo.
<i>A. platy-rotundo-cuspidator</i> , Munchberg.	<i>Anisoptera & Zygoptera</i> .	Munchberg, 1952	Ins. Odo.
<i>A. papillator</i> , Müller.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. pollictus</i> , Marshall	4 <i>Lestes</i> species.	Mitchell, 1959	Ins. Odo.
<i>A. pustulator</i> , Müller.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. radiatus</i> , Piersig.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. robustus</i> , Koenike.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. tetracyphus</i> , Piersig.	Libellulidae.	Munchberg, 1935	Ins. Odo.
<i>A. tricuspidator</i> , Müller.	Libellulidae.	Munchberg, 1935	Ins. Odo.

A.virens, Neuman.	Libellulidae.	Munchberg, 1935	Ins. Odo.
A.wallensis, Cook.	Libellulidae.	Mitchell, 1959	Ins. Odo.
A.(s.str.) 122 species.	No information.		
Sub-genus Megaluracarus, Viets.			
A.buccinator, Müller.	Various mosquitoes.	Munchberg, 1935.a & 1936.	Ins. Dip.
A.globator, Müller.	Zygoptera.	Jones.	Ins. Odo.
A.medio-rotundatus, Thor.	Various mosquitoes.	Munchberg, 1936, 37, 38.	Ins. Dip.
A.(Mega) 161 species.	Anopheles claviger, Meigen.	Jones.	Ins. Dip.
	No information.		
Sub-genus Truncaturus, Thor.			
A.knauthi, Koenike.	Mosquitoes.	Munchberg, 1936	Ins. Dip.
A.nodosus, Koenike.	Mosquitoes.	Munchberg, 1936	Ins. Dip.
A.stecki, Koenike.	Mosquitoes.	Munchberg, 1936	Ins. Dip.
A.truncatellus, Müller.	Mosquitoes.	Munchberg, 1937	Ins. Dip.
A.(Truncaturus) 22 species.	No information.		
Sub-genus Micruracarus, Viets.			
A.bisulcicodulus, Piersig.	Mosquitoes.	Munchberg, 1937	Ins. Dip.
A.integrator, Müller.	Mosquitoes.	Munchberg, 1938	Ins. Dip.
A.pugionifer, Koenike.	Mosquitoes.	Munchberg, 1936	Ins. Dip.
A.sinuator, Müller.	Tanytus punctipennis, Meigen.	Munchberg, 1936	Ins. Dip.
A.(Micruracarus) 67 species.	No information.		
Arrenurus species named from the females, and sub-genus therefore uncertain.			
A.78 species.	No information.		

A. spp.

Dixa aestivalis, Meigen.

Jones.

Ins. Dip.

A. spp.2.

Anatopynia varia, Johnston.

Jones.

Ins. Dip.

Bibliography.

Absell, A.:

1948. On the Distribution of certain British Hydrachnidae.
J. Queckett.micr.cl. 2.4, (221-222).
1949. On the Distribution of certain water mites in Europe.
J. Queckett.micr.cl. 2.6, (335-338).
1951. Water-mites. A surprising discovery. J. Queckett.
micr.cl. 3.4, (297-298).

Alabaster, A.W.:

- The Hydracarina of Devon. Trans. Plymouth Fld.Cl., 1916-1917.
No.5, (16-19).

Andre M. & Lamy E.:

1930. Les Acariens parasites des Mollusques. J.Conchyliol.
74, (199-221).
1930. Les Acariens parasites des Mollusques. Notes Complement-
aires. J.Conchyliol. 74, (322-327).

Angelier, C.:

- 1951a. Les rapports entre la flore aquatique et la faune
Hydracarienne. Bull.Soc.Cot.N.Fr. 3.3, (55-56).
1951b. Les Hydracariens des eaux stagnantes et la vegetation.
Bull.Soc.Cot.N.F. 4.2, (34-36).

Angelier, E.:

- 1954a. Contributions a l'etude de la faune d'eau douce de Corse.
Acariens psammiques. Vie et Milieu. 4.3, (505-539).
1954b. Contributions a l'etude de la faune d'eau douce de Corse.
Acariens des eaux superficielles. Vie et Milieu. 5.1, (74-148).

- 1954c. Écologie et Bibliographie des Hydracariens des eaux superficielles de Corse. Vie et Milieu. 5,2, (258-272).

Arndt, W. & Viets, K.:

1938. Die Biologischen (parasitologischen) Beziehungen zwischen Arachnoideen und Spongien. Z. Parasitenk. Berlin. 10.1. (67-93).

Beneden, P.J.:

1848. Recherches sur l'histoire naturelle et le développement de l'Atax ypsilophora (Hydrachna concharum) acaride vivant en parasite sur les Anodontes. Mem.Acad.R.Belg. T.1., 24, (1-24).

Besseling, A.:

1939. De levenswijze van Sperchon setiger, Thor. Ent. Ber. Amsterdam. 10, (143-144).

Bessels, E.:

1871. Observations on the species of Atax parasitic on our fresh-water mussels. Ann.Mag.Nat.Hist.London. 4.7, (55-59).

Brumpt, E.:

1929. Fréquence du parasitisme d'Hydrachna processifera sur le Dytiscus marginalis en Normandie. Ann.Parasit.hum.comp. 7.4, (290-302).

Bruyant, L.:

1908. Sur les larves d'Hydrachnides parasites des Culicides. C.R.Soc.Biol.Paris. 65, (706-707).

Campion, F.W. & H.:

1909. Notes on dragonfly parasites. (Larval water-mites). Entomologist, 42.557, (242-246).

Chandler, E.R.:

1934. Unionicola aculeata Koenike, in snails in North Carolina.
J.Parasit, 20.5, (312).

Chatterjee, G.Ch.:

1901. Parasites in Anopheles. Indian.Med.Gaz. 36.10, (371-372).

Cook, D.R.:

1955. Preliminary Studies of the Hydracarina of Michigan. The
sub-family Foreliinae Viets. Ann.ent.Soc.Amer. 48.4,
(299-307).

Crisp, D.J.:

1959. Hydracarines and Nematodes parasitising Corixa scotti
(D & S) in Western Ireland. Irish Nat.J. 13.4.

Crowell, R.M.:

1953. Morphology and Development stages of Piona linguaplax n.sp.
(Hydracarina Pionidae) a water-mite from N.Carolina.
Amer.Midl.Nat. 50.2, (426-432).

Crowell, R.M.:

1960. Taxonomy, Distribution and Development stages of Ohio
Water Mites. Bull.Ohio,Biol.Soc. 1.2.

Davies, M.D.:

1959. The parasitism of Black Flies (Diptera, Simuliidae) by
Larval water-mites mainly of the genus Sperchon.
Canad.J.Zool. 37, (353-369).

Efford, I.E.:

1960. A Population Study on Water-Mites. Unpublished Thesis for
Degree of Ph.D. at Oxford University.

Fearnside, C.J.:

1900. Parasites found on Mosquitoes. Indian Med.Gaz.

Feng, Lang-chou.:

1933. Some parasites of mosquitoes and flies found in China.
Lingnan.Sci.J. 12.Suppl. (23-31).

George, C.F.:

1899. Fresh water mites and Corixa. Sci.Gossip. (n.s.) 5, (316).

Greenier, P.:

1943. Observations sur quelques stations de Simulies. Parasites
et Prédateurs des larves et Nymphes. Bull.Soc.Pat.exot.
36.3-4, (105-110).

Gros, H.

1904. Sur un Acarien parasite des Anopheles. C.R.Soc.Biol.
Paris. 56.2, (56-57).

Humes, A.G. & Jamnback, H.A.:

- 1950a. Najadicola ingens, Koenike, a watermite parasitic in
fresh-water clams. Psyche,Camb.Mass. 57.3, (77-87).
1950b. Distribution and host relationships of a mite parasitic
in freshwater clams. J.Parasit. 36.6, sect.2, (32).

Hughes, T.E.:

1959. Mites, or the Acari. The Athlone press. London.

Imamura, T.:

- 1950a. On the Life History of the Water-Mite Hygrobates longipalpis,
Herm. Gakugei, Hokkaido Univ. 2.1, (74-78).
1950b. On the Life-History of Partnunia uchidai, a Water-Mite
parasitic on Stone-flies. Annot.Zool.Jap. 24, (54-58).

- 1951a. A New Water-Mite, Arrenurus daisetsuensis n.sp. with a note on its Life-History. J.Fac.Sci.Hokkaido Univ. 6. Zool. 10, (106-112).
- 1951b. Studies on three Water-mites from Hokkaido, parasitic on midges. J.Fac.Sci.Hokkaido Univ. 6. Zool. 10, 3.4, (274-288).
- 1953. Water-Mites from Gifu Prefecture. J.Fac.Sci.Hokkaido Univ. 6. Zool. 11, 3.4, (411-471).
- 1954. Studies on Water-mites from Hokkaido. J.Hokkaido Gakugei Univ.Sec.B.Suppl. 1.
- 1958. Water-Mites of Marsh Hinuma. Bull.Fac.Lib.Arts.Ibaraki Univ. No.8.

Jones, J.R.E.:

- 1940a. A Study of the Zinc-polluted river Ystwyth in North Cardiganshire, Wales. Ann.appl.Biol. 27, (368-378).
- 1940b. The Fauna of the River Melindwr, a lead polluted tributary of the R. Rheidol in North Cardiganshire, Wales. J.Anim.Ecol. 9, (188-201).
- 1941. The Fauna of the river Dovey, W. Wales. J.Anim.Ecol. 10, (12-24).
- 1943. The Fauna of the R. Teifi, West Wales. J.Anim.Ecol. 17.1, (51-65).
- 1949. An Ecological study of the R.Rheidol, N. Cardiganshire, Wales. J.Anim.Ecol. 18.1, (67-88).
- 1951. An Ecological study of the R. Towy. J.Anim.Ecol. 20, (68-86).

Killington F.J. & Bathe, E.C.:

- 1947a. Acarine parasites of Odonata, II. Arrenurus leuckarti,
Piersig, A.ornatus, George, A.neumani, Piersig & A.spp.nova.
Entomologist's Mon.Mag. 4 vol.8. no.90 = 83. no.996.
(116-124).
- 1947b. Acarine parasites of Odonata, III, Limnochares aquaticus, L.
Entomologist's Mon.Mag. 4. 8. no.90. = 83. no.997.
(145-147).

Kramer, P.:

1890. Zur Entwicklung der Hydrachniden. Zool.Anz. 13. 341, (427-
428).
1891. Über den Typen der postembryonalen Entwicklung bei den
Acariden. Arch.Naturgesch. 57. 1, (1-14).

Laird, M.:

1947. Some natural enemies of mosquitoes in the vicinity of
Palmaal, New Britain. Trans.Roy.Soc.N.Z. 76.3, (453-476).

Laveran, C.L.A.:

1902. De quelques parasites des Culicides. C.R.Soc.Biol. Paris.
54. 8, (233-235).
1904. Note sur un Acarien parasite des Anopheles. C.R.Soc.Biol.
Paris. 56,2. (57).

Leon, N.:

1924. Action des ectoparasites sur les Culicides. Ann.Parasit.
hum.comp. 2.3, (211-213).

Lundblad, O.:

1924. Ein unerwartetes, interessantes Verhaltnis in der Epimorphose

einer schwedischen Hexalebertia. Ent.Tidskr. 45, (72-79).

1927. Die Hydracarinen Schwedens. Zool.Bidr. Uppsala.
11, (185-540).

1941. Eine Übersicht des Hydrachnellensystems der Gattungen
dieser Gruppe. Zool.Bidr. Uppsala. 20, (359-379).

Marshall, J.F. & Staley, J.:

1929. A newly observed reaction of certain species of mosquitoes
to the bites of larval Hydrachnids. Parasitology.
21. 1-2, (158-160).

1930a. Specimen of Tubular Processes produced in mosquitoes by
the bites of larval mites. Trans.R.Soc.Trop.Med.Hyg.
23.4, (331).

1930b. Tubular processes produced in a mosquito by the bites of
larval Hydrachnid mites. Rep.Brit.Mosq.Contr.Inst. (6-7).

Marshall, Ruth.:

1929. The Morphology and Developmental stages of a new species of
Piona. Trans.Wis.Acad.Sci.Arts Lett. 21. (401-404).

1933. Water-mites from Wyoming as fish food. Trans.Amer.micr.Soc.
52.1, (34-41).

1935. A new parasitic Unionicola. Univ.Toronto stud.biol.
39, (99-102).

1940. On the occurrence of water-mites in the food of turtles.
Amer.Midl.Nat. 24.2, (361-364).

Masuda, Y.:

1934. Notes on the life history of Hydrachna (Schizohydrachna)
nova. Marshall. J.Sci.Hiroshima.Univ. Ser.B.Div.1.3.4, (33-43).

Mitchell, R.D.:

- 1954. A description of the water-mite Hydrovolzia gerhardi, n.spp.
with observations on the ecology and life history. Nat.Hist.
Misc. no.134.
- 1955. Anatomy, Life-History and Evolution of the mites Parasitizing
Fresh-Water Mussels. Misc.Publ.Mus.Zool. Univ.Mich. no.89.
- 1957a. On the Mites parasitizing Anodonta. (Unionidae; Mollusca).
J.Parasit. 43.1, (101-104).
- 1957b. Evolutionary Lines in Water-mites. Syst.Zool. 6.3.
- 1959. Life-histories and Larval Behaviour of Arrenurid Water-Mites.
J.N.Y.Ent.Soc. 67.1.

Motas, C.:

- 1925. Introduction a l'etude des Hydracariens. Trav.Lab.Piscic.
Univ.Grenoble. Ann.17.
- 1928a. Contribution a la connaissance des Hydracariens francais
particulierement du Sud Est de la France. Trav.Lab.Piscic.
Univ.Grenoble. Ann.20.
- 1928b. Considerations generales sur la repartition des Hydracariens
dans les eaux stagnantes et courantes et leur distribution
geographique particulierement dans le Sud Est de la France.
Bull.Soc.sci. Dauphine. 49, (1-65).
- 1929. Sur le developpement postembryonnaire de Calonyx brevipalpis
(Maglio) et sur les affinites des Protziidae. Ann.Sci.Univ.
Jassy. 16. 1-2, (250-265).

Munchberg, P.:

- 1935. Über die bisher bei einigen Nematocerenfamilien (Culicidae

- Chironomidae, Tipulidae) beobachten ektoparasitieren
Hydracarinienlarven. Z.Morph.Okol.Tiere. 29.5, (720-749).
- 1936a. Zur Morphologie der Arrhenurus und Georgella Larven und
Nymphen, mit besonderer Berücksichtigung der Libellenparasiten.
Arch.Naturgesch (N.F.) 5,1, (93-115).
- 1936b. Zur Kenntnis des Larvenparasitismus der Thyasinae 'Hydracarina')
zugleich ein Beitrag Über Schmarotzer der Limnobiinae.
(Diptera) Int.Rev.Hydrobiol. 33, (313-326).
- 1936c. Über Libellenschmarotzer. Aus.d.Heimat.Stuttgart.
49.6, (179-182).
- 1936d. Über die an Culicinae (Diptera) schmarotzenden Arrhenurus-
Larven (Hydracarina) I. Arch.Hydrobiol. 30, (557-573).
- 1937a. Über die an Culicinae (Diptera) schmarotzenden Arrhenurus-
Larven (Hydracarina) II. Int.Rev.Hydrobiol. 34, (353-372).
- 1937b. Wassermilbenlarven als Stechmücken-schmarotzer. Mikrokosmos,
Stuttgart. 30.9, (141-142).
- 1937c. Über den Parasitismus der Wassermilbenlarven an Luftinsekten.
Dtsch.Ent.Z. 1937 1-2, (19-34).
1938. Dritter Beitrag über die an Stechmücken schmarotzenden
Arrhenurus Larven (Hydracarina) Arch.Hydrobiol. 33, (99-116).
1951. Ein zweiter Beitrag über die an den U.S.A. eine odonaten-
parasitische Larvenphase aufweisenden Arrhenurus-Arten.
Arch.Hydrobiol. 45.3, (378-388).
1952. Über Fortpflanzung, Lebensweise und Körperbau von Arrhenurus
planus Marshall, zugleich ein weiterer Beitrag zur Ökologie
und Morphologie der im arctogaischen Raum eine Libellen-

parasitische Larvenphase aufweisenden Arrenuri (Hydracarina)
Zool.Jahr.Syst. 81 1-2, (27-46).

1953. Vierter Beitrag zur Kenntnis der im Noramerikanischen Raume
an Odonaten parasitierenden Arrenurus-Arten. (Ord:Hydracarina)
Zool.Jahr.Syst. 82. 1-2, (47-57).

1954a. Kurtze Mitteilung über die an Steinfliegen (Plecoptera)
schmarotzenden Wassermilbenlarvel. Arch.Hydrobiol.
49.3, (414-420).

1954b. Zur Kenntnis der an Culiciden (Diptera) schmarotzenden
Arrenurus Larven (Hydracarina) sowie über die Bedeutung
dieser Parasiten für Wirt und Mensch. Z.Parasitensk.
16, (298-312).

Pearce, E.J.:

1922. Haliphus obliquus. E.R. infested with scarid parasites.
Entomologist's Mon.Mag. 3.8. 58, (37).

Perez, G.:

1904. Sur les Larves d'Hydrachnes. C.R.Soc.Biol. Paris.
56, (263-264).

Piersig, R.:

1897-1900. Deutschlands Hydrachniden. Zoologica 22, (1-601).

Piatakow, M.L.:

1915a. On the Development of Eylais and Hydrachna larvae on the
wings of Dytiscidae. (Russian with summary in English)
Rev.Russe.Ent. 15.2, (125-130).

1915b. On the development of other Eylais and Hydrachna larvae
under the wings of Dytiscidae and Gyrinidae. (Russian with
summary in English). Rev.Russe.Ent. 15.4, (508-510).

1927. Zur Zucht der an Libellen schmarotzenden Arrhenurus Larven.
Zool.Anz. 74. 11-12, (248).

Sellnick, M.:

1939. Milben als Parasiten von Insekten. 7th.Int.Congr.Ent.
Berlin. 1938. 2, (1300-1307).

Sergent, E. & Sergent, E.:

1904. Note sur les Acariens parasites des Anopheles.
C.R.Soc.Biol. Paris. 56.3, (100-102).
1910. Note sur les Acariens parasites des Anopheles. In Ed.
Sergent: Recherches experimentales sur la Pathologie
Algerienne. Microbiologie, Parasitologie, 1902-1909.
Alger, 1910.

Smith, K.V.G.:

1951. Acarine larvae on Limonia tripunctata F.(Diptera, Tipulidae)
and on a species of Chironomid. Entomologist's Mon.Mag.
87, (63).

Soar, C.D.:

1901. Note on the occurrence of Larval water-mites on various
aquatic animals. J.QUECKET Micr.cl. 8.48, (65-66).
1903. Note on the occurrence of a living Hydrachnid larva in the
stomach of a trout. J.QUECKET Micr.cl. 8.52, (463-464).
1906. Notes and observations on the life history of fresh-water
mites. J.QUECKET Micr.cl. 9.59, (359-370).

Soar, C.D. & Williamson:

1925. The British Hydracarina. Ray Society.
1927. The British Hydracarina. Ray Society, Vol.II.
1929. The British Hydracarina. Ray Society, Vol.III.

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SPARING, I

1959 DIE LARVEN DER HYDRACHNELLAE, IHRE
PARASITISCHE ENTWICKLUNG UND IHRE
SYSTEMATIK.

GUSTAV FASCHER, JENA.

H.P. May

Sokolow, I.I.:

1924. Untersuch-ungen über die Eiablage und den laich der Hydracariden. Arch.Hydrobiol. 15.3, (383-405).
 1925. Untersuch-ungen über die Eiablage und den laich der Hydracariden. II. Z.Morph.Okol.Tiere. 4.3, (301-332).

Stankovitch, S.:

1921. Etude sur la morphologie et la nutrition des alevins des poissons Cyprinides. Bull.Soc.Sci.Isere. 42, (31-212).

Stout, V.M.:

- 1953a. Eylais waikawae, n.sp., (Hydracarina) and some features of its life-history and anatomy. Trans.Roy.Soc.N.Z. 81.3, (389-416).
 1953b. New species of Hydracarina with descriptions of the life history of two. Trans.Roy.Soc.N.Z. 81.3, (417-466).

Thon, K.:

1899. Über ein interessantes Beispiel des Parasitismus bei den Hydrachniden. Verh.zool.bot.Ges. Wein. 49, (484-485).

Uchida, T.:

1932. Some Ecological Observations on Water-Mites. J.Fac.Sci.Hokkaido.Univ. Zool.1.4, (143-165).

Uchida, T. & Imamura, T.:

1951. Some Water-Mites from China. J.Fac.Sci.Hokkaido Univ. Zool.10. 3-4, (324-358).

Uchida, T. & Miyazaki, I.:

1935. Life history of a water-mite parasitic on Anopheles. Proc.Imper.Acad. Japan. 11.2, (73-76).

Viets, K.:

- 1936. Wassermilben oder Hydracarina. (Hydrachnellae und Halacaridae). F.Dahl. Tierwelt Deutschlands. G. Fischer, Jena.
- 1939. Piona rotunda Kramer, (Hydrachnellae) in der Kiemenhöhle von Krebsen. Arch.Hydrobiol. 12, (115-116).
- 1955. Die Milben des Süßwassers und des Meeres. Teil I Bibliographie.
- 1956. Teil II Katalog. Gustav Fischer, Jena.

Vitzthum, Graf von Eckstaedt,:

- 1940-43. Acarina. In Bronn, H.G. Klassen und Ordnungen des Tierreichs. Bd.5., Abt.IV., Buch, 5, (1-1011).
- 1941a. Über den Parasitismus der Hydryphantes - Larven. Z.Parasitenk. 12.2, (144-156).
- 1941b. Über den Parasitismus der Feltria Larven. Z.Parasitenk. 12.3, (362-371).

Walter, C.W.:

- 1915. Notizen über die Entwicklung Torrentikoler Hydracarinen. Zool.Anz. 45.10, (442-456).
- 1917. Beitrag zur Kenntnis der Entwicklung bachbewohnender Milben. Verh.Naturf.Ges.Basel. 28. 1-2, (148-164).

Webster, F.M.:

- 1914. Natural Enemies of Simulium. Psyche.Camb.Mass. 21, (95-99).

Welsh, J.H.:

- 1930. Reversal of phototropism in a Parasitic Water Mite. Biol.Bull.Woods Hole. 59.2, (165-169).

1931. Specific Influence of the host on the Light Response of
Parasitic Water Mites. Biol.Bull. Woods Hole.
61.3, (497-499).

1932a. A Laboratory Experiment in Animal Behaviour.
Science (N.Y.) 75, No.1953, (591-592).

1932b. Photokinesis and Tonic effect of Light in Unionicola.
J.Gen.Physiol, Baltimore. 16.2, (349-355).

Wesenberg-Lund, C.J.:

1918. Contributions to the Knowledge of the Postembryonal
Development of the Hydracarina. Vidensk. Medd.Dansk
naturh.Foren.Odense. 70, (5-57).

Williamson, W.:

1909. Paniscus michaeli, Koenike, in Selkirkshire.
Ann.Scot.Nat.Hist. No.70, (121).

Wolcott, R.H.:

1899. On the North American Species of the Genus Atax, Fabr.
Stud.Zool.labor. Nebraska, Lincoln No.30.

Womersley, H.:

1953. An Interesting new Larval Species of Panisopsis (Thyasidae,
Acarina) from New Zealand. Rec.Canterbury, (N.Z.) Mus.
6.3, (233-235).

Summary of Thesis entitled "An Investigation into the life-histories
and Ecology of the Hydracarina".

The work described in this thesis was designed to throw some light on the problems of the larval behaviour and way of life of the British Hydracarina. Although these animals are a common and numerous element in nearly all fresh-water habitats the full life-histories are known for very few.

The principal method of investigation used in this work was by catching and examining aquatic invertebrates and attempting to identify any mite larvae which they were carrying. The lack of any complete key made it necessary to attempt to breed these larvae through to the adult stage and this was done successfully in five cases. The hosts for a further three species were found by using larvae bred in the laboratory to produce parasitic infections of hosts under experimental conditions, while another seven species of larva were identified on the host from Sparing's key and by comparison with bred specimens.

The actual transfer of the larvae onto their hosts was observed for an Arrenurus species, parasitic on Zygopteran adults, and for Protzia eximia, Protz, whose larvae jump distances of up to 2 cm. from the water or land surface to reach their positions on their Empid or Trichopteran hosts.

The larvae of two Unionicola spp., believed since the time of Benz, 1783 to be free-living, were shown to be parasitic on Chironomids, thus making the position of the Unionicolidae in the Super-family Pionae much more comprehensible than it had hitherto appeared.

Collections of large numbers of Chironomids showed the great importance of this group in the life cycles of the Hydracarina, and it also became obvious that the Nematocera in general appear to be by far the most important host group for the water-mites.

In the appendix are descriptions of three previously unknown larvae together with a table summarising present knowledge of the hosts of water-mites.