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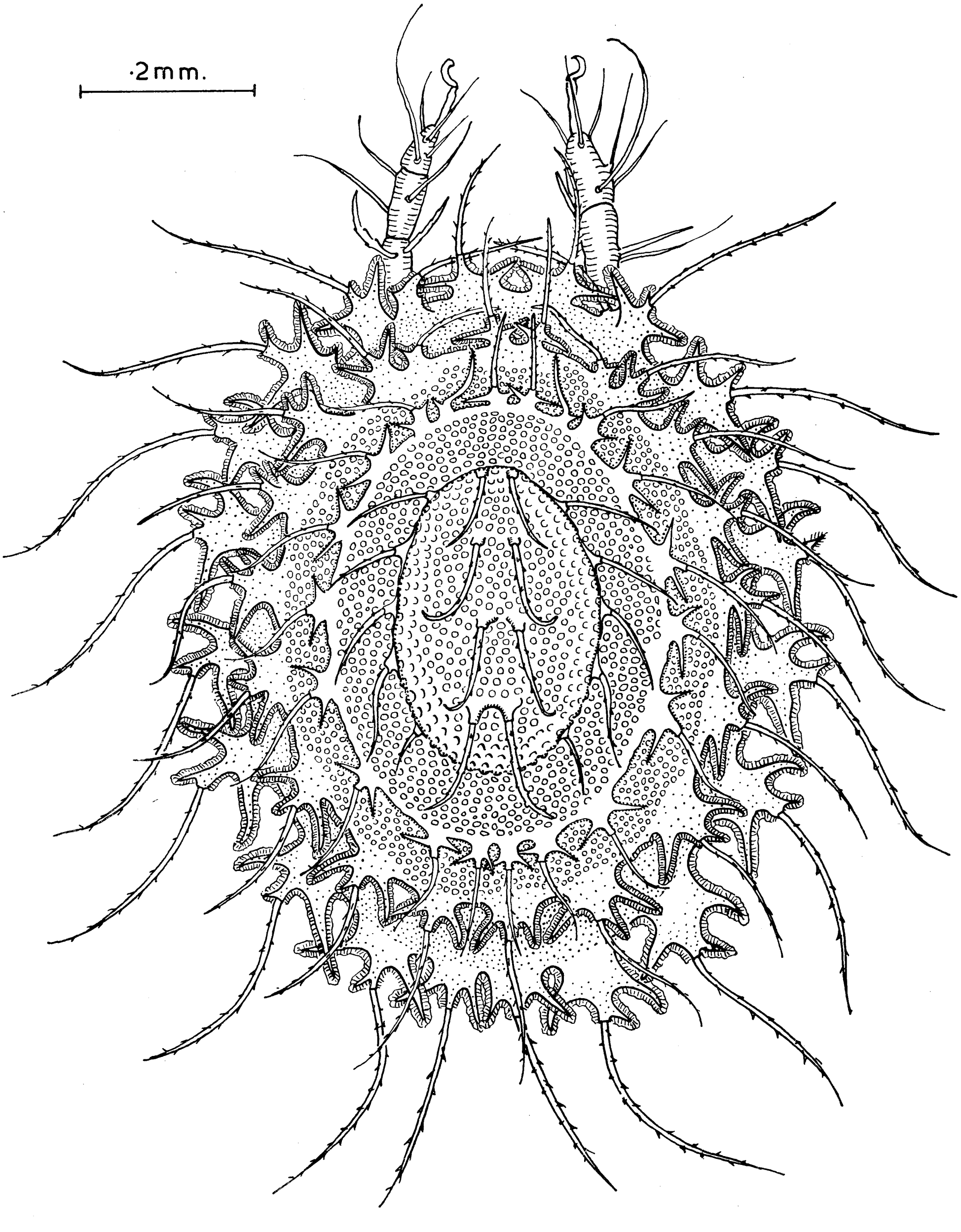

Cepheus dentatus (Michael) Tritonymph.
From a decaying tree stump, Petts Wood, Kent.

MITES
OR THE ACARI

by

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Preface

No general account of the Acari, apart from taxonomic studies, has appeared in English since the work of Nathan Banks. There exists a large but scattered literature on this group of animals, which are being studied because of their economic importance and their zoological interest. It was, therefore, felt that a descriptive account of this remarkable assemblage of species would be of use both to students and to working acarologists.

It is quite obvious that I owe a great deal to H. Graf Vitzthum, who in his works on mites presented an enormous amount of information gathered over a long lifetime. I should like to thank, too, all those with whom I have discussed mites, and in particular Dr. Owen Evans and Mr. E. Browning for their unfailing kindness and help both in discussions and in verifying references; I am also grateful to the Governors of this College for a grant towards the cost of publication.

Some of the figures have been published before, though their presentation in this volume has been slightly altered. I am grateful to the editors of *Annals of Tropical Medicine and Parasitology*, *Proceedings of the Zoological Society of London*, *Annals and Magazine of Natural History*, *The Quarterly Journal of Microscopical Science*, and *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, for granting me permission to reproduce them here.

In conclusion I should like especially to acknowledge the help of my wife, many of whose drawings I have used.

Birkbeck College, London T.E.H.
1 *August* 1957

TO THE MEMORY OF

H. GRAF VITZTHUM

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Dear Madam, did you never gaze,
Thro’ Optic glass on rotten cheese?
There, Madam, did you ne’er perceive
A crowd of Dwarfish Creatures live?
The little things, elate with Pride,
Strut to and fro, from side to side:
In tiny Pomp and portly vein,
Lords of their pleasing Orb, they reign;
And, fill’d with harden’d Curds and Cream,
Think the whole Dairy made for them.
So men, conceited Lords of all,
Walk proudly o’er this pendent Ball,
Fond of their little Spot below,
Nor greater Beings care to know;
But think, those Worlds *which deck the skies,*
Were only form’d to please their *Eyes.*

STEPHEN DUCK (1736)

CHAPTER I

The Free-living Acari

THE free-living terrestrial mites occur at high altitudes (H. Franz, 1943, 1944) and are very early inhabitants of partially formed soils (W. Kuhnelt, 1942, 1950) on mountains. They extend down to the shore and, through an intertidal fauna, merge with marine forms; alternatively, by way of denizens of marsh and bog, they are continuous with a freshwater fauna. The Acari are usually noticed, if at all, because of their impact on some human activities. They may become noticeable as direct parasites, or as the vectors of disease to man or domestic animals. The interest aroused of recent years in trombiculid larvae is the outcome of their powers of transmission of scrub typhus in certain species. They have also attracted considerable attention as plant parasites and as the infestors and destroyers of many stored food products. The free-living mites, however, show a great diversity of adaptation to a wide range of ecological niches, perhaps as wide a range as that other versatile group of arthropods, the insects.

The free-living forms occur in all those situations where vegetation is found, amongst the decaying debris and in association with mosses and lichens. The richest sources are mosses and the rich top soils of woods and forests, where they may form 70 to 80 per cent or more of the total population,[1] and the same is true of the soil faunas of fenland with its high humus content (A. MacFadyen, 1948), while on natural heathland (P. W. Murphy, 1950) they may represent 95 per cent of species of the arthropod fauna of the soil. As in any other group with diversity of habit as well as habitat, these populations of mites in the surface vegetation and upper layers of the soil include forms which are vegetarian, feeding on the decaying plant remains, scavengers consuming decaying animal remains, and some coprophilous forms. On this basic population lives a variety of predatory mites which include in their diet other small arthropods, like Collembola, the eggs and larvae of insects, and small oligochaetes.

The mites fall into the following five suborders.

The suborder Parasitiformes is divisible primarily on the one hand into the Mesostigmata, which includes an assemblage of free-living forms—predaceous,

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[1] The same sort of thing holds on wave-beaten rocks apparently (H. Gorvett, *Nature*, London, **182**, 1653).

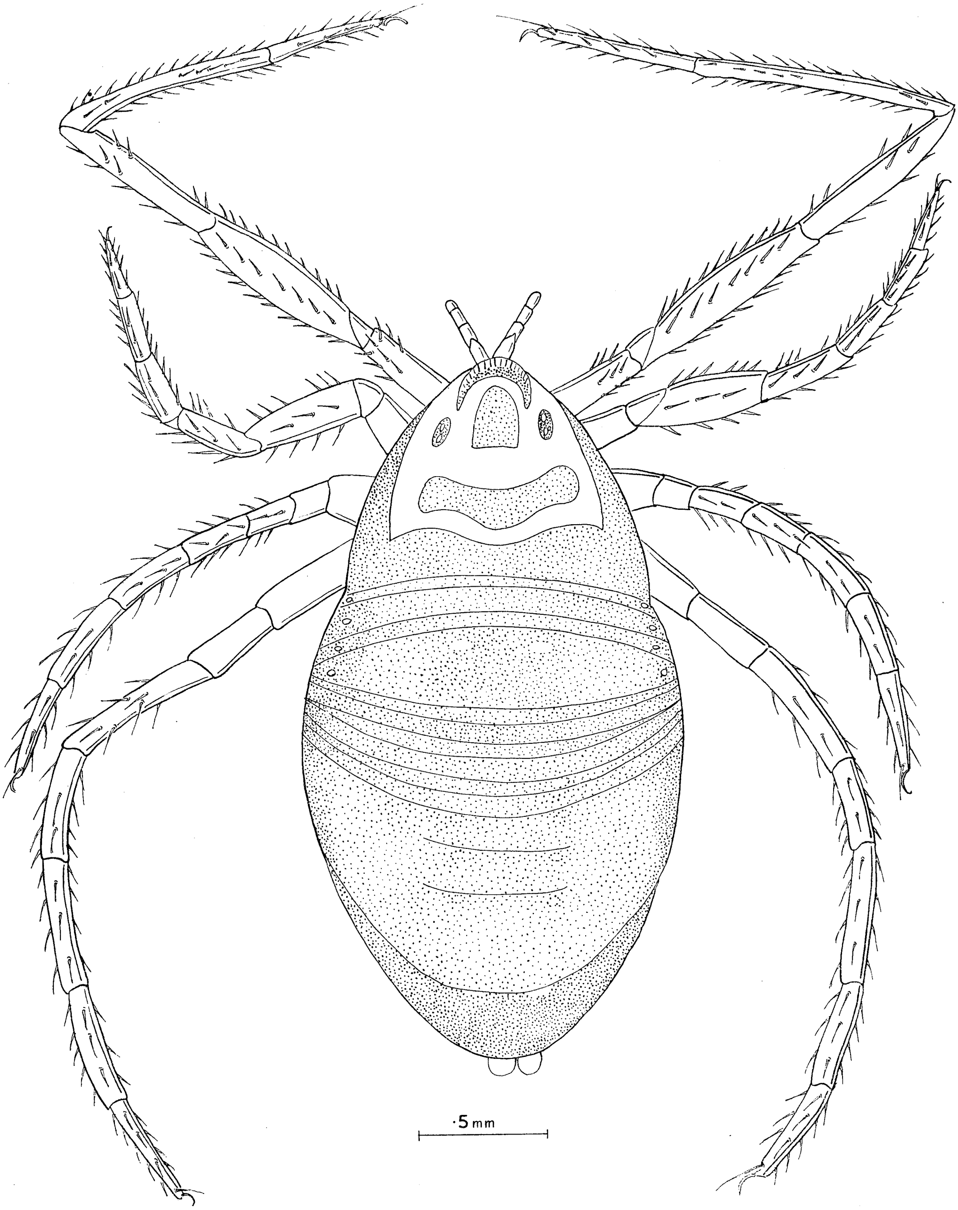


PLATE 1. *Opilioacarus* sp.; dorsal view.

plant-feeding and coprophilous—together with numerous parasites of animals and, on the other hand, the wholly parasitic Ixodides. The Mesostigmata, broadly speaking, are further divisible into the Uropodina which, so far as is known, are feeders on fungal mycelium and spores and decaying plant material, and the Gamasides, which show a remarkable range of forms.

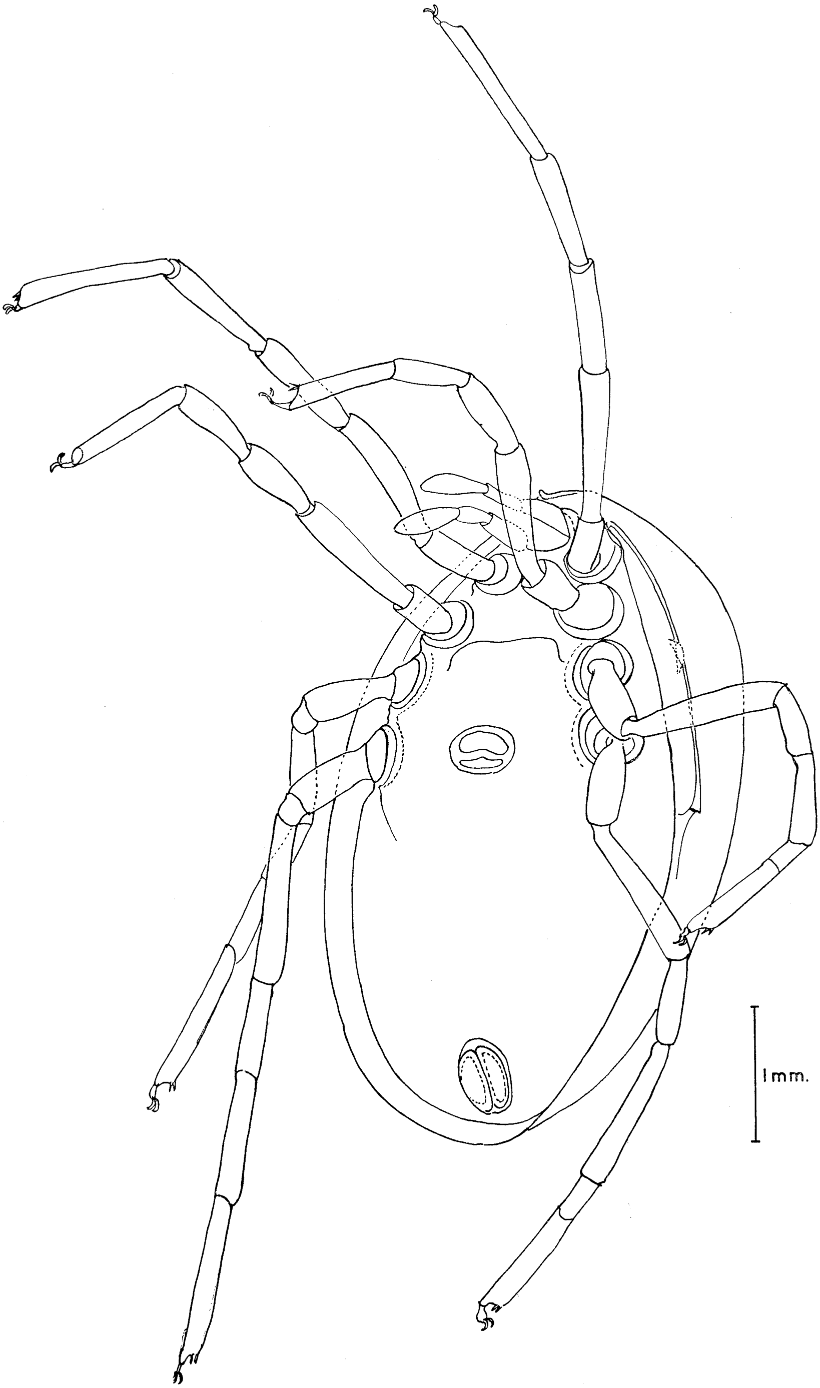
The suborder Trombidiformes includes a wide range of free-living forms comparable to the Gamasides, as well as a great range of parasites and a rich aquatic fauna. The majority of the group constitute the Prostigmata, and those species of the Prostigmata which are either free-living throughout their life or else completely parasitic are grouped into the Eleutherengona. They include many predators of other mites and small insects. On the other hand the Parasitengona include all those trombidiform mites which are parasitic as larvae, but free-living as nymphs and adults. I think it most suitable to consider them as free-living species and to discuss their peculiar larval habits when dealing with parasitism generally. In their free-living stages many are predaceous forms, found in decaying plant debris and moss.

The suborder Sarcoptiformes is divided into two groups: the Acaridiae containing free-living and parasitic forms, and the Oribatei which are all free-living. Unlike the preceding suborders, the Sarcoptiformes are predominantly feeders upon vegetable materials. Nevertheless, many show a predilection for a high protein content in their food and this sometimes leads them into feeding on animal substances. The suborder as a whole has departed far from the primitive arachnid habit of active predation.

The suborder Notostigmata (Plate I) has been collected from under stones and in damp soil crevices in regions as far apart as the Mediterranean regions, the Argentine and Uruguay; it is therefore probably a suborder of cosmopolitan habit, as far as subtropical and warm climates are concerned. These large and active mites are predators on other arthropods, the curiously modified labrum being used to rasp the prey, so that the gut contents come to include small bits of exoskeleton of the prey, as well as the soft parts. In respect of feeding habits, they are paralleled by the suborder Holothyroidea (Plate II): these active heavily sclerotized predators occur in Mauritius, Ceylon, Australia and New Zealand, under stones and amongst decaying vegetation where their arthropodan prey abounds. These two suborders, of small size, have, from a biological point of view, scarcely been studied.

Some of the free-living Eleutherengona are found in high mountains; *Anandia alticola* (S. Hirst, 1927), family Anystidae, was collected on Mount Everest at a height of 5,000 metres. The Caeculidae, which occur high in the Austrian Alps, have also been collected in Kashmir at 5,000 metres above sea level. These mites live under relatively dry conditions. The vast bulk of the known mite fauna is found, however, in soil and plant debris at lower altitudes and under more humid conditions.

Many of the Gamasides are active predators and are found in such places as their prey frequents. Many of the Parasitidae, Macrochelidae and Laelap-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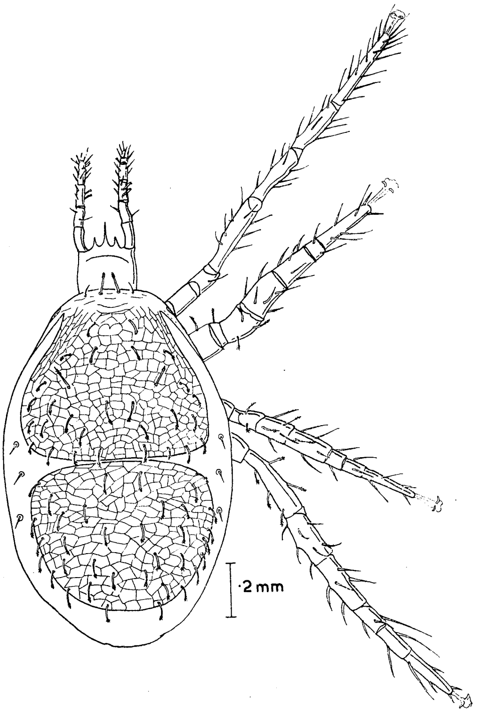
tidae are found in dung or associated with dung beetles; it is highly probable that these mites are in many cases not coprophilous themselves, nor are they parasitic on the insect 'hosts', but use them as a means of transport from one dung mass to another, feeding on the eggs, larvae and pupae of insects which there abound, and also probably on small worms. In moss and leaf mould, members of the Parasitidae and other Gamasides (Plate IV, figs. 1, 2) are found preying on other mites and Collembola. Species of *Eugamasus* (Plate III, fig. 1), *Pergamasus* (Plate XXVII, fig. 3) and *Veigaia* (Plate XXVII, fig. 1) are found in organic debris in holes and crevices in the ground, where it may have accumulated under the effects of wind or winter rains. They prey on the other arthropod fauna there.

The other groups of Mesostigmata, the Uropodina and Trachytina (Plate III, figs. 2, 3), are never predatory, their long rather weakly developed chelicerae being adapted for feeding on fungal mycelia and decaying vegetable materials. They occur in leaf mould, moss, compost heaps and decaying dung. Their highly developed and heavily sclerotized exoskeleton gives very complete protection against the lesser predatory arthropods, and also enables them to become commensals of ants and termites.

The Trombidiformes (Plate V, figs. 2, 3, 4) occur as predators in moss and humus-rich soil, or plant debris. For example, the Rhagidiidae (Plate III, fig. 4) are frequently found in moss and the debris in holes and crevices; some species seem to have become restricted to caves and smaller similar holes; the variety *longipes* (I. Trägårdh, 1911) of *Rhagidia terricola* (C. L. Koch, 1836) appears to be such a one. The Eupodidae and Penthaleidae are found in a similar range of habitats, forms which have become cavernicolous showing a reduction of the eyes, which are normally well developed in the Trombidiformes. A genus of the Anystidae, *Erythracarus*, is frequently found on rocks and sandy soils warmed by the sun, but one species *parietinus* (J. Hermann, 1804) was recorded from old books in a library, where it was probably feeding on psocids. The Cheyletidae are a free-living predaceous family feeding on other mites and small insects, and so are found under conditions favourable to other families, like the Acaridae, among the Sarcoptiformes.

Parasitengona of similar predatory habits are also common; the subfamilies Trombellinae and Tanaupodinae (of the family Trombidiidae) are large red mites (0·04 to 4·0 mm. long) which dig down into the leaf mould of woods and prey on the small arthropods there. Other forms such as *Allothrombium*, *Erythracarus* and *Trombidium* live, for the most part, under stones, in mole runs and under grass roots. In the spring of the year, however, they appear above ground on sun-warmed patches of soil or rock, and appear to be searching for mates or sites for oviposition. On the other hand, the subfamily Trombiculinae, except for the parasitic larval stage, live a subterranean life in the interstices of the soil. The habit of *Allothrombium* and other

PLATE II. *Holothyrus coccinella* (Gervais)♂; ventro-lateral view.



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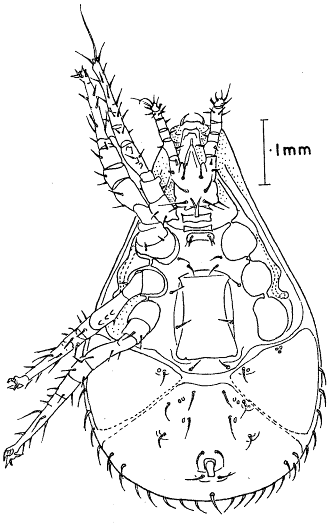

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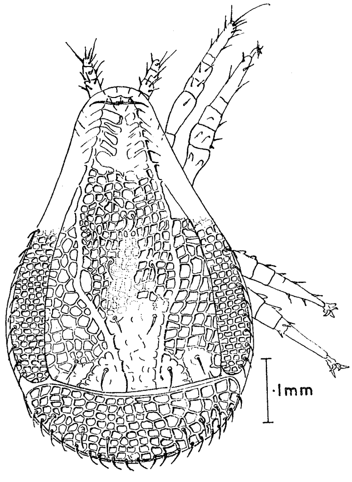

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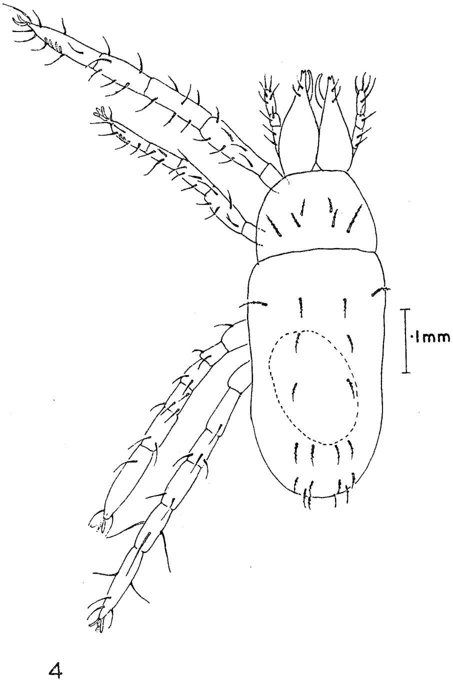

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genera of appearing in the spring is sometimes very striking; the species *Balaustium murorum* (J. Hermann, 1804, family Erythraeidae) sometimes appears in huge numbers from the cavities of dry stone walls, or the crevices of brickwork, or from under stone paving. This peculiarity is sometimes shown by a species *Bryobia praetiosa* (Plate XXI, fig. 2) (C. L. Koch, 1836, family Tetranychidae), which is a plant parasite throughout its life. Thus it would seem that a wide variety of forms overwinter as adults or possibly in the final nymphal stage, appearing fully developed in spring and proceeding to egg-laying.

Many of the Trombidiformes are less fond of moisture than are the soil and moss inhabitants, and occur as adults in relatively dry places. The subfamily Trombidiinae of the family Trombidiidae includes the largest mites, apart from the ticks, attaining a length of a centimetre or more (e.g. *Dinothrombium* species). These large scarlet mites with velvet surface occur in warm countries in fairly dry sandy soils in Madeira, the Sudan and South-East Asia. Perhaps the most remarkable sand-dweller is *Lucasiella plumipes* (C. L. Koch, 1836), of the Mediterranean countries, but which extends into Switzerland and the Channel Islands. This active mite, a member of the Erythraeidae, has the fourth pair of legs modified into sensory organs like flue brushes (Plate V, fig. 1), and carries them above its back. While in motion, it moves them up and down continuously.

The Oribatei are found in large numbers in moss, humus, surface vegetation and the crevices of bark. Their immature stages are soft-bodied, only the adults being dark and heavily sclerotized (Plate VII, fig. 1). As a group, they have exacting requirements as regards humidity, especially the young stages which require an atmosphere approaching saturation. This may be the main factor in making them the predominant Acari in soil faunas of all types. In the soil they appear to play an important part in the breaking up of decaying detritus into small particles. In all stages of the life cycle they have biting mouthparts and, so far as is known, feed either on partially decayed plant debris, or by cropping the mycelia or fruiting bodies of fungi which grow on this material. P. W. Murphy (1953), in his discussion of soil fauna, said that Oribatei will not feed on plant material unless it is fully saturated and, moreover, show a preference for one type of forest litter over another; thus *Steganacarus* species prefer the broad leaves of deciduous trees to the needles of conifers. There is also a preference for partially decayed leaves, the freshly fallen ones not being attacked. This liking for plant material, after it has been attacked by fungi or bacteria, is a marked feature of many groups. H. Vitzthum (1943) stated that the young stages of *Oribotritia* bore into decaying wood. The nymphs of Phthiracaridae burrow into conifer needles (A. P. Jacot, 1939), once the mesophyll has become invaded by fungi. Each

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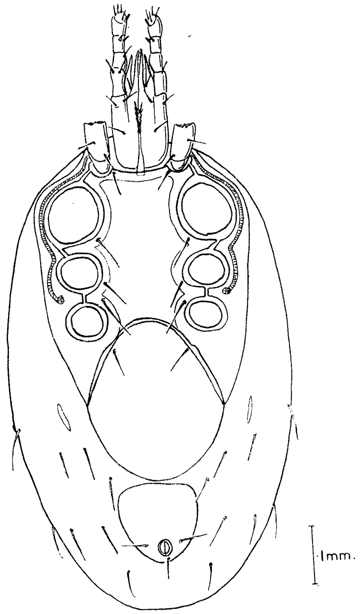
PLATE III. **1.** *Eugamasus magnus* (Kramer) ♀; dorsal view. **2.** *Trachytes* sp. ♀; ventral view. **3.** *Trachytes* sp. ♀; dorsal view. **4.** *Rhagidia gelida* (Thorell) ♀; dorsal view.



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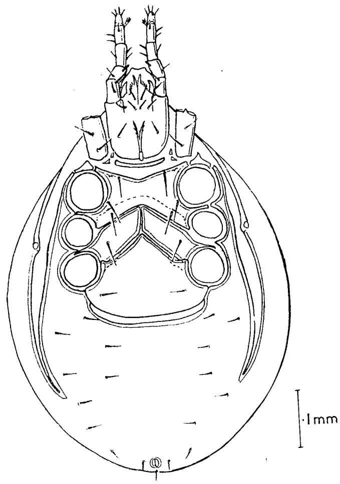

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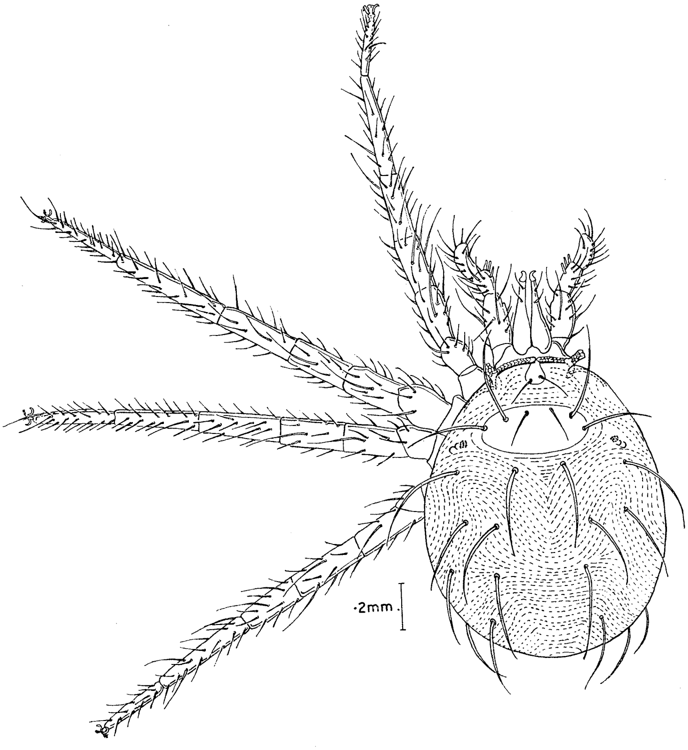

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needle usually contains a single nymph which works its way along the needle, undergoing its nymphal ecdyses and emerging as an adult.

H. Vitzthum (1943) stated that under certain conditions *Oribella castanea* (J. Hermann, 1804, family Eremaeidae) becomes a predator. When tyroglyphid (Acaridiae) mites build up large populations in tobacco stores this oribatid has been seen to feed on them. *Nothrus ovivorus* (A. Packard, 1870, family Camisiidae) feeds on the eggs of Microlepidoptera. The coccid *Aspidiotes gloveri*, on citrous fruit, is preyed on by *Oribates aspidiota* (W. Ashmead, 1879); whilst the parasitic hymenopteran *Polygnotes zosini*, which attacks the ceccidomyid fly *Mayeticola destructor*, is eaten while in the fly pupa by *Scheloribates laevigatus* (C. L. Koch, 1836). Thus although most of the group are now adapted to a diet of vegetable materials, a few scattered genera retain or have returned to the predaceous method of feeding.

Species living in moss and decaying vegetation are under fairly humid conditions; in much drier conditions are found mesostigmatic forms, such as *Typhlodromus* and *Amblyseius* (Gamasides), preying on the insect parasites of plants which they hunt on the leaves and stems. The Anystidae (Prostigmata) show a similar habit to these Phytoseiidae among the Gamasides, many living on leaves of plants and preying on plant parasites. It seems probable that there is a restriction of *Anystis* (Plate IV, fig. 3) to certain plant types by reason of the specificity shown by plant parasites.

The fact that so many mites live in places devoid of the normal stimulus of light has perhaps been responsible for the development of cavernicolous forms in some groups. Apart from those cavernicolous Trombidiformes already mentioned, some of the Mesostigmata have become largely restricted to a subterranean existence in caves, seldom being found elsewhere. *Eugamasus loricatus* (H. Wankel, 1861), *Eugamasus magnus* (P. Kramer, 1876) (Plate III, fig. 1) and *Cyrtolaelaps mucronatus* (G. and R. Canestrini, 1881) are often cavernicolous species. From among the Sarcoptiformes, H. Vitzthum (1932) also recorded floating colonies of *Schwiebea cavernicola* on the water of a subterranean pond. The tendency to live in regions of high humidity becomes emphasized in some of the Mesostigmata; the *Rhodacaridae* live underground in saturated soil usually overlaid by decaying vegetation, while *Hydrogamasus antarcticus* (I. Trägårdh, 1907) was found in wet moss on Paulet Island. *Hydrogamasus salinus* occurs in crevices of rocks on the European coasts and extends down into the intertidal zone, and *Halolaelaps* species occur in similar situations, *Halolaelaps celticus* (J. Halbert, 1915) having been recorded from the Irish and Welsh coasts, while *Halolaelaps marinus* (G. Brady, 1875) occurs on the Atlantic coast of Europe from Norway to Spain. *Cyrthydrolaelaps hirtus* (A. Berlese, 1904) also occurs on the European coast in rock crevices and *Hydrogamasus littoralis* (G. and R. Canestrini, 1881) is

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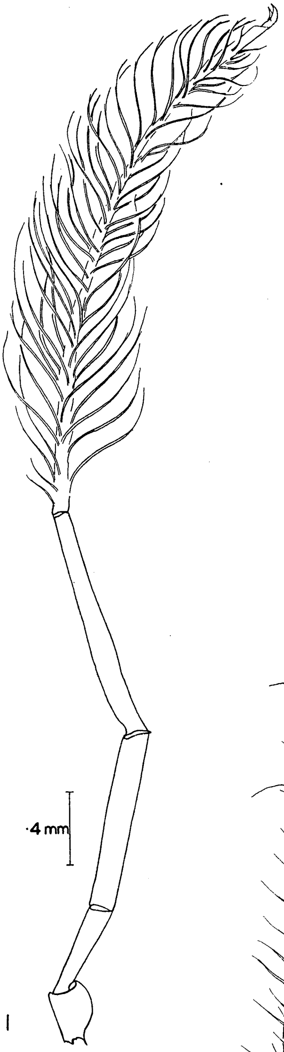
PLATE IV. **1.** *Pachylaelaps* sp. ♀; ventral view. **2.** *Ologamasus* sp. ♀; ventral view. **3.** *Anystis baccarum* L; dorsal view.



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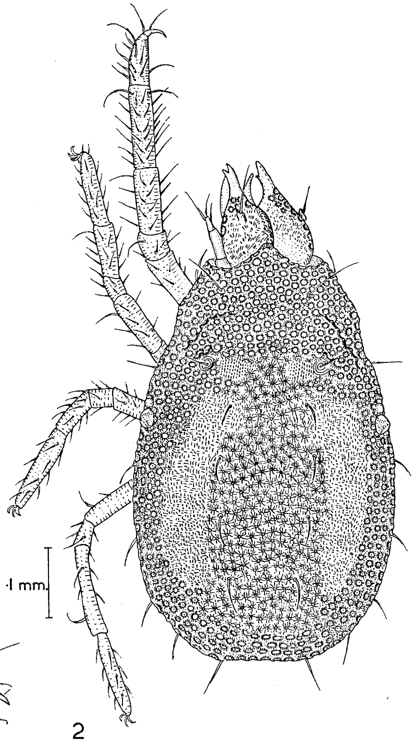

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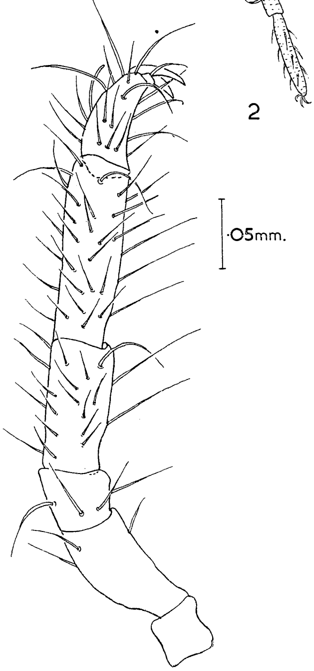

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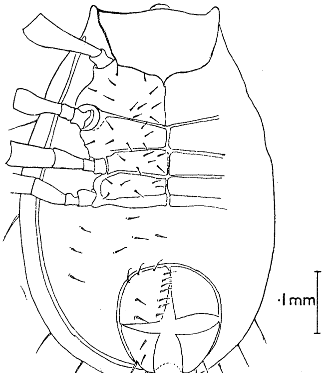

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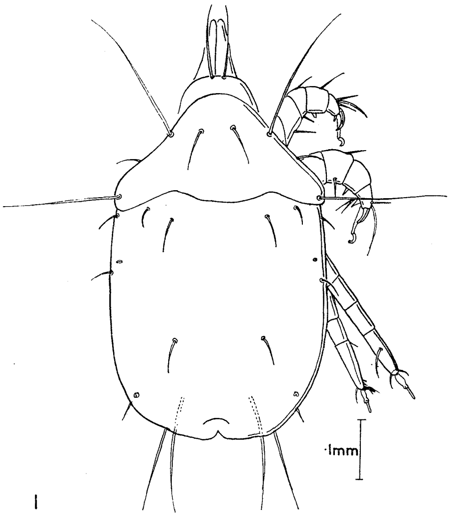
found round the Adriatic coast. All these forms are capable of withstanding tidal submersion, although they have the tracheal system of typically terrestrial forms. Either they survive on the actual oxygen contained in the peritremata, or this air, separated at most by an extremely thin membrane from the water, acts as an absorbent mechanism for dissolved oxygen. The Gamasides give rise to no completely aquatic forms.

Although, as already mentioned, the Trombidiformes include forms found in rather dry conditions at high altitudes or on sandy soils, certain families, for example the Bdellidae and the Cunaxidae, are moisture-loving creatures. The former are littoral animals and can be intertidal in distribution, *Bdella interrupta* (O. Evans, 1952) being found on the Welsh and Channel coasts in rock crevices. The Cunaxidae live in saturated moss in close proximity to water in marsh or boggy ground.

These moisture-loving families are related to true aquatic families. The Eleutherengona are poorly represented in fresh water by a small family, the Porohalacaridae; they occur on the bottoms of lakes and ponds and on marshes, preying on the inhabitants of mud; they do not appear in waters with a clean bottom, and have no adaptations for swimming. The family occurs both in America and Europe.

Relatively few mites have been recorded from brackish water; K. Viets (1928) described one species, *Caspihalacarus hyrcanus* (Porohalacaridae), from the harbour at Baku where the salinity is 1·25 per cent, and another, *Copidognathus oxianus*, from the Aral sea where the salt content is as low as 1 per cent. *Copidognathus oxianus* is a member of the family Halacaridae, and this family is the marine representative of the Eleutherengona; although aquatic the animals cannot swim, and the tracheal system is greatly reduced or absent. These mites are found feeding on animals which are epizoic on seaweeds, on sandy bottoms and on rocks. The majority of them live intertidally or in the coastal waters, though some have been found in deep water: for example, *Agaue abyssorum* (E. Trouessart, 1896) from a depth of 1,400 metres. The genera *Rhombognathus* (Plate VI, fig. 2), *Halacarus*, *Agaue*, *Copidognathus* (Plate XXXI, fig. 1) and *Agauopsis* have been recorded from both tropical and boreal coasts, but *Copidognathus* appears to predominate in tropical habitats, at any rate on the American Atlantic coast. *Rhombognathides*, *Metarhombognathus*, *Isobactrus*, *Arhodeoporus* and *Lohmannella* have never been recorded from the tropics. In sand are found *Halacarus anomalus* (E. Trouessart, 1894), *Halacarellus capuzinus* (Lohmann, 1893) and *Halacarus subterraneus* (E. Schulz, 1933); these species dig quite deep into the sand in intertidal zones, whilst *H. anomalus* can be collected above high-water mark. Species of *Copidognathus*

PLATE V. **1.** *Lucasiella* sp.; right leg IV. **2.** *Labidostoma luteum* (Kramer); dorsal view. **3.** *Labidostoma luteum* (Kramer); dorsal view of leg I. **4.** *Labidostoma luteum* (Kramer); ventral view. The gnathosoma has been removed and the reticulate thickening of the surface cuticle is not shown.



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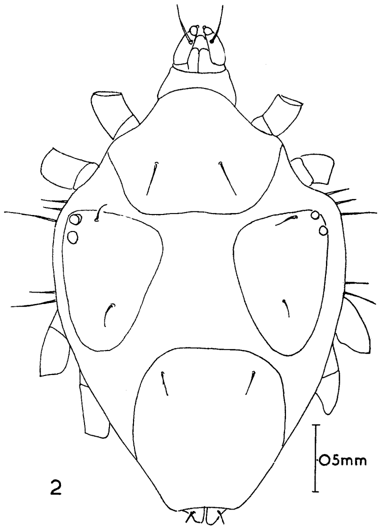

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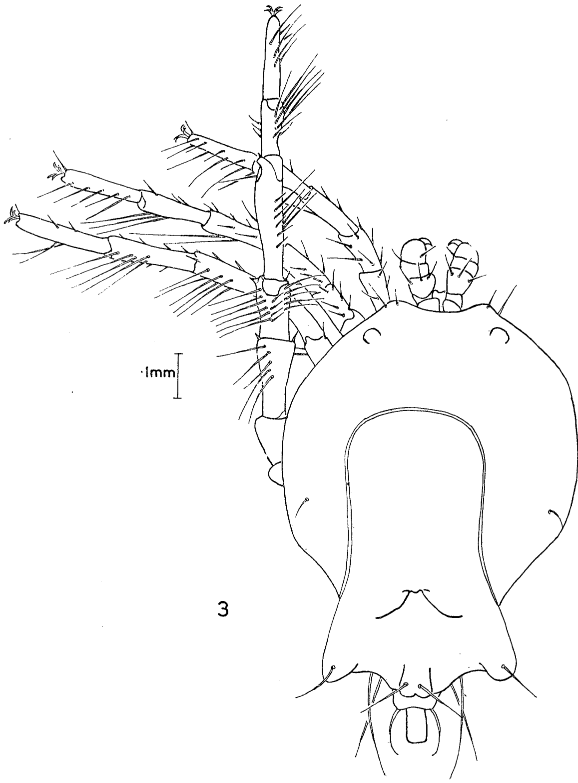

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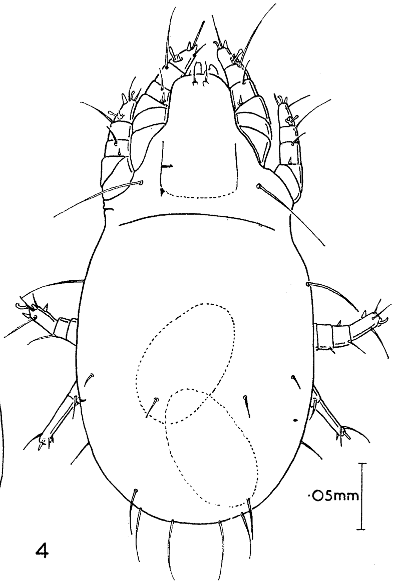

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are also frequently found in sandy situations. *Actacarus pygmaeus* (E. Schulz, 1937) lives in the sands of the Friesian islands but, like *Halacarus subterraneus*, probably occurs on both sides of the Atlantic.

Halacarids have also been recorded from subterranean waters in caves. C. Walter (1917) described *Soldanellonyx chappuisi*, *S. monardi* (1919) and *Hamohalacarus subterraneus* (1931) from the Donnelson caves of Indiana; the two former species have also been recorded from caves in the Pyrenees and Crete, none of them being restricted to subterranean waters. Viets, however, in 1937, described *Parasoldanellonyx typhlops* and *Stygohalacarus scupiensis* (1934) as truly cavernicolous forms, lacking eye spots and pigmentation.

Apart from water temperatures and type of substratum acting as factors limiting distribution, some Halacaridae are feeders on the algae themselves and are, therefore, found in those conditions which favour algal growth. The whole of the subfamily Rhombognathinae is thus restricted, though otherwise cosmopolitan in distribution.

Just as the Eleutherengona have their aquatic forms, so the Parasitengona have their freshwater and marine representatives. The marine fauna is slight, being represented by a single family, the Pontarachnidae, which includes only two genera, *Pontarachna* (Philippi, 1840) and *Litarachna* (C. Walter, 1922). The freshwater fauna of the Parasitengona is, on the other hand, peculiarly rich, and forms the convenient, but taxonomically heterogeneous, group—the Hydrachnellidae—some of which can be cavernicolous. *Hygrobates longipalpis* (Hermann, 1804), *Neumania limosa* (C. L. Koch, 1836) and *Arrenurus albator* (O. F. Müller, 1776) all occur in caves in Germany.

Unlike the eleutherengonan Halacaridae, none of which can swim, the hydrachnellids include many forms with natatory hairs on the legs (Plate XLV, fig. 5), particularly the third and fourth pairs. The fully aquatic forms are linked ecologically with the terrestrial ones, by such groups as the subfamily Johnstonianinae of the family Trombidiidae, and the Calyptostomidae, which occur in extremely wet habitats. Moreover, some of the aquatic mites can crawl out of the water; for example, the Thyasidae occasionally do this and *Euthyas* overwinters in the ground near water. Species and genera inhabiting waters liable to dry up can aestivate in the dried-out mud for considerable periods. The fact that the hydrachnellids include some forty families shows how successful this invasion of the fresh water has been.

Fresh water can be broadly divided into two types of habitat, running water and standing water. The hydrachnellids of running water are the non-swimming forms; provided with powerful tarsal claws, they cling to and creep among the water plants on stones in rivers and mountain brooks. *Protzia eximia* (G. Piersig, 1897, family Protziidae) is confined to running

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PLATE VI. **1.** *Hyadesia algivorans* (Michael) ♀; dorsal view. **2.** *Rhombognathus notops* (Gosse) ♂; dorsal view. **3.** *Arrenurus maculator* (Müller) ♂; dorsal view. **4.** *Schwiebia talpa* (Oudemans) ♀; dorsal view.

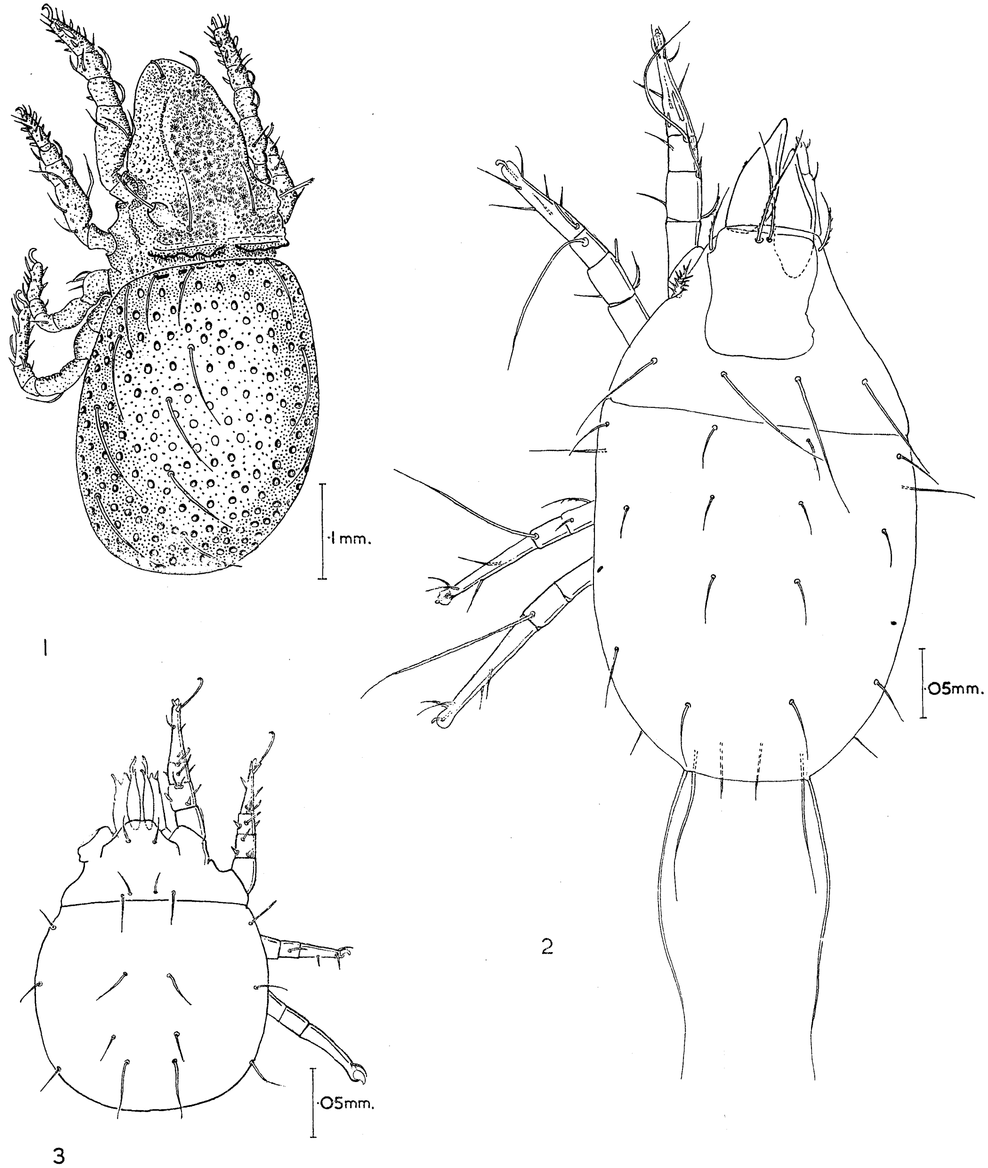


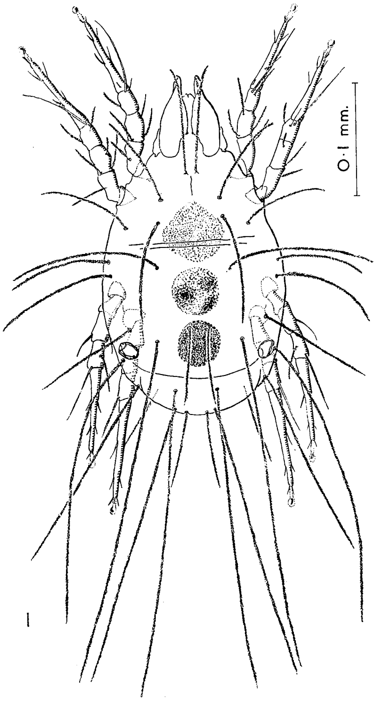
PLATE VII. **1.** *Nanhermannia nana* (Nicolet) ♀; dorsal view. **2.** *Acarus siro* (L) (= *Tyroglyphus farinae*) ♀; dorsal view. **3.** *Histiostoma* (= *Anoetus*) sp.; dorsal view.

water, *Bandakia* (=*Drammenia*) *crassipalpis* (Sig Thor, 1913, family Mamersopsidae) lives in submerged mosses in mountain streams, *Atractides anomalus* (C. L. Koch, 1837, family Atractideidae) also occurs in fast-running rivers and streams in Europe, Russia and Pakistan, and the members of the Feltriidae are similarly adapted for life in moving waters. On the other hand, the Pionidae, Hydrachnidae and Arrenuridae (Plate VI, fig. 3), for example, are provided with natatory hairs and live in lakes and ponds, or slow-moving rivers and streams. *Unionicola crassipes* (family Unionicolidae) with elongated legs has been taken as a free-swimming adult and nymph from depths down to 140 metres; it has also been taken out of *Anodonta fragilis* in Lake Michigan.

Apart from the effect of water movement on the type of hydrachnellid found in any given habitat, temperature also has a considerable effect. *Diplodontus despiciens* (O. F. Müller, 1776) can live over a wide range of temperature, from the cold waters of mountain lakes to the relatively warm ponds of the lowlands. A number of genera have been described as inhabitants of hot springs in various parts of the world; *Eylais thermalis* (Uchida, 1927, family Eylaidae) was found in a hot spring in Formosa, *Thermacarus thermobius* (I. Sokolow, 1927, family Thermacaridae) in hot springs near Lake Baikal and in springs between Kashmir and Tibet, *Thermacarus nevadensis* (Marshall, 1928) in various hot springs of the United States of America and *Partnuniella thermalis* (K. Viets, 1928, family Protziidae) has also been recorded from the United States.

To a very much lesser extent, the Sarcoptiformes show the same sort of transition from damp habitats to a truly aquatic habit. From the habit of living in the moist conditions of moss and decaying leaves, it is but a short step to the amphibious habits of some genera. Among the Oribatei *Scapheremaeus petrophagus* (N. Banks, 1906, family Cymbaeremaeidae) was found on the water-splashed rocks near waterfalls in Yellowstone Park. The mite feeds on the lichen growing on the rock surfaces and shelters in pits in the lichen or in the soft rock. Another species of this genus, *S. marinus*, is found intertidally. *Trimalaconothrus* (family Malaconothridae) lives in aquatic mosses. The genus *Hydrozetes* is aquatic, living on water plants and mosses; *Ceratozetes furcatus* (N. Pearce and C. Warburton, 1905) and *Heterozetes palustris* (C. Wallman, 1917), living under similar conditions, can move on the water surface, as can *Oribatella aquatica* (N. Banks, 1895), although *Hydrozetes* is unable to do so. Like *Scapheremaeus marinus*, *Halozetes* species live intertidally on seaweeds and the family Ameronothridae can also live intertidally, though they are more numerous above the high-water mark.

As in the Oribatei, certain members of the Acaridiae have become aquatic. *Hyadesia* sp. (Plate VI, fig. 1) are found intertidally, and above the tide in the spray zone, where fresh water drains into the sea. A. D. Michael (1901) found the species *algivorans* near Land's End where a small stream flowed across rock in the spray zone. The species *fusca* (H. Lohmann, 1896) has been found in the British Isles and in Patagonia, *uncinifer* (Mégnin, 1889)



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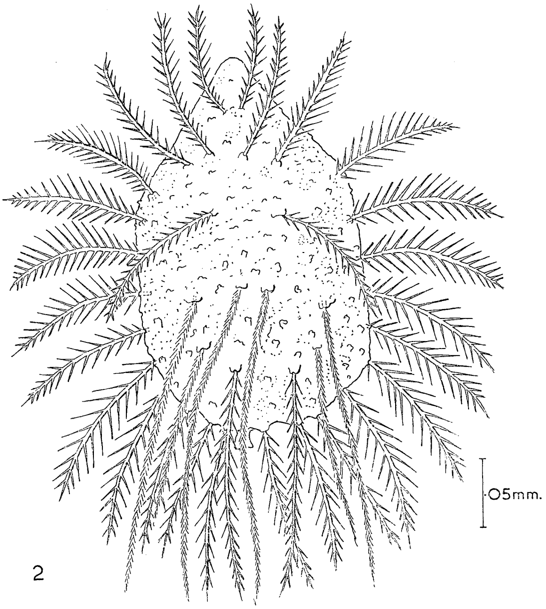

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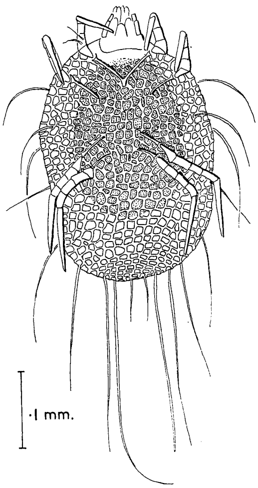

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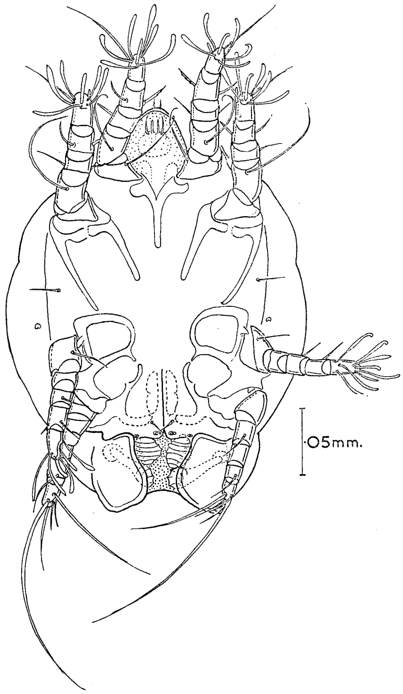

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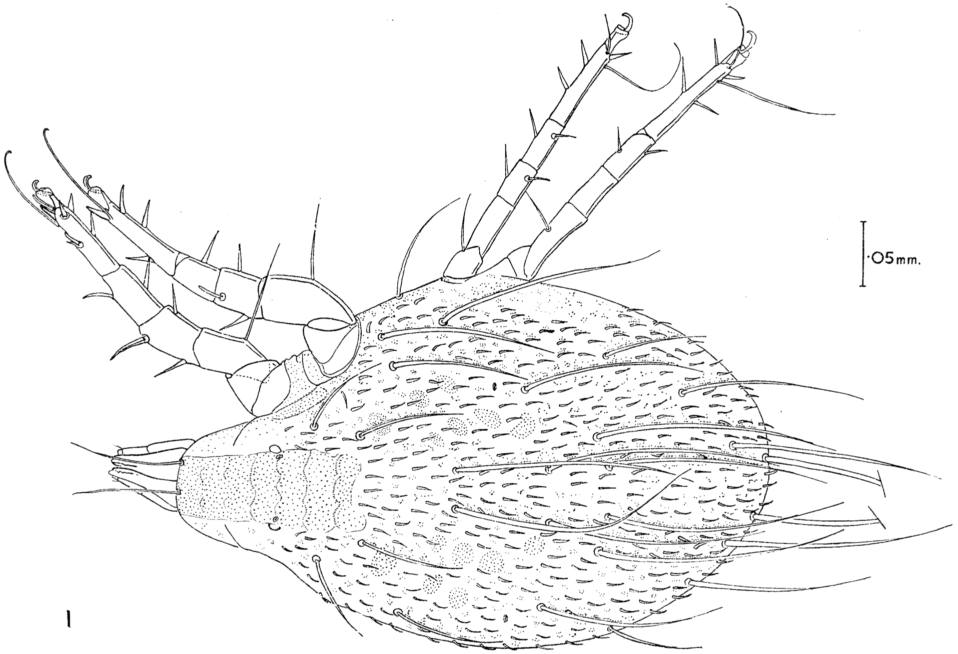
was also found in Patagonia, while on the shore of the Kerguelen Islands a species *kergulensis* (H. Lohmann, 1907) was found. A second genus *Algophagus* (A. M. Hughes, 1955), larger in size and living in fresh water, also occurs on the Kerguelen Islands.

Much more marked, however, is the tendency of the Acaridiae to live in rather drier conditions. Although even as adults they are lightly sclerotized, they appear not to be restricted to such moist habitats as moss, leaf mould and surface vegetation in the same way as the Oribatei, but are able to thrive in somewhat drier situations, though many of them do best in humidities of 70 per cent R.H. and upwards. It may well be that this ability has been a decisive factor in enabling members of this group to become adapted as ectoparasites of birds and mammals, where the humidity of the micro-climate is not very high. The ability to live in drier situations than the soil has undoubtedly enabled them to form a close association with man as pests of stored grain and cereal foods generally, as well as a number of other types of stored products; thus they closely parallel the similar adaptation of some insects to the utilization of human stores, though not to the extent that some of the stored product insects can withstand low humidities.

The Acaridiae do not occur in the soil to any great extent, though *Schwiebea* (Plate VI, fig. 4) is present in many soils and penetrates into the mineral soil below the humus (P. Murphy, 1953). According to C. V. Sorokin (1951a), Glycyphagidae and Acaridae (=Tyroglyphidae) are present in arable soils. This was shown by putting down ground bait in the form of sterilized bags of hay or grain at varying depths in the soil. In view of the fact that other soil investigators have failed to find these forms, these results need careful confirmation. Though the bait, shovels and so on were sterilized, it must be borne in mind that, owing to the small size of these creatures, they can be carried on the boots and clothes of people going into stores to get the bait for filling the bags. The difficulty of deciding where the original habitats of the majority of free-living Acaridiae may have been, arises from the fact that they have become more closely associated with man's activities than the other sub-orders of mites. Thus when they are found in the field, it is not possible to know whether they occur there naturally or have spread from houses, stores and so on in the neighbourhood. Various families, Glycyphagidae (Plate VIII, figs. 1, 2), Acaridae (=Tyroglyphidae), for example, have been found in rodents' nests and in moles' nests. The rodents undoubtedly are vectors between the nests and buildings, though which is the original source it is now impossible to say. In Europe and America such nests, like birds' nests, are reservoirs from which infection spreads to stores, houses and ricks. It therefore happens that the majority of species of free-living Acaridiae have been

PLATE VIII. **1.** *Glycyphagus domesticus* (Degeer); nymph, dorsal view. **2.** *Ctenoglyphus plumiger* (Koch) ♀; dorsal view. **3.** *Glycyphagus destructor* (Schrank); hypopus in protonymphal cuticle, ventral view. **4.** *Labidophorus sciurinus* (Koch), hypopus; ventral view.



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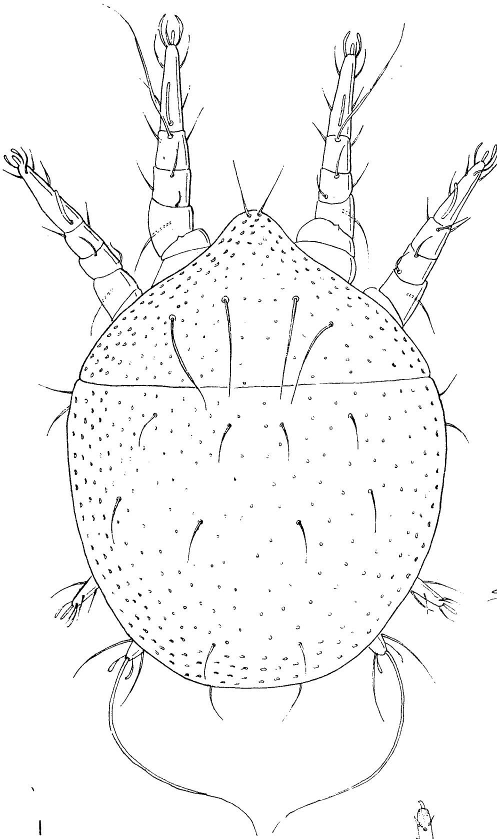
described from specimens collected from such sources. The recent papers of G. E. Woodroffe (1953, 1954) show that birds' nests in dry situations support a mite population which usually includes *Glycyphagus* (Plate VIII, fig. 1), *Acarus* (=*Tyroglyphus*) (Plate VII, fig. 2) and *Tyrophagus* as a regular thing. It may well be that these nests, together with chance accumulations of dry organic material, and the nests of small mammals, are, in fact, the natural habitat rather than the soil, and that the great development of the populations of what were originally rather restricted species is due entirely to their associations with human activities. In this respect the Acaridiae as free-living forms certainly appear to differ from the Oribatei, where huge naturally occurring populations exist in the soil.

Although this group is primarily a vegetable-feeding one, there is a general tendency to select food of a high protein content where this is available. Thus *Acarus siro* (= *Tyroglyphus farinae*) (Plate VII, fig. 2), feeding on grain, by preference attacks the germ first; *Tyrolichus casei* (C. Linnaeus, 1758), which is an occasional inhabitant of nests, is also the typical cheese mite, again showing a preference for a food of high fat and protein content. In parts of France and Germany where farmhouse cheese-making is an industry, deliberate infection of cheeses with mites is carried out to impart the particular bouquet and appearance to the cheese. *Dermatophagoides* (= *Mealia*) (Plate XVI, fig. 2) feeds on animal hair, being found on hides and fur coats, and is also an inhabitant of nests. *Lardoglyphus zacheri* (A. C. Oudemans, 1927) also feeds on animal substances such as hides, *L. konoi* (=*Hoshikadania*; Sasa and Asanuma, 1951) (Plate IX, fig. 2) on dead crabs and the offal which is used for making fertilizers.

There is also a tendency within the group to feed on fungal hyphae and fruiting bodies. The Glycyphagidae show this, cropping the moulds which grow on damp hay and straw. This habit sometimes leads to the building up of serious infestations in damp houses containing furniture upholstered with vegetable fibre, such as dried Algerian fibre (A. M. Hora, 1934). *Caloglyphus spinitarsus* (J. Hermann, 1804) can be a serious pest of cultivated mushrooms, attacking the fruiting bodies. *Caloglyphus* species have been found on decaying animal bodies, and several species have been recorded from bat guano. It seems quite probable that in these latter cases they were feeding on coprophilous fungi. The species of *Rhizoglyphus* feed on decaying plant material, particularly bulbs and other storage organs. On vines they are frequently associated with the bug *Phylloxera vastatrix* which causes the initial damage. It is doubtful whether *Rhizoglyphus* ever attacks healthy undamaged tissue. I have had the species *echinopus* (A. Fumouze and C. Robin, 1868) from the contact beds of sewage disposal works, where the stones were carrying a heavy fungal growth. *Histiogaster corticalis* (A. D. Michael, 1885) occurs on fungus-infested bark of trees, and other species enter decaying reeds.

PLATE IX. **1.** *Hericia hericia* (Robin) ♀; dorsal view. **2.** *Lardoglyphus konoi* (Sasa and Asanuma) ♀; ventral view.



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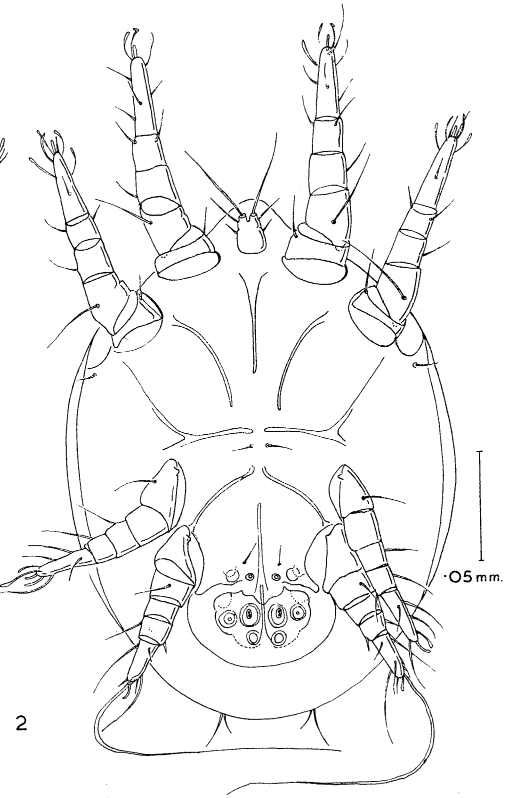

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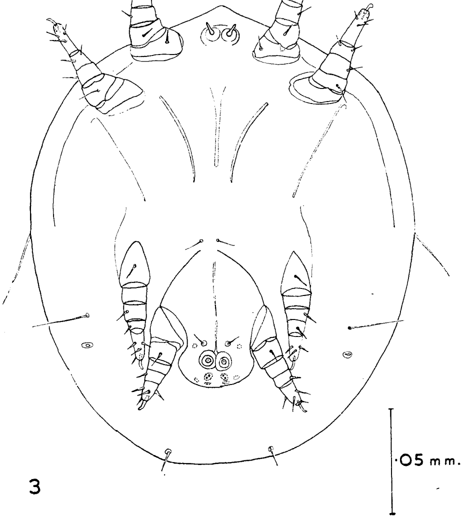

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The genus *Carpoglyphus* contains few species. *Carpoglyphus lactis* (Linnaeus, 1758) shows a predilection for food substances containing sugars, from which bacterial or fungal activity gives rise to the lower fatty acids, like lactic, acetic or succinic acid. The species has, therefore, become a pest of the dried fruit industry, and at times occurs in dried milk powder. It also lives in sweet wines, forming colonies in the neck of the bottle and eventually giving rise to a floating scum on the surface of the wine. The presence of the mite does not lead to any noticeable deterioration of the wine. Another species, *Carpoglyphus munroi* (A. M. Hughes, 1952), was found in a mixture of dead flies and cobwebs in a clock tower, and has since been found in bat roosts; presumably in both cases it was feeding on decaying animal matter. In all these forms there is a tendency to feed on materials which are, or have been, subjected to bacterial or fungal activity.

Perhaps the most remarkable family is that of the Anoetidae (Plate VII, fig. 3); they occur on rotting vegetable matter if it is covered with a fluid film, in the fluid of the pitchers of pitcher plants and other accumulations of water in the axils of plants or inflorescences of tropical plants, and I have had them off the filter beds of sewage works. The original species, *Histiostoma pectineum*, was found on the stove-in end of a barrel of sauerkraut by P. Kramer in 1876. They may also sometimes be found in sap fluxes from damaged trees. The common feature of these diverse habitats is that they all contain a considerable fauna of bacteria and unicellular fungi. The Anoetidae have highly modified mouthparts (T. E. Hughes, 1953) and are filter feeders, combing these micro-organisms from the fluid in which they live by means of the curious chelicerae. To all intents and purposes the family is an aquatic one. In plant sap oozing from damaged trees and resinous exudations, Acaridiae are also found. The genus *Hericia* (Plate IX, fig. 1) is restricted to this type of habitat.

The tendency to feed on foods of a higher protein content than that of the Oribatei, has led in the Acaridiae to the development, not only of parasitic forms, but also of a limited number of predaceous forms, which feed on the eggs of other animals. *Hemisarcoptes malus* (C. Shimer, 1868) feeds on the eggs of the coccid *Mytilococcus pinnaeformis*, *Chionaspis salicis* and *Matsucoccus pini*, while some of the genus *Acotyledon* (family Acaridae) feed on the eggs of Acrididae. In laboratory cultures of insects, such as *Tenebrio molitor*, *Caloglyphus* species, which apparently initially live on the substrate, may increase their food by eating eggs and first instar larvae. A number of other Acaridiae are associated with insects, sometimes quite specifically; for example, *Vidia concellaria* (J. Cooreman, 1948) is found in the nests of hymenopterans of the genus *Cerceris*. In species with restricted habitats, like that of *Hericia* (Plate IX,

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PLATE X. **1.** *Acarus siro* (L) (= *Tyroglyphus farinae*); dorsal view of motile hypopus. **2.** *Acarus siro* (L) (= *Tyroglyphus farinae*); ventral view. **3.** *Acarus siro* (L) (= *Tyroglyphus farinae*); ventral view of inert hypopus.

fig. 1) and the Anoetidae, and among forms associated with specific insects, distribution is largely dependent on the development of the hypopial or 'Wandernymph' stage in the life cycle. This peculiar nymph of the Acaridiae arises as the second nymphal stage in the life cycle of some individuals only. Its production appears, in some cases, to coincide with the presence in the habitat of some species suitable to act as a vector to new localities. The hypopus (Plate X, figs. 1 to 3) is a non-feeding form adapted to cling to other creatures, usually insects, and its function must be one of distribution of the species. In *Hericia hericia* (C. Robin, 1868) I. Robinson (1953) showed that the hypopus appeared at the time of year when the sap flux in which it lived was visited for oviposition by Diptera. *Ensliniella parasitica* (H. Vitzthum, 1925) lives in the nests of *Odynerus delphinalis* and produces these heteromorphic deutonymphs when the *Odynerus* young are about to become the imaginal form, so that the mite becomes carried to new nests.

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CHAPTER II

Associations with other Animals

THE mites enter into relationships of varying degrees of intimacy with a wide variety of other animals. In a great many cases it is not possible to decide what the exact nature of the relationship is. Thus a description of these associations in terms of the precise classification of P. Deegener (1917) does not appear to be justified. Here they are treated under the broader, more general terms of commensalism and parasitism.

Mites may be associated with animals whose way of life provides a source of food for them, and this may degenerate into preying on the 'host' or its eggs. Predaceous mites may utilize such commensals as food, or they may feed on the ectoparasites of other creatures and therefore come to be associated with them. The utilization of particular food sources, also used by other animals, may lead to the exploitation of these animals as a means of transport to new feeding grounds. This type of association is widespread, since mites have no great powers of unaided dispersal.

The building of nests by various vertebrate and invertebrate animals creates localized sources of food, such as organic debris of various kinds. These have been used by a variety of mites as food, and so have often led to associations between the nest-builders and mites which scavenge in the nests. The social insects provision their nests so that, apart from organic detritus feeders, mites are found which pillage these stores just as they do those of man.

The class of association with the inhabitants of colonies, or with animals used as a means of conveyance from one source of food to another, appears to lead to yet another type of association. The secretions of dermal glands, or the desquamated skin of the host, have been utilized by many species as food. The forms deriving their nourishment from the surface of another animal represent a transitional stage between the commensal and truly ectoparasitic forms.

Simple associations

Examples of associations of a simple kind are shown by the Tetrapodili which include various mites, for example the Eriophyidae, which are parasitic on plants and evoke the formation of a variety of galls on the host plant. In these galls live other non-gall-forming species which derive shelter and food from the association. An example of this is the mite *Epitrimerus armatus* (G. Canestrini, 1890) in the bud galls produced by *Eriophyes crategei* (G. Canestrini, 1896) on *Crataegus oxycantha.* This type of association parallels the conditions found in galls induced by insects. Scheuten (1857) figured the mites from the blister galls on pear leaves and took them to be immature forms, because they had only two pairs of legs. With them was an adult which he assumed was the mature stage; in point of fact, his figure shows it to be a parasitid which was doubtless preying on the eriophyid.

The feeding on prey which is itself parasitic is also seen among the Trombidiformes. Many small mammals, particularly rodents, carry on their fur listrophorid mites which are preyed on by *Cheyletiella parasitivorax* (P. Mégnin, 1878), whilst the species *heteropoda* (P. Mégnin, 1878) feeds on the various feather mites which are members of the Acaridiae and live on the feathers or skins of birds. The cheyletid *Syringophilus* (Plate XV, fig. 2) will prey on the acaridian *Syringobia* inside the quills of the flight feathers of geese and similar birds, though it is probable that it can also feed on material inside the quill. The predaceous habit may also lead to associations with animals, the eggs of which are used as food. *Cosmoglyphus dampfi* (A. C. Oudemans, 1928) feeds on the eggs of Acrididae; *Blattiosocius tineivorus* (A. C. Oudemans, 1929) on the eggs and first instar larvae of *Ephestia kuehniella* and *Sitotroga cerealella* and they are found associated with these grain pests. *Acarophenax tribolii* (R. Newstead and H. Duval, 1918) lives under the wings of *Tribolium confusum* and *T. ferrugineum*, feeding on the eggs when laid.

A somewhat similar state of affairs exists between mites and some pagurid crabs. M. André (1937) described *Laelaps pagurophilus* and *Hydrogamasus conchylicola* associated with the ovigerous females of pagurids from the New Hebrides. This association is only temporary, and non-ovigerous females do not carry these mites.

Among the Halacaridae are various genera associated with *Mytilus* and similar molluscs. Species of *Rhombognathus* (Plate VI, fig. 2), for example, live among the byssus threads of the host, and these provide a wet shelter during intertidal periods and a source of food, since various algae grow attached to the byssus. The mites concerned are algophagous and belong to the subfamily Rhombognathinae. The shells of such molluscs often afford a substrate for barnacles, creating a rough surface from which grow filamentous algae. Under such conditions the algicolous mites are often preyed upon by species, such as *Halacarus balticus* (H. Lohmann, 1889).

Distribution

A more enduring type of association occurs when mites make use of some other animal as a means of distribution to new feeding sites. *Eriophyes ribis* (J. O. Westwood, 1869) (Plate XXI, fig. 4), which causes 'big bud' on blackcurrant bushes, comes on to the surface of the gall or on to the leaves, and rears up on to its opisthosoma, swaying the anterior part of its body about in the air. It can hold this position for two or three minutes. Should the mite come into contact with an aphid, ladybird or other insect, it will cling on with the two pairs of legs and get carried away. *Cheletomorpha lepidoptorum* (G. Shaw, 1794) (Plate XXXII) has been found clinging on to hairs of moths by means of the chelate pedipalps. The habits of these mites presumably serve to distribute them more effectively than their own unaided powers of locomotion. Some groups of mites have developed particular structures in certain stages of the life cycle for the exploitation of this type of dispersal. Many of the Acaridiae have a heteromorphic nymphal stage, following the first nymphal instar, called a hypopus or deutonymph; all the members of the species do not, however, pass through this stage. The hypopus has a reduced gnathosoma and does not feed. It is more heavily sclerotized than the other stages of the life cycle and has, on the posterior part of the ventral surface, a complex arrangement of suckers for attachment to a host. Many of the Uropodina have in the second nymphal instar, through which they all pass, a slightly enlarged anal opening. Through this they can eject a thread of sticky material which dries quickly in the air and attaches them to the host (Plate XI, fig. 3). The Parasitidae, which as deutonymphs often make use of other animals as a means of transport, have no very marked modifications of this sort, but cling on to their host by means of their claws. The same methods are adopted by the adult females of the Macrochelidae, Laelaptidae and Tarsonemini, which use this method of distribution. The forms which cling on by means of claws usually choose a sheltered site on the host, such as the 'hairs' between the coxae, if it is an insect. The deutonymphs of the Uropodina and Acaridiae like a smooth surface to adhere to. The animals which serve these mites as distributive agents are those which share with them a common habitat or food source. The coprophagous beetles of the families Scarabaeidae and Histeridae come into contact with mites which may themselves be coprophagous, feed on the mycelia or spores of fungi growing in dung, or which are predaceous on insect eggs and larvae or other mites, and such beetles are frequently found carrying mites. The deutonymphs of *Caloglyphus* species can be found under the elytra of *Geotrupes sylvaticus*, and *Uropoda orbicularis* (O. F. Müller, 1776), *Fuscuropoda marginata* (C. L. Koch, 1839) (Plate XI, fig. 1) and species of *Macrocheles* are common on such beetles too.

The carrion-feeding Carabidae and Silphidae also act as distributors of *Macrocheles glaber* (J. Müller, 1859) and *Parasitus coleoptratorum* (C. Linnaeus, 1758), and species of *Necrophorus* frequently carry *Poecilochirus subterraneus* (J. Müller, 1859, family Poechilochiridae). The Uropodina are, in all probability, mycelium feeders in the majority of cases and are also found as deutonymphs on woodlice, which scavenge wet and decaying organic detritus of various kinds. Thus *Uropodina orbicularis* (Plate XI, fig. 3) has been found on *Oniscus armadillo* and *Fuscuropoda marginata* (Plate XI, fig. 1) on *Porcellio scaber*. Diptera, too, serve as transport for several of the coprophilous

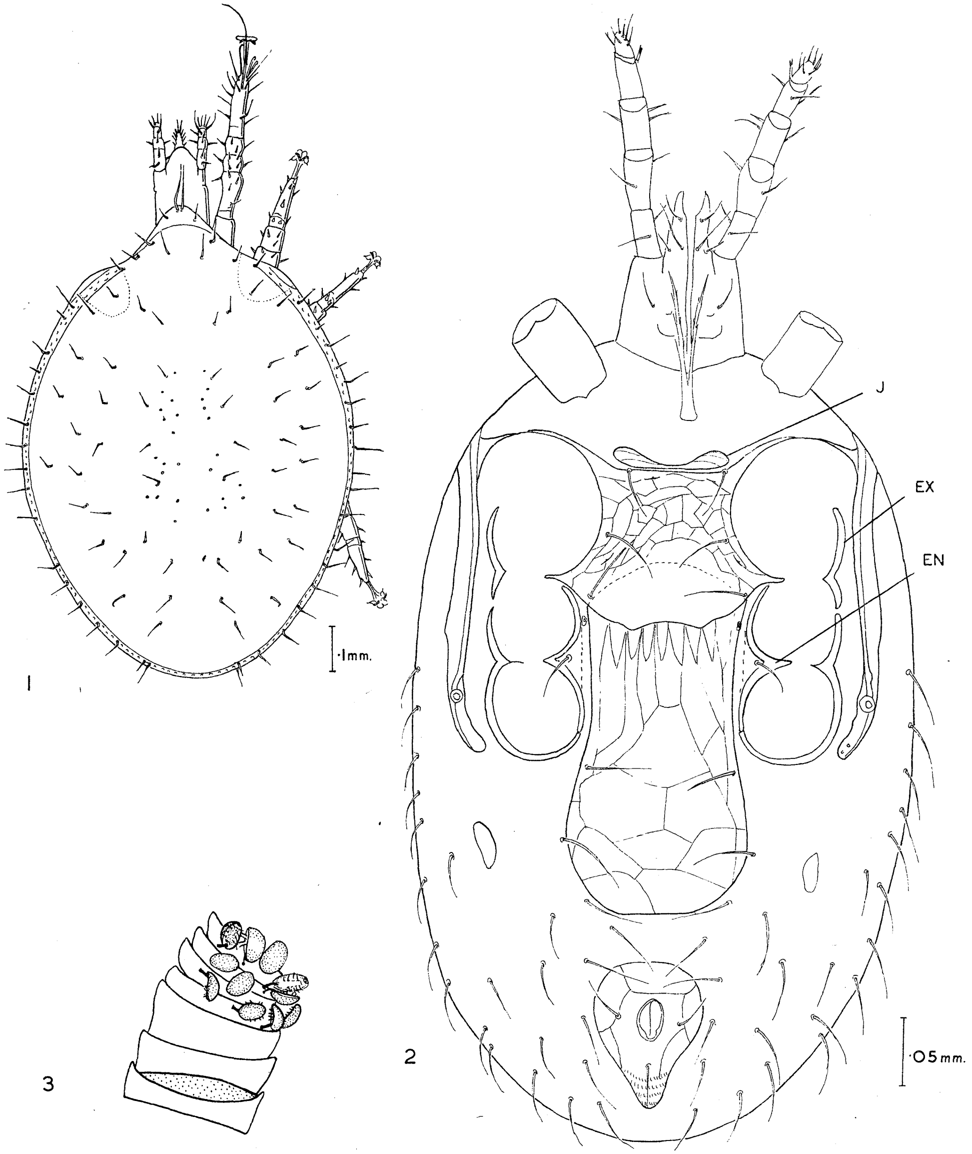


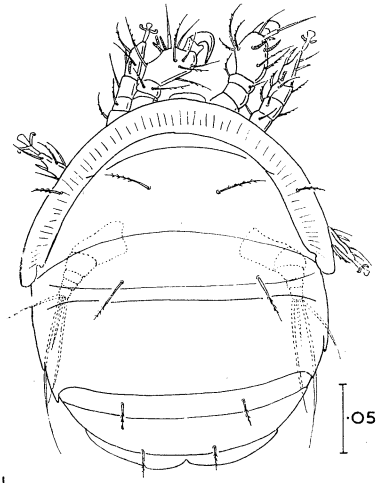
PLATE XI. **1.** *Fuscuropoda marginata* (Koch) ♀; dorsal view. **2.** *Hypoaspis smithii* (Hughes) ♀; ventral view. EN endopodal plate, EX exopodal plate, J fused jugularia. **3.** Uropods on posterior segments of woodlouse.

and carrion-frequenting species. *Macrocheles glaber* has been found on *Calliphora erythrocephala*, *Musca domestica* and *Sarcophaga carnaria*; *Uroseius acuminatus* (C. L. Koch, 1847, family Trachytidae) on boborid flies, and *Parasitus lunaris* (A. Berlese, 1881) on empid flies; whilst females of *Macrocheles muscae* (J. Scopoli, 1771) occur on *Musca domestica*. These relationships are obviously very variable and the host can be any one of a number of species frequenting a common habitat or source of food. The same conditions hold for the hypopi of the Anoetidae; *Histiostoma sapromyzarum* (L. Dufour, 1839) was found on the fly *Sapromyza blepharopteroides*, but has also been found on myriapods and beetles, *Histiostoma formicarum* (H. Vitzthum, 1941) was found on *Myrmica salcinodis*; other anoetid deutonymphs have been found on phytophagous beetles, whilst that of *Histiostoma polypori* (A. C. Oudemans, 1914) is always found on the neck of the earwig *Forficula auricularia*, but what the significance of this choice of site may be, is unknown. Since the anoetids feed on microorganisms in fluid or semifluid media, they are associated with insects, such as beetles and flies, which frequent the accumulations of water in plants or the decaying material in which the active stages of the life cycle find their food; the hypopus *Histiostoma neglectus* (A. Berlese, 1903) was, for example, found on *Necrophorus humator*. In the same sort of way, ectoparasites may carry the hypopi of acarid mites which live in the nests of the ectoparasites' hosts as scavengers; thus the hypopi of *Acarus siro* (=*Tyroglyphus farinae*) (Plate X, figs. 1, 2) have been found on the mole flea *Hystrichopsylla talpae* and the rat flea *Ceratophyllus fasciatus*.

Bark and wood-boring beetles frequently carry mites (e.g. females of Tarsonemini and deutonymphs of Uropodina and Acaridae), the active stages of which live in the tunnels and crevices made by the beetle larvae. *Histiogaster hylecoeti* (see J. Cooreman, 1952) is carried as a hypopus by the wood-boring beetle *Hylecoetus dermestoides* (Lymexilidae), the other stages of this acarid being found in the tunnels of the beetle larvae.

From the examples given, it can be seen that the insects are the most useful group of animals to mites as a means of transport and distribution, though other groups are used as well. The littoral uropod mite *Phaulodinychus orchestiidarum* (T. Barrois, 1887) uses amphipods to distribute the deutonymphs. Mites of the genera *Labidophorus* and *Xenoryctes* (family Acaridae) have hypopi adapted for clinging on to the fur of the small mammals in whose nests they live (Plate VIII, fig. 4); for example *Labidophorus talpae* (P. Kramer, 1877) is found in moles' nests, and *Xenoryctes desmanae* (A. Zachvatkin, 1941) with the musk rat.

In the case of many beetles, it may be that the relationship between mite and beetle extends beyond that of the mite being a mere passenger. The immature stages and, in some cases, the adult mites can obtain food from the excretions of the beetle larvae, or from their dermal secretions. *Coleolaelaps* species, from the larvae to the newly fertilized female, feed on the oily secretions of the larvae of phytophagous scarabaeids. *Hypoaspis krameri*



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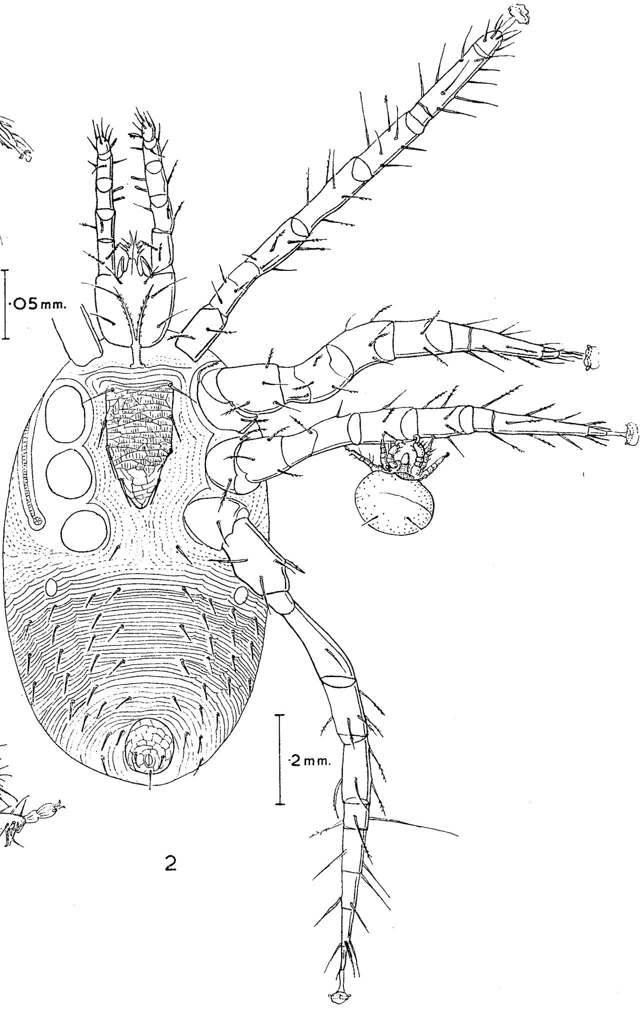

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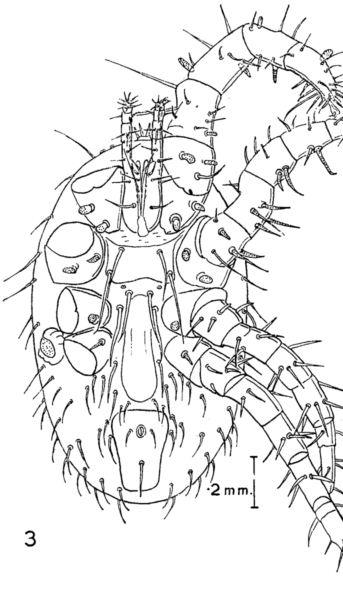

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(G. and R. Canestrini, 1881) and *Coleolaelaps campestris* (A. Berlese, 1887) are associated in this way with *Anoxia matutinalis*, and *Caloglyphus spinitarsus* (O. Hermann, 1804) with *Osmoderma eremita*, the adult beetles spreading the mites to the new breeding sites. It appears very probable that some such relationship exists between the host and many of the mites found as adult laelaptids or deutonymphs of acarids on beetles.

Nest dwellers

There are many mites which obtain food and shelter by association with animals which build nests. The mites may be general scavengers of the nests or they may eat food stored by the rightful owners of the nests. The species of *Labidophorus* and *Xenoryctes*, mentioned above, together with other Acaridiae found in the nests of mammals and birds, are, so far as is known, scavengers of organic detritus. *Eulaelaps* species, also associated with small mammals' nests, are said by H. Vitzthum (1943) to be coprophilous; but they also occur frequently with acarid mites on stored grain. Though it is possible that they are dropped by chance from mice or rats, their frequency does not suggest this, and it seems probable that they are predaceous on other mites and are feeders on organic detritus, too. The same sort of association also occurs with *Haemogamasus nidi* (A. D. Michael, 1892) which may carry females of *Scutacarus talpae* (A. C. Oudemans, 1913), just as *Eulaelaps cricetuli* (H. Vitzthum, 1930) carries the deutonymphs of *Cilliba eulaelaptis* (H. Vitzthum, 1930, family Uropodidae); *Eulaelaps stabularis* (C. L. Koch, 1839) occurs in the nests and on the animals and can be found containing blood, so that it can be parasitic as well as probably scavenging. *Haemogamasus pontiger* (A. Berlese, 1889) is also found containing blood in nests and on animals such as mice and rats and it also occurs among acarid mites on stored grain and does not then contain blood. This species can be bred through its life cycle on Bemax (wheat germ), so that it, too, is a facultative parasite (personal communication, A. M. Hughes). Typical scavengers (Plate XI, fig. 2) and detritus feeders, such as *Hypoaspis dasypus* (G. Menzies and R. Strandtmann, 1952) found in an armadillo's nest, also occur; and in birds' nests, *Acarus siro* (C. Linnaeus, 1758 (= *Tyroglyphus farinae*)) and *Glycyphagus domesticus* (K. Degeer, 1778), with their cheyletid predators—*Cheyletus eruditus* (Schrank, 1781) and *Acaropsis docta* (A. Berlese, 1886)—are also found. Some forms, e.g. *Labidophorus* and *Xenoryctes*, only live in such associations, as do *Talpacarus platygaster* (A. D. Michael, 1886) and *Oryctoxenus dispar* (A. D. Michael, 1886), both of which species frequent moles' nests. Uropodina and Oribatei also occur in mammals' nests. For example, the oribatid *Nanhermannia hirsuta* (A. G. Hartman, 1949) has been found in an armadillo's nest, and *Leiodinychus jeanneli* (M. André, 1945)—a uropod—in

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PLATE XII. **1.** *Scutacarus* sp.; dorsal view. **2.** *Parasitus fucorum* (Degeer); from *Bombus* sp., with *Scutacarus* attached to it. **3.** *Dinogamasus* sp. from a xylocopid bee.

the nest of a mole rat, but these, like *Acarus siro* and *Glycyphagus domesticus*, are, as it were, casual visitors capable of living elsewhere.

The social insects build nests of varying degrees of complexity which contain stores of food and a certain amount of detritus, and it is, therefore, not surprising that these nests support a considerable fauna of mites. *Ensliniella parasitica* (H. Vitzthum, 1925) lives in the earthen cells of the wasp *Odynerus*, and spreads as the deutonymph, which is carried by the female wasp. The related *Vidia concellaria* (see J. Cooreman, 1948) lives with the sphecid wasp *Cerceris aranaria*; the immature stages and adults feed on the curculionids provided by the wasp for its own larvae, and the hypopi are spread by the female wasps, when they emerge. Other species occur with megachiline bees. *Parasitus vesparum* (A. C. Oudemans, 1905) lives in the nests of *Vespa vulgaris* and appears to be coprophagous, since it also occurs on the accumulations of faeces under the nests; its methods of distribution are unknown.

Bees of the genera *Bombus* and *Psithyrus* are often found carrying the deutonymphs or adults of *Parasitus fucorum* (K. Degeer, 1778) (Plate XII, fig. 2), and other species of *Parasitus*, the hypopi of *Tyroglyphus fucorum* (A. C. Oudemans, 1903) and, occasionally, females of *Pneumolaelaps* species. The females of *Scutacarus femoris* (G. Le Gros, 1848) are also very commonly carried. The nests of the bees have not been investigated to any extent, but it seems highly probable that the species of *Parasitus* are coprophagous and detritus feeders. The Tarsonemini (Plate XII, fig. 1), like *Scutacarus femoris*, have mouthparts suitable for piercing and sucking. It is, therefore, not unreasonable to suppose that they either parasitize the larvae, a habit of other tarsonemids, or else steal honey from the bees' food store.

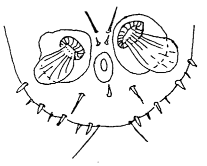
The xylocopid bees are associated with the genus *Sennertia* (family Acaridae), *Xylocopa violacea* of Southern Europe is associated with *Sennertia cerambycina* (J. Scopoli, 1763), *Xylocopa frontalis* with *Sennertia donaldi* (F. A. Turk, 1948), the hypopi being carried by the adult bee. The other stages of the mite probably feed on the pollen with which the cells are provisioned. Of the various species of *Chaetodactylus* which have been taken as hypopi from species of *Osmia, Andrena* and *Megachile* (such as *Chaetodactylus dementjevi* (A. Zachvatkin, 1942) from *Megachile* species and *Pseudovespa germanica*), nothing is known as to the feeding stages in the life cycle. It is known, however, that the active stages of *Chaetodactylus ludwigi* (E. Trouessart, 1904) live on the food made from pollen by *Lithurges dentipes*; and it is to be assumed that the others, too, steal the provisions for the larvae of the host.

The bees of the genus *Mesotrichia* (Xylocopidae) have a cavity beneath the first abdominal tergite which opens to the exterior by a median slit. In this cavity are usually to be found adult female mites of the genus *Dinogamasus* (family Laelaptidae). The various species of *Dinogamasus* (Plate XII, fig. 3) show great specificity for particular species of the various subgenera of *Mesotrichia*. *Dinogamasus villiosior* (A. Berlese, 1918) is restricted to the subgenus *Mesotrichia s. str.*; a group of species is restricted to the African species of *Koptorthosoma*, a second group to the Asiatic species, being recorded from Java, Sumatra and the Philippines. The other two subgenera, *Platynopoda* and *Cyanoderes*, each have their own groups of *Dinogamasus* species. The immature stages live in the nests of the bees, and it is known that females transported to new nests lay their eggs with the bees' eggs or on the pupae when these develop. N. Le Veque (1930) thought the mites feed on pollen, but they might equally well be coprophagous and scavenging.

The stingless bees have, living in their nests, Macrochelidae of the genus *Trigonholaspis*. These mites are coprophilous, as are many Macrochelidae, for example *Macrocheles coprophila* (H. Womersley, 1943), and trigonid bees accumulate quantities of faeces in their nests. Meliponid bees harbour species of *Hypoaspis* in their nests, *Hypoaspis favosus* (see F. Turk, 1948) is found with *Melipona favosa* and *Hypoaspis alphabeticus* (A. Berlese, 1904) with *Melipona interrupta*; they are presumably general detritus feeders like other species of *Hypoaspis*.

The honey bees of the apiarist commonly support *Acarus siro* (*Tyroglyphus farinae*) and *Glycyphagus domesticus*, the pollen the bees collect being the probable attraction; *Tarsonemus apis* (J. Rennie, 1918) is extremely common, though it is not known how it feeds. H. Homann (1933) has reported the presence of *Parasitus coleoptratorum* (C. Linnaeus, 1758) and *Chaetodactylus osmiae* (L. Dufour, 1839) in sound stocks of bees, and bees suffering from virus or bacterial infections are said to be subject to associations not found in sound stocks, such as *Uroseius acuminatus* (C. L. Koch, 1847, family Trachytidae).

Ants' nests also harbour mites from many families. Many of these are oribatids and parasitids which get into the nests by chance, but others form lasting associations with the ants. *Macrocheles vagabundus* var. *neotropicum* (A. Berlese, 1918) and *Coprholaspis mundus* (A. Berlese, 1918, family Macrochelidae) are found with *Acromyrmex lundi*; *Gymnolaelaps laevis* (A. D. Michael, 1891) is widespread among the species of *Formica*. These and other Mesostigmata, such as species of *Hypoaspis*, *Androlaelaps* and *Pachylaelaps* (Plate IV, fig. 1), are scavengers of bodies, exuvia and other detritus, the Macrochelidae being also coprophagous. Many genera of Uropodina live with ants and probably feed on the mycelia and spores of fungi, and on organic detritus. For example *Uroobovella obovata* (G. Canestrini and A. Berlese, 1884) is found with *Lasius alienus* and the genera *Urojanetia*, *Urodiscella*, *Oplitis* and *Marginura* include many forms distributed among the various species of ants all over the world. The Acaridiae are represented by *Forcellinia wasmanni* (R. Moniez, 1892) in the nests of *Camponotus ligniperdi*, *Formica sanguinea* and *Lasius juliginosum*; they are probably general scavengers of these nests. H. Vitzthum (1919) described a deutonymph *Froriepia vimariensis* on *Lasius fuliginosum* and in 1941 *Histiostoma formicarum* on *Myrmica salcinodes*. Here the ants are acting as a means of distribution of mites, the other stages of which live in places frequented by the ants, rather than in their nests. The Trombidiformes



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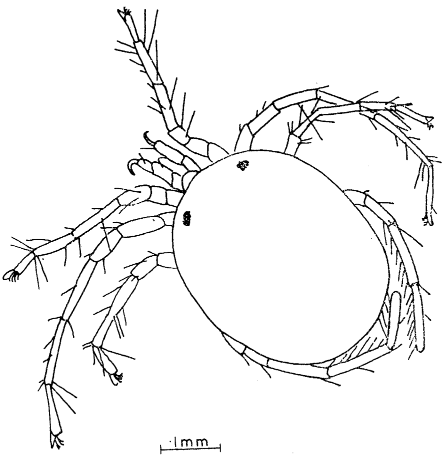

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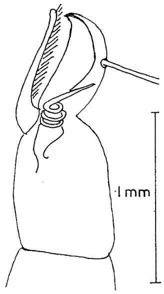

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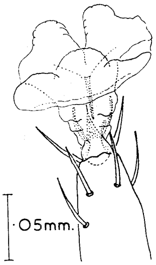

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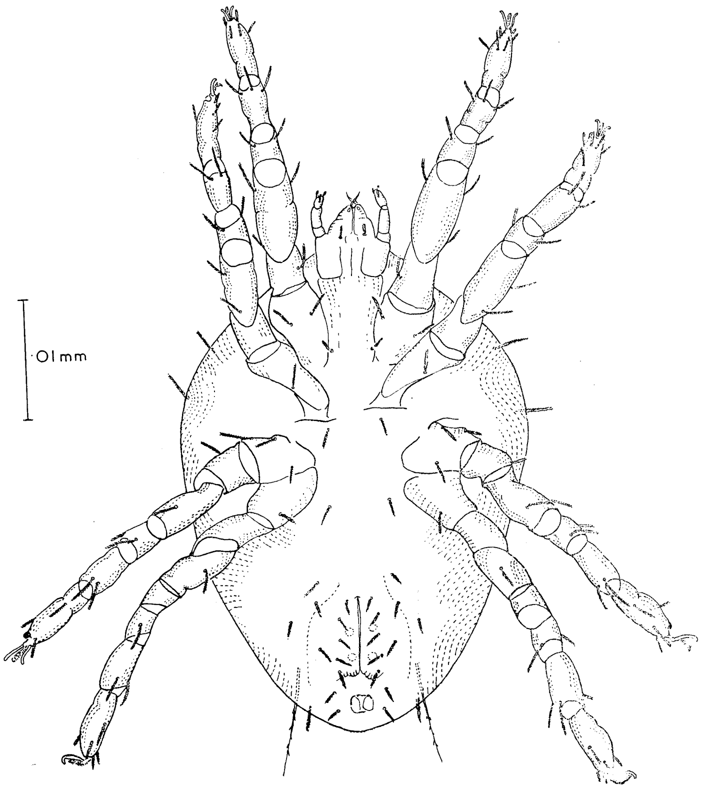

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are represented by *Scutacarus longisetus* (G. Paoli, 1911) in nests of *Lasius flavus*, *Scutacarus circularis* (A. Berlese, 1903) with *Camponotus aethipos*, *Leptothrombium oblongum* (I. Trägårdh, 1904) in nests of species of *Messor*, and more recently, H. Womersley (1944) has reported *Caecothrombium burraensis* from ants' nests in Australia. Nothing is known of the biology of these forms.

A very similar fauna of scavenging forms is found in the nests of termites. The Mesostigmata include species of *Urozercon* (Laelaptidae), *Hypoaspis hospes* (A. Berlese, 1923), *Zuluacarus termitophilus* (I. Trägårdh, 1906, family Liroaspidae) and, among the Acaridiae, *Caloglyphus viduus* (A. Berlese, 1901). These forms are probably all general scavengers. Various uropods have also been found, such as *Urojanetia termitophila* (I. Trägårdh, 1906) and *Dentidinychus zikani* (M. Sellnick, 1926); they are probably feeding on mycelia of fungi which grow in termites' nests. Among the Trombidiformes are *Leptothrombium oblongum* and *Eucheyla panamensis* which were reported on the eggs of termites by E. W. Baker (1949), and *Tarsonemoides termitophilus* (I. Trägårdh, 1904). The trombid mites may well be predaceous on other small inmates of the nest, or suck the eggs and larvae of the termites. *Eucheyla loricata* (A. Berlese, 1913) was found in moss, and species of *Eucheyla* and tarsonemids, too, have been found with acarid mites on stored grain and also in birds' nests, and in these cases they are almost certainly predaceous.

Feeding on the surface of the host

Mites may also form more intimate associations with animals, living on their bodies and obtaining food from the secretions of skin glands and the debris of skin or cuticle. Among the Arthropoda, the Myriapoda, Insecta and Crustacea can all support various mites in this way, and the lamellibranch and pulmonate molluscs, freshwater sponges, birds and mammals also take part in this type of relationship.

Some of the Hydrachnellida are associated with lamellibranchs, the commonest species belonging to the genus *Unionicola* (Plate XIII, fig. 2) (family Unionicolidae) and its subgenera *Pentatax* and *Hexatax*. The eggs are laid on the inside of the mantle which forms a cyst round them. *Unionicola ypsilophora* (Bonz, 1783) has larvae which leave the mollusc, whilst *Pentatax intermedia* (F. Koenike, 1882) lives its whole life in the mantle cavity of *Anodonta* species; in this case food is derived from the ciliary currents set up by the mollusc's gills. Various other types of life cycle are known in which the larval or nymphal stages return to the shelter of the mollusc to moult. Some species of *Hexatax* lay eggs in the freshwater sponges of the genus

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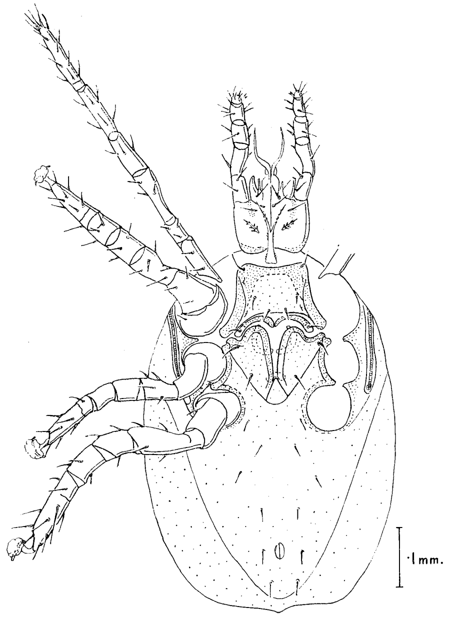
PLATE XIII. **1.** Discozerconidae, ♂ from Myriapod; ventral view of hind end of idiosoma. **2.** *Unionicola* sp. nymph from *Unio* sp.; dorsal view. **3.** Discozerconidae; chelicera of ♂ showing spiral spermatophore-carrier and comblike setae. **4.** *Julolaelaps* sp. from Myriapod; tarsus I. **5.** *Riccardoella limacum* (Schrank) from slug; ventral view.



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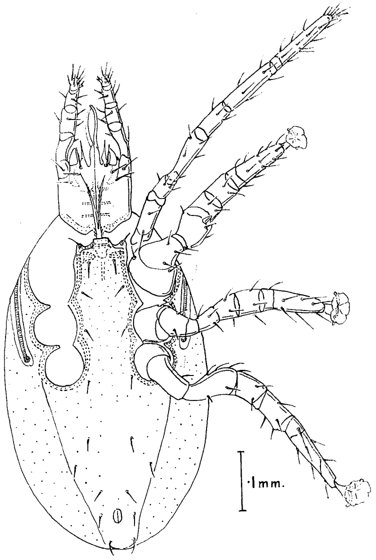

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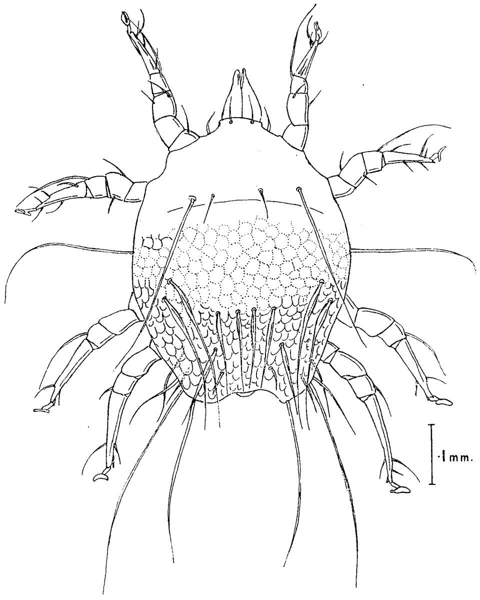

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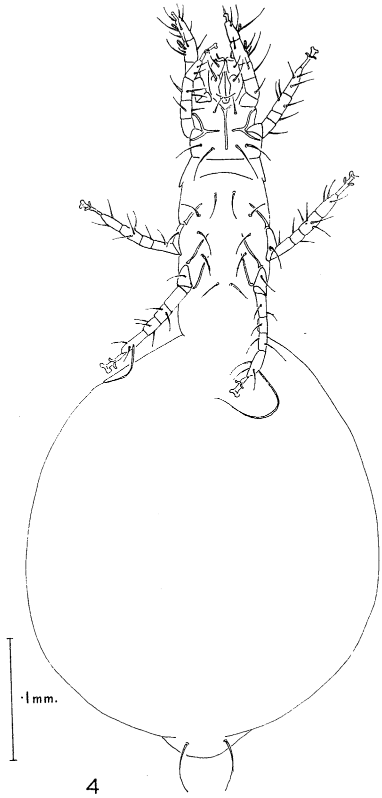

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Spongilla, and *Unionicola ampullaria* (F. Koenike, 1890) was found in a South American species of *Ampullaria*. The terrestrial pulmonates usually harbour species of *Riccardoella* (family Ereynetidae) in their mantle cavities. The eggs are stuck on to the inside of the pulmonary cavity, and the active stages feed on the mucus and sloughed cells from the mantle surface. *Riccardoella limacum* (Schrank, 1781) (Plate XIII, fig. 5) is of widespread occurrence and *Riccardoella oudemansi* (Sig Thor, 1931) was reported from *Helix pomatia* in Mexico by E. W. Baker (1945).

Mites may also live in the branchial chamber of freshwater decapods. Species of Halacaridae of the genera *Porolohmannella* and *Porohalacarus* have been found in *Potambius astacus*. They can obtain food from the respiratory current of the crayfish, which is perhaps easier than swimming about in search of it. The pagurids, which have already been mentioned in connection with mites that probably steal their eggs, can also carry mites in their branchial chambers or on the body surface. Von Frauenfeld (1868) gave a description of mites found on the soft-shelled abdomen of *Calcinus tibicen* living in a Triton shell and called the mite *Cyclothrix carcinicola*. H. Vitzthum (1928) described mites from species of *Coenobita* from Sumatra which he considered to be the same species of mite. These mites, of the family Megisthanidae, spend their entire life cycle within the shelter of the mollusc shell inhabited by the crab, and feed on detritus and the exudations of the host. The land crab *Birgus latro* frequently houses, in its respiratory chamber, adults of *Cyclothrix latronis* (H. Vitzthum, 1937), together with the hypopi of *Caloglyphus birgophilus* (H. Vitzthum, 1937). The other stages of the life cycles of these mites may be spent in the holes or burrows which *Birgus* makes according to H. Vitzthum (1937). A. Pearse (1929) described *Laelaps cancer*, adult females, nymphs and eggs from the branchial chamber of *Geocarcinus lateralis* (Decapoda, Brachyura) from the islands of the Dry Tortugas. It is noticeable that in the case of the pagurids and this brachyuran, the mites are related to terrestrial groups, since Megisthanidae occur typically on beetles, and the crabs have become terrestrial in that they may be said to live above the tide line.

The Myriapoda carry a surprising number of mites of the families Antennophoridae, Parantennulidae, Heterozerconidae and Discozerconidae (Plate XIII, fig. 1), and the method of clinging on to the smooth surface of the host varies with the different families. The Antennophoridae are the least specialized, having claws and suckers on the last three pairs of legs; the Parantennulidae rely on tarsal suckers, the claws being very reduced. The other two families have developed a large sucker on either side of the anus

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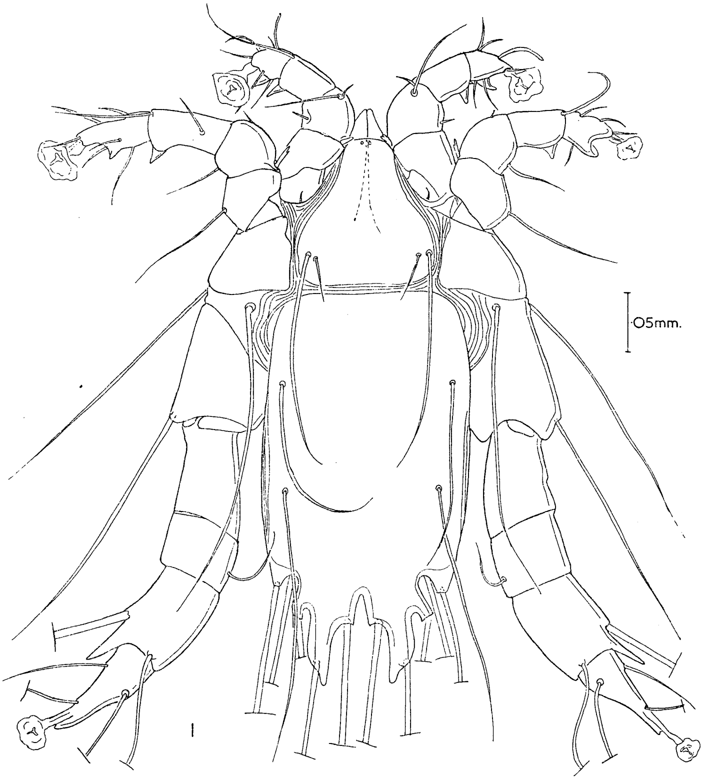
PLATE XIV. **1.** *Lobogynium* sp. (Diplogynidae) ♀; from a Hercules beetle; ventral view. **2.** *Lobogynium* sp. (Diplogynidae) ♂; ventral view. **3.** *Percanestrinia* (*Percanestrinia*) *saetolata* (Cooreman) from a carabid beetle; dorsal view. **4.** *Pyemotes ventricosus* (Newport) ♀; ventral view.



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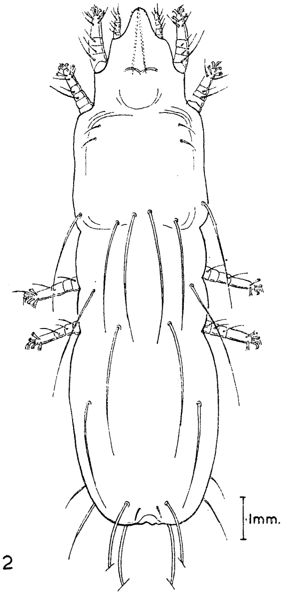

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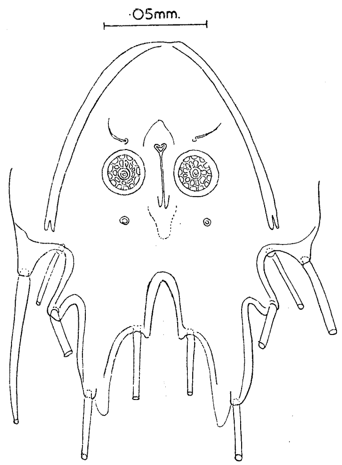

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and extending forward to the region just behind the fourth pair of legs; it may be an enlarged and modified metapodal plate. The Antennophoridae, Discozerconidae and Parantennulidae have chelicerae provided with numerous flap-like projections on the digits, and it is thought that these may be used in wiping the secretions of the dermal glands from the myriapods' body surface. There are a few species of laelaptids (Plate XIII, fig. 4) found on myriapods: *Hypoaspis spirostrepti* (A. C. Oudemans, 1914) and *Hypoaspis indicus* (H. Vitzthum, 1921), *Jacobsonia minor* and *J. submollis* (A. Berlese, 1910); the two latter species were found on scolopendrids in Sumatra and Java. *Jacobsonia minor* is always associated with *Heterozercon audax* (A. Berlese, 1910), which suggests some more complex relationship than is at present understood.

In all these cases it appears that both sexes of adults can be found on the myriapods; the rest of the life cycle, in some cases at any rate, seems to be free-living. *Neomegistus juliolicola* (I. Trägårdh, 1906, family Antennophoridae) has immature stages which live in rotting vegetation. The laelaptids which are found as adults on myriapods are, presumably, making use of the ability to feed on organic residues, which so many of the group possess.

The Megisthanidae, Antennophoridae, Diplogynidae (Plate XIV, figs. 1, 2) and Fedrizziidae, which have similarly modified chelicerae, are also found on beetles under their elytra. *Fedrizzia helleri* (A. C. Oudemans, 1929) occurs in the Argentine on passalid beetles, *Megisthanus thorelli* (H. Womersley, 1937) on passalids in Australia, and *Antennurella trouessarti* (A. Berlese, 1903) on passalids in Brazil. These families seem to show a choice for passalids and the mouthparts appear to be suitable for making use of glandular secretions of the beetles. *Pachylaelaps penicilliger* (A. Berlese, 1920) is found on phytophagous scarabaeids and *Gamasellus cultriger* (G. Lombardini, 1946, family Allolaelaptidae) as a nymph on a passalid beetle. It is thought, since in no case do all the stages of the life cycle occur on the beetle, that the other stages are probably associated with the beetle larvae. There are, however, mites which spend their entire life cycle on beetles, living under the wings on the body surface. The Acaridiae include two families, the Canestriniidae (Plate XIV, fig. 3) and the Linobiidae which are confined entirely to phytophagous beetles. *Paramansia menthastri* (J. Cooreman, 1950) lives on the chrysomelid *Chrysomela menthastri* and *Photia chrysocarabi* (J. Cooreman, 1950) on *Chrysocarabus auronitens* and *Carabus nemoralis*. *Linobia coccinella* (J. Scopoli, 1763) was collected from a Mexican chrysomelid. It seems possible that the acarid *Melisia melisia* (G. Lombardini, 1944), both males and females of which were found under the elytra of an American passalid, might also be restricted to the beetle.

Mites which derive their sustenance directly from their hosts are found in

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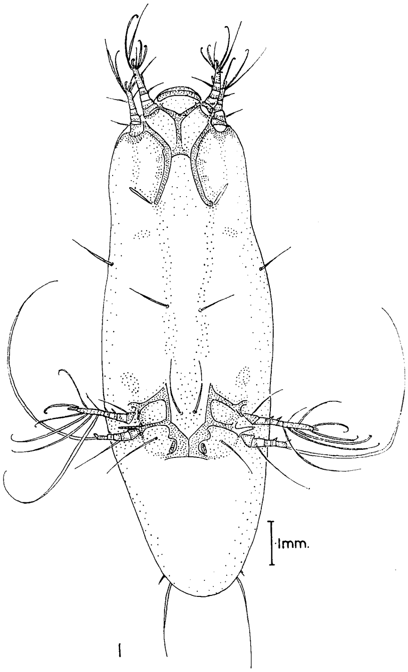
PLATE XV. 1. *Mesalges similis* (Berlese) ♂; dorsal view. 2. *Syringophilus* sp.; dorsal view. 3. *Mesalges similis* (Berlese) ♂; ventral view of posterior end of idiosoma.



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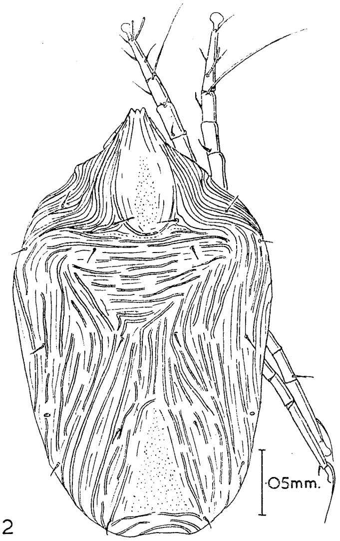

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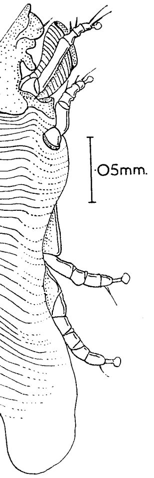

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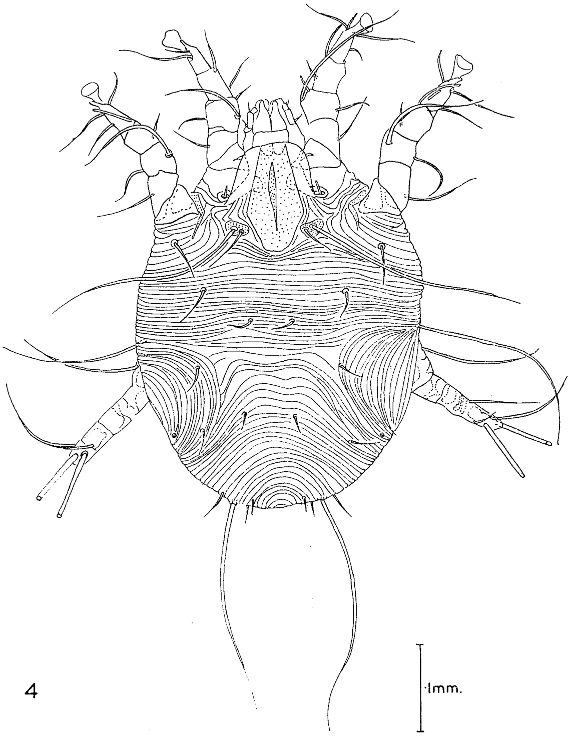

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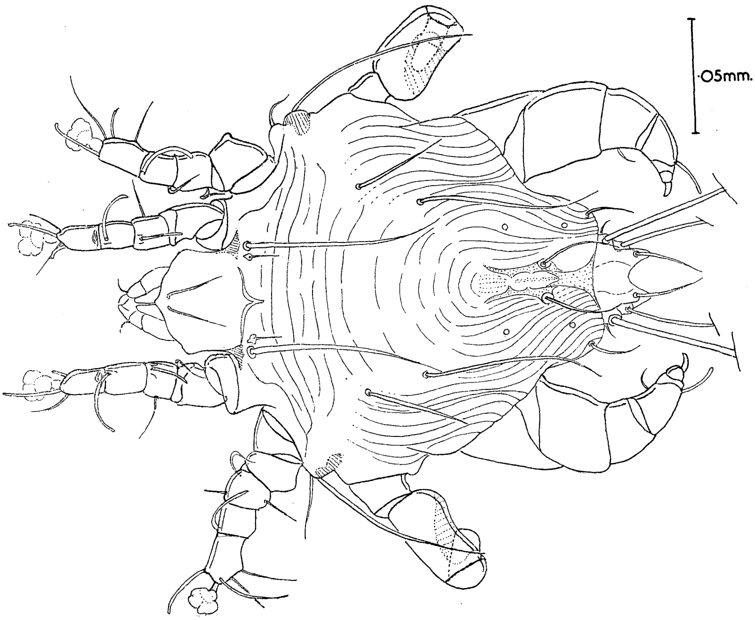
ants and termites' nests. *Holostaspis isotricha* (F. Kolenati, 1858, family Laelaptidae) is said to feed on the saliva deposited on the eggs of *Formica* species by the worker ants, and *Eucheyla panamensis* (E. W. Baker, 1949) might be occupied in the same way with the eggs of termites, though it is more probably eating them. Many laelaptid species cling on to the bodies of ants; A. D. Michael (1891) described *Laelaspis equitans* riding on workers of *Tetramorium caespitum*, and I. Trägårdh (1906), *Myrmonyssus equitans* on *Pheidole* species; *Myrmonyssus eidmanni* (see M. Sellnick, 1945) was found on *Cremastor impressa.* The method of feeding is probably the same as that of the Antennophoridae which ride on ants. In their case they have exploited the habit of trophyllaxis or reciprocal feeding which plays such an important part in the economy of ant societies, and, according to Wheeler, this may be to a great extent responsible for holding such societies together. The species of *Antennophorus*, such as *forelli* (E. Wasmann, 1897) on *Lasius alienus* or *emerginatus* (N. Banks, 1916) on *Ponera lutea*, takes up a position beneath the ant's head, facing forwards. When the ant regurgitates a drop of fluid to feed a fellow ant, the antennophorid uses its modified chelicerae to whisk a part of the drop into its own mouth. These forms are, thus, really parasitic on the ants.

Transition to ectoparasitism

The mites which live on vertebrates and derive their food from secretions of the skin and debris are much more restricted. Antennophoridae of the genus *Ophiomegistus* are found on snakes and lizards. The majority of epizoic species, however, are found on birds and to a much lesser extent on small mammals, and all belong to the Acaridiae. Sitting along the barbs of the stiff flight feathers of birds and on the stiffer parts of the contour feathers in rows, can be found members of the Analgesidae (Plate XV, fig. 1), Falculiferidae, Pterolichidae and Proctophyllodidae. In the shafts of the quill feathers live Dermoglyphidae, and on the skin Epidermoptidae and Heteropsoridae. The forms found on the vanes of the feathers are, it is said, feeding on the oily secretions of the coccygeal gland with which the feathers are lubricated (E. Lönnfors, 1931). Though this may well be so, the quite normally developed chelate chelicerae suggest that they may also eat scales from the feather surface and skin, and G. Haller (1880) has found feather fragments in the guts of feather mites. Moreover, feather mites occur on birds such as the ostrich and bustard, which are said not to possess a coccygeal gland.

There does not appear to be any very great host specificity among the feather mites. The Falculiferidae are restricted to the Columbidae and *Microspalax chanayi* (E. Troussart, 1885) is found only on the turkey *Melleagris*

PLATE XVI. **1.** *Falculifer* sp. hypopus; ventral view. **2.** *Dermatophagoides longior* (Trouessart) ♀; dorsal view. **3.** *Listrophorus leuckarti* (Pagenstecher); lateral view. **4.** *Otodectes cynotis* (Hering) ♀; dorsal view.



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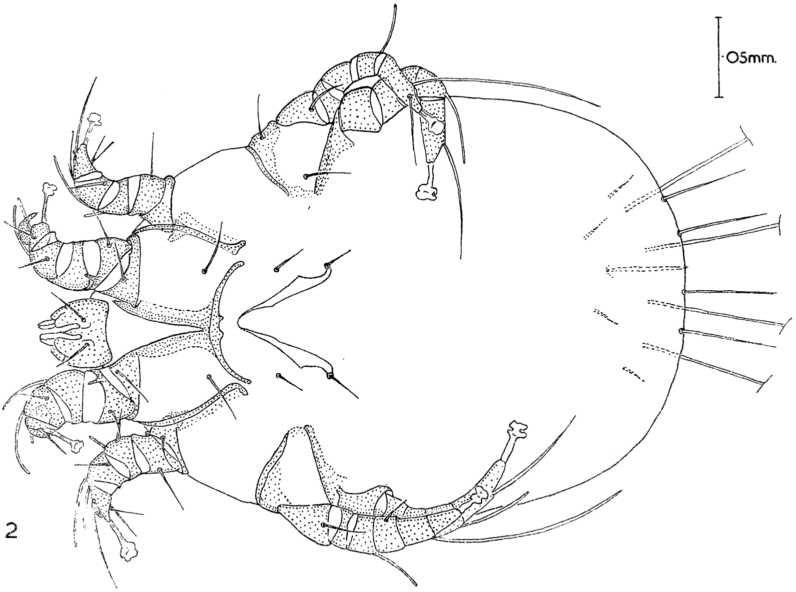

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PLATE XVII. **1.** *Myocoptes musculinus* (Koch) ♂; dorsal view. **2.** *Microlichus uncus* (Vitzthum) ♀; ventral view.

gallopavo. Some of the feather mites give rise to a hypopial form in the subcutaneous tissue of the host, for example *Falculifer rostratus* (R. Buckholz, 1869) (Plate XVI, fig. 1) and the genera *Michaelichus*, *Pterolichus* and *Kramerella*. Such hypopi may serve to perpetuate a colony over the moulting period of the host. It is not at all clear how the hypopi get into the subcutaneous tissues; no exuvia is found with them, so that the moult to and from the hypopial stage must take place on the feathers. Having no mouthparts and very reduced legs, it is not possible for them to bore their way in. G. M. Spurlock and J. T. Emlen (1942) suggested that the migration is through the feather follicles or respiratory tract for *Falculifer rostratus*, and H. Vitzthum (1943) favours a movement through the superior umbilicus of the developing feathers and out of the inferior umbilicus of the fully developed feather. This is presumably the method of entry used by the Dermoglyphidae which live in the feather shafts, since there is no other opening into the quill at any period.

The forms living in quills and feeding on the substance of the quill are, in effect, parasites. The Epidermoptidae, e.g. *Microlichus uncus* (H. Vitzthum, 1934) (Plate XVII, fig. 2) and Heteropsoridae may feed on desquamated cells from the skin, but they can also abrade the surface with their chelicerae and give rise to skin irritation and excessive desquamation.

Small mammals carry members of the Listrophoridae in their fur. The pedipalps of the genus *Listrophorus* (Plate XVI, fig. 3) are modified for gripping the hair; in other genera the legs are used. In the genus *Myocoptes* (Plate XVII, fig. 1) the third and fourth pairs of legs carry curved and broadened tarsal claws for this purpose. In the genus *Labidocarpus* the first and second legs are highly modified; they possess a short femur, followed by a broad curved structure composed of the other leg segments fused together; these form powerful clasping organs.

Species of *Listrophorus* feed by rasping scales off the hair surface and on sebaceous secretions on the hair; *Myocoptes musculinus* (C. L. Koch, 1844) (Plate XVII, fig. 1), however, pushes its gnathosoma down beside the hair into the follicle and feeds on the softer tissue there. This can cause considerable irritation of the skin, and in laboratory stocks of mice this species produces a sort of mange. The examples of mites living on vertebrates show quite clearly how the association of mite and host may pass from one of a harmless epizoic relationship of mite to host to one of ectoparasitism by the mite, producing pathological effects.

Despite the considerable number of species already described in the literature as being associated with various other animals, there is, however, in only a very limited number of cases any precise knowledge of what the mite does. An urgent need is for an increased knowledge of the biology of the commoner species, for without this it is not possible to arrive at even a relatively true appreciation of the relationships of mites to the general problems of animal ecology.

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CHAPTER III

Ectoparasitism

PARASITES OF MAMMALS

ECTOPARASITISM may take various forms. The parasites may live on the surface of the host feeding upon exudations and abrading the surface. They may, however, invade the surface tissue and attack the living cells and drink the tissue fluids. Finally, the parasite may remain upon the surface of its host but, by modified mouthparts, pierce this surface and suck tissue fluid, or perhaps blood, from the underlying regions. In this last type of relationship, the parasite may visit the host only at intervals, or it may remain more or less permanently attached.

Speaking in a very general way, one may say that the Acaridiae, among the Sarcoptiformes, pursue the first two courses, while the Trombidiformes and Parasitiformes favour the third. There are, of course, many exceptions.

Surface feeding

Among the Acaridiae are many forms of mites which, in varying degree, parasitize warm-blooded animals, particularly mammals. Psoralgids and psoroptids feed on the surface of the skin of mammals on skin scales. Such mites may cause intense irritation; for example, *Caparinia tripilis* (A. D. Michael, 1899) occurs on the hedgehog, particularly on the belly, and may cause the death of the animal. *Chorioptes* species, such as *bovis* and *equi* (E. Hering, 1845) and a number of others described from various hosts, all cause skin irritation by abrading the surface. Probably there are only two morphologically distinct species of *Chorioptes*, *equi* with a number of varieties of which *bovis* is one, and *texanus* (S. Hirst, 1924) from American goats.

Psoroptes communis (M. H. Fürstenberg, 1861) causes mange on horses, sheep and cattle particularly on the rump, and has also been known to invade the ears of goats and rabbits. In sheep, the mite gives rise to the condition known as sheep scab. Alone among the acarid mites, psoroptids have mouthparts long enough to pierce the epidermis and reach the dermal capillaries. The puncturing of the skin causes irritation and an excematous eruption. Rubbing and biting at the skin leads to loss of coat and the formation of scabs. In horses the site of infection is usually under the mane, between the jaws or at the root of the tail.

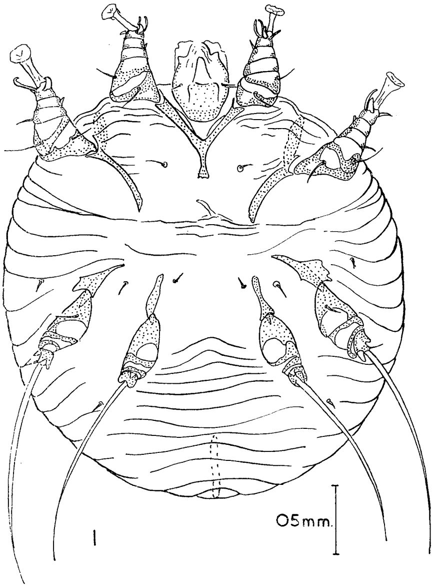
Another mite which invades the ear is *Otodectes cynotis* (Plate XVI, fig. 4) (E. Hering, 1838) which attacks cats, dogs, ferrets and foxes; the irritation produced causes an excessive production of cerumen which is often mixed with blood, due to the scratching of the host. The presence of *Otodectes* is usually the initiating cause of secondary bacterial infections. The ears of cattle are attacked by *Raillietia auris* (J. Leidy, 1872, family Laelaptidae) which, having long chelicerae like other parasitic Mesostigmata, cause bleeding by their attacks on the lining of the outer ear.

Invasion of the tissues

The other acarid mites parasitic on mammals usually burrow into the skin to reach the lymph of the malpighian layer and the stratum spinosum above it. The presence of such mites stimulates the malpighian layer to greater activities and so tends to produce an excessive cornification. This may be strictly localized and produce a cup-like structure with the mite sunk in its base, as is the case when the female *Teinocoptes epomophori* (see J. Rodhain, 1921, family Sarcoptidae) parasitizes *Micropteropus purillus* or *Epomorphus* species, where it prefers the less hairy parts of the body, particularly the hind border of the patagium; the males are free on the body surface and perhaps do not feed. The immature stages burrow into the skin for about half their length, but do not provoke the skin to grow up round them. Other parasites on bats, such as *Nycteridocoptes poppei* (A. C. Oudermans, 1897, family Sarcoptidae) on *Vespertilio murinus* produce patches of scurf on the hairy parts, or small cornified patches on the non-hairy. Beneath these patches the females destroy the skin down to the muscle layers, and under them the eggs are laid and the young stages develop.

Sarcoptes scabei (C. Linnaeus, 1758) on man and animals burrows through the cornified layers and feeds on the lymph bathing the cells of the stratum spinosum, which it also destroys; vesicles form in the stratum spinosum and fill with lymph, which may contain leucocytes. The mites bore tunnels along the stratum spinosum, the walls of which cornify behind them. By the activity of the malpighian layer, these tunnels are raised into the cornified layer, but the mites are always at their lower ends in the region of the living cells of the skin. There is, thus, a continuous struggle between the mites and the process of cornification. If this process is sufficiently rapid to isolate the mite from its food sources, an infection is not set up. The female mite always bores in between folds of the skin and usually takes about thirty minutes to bury itself (J. W. Munro, 1919). It usually places itself across the furrow of the skin which it has selected, resting the last pair of legs with their long setae on the top of the ridge behind it and with its anterior legs clinging to the skin in the bottom of the trough. Moving the gnathosoma rapidly from side to side, and possibly cutting with the chelicerae, it quickly raises a scale of cornified cells and, as soon as the free edge of the scale is long enough, the fore legs are also brought into play. The mite then slowly turns its body from side to side and at intervals lowers the hind end, and in this way forces its way in under the surface and continues to burrow into the cornified layer. The posterior legs may be directed laterally, the claws gripping on to the sides of the burrow, or directed inwards under the animal (B. Heilesen, 1946), suggesting that the long setae act as springs tensed against the floor of the burrow and holding the mite firm. Eggs are laid in the burrow, only the driving face of which is in, or in contact with, the spinose layer, all the older parts being surrounded by keratinized cells. The cycle from egg to ovigerous female takes ten days to a fortnight, only about 10 per cent of the eggs surviving to give rise to adults, since scratching dislodges many and may even destroy the adults. K. Mellanby (1942 a and b) considered that the initial infection gives rise to a sensitized condition and subsequent infection causes rapid irritation; scratching and dislodgement of the mite may result, thus cutting down chance of infection. The commonest source of infection in man, though by no means the only one, is sexual intercourse with infected subjects. Normally, apart from vesicles caused by intra- and extra-oedema of the cells of the stratum spinosum, there is no violent skin reaction in the form of excessive keratinization, for example. It does happen that in cases of infection with *Scabies norvegica*, the corneum thickens and loose patches of cornified cells are held on by exudations of lymph and blood from scratching and thus form an atypical crust, below which the mites live and in which are found eggs and young stages near its base. Transference of scabies mites from hosts of one species to another can produce an evanescent infection, but the mites fail to get established; thus there are physiologically distinct varieties which are morphologically indistinguishable. Man would appear to be the specific host for *Sarcoptes scabaei*. In horses, dogs and cattle, infection is associated with a previous loss of condition. In the Austrian Alps goats in overcrowded winter quarters may develop scabies and spread this to the chamois during the summer while they are on the mountain pastures. With the onset of winter and falling off of food supplies, the chamois lose condition and may become heavily infected. According to H. Vitzthum (1943), the eyelids may become so thickened as to produce blindness and death.

Another mite which burrows into the skin of mammals is *Notoedres cati* (E. Hering, 1838), producing mange on the heads of cats; it will also live on rabbits and man. The species *alepis* (A. Railliet and Lunet, 1893) and *muris* (P. Mégnin, 1877) (Plate XVIII, fig. 1) live on rats, while *Notoedres vanschaïki* was reported from bats by G. L. van Eyndhoven in 1946. These mites burrow straight down to the malpighian layer where they feed at the bottom of their hole. For purposes of oviposition or ecdysis, horizontal tunnels are made from the bottom of the bore-hole. The irritated malpighian layer cuts off cells which progressively cornify; blood and lymph from scratches form, with this excessive keratinized tissue, a leathery crust which grows progressively from below. The surface of this thickened area becomes wrinkled and



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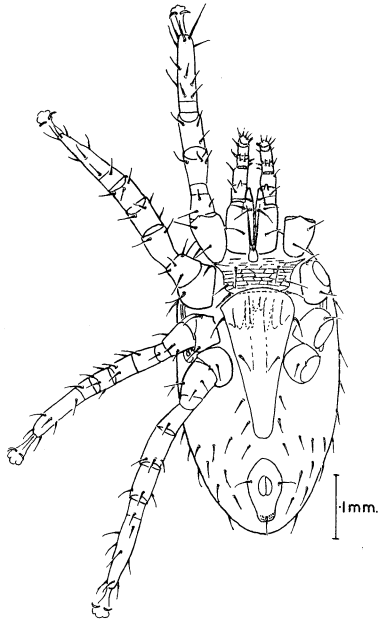

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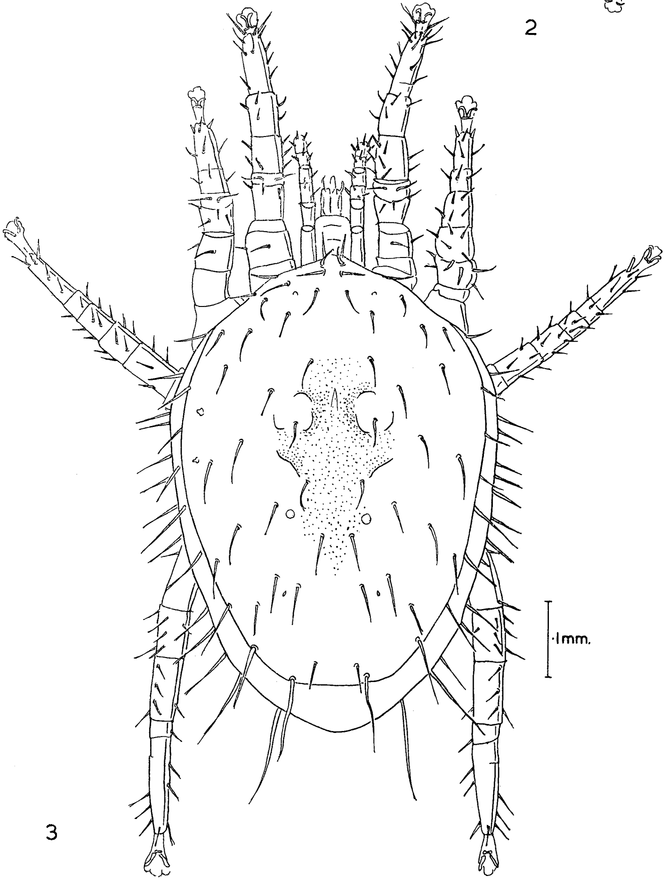

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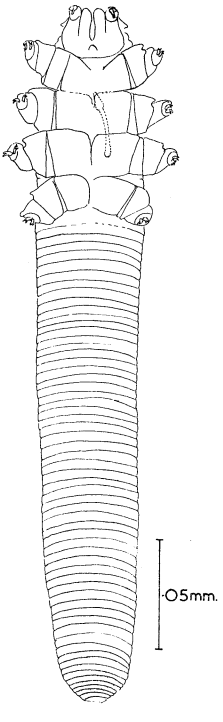

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corrugated. The various developmental stages are found in the lower parts of this crust, while the gravid females lie in the bottom of the pores which penetrate it. This species easily passes from cat to man and sets up a transient infection. It is said that species attacked by *Notoedres* are not naturally very susceptible to *Sarcoptes scabei.*

Among the Epidermoptidae, the genus *Dermataphagoides* (Plate XVI, fig. 2) was founded by A. Bodganow (1864) for mites of this family causing human dermatitis, and J. R. Traver (1951) described in detail the effects of infection by the species *scheremetewskyi* (A. Bogdanow, 1864) from personal experience. This mite, too, produces papules and a thickening of the skin.

Among the Trombidiformes are some of the Eleutherengona, which superficially resemble acaridians and parasitize mammals. The Myobiidae parasitize insectivores, rodents and bats and there appears to be a strong host specificity. The eggs are stuck on to the hair like those of lice, and the young stages probably live in the hair follicles like those of the myocoptids mentioned in the previous chapter. *Myobia musculi* (F. v. P. Schrank, 1781) occurs on mice, the species *pipistrellia* (C. Radford, 1938) on the bat *Pipistrellus pipistrellus*, which is also the host of *Myobia chiropteralis* (A. D. Michael, 1884). Larger mammals are also involved; H. B. Carter in 1941 described a mite, *Psorergates ovis*, from sheep in Australia which causes intense irritation and inflammation, presumably by feeding in the hair follicles. This type of parasitism is carried further by the Demodicidae, which burrow down the hair follicle, feeding on sebaceous secretions; in correlation with this habit, the body is elongated and wormlike. Increase in numbers of the mites in the hair follicles leads to loss of hair without, however, causing irritation. *Demodex folliculorum* (G. Simon, 1892) (Plate XVIII, fig. 4) is said by F. Fuss (1933) to be practically universally present on man and to have preferred sites such as the chin, eyelids, root of the nose and scalp. The species *canis* (F. Leydig, 1859) causes loss of coat in dogs, and its presence is usually accompanied by staphylococcal infections, the two together giving the typical follicular mange. The water rat *Apodemus sylvaticus* is the specific host of *Demodex longior* (S. Hirst, 1918).

Piercing and sucking of tissue fluid

The habit of piercing and sucking up tissue fluid without actual invasion of the tissues by the mite may also occur.

The Trombidiformes includes a large number of Parasitengona, parasitic in the larval stage only, which have been described from mammalian hosts. In very few cases have these larvae been linked with the subsequent developmental stages. The Trombiculidae have larvae known as chiggers and many

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PLATE XVIII. **1.** *Notoedres muris* (Mégnin) ♂; ventral view. **2.** *Ornithonyssus sylviarum* (Canestrini and Fanzago) ♀; ventral view. **3.** *Laelaps hilaris* (Koch) ♀; dorsal view. **4.** *Demodex folliculorum* (Simon) ♂; ventral view.

of them attack man and his domestic animals. There are a large number of genera and species, all based on larvae; in 1953 alone fifty new species were recorded. *Trombicula autumnalis* (G. Shaw, 1790) (Plate XXXIII, fig. 1) is the harvest bug of this country, the rouget of France, and it is found extending across Europe in a south-easterly direction, being absent in the north and in the south (R. Gasser and H. Mooser, 1954). The bright red larvae feed on any mammal that comes their way and in August and September the inside of the ears of rabbits may be coated with them. When they attack man, they produce in many individuals intense irritation and a rash or dermatitis. *Trombicula irritans* (C. V. Riley, 1873) which occurs in North America, *akamushi* (E. Brumpt, 1913) in Japan and Formosa, and *hirsti* (L. W. Sambon, 1927) in Queensland, all attack man, and may act as vectors of rickettsial diseases. Trombiculid larvae normally feed on small mammals. The secretion of the salivary glands evokes a reaction in the host tissues which was first described by M. André (1927). There is a histolysis, followed by a hardening of the periphery of the histolysed region, which creates a tube through the deeper layers of the epidermis down to the malpighian layer and the underlying dermis. This tube allows the larva to suck lymph up it, its own mouthparts being much too short to allow it to reach this source of food unaided. The nymphs and adults, so far as is known, live in the soil and probably feed on insect eggs or Collembola and other small creatures. The larvae of *Trombicula autumnalis* are not uniformly distributed in countries where they occur. In this country they are more frequent on chalk than on clay soils, in France the reverse is true; H. Vitzthum (1943) suggests that soil humidity may be a determining factor in oviposition.

The sucking of blood

The mites so far considered, with the possible exception of *Raillietia* and *Psoroptes*, are not primarily concerned with tapping the capillary bed of the dermal layers of the skin as a source of food. There is, however, a diverse fauna of blood-sucking Mesostigmata which parasitize many small mammals, species of *Laelaps*, *Haemolaelaps* and *Eulaelaps* being found on rodents and insectivores. It seems probable that the larvae and first nymphs feed on lymph, their mouthparts being inadequate to reach blood, the second nymphs and adult females feed on blood; the males probably do not feed at all. Species of *Myonyssus* (family Dermanyssidae) from rats apparently feed entirely on lymph; at any rate, they have never been recorded as containing blood. *Echinolaelaps echidninus* (A. Berlese, 1887) is found on rats and on *Perameles gunni*, *Neolaelaps magnistigmatus* (H. Vitzthum, 1918) on *Pteropus* species, *Acanthochela chilensis* (H. E. Ewing, 1933, family Haemogamasidae) on *Didelphys elegans*. None of these mites parasitize large mammals and the same may be said of the mites belonging to the genera *Ornithonyssus* and *Dermanyssus* (family Dermanyssidae). Many of these mites are viviparous, giving birth to first-stage nymphs; and the host specificity appears to be low.

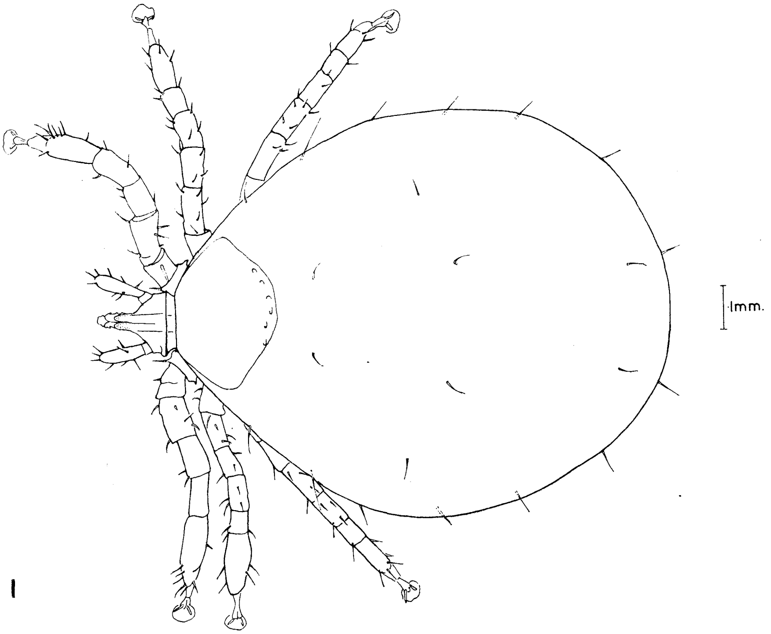
Steatonyssus periblepharus (F. A. Kolenati, 1858) is found on rodents and bats, *Ornithonyssus bacoti* (S. Hirst, 1913)—normally a parasite of tropical and subtropical rodents—will, in default of its normal host, feed on man and is said to do this to a considerable extent in parts of Australia. *Dermanyssus murinus* (A. C. Oudemans, 1929), also a rat parasite, has become a nuisance in some ports because it too may attack man, as will the species *gallinae* (K. Degeer, 1778)—a common parasite of birds. In all these forms there is a tendency for the chelicerae to be long, with reduced denticles, or even to lose the chelate character and become stylet-like, as they are in the genus *Dermanyssus*. The claws and pulvilli do not usually appear particularly well developed as compared with those of free-living Mesostigmata.

The Spinturnicidae and Spelaeorhynchidae have become specialized for parasitizing bats, and the former family does have enlarged claws and pulvilli for clinging to the host. Among the Spinturnicidae the genus *Spinturnix* is of world-wide distribution and, together with the genus *Periglischrus*, is confined to insectivorous bats, while the genera *Meristaspis* and *Ancystropus* are confined to fruit eaters, like *Pteropus*. The Spelaeorhynchidae are found in Central and South America, *Spelaeorhynchus praecursor* (K. W. Neumann, 1902) being recorded from Brazil. These mites, though classified with the Mesostigmata, differ from the others in having a very deep camerostome into which the gnathosoma withdraws; on account of this Banks and Neumann considered them to be in some way allied to the ticks. Apart from these mites peculiar to themselves, bats are also attacked by species of *Ornithonyssus*.

The most accomplished of the blood-sucking mites are the ticks or Ixodides (Plate XIX, fig. 1). All ticks suck blood or lymph in every stage of their life history as a general rule, though *Ornithodorus moubata* (A. Murray, 1877) and *O. savignyi* (J. V. Audouin, 1827) among the Argasidae have larvae which do not feed at all, and this is probably true of the males of several species of *Ixodes*, such as *autumnalis* (W. E. Leach, 1858) and *vulpis* (P. Schulze, 1937). Some ticks, however, are known to feed only in the larval stage, moult direct to adults and then proceed to reproduction; for example, *Otobius mégnini* (A. Dugès, 1883, family Argasidae).

The adult Argasidae (Plate XXV, fig. 5) typically have the habits of the bedbug *Cimex*, feeding at intervals and laying small batches of eggs between feeds. The larvae attach to the host for some time, usually two or three days, the nymphs usually complete their feed in about an hour, and the adults are even quicker. These ticks inhabit the burrows, roosts or houses of their hosts. *Ornithodorus talaje* (F. E. Guérin Meneville, 1849) lives in cracks in house walls in Mexico, and *moubata* (A. Murray, 1877) is a domestic pest of Africa; *Argas testudo* (A. Risso, 1780) is found in bats' roosts.

The Ixodidae prefer a higher humidity than the Argasidae and as adults they normally feed but once; after this the females lay a clutch of some thousands of eggs. The life cycle consists of egg, larva, nymph, adult, and each active stage remains attached to the host for some days before becoming



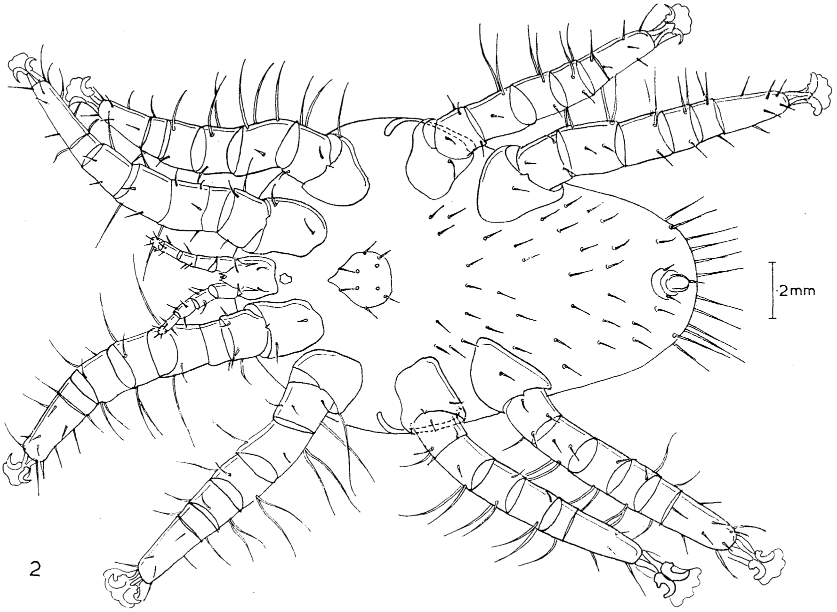


PLATE XIX. **1.** *Ixodes ricinus* (L), larva; dorsal view. **2.** *Spinturnix* sp. nymph; ventral view.

gorged. The host is not necessarily the same species at each stage of the life cycle and, indeed, host specificity appears to be low, with, perhaps, the exception of some of the bat parasites, such as *Eschatocephalus vespertilionis* (C. L. Koch, 1841) which is always recorded in association with bats. *Ixodes ricinus* (C. Linnaeus, 1758) will, on the other hand, feed on cattle, sheep, dogs and man. There are minor variations in the life cycle as to the number of hosts attacked. Thus *Boophilus annulatus* (T. Say, 1821) remains on the one host, cattle, from larva to adult and only leaves it for oviposition; while *Rhipicephalus bursa* (G. Canestrini and F. Fanzago, 1877) passes larval and nymphal stages on one host, drops off to moult to the adult and the females seek another host before proceeding to egg-laying.

The habit of ticks of remaining attached often leads to their becoming surrounded by a cup-like proliferation of skin, brought about by their effects on the malpighian layer, and they may become completely covered by the skin. *Ixodes autumnalis* has been found subcutaneously on horses, and this is the normal position for *Hyalomma rhipicephaloides* (L. G. Neumann, 1901) on the gazelle, which it usually parasitizes. D. Arthur (1947) records a case of *Ixodes hexagonus* being found beneath the skin of a man's chest.

The sensory physiology and behaviour of *Ixodes ricinus* has been investigated in some detail by A. D. Lees (1948a) and it is probable that his findings hold for ixodid ticks in general. The unfed female, when walking, waves its first pair of legs like antennae. On the tarsus of the first leg is Haller's organ, containing sensilla stimulated by scents and humidity. The ticks climb grass stalks and at intervals quest by waving the first pair of legs in the air. This reaction is brought about by mechanical disturbance or shading, such as would be produced by the approach of a host animal. There is a strong reaction to rise in temperature accompanied by the smell of animal hair. The olfactory sense organs are the peg-like chemoreceptors in the capsule of Haller's organ, the temperature receptors are short setae on the dorsal surfaces of the legs. Light sensitivity is a general cutaneous property. Under these conditions, the tick clings and climbs on to anything brushing against it. The sensory pads on the tips of the pedipalps are used in selecting a site on the host for fixation. Unfed ticks remain on the grass till desiccation evokes a kinesis and, under the influence of this, they move down into the more humid conditions at the base of the herbage, where they absorb moisture through the cuticle. The movements of engorged ticks into the mat at the base of the grass are guided by avoidance of direct illumination.

The sensitivity to humidity is very marked in *Ixodes ricinus* and most of its life is spent in microclimates approaching saturation. The life cycle in this country has been extensively studied by Milne (1943–52). During a life of some three years, the tick spends a total time of about three weeks attached to hosts, the rest of the time is spent in the mat of dead and decaying vegetation at the base of the rough hill and moorland pastures where it occurs. In the spring there is a period of activity in the tick population lasting from

March to June; in the West of England and Wales there is a second similar period in the autumn. During the period of activity, unfed larvae, nymphs and adults ascend the herbage about them and behave as has just been described over periods of 4–5 days; these periods of activity are some five in number spread over about three months, or they may terminate in fixation to a host. Gorged ticks, on falling from the host, descend vertically into the dead vegetation where they enter into a period of inactivity. The distance a gorged female moves, apart from downwards, is very limited, some three inches only, so that unless they drop in favourable positions, survival is not possible.

The dependence of these mites on a microclimate of high humidity is the principal factor controlling their distribution in the British Isles. It is correlated with the ability of water vapour to be absorbed through the cuticle, presumably by the epidermal cells (Lees, 1946, 1947, 1948b). Ixodid ticks can take up water from saturated or nearly saturated air, even when the spiracles are occluded. The periodic descents of the active *Ixodes ricinus* into the mat at the base of the herbage serves to make good the water losses suffered while it is exposed on the foliage above and questing for a host.

Lees (1947, 1952) has shown, too, that this sensitivity to humidity conditions is an important factor in determining the distribution of various species. *Ixodes ricinus* loses water much faster than the related *I. canisuga* (Johnston, 1849), which can therefore survive in drier habitats, such as foxes' earths, dog-kennels and the burrows of sand martins. In a series of ticks investigated regarding rate of water loss in dry air, he showed that *Dermacentor andersoni* (Stiles, 1908) loses water very slowly compared with *I. ricinus*. In North America in Montana, it is found on scrub-covered hillsides supporting heavy rodent populations, and where the soil often becomes very dry. The argasid ticks lose water much more slowly than the ixodids. *Argas persicus* (C. Oken, 1818), widely distributed in warm countries, lost only 0·7 per cent body water in 24 hours in dry air, as compared with a loss of 7·9 per cent by *I. ricinus* females. An even more resistant form is *Ornithodorus delanoei acinus* (Whittick, 1938) which, like *O. savignyi* (Audouin, 1827), is found in dry sand where camels and caravans rest. An exceptionally resistant ixodid is *Hyalomma savignyi* (Gervais, 1844) which is often found in the heat of the sun on sand dunes in Palestine. Browning (1954) investigating the uptake of water by *Ornithodorus moubata* (Murray, 1877) found that in the gorged female, or in conditions of high external CO_2 tension, the water control was impaired, whereas low oxygen tensions had no effect.

PARASITES OF BIRDS

Invasion of skin and quills

Birds, like mammals, are parasitized by mites other than the epidermoptids already mentioned as living on the skin. The genus *Cnemidocoptes* (family Sarcoptidae) burrows into the skin, causing quite typical lesions. *Cnemi-*

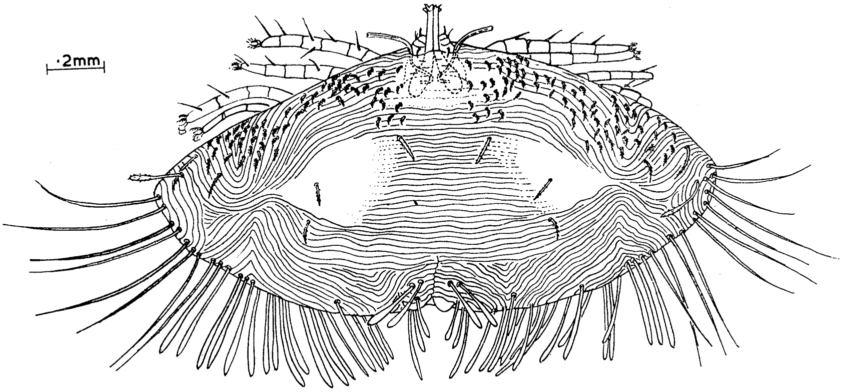
docoptes mutans (C. Robin, 1860) causes the disease known as scaly leg in chickens and other Phasianidae. The mites burrow in below the larger leg scales, their presence producing an excessive proliferation and keratinization, which takes the form of a white floury scurf and raises the edges of the scales. The mites live between the dermis and the epidermis and stimulate desquamation, the desquamated scurf often becoming wet with exuded lymph which coagulates into a spongy crust. The feet become grossly malformed as the toes become affected and the birds are lamed. These mites sometimes also attack the bare parts of the head and face and extend on to the neck. The species *laevis* (A. Railliet, 1885), of which there are probably several varieties, causes depluming itch in fowls. The mites live in the scales at the base of the quills and cause a loosening and loss of feathers. A completely subcutaneous mite is *Laminosioptes cysticola* (F. Vizioli, 1870, family Laminosioptidae) which is found under the skin of turkeys in the connective tissue; calcareous cysts form round the dead mites like minute sand grains, and give a peculiar and typical appearance to the tissue.

The parasitic larvae of the Trombiculidae have less opportunity for getting on to birds than they have of attacking mammals. *Trombicula wichmanni* (A. C. Oudemans, 1905) is frequently found on the crown pigeon in New Guinea; *Neoschöngastia edwardsi* (C. E. M. Gunther, 1939), as well as some species of *Schöngastia*, is found on the scrub turkey. Among the Eleutherengona, the pseudoleptid *Pseudoleptus arechavaletae* (L. Bruyant, 1911), which is a parasite of grasses, occasionally attacks the face of the bush turkey *Nothura maculosa* in South America, causing a rash and irritation. The Myobiidae are represented on birds by the genus *Harpirhynchus*; the species *nidulans* (C. L. Nitzsch, 1818) lives in cysts round the base of feathers on pigeons, each cyst containing a little colony of mites. *Harpirhynchus pilirostris* (A. Berlese and E. L. Trouessart, 1889) occurs on the common sparrow in the skin about its head.

The sucking of blood

Blood-sucking Mesostigmata are principally represented by species of *Dermanyssus* and *Ornithonyssus* (Plate XVIII, fig. 2). *Dermanyssus gallinae* (K. Degeer, 1778) feeds on birds while they roost and is the red fowl mite of poultry keepers, spending the day in cracks and crevices in fowl roosts or in the nests of birds; it will, in default of birds, attack mammals. As in the case of other blood-sucking Mesostigmata, such as *Ornithonyssus bacoti*, after a blood meal the female lays a small clutch of eggs in the course of the following two or three days, and then feeds again. Other species of *Dermanyssus* include *hirudinis* (J. F. Hermann, 1804) which can occur on any species of small bird, and *quintus* (H. Vitzthum, 1921) which was taken off a woodpecker. In subtropical and tropical regions the common bird parasite of this type is *Ornithonyssus bursa* (A. Berlese, 1888), the tropical fowl mite, replacing *Dermanyssus gallinae* which is unable to live in warm conditions. Since these

Ectoparasitism



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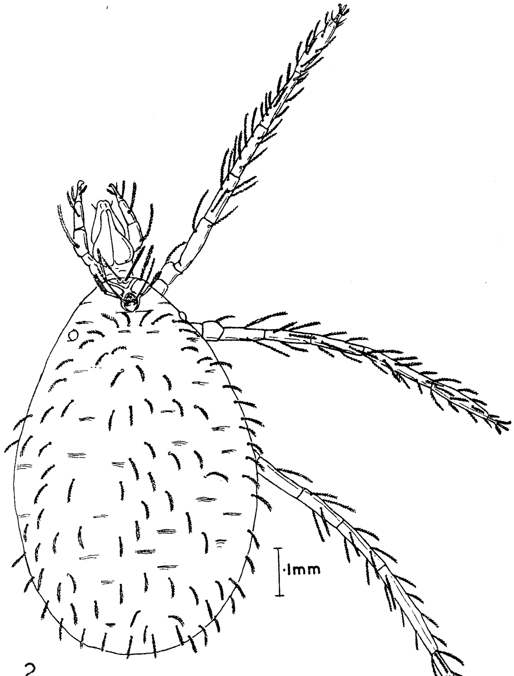

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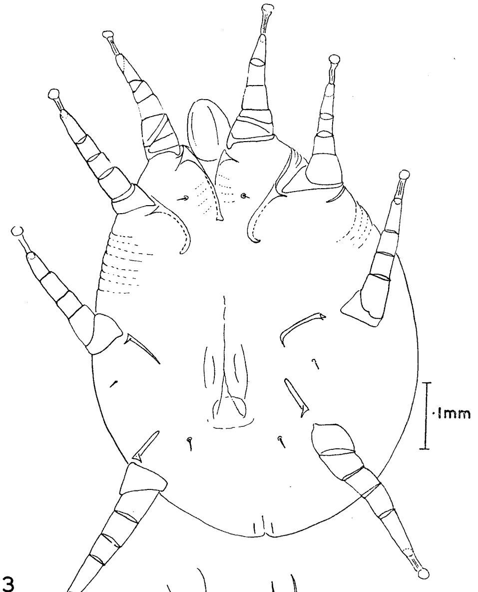

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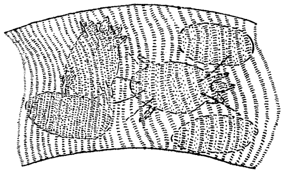

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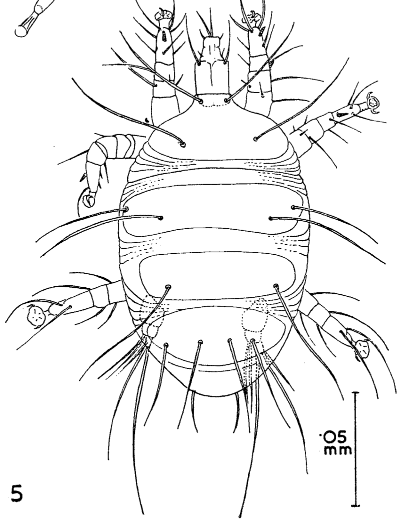

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mites may occur in large numbers, they can cause considerable debility among domestic fowls. Separated from the host, *D. gallinae* may survive eighty days, and the larva can ecdyse into the first nymphal stage without taking a blood meal.

Ticks will also attach themselves to birds and, indeed, the specific host of some ticks would appear to be birds, in so far as ticks show host specificity. Thus *Argas columbarum* (G. Shaw, 1793) is associated with pigeons and is often found in their roosts, whilst *Argas persicus* (C. Oken, 1818) is a pest of domestic poultry over most of the world and in parts of its range a domestic pest as well, living in cracks in houses and attacking man. *Ceratixodes uriae* (J. White, 1852) is found on sea birds and, as F. Zumpt (1952) pointed out, is of interest in that its territory comprises the surroundings of both poles. The most frequently recorded hosts are gulls, albatrosses, petrels, shearwaters and penguins. The males do not feed and occur on the nesting sites. The explanation of its odd geographical distribution is, probably, to be sought in the very considerable migratory movements of some sea birds, such as the storm petrel *Oceanites oceanicus* which breeds in the Antarctic but migrates as far north as Greenland and this country. *Ornithodorus talajae talajae* (F. E. Guérin-Meneville, 1849) infests a wide range of mammals, including rodents in South America, and extends into Texas and Florida; it infests old houses and causes painful bites on man. Two varieties of this tick are known from sea birds; *capensis* (L. G. Neumann, 1901) is common in the nests of the South African penguin *Spheniscus demersus*, and the variety *sanctipauli* (P. Schulze, 1941) has been taken from nests of *Anosus stolidus* on the Saint Paul rocks.

Except for the Sarcoptiformes, the various suborders of mites which parasitize the warm-blooded vertebrates also have members which feed on reptiles and Amphibia.

PARASITES OF LOWER VERTEBRATES

Among the Mesostigmata there are species of *Hemilaelaps* which feed on snakes; H. E. Ewing (1933) described two species, *americanus* on a snake of the genus *Drymarchon*, and *distinctus* on *Elaphe obsoleta*, and had previously (1923) described *Liponyssus triangulus* from *Lampropeltis calligaster*. The genus *Liponyssus* is also represented by the species *lacertarum* (N. Contarini, 1847) on *Lacerta viridis*. The genus *Ophionyssus* is confined to snakes, the species *natricis* (P. Mégnin, 1884) being found on a species of *Tropidonotus*; S. Hirst (1915) described a species *serpentium* from North American snakes, but it also occurs in India on Russell's viper and on the coral snake of Brazil, while *Ophionyssus*

PLATE XX. **1.** *Pterygosoma neumanni* (Berlese); dorsal view. **2.** Erythraeid larva; dorsal view. **3.** *Cytodites nudus* (Vizioli) ♀; ventral view. **4.** Trachea of bee containing *Acarapis woodi* (Rennie). **5.** *Acarapis woodi* (Rennie) ♀; dorsal view.

variabilis was described in 1951 by A. A. Zemskaya from *Echis carinatus* in Russia. This genus seems to have a preference for feeding round the eye orbit. The adult females of the family Ixodorhynchidae have the habit of attaching themselves under the scales of snakes in the manner of ticks, the males and immature stages remaining freely mobile. The species *butantanensis*, described by F. da Fonseca in 1934, was from a Brazilian grass snake. The true ticks also attack reptiles, the genera *Aponomma* and *Haemalastor* attacking lizards, snakes and tortoises. *Aponomma pulchrum* (F. H. Roberts, 1953) was found on *Varanus*, while sea snakes of the genus *Platurus* are parasitized by *Haemalastor nitidus* (S. and L. F. Hirst, 1910). *Aponomma gervaisi* (H. Lucas, 1847) is common in Australia, India and Malaya and infests tortoises, while the Grecian tortoises sold in this country often carry *Hyalomma syriacum* (C. L. Koch, 1847).

The eleutherengonans (family Pterygosomidae) (Plate XX, fig. 1) parasitize geckos and lizards; A. Berlese (1892) records *Geckobia insignis* from the Italian gecko *Platydactylus muralis*, and S. Hirst in 1917 described a form which he called *Pimeliaphilus tenuipes* from a South American gecko *Gonatodes albigularis*. I. Trägårdh's species *podapolipophagus* (1904)—the type species of the genus *Pimeliaphilus*—was originally placed in the Rhaphignathidae, and H. Vitzthum (1943) suggests the generic name *Pimeliaphiloides* for the two species *insignis* and *tenuipes*, which are pterygosomids superficially resembling *Pimeliaphilus*. There appears to be a good deal of host specificity. *Pimeliaphiloides* species are found on geckos and the genus *Pterygosoma* on agamid lizards. *Geckobia guyanensis* (H. Floch and E. Abonnenc, 1944) was found on a species of *Platydactylus*. Among the cheyletid mites the genus *Hirstiella* occurs on reptiles, the species *bakeri* (F. Cunliffe, 1952) was described from material off a Californian iguanid and *pelaezi* (F. Cunliffe, 1949) from *Sceloporus ferrari perezi*. Related to the genus *Myobia*, which occurs on mammals, is the genus *Ophioptes*; mites of this kind live sunk into little pits in the softer parts of the scales. *Ophioptes tropicalis* (H. E. Ewing, 1933) occurs in British Guiana on *Erpetodryas carinatus*, and the species *coluber* (see C. Radford, 1947) on the copper-headed rat snake of India, *Coluber radiatus*.

Some of the parasitengonan larvae of trombid mites feed on reptiles in default of mammals. *Trombicula irritans* (C. V. Riley, 1873) has been found on terrapins and colubrine snakes in America and it is said that they remain attached for a greater length of time than when they feed on mammals, often remaining on snakes until the skin is sloughed. *Trombicula ewingi* and *T. ophidica* (F. da Fonseca, 1932) was found on *Ophis merremii*. The genera *Schöngastia* and *Neoschöngastia* are also found on reptiles as well as mammals, *Schöngastia bidentata* (see G. W. Wharton and H. S. Fuller, 1952) on skinks in Australia, *Neoschöngastia scelopori* (H. E. Ewing, 1931) on the lizard *Sceloporus spinosus*.

Larvae of the genera *Hannemania* and *Endotrombicula* feed on amphibians and tend to sink into the skin. *Hannemania hylodeus* (A. C. Oudemans, 1910) becomes ringed round by a ridge of epidermis, while the species *hylae* (H. E. Ewing, 1926) is practically buried in the skin of its host, *Hyla arenicolor*. *Endotrombicula penetrans* (H. E. Ewing, 1931) becomes subcutaneous on *Arthroleptis minutus* of East Africa. A subgenus of *Endotrombicula*, *Phrynacanis*, was found by R. F. Lawrence (1949), as the species *fitsimonsi* on a snake *Heleophryne regis* in South Africa. Ticks have also been recorded from amphibians; *Amblyomma dissimile* (C. L. Koch, 1844) was recorded by H. E. Evans (1947) from *Bufo marinus*.

INVERTEBRATE HOSTS

Insects

Apart from the vertebrates, the only other phylum of animals to be extensively parasitized by the mites is the Arthropoda. The Orthoptera are extensively used as host by trombidiform mites, tarsonemids of the family Podapolipodidae, for example *Podapolipus grassii* (A. Berlese, 1897), being found on *Locusta migratoria* and other species of locust. The females of this family show a reduction in number and development of the legs and a tendency to physogastry in some genera, such as *Podapolipus*. The males retain four pairs of legs in *Tarsopolipus* but in other genera have lost the fourth pair. The females remain attached to their hosts and in some cases give rise to a cytostome in the host tissues similar to, but more extensive than, that induced by trombiculid larvae in mammalian skin. Among the parasitengonan trombidiform mites, many larvae attack Orthoptera, larvae of species of *Eutrombidium* being found on the bodies of mantids, grasshoppers, crickets and locusts. *Balaustium berlesianum* (G. Paoli, 1937, family Erythraeidae) occurs on acridids, and, in fact, erythraeid larvae (Plate XX, fig. 2) parasitize insects in the same generalized way that trombiculids parasitize vertebrates. E. W. Baker and G. W. Wharton (1952) state that *Pimeliaphilus podapolipophagus* (I. Trägårdh, 1904) is a parasite of cultures of cockroaches in the United States; they make the genus synonymous with *Pimeliaphiloides* (H. Vitzthum, 1943) and place it in the family Pterygosomidae. In point of fact Trägårdh described specimens from under the elytra of tenebrionid beetles, where they were associated with *Podapolipus apodus* (I. Trägårdh, 1902) on which he thought they fed, this suggesting the specific name. Vitzthum (1943) on page 612 is at pains to point out that his suggested name *Pimeliaphiloides* is for two species of Pterygosomidae parasitic on reptiles. There thus appears to be some confusion over these mites. The relationship of these genera is discussed by F. Cunliffe (1952).

The Coleoptera are also hosts for some species of mites. The passalid beetles are parasitized by gamasids, e.g. the Diplogynidae (Plate XIV, figs. 1, 2), and I. Trägårdh (1946) created a second family Diarthrophallidae for three genera found on them; *Diarthrophallus similis* (I. Trägårdh, 1946) was found on *Proculus goryi*, *Passalobia quadricaudata* (G. Lombardini, 1926) on a

Brazilian passalid and *Brachytremella spinosa* (I. Trägårdh, 1946) on *Protomocercus* species in New Guinea.

The ticks very rarely affect arthropods, but *Aponomma ecinctum* (L. G. Neumann, 1901) occurs on the beetle *Aulacocyclus kaupi.*

The trombidiform mites occur on beetles as parasites either in the larval instar, for example hydrachnellids, or as adults; sometimes only the females are parasitic, as in the tarsonemids. *Pyemotes scolyti* (A. C. Oudemans, 1936) occurs on the larvae of the bark beetle *Scolytes multistriatus*, the species *rhynchitinus* (M. H. Debey, 1849) on a larval curculiond, *Rhynchites betuleti.* The females become physogastric and produce adult males and females. The males wait upon the birth of the females and pair with them. A. Herfs (1926) showed that *Pyemotes ventricosus* (G. Newport, 1850) (Plate XIV, fig. 4), which normally parasitizes lepidopterous larvae, will also feed on coleopterous larvae. This species sometimes occurs in large numbers on the larvae of the grain moth *Sitotroga cerealella* and causes dermatitis in people handling infected grain. A similar species *tritici* (A. Lagreze-Fossat, 1851) was a considerable nuisance to the Japanese during the Manchukuo campaign, according to H. Vitzthum (1943).

Another tarsonemid which attacks adult beetles is *Acarophenax tribolii* (see R. Newstead and H. M. Duval, 1918) found on species of *Tribolium* which infest grain. These mites pierce the intersegmental membranes of the abdomen and are often found in large numbers under the elytra. The Podapolipodidae also parasitize adult beetles, the females being attached to the body—usually round the wing bases—the males remaining freely mobile. *Tarsopolipus corrugatus* (A. Berlese, 1911) occurs on scarabaeid beetles in Southern Europe, *Podapolipus apodus* (I. Trägårdh, 1902) on tenebrionids, while the species *rhyncophori* (H. E. Ewing, 1924) was found on curculionids, and *Eutarsopolipus desani* on carabid species from the Belgian Congo by J. Cooreman (1952). Doubtless other families of beetles will be found to carry mites of this family.

The water beetles come into contact with the parasitic larvae of hydrachnellids and are attacked by species of *Hydrachna* and *Rhabdohydrachna*, which move in the surface film of water; here, too, are found the larvae of *Eylais* which attack dytiscid and other beetles.

Parasitized by the same species of larvae as the aquatic beetles, are many aquatic Hemiptera, such as *Nepa* and *Ranatra.* The terrestrial hemipterans also serve as hosts for a number of mites, Neumann (1901) describing a tick *Rhipicephalus maculatus*, the host of which was a terrestrial pentastomid, *Platymeris horrida.* The trombidiform mites are, however, the main parasites of bugs, as of other insects. *Pimeliaphilus triatomae* (F. Cunliffe, 1952) was taken from *Triatoma infectans* and aphid and other plant-sucking bugs are parasitized by Erythraeidae (Plate XX, fig. 2); *Balaustium* larvae, probably *B. murorum* (J. F. Hermann, 1804), are found on aphids, as well as a larval Allothrombium. *Paratrombium teres* (M. André, 1928) was found on the capsid

Brachytropis calcarata and *Balaustium cristatum* (H. Womersley, 1934) occurred on jassid bugs in Australia.

Dipterous insects, too, are frequently parasitized by trombidiform mites. Many of the water mites attach themselves as larvae to Diptera which have aquatic larvae, and thus the larval instar of the mite may be spent out of the water on the body of the insect imago. Anopheline and culicine mosquitoes are parasitized by the larvae of the Hydryphantidae; the larvae probably attach themselves during the emergence of the adult from its pupa. Many of the Arrenuridae seem to have a preference for anopheline mosquitoes. Chironomids are parasitized by larvae of *Piona disparilis* (F. Koenike, 1895) in the adult stage, and as pupae by other pionid larvae which leave it before the imago emerges. The Chironomidae are also made use of by larval Sperchonidae. *Corethra* species are the hosts of Hydrodromidae and Hygrobatidae. The Thyasidae have very active larvae which crawl up the stems of water plants such as reeds, or else on to the shore; they can also jump and are found attached to Diptera flying over water, such as mosquitoes and tipulids. The larvae of *Johnstoniana* and of the Calyptostomidae, which always live near water, are also of frequent occurrence on tipulids.

Before considering the purely terrestrial Diptera, it may conveniently be said here that other insects with aquatic larvae, such as dragonflies (see R. D. Mitchell, 1953), are also parasitized by hydrachnellids. The Hydryphantidae and species of *Arrenurus* are often found on libellulids. They also act as hosts for the terrestrial trombids, such as *Leptus phalangi* (K. Degeer, 1778), but this genus also parasitizes a wide range of other arthropods, including arachnids. Trombiculid larvae are found on terrestrial dipterans; *Microtrombidium demeijerei* (A. C. Oudemans, 1909) has been taken from species of *Anthomyza* and *Platyparea*. Frit-flies, such as *Oscinella frit*, have been found with trombiculid larvae and species of *Enemothrombium*. The Hippoboscidae, themselves parasitic on birds, are parasitized by a few species of acarid mites, *Microlichus* species and *Myialges* species; the latter also parasitize bird lice.

The Lepidoptera may also be parasitized by mites. The occurrence of pyemotid mites on grain moths, such as *Sitotroga*, and on clothes moths, such as *Tineola biseliella*, has been mentioned previously. In this country, *Melanargia galathea* frequently carries the larvae of *Trombidium holosericeum* (C. Linnaeus, 1758), but it is found on other Lepidoptera, too. *Erythraeus ojimai* (J. Kishida, 1929) was found on rice moths in Japan. Species of Psychidae have been found parasitized as larvae by *Pyemotes ventricosus*. The Hymenoptera do not appear to be parasitized to any great extent although, as has been previously mentioned, they are associated more or less intimately with many types of mites. *Paratrombium egregium* (L. Bruyant, 1910) occurs on the wasp *Pompilus pectinipes*. The uropod *Tricocylliba comata* (D. G. Leonardi, 1895) is said to parasitize *Lasius mixtus*, being the only known example of a parasitic uropod.

Other groups of Arachnida may carry mites as ectoparasites and some of the larger spiders have been found acting as hosts. S. Finnegan (1933) described *Peletiphis bristowi* (family Laelaptidae) from the Malayan spider *Liphistius malayanus*, and in 1932 A. C. Oudemans described *Ljunghia selenocosmiae* (family Hypoaspidae) from the spider *Selenocosmia javanensis*. From scorpions M. André (1953) has described *Leptus pyrenaeus* from *Buthus occitanus* and erythraeid larvae were found on *Parabuthus mixtus* from Abyssinia by G. Lombardini (1947), and F. Cunliffe (1949) records *Pimeliaphilus isometri* from a species of *Isometrus*. M. André had previously (1949) described *Isothrombium oparbellae* from a solifugid *Oparbella fagei*. Among the smaller arachnids, species of *Leptus* are often found on phalangids and pseudoscorpions.

Crustacea

The Crustacea are in some cases parasitized by mites which attach themselves to the gill lamella and, presumably, suck the blood. W. A. Haswell (1922) described a hydrachnellid, *Astacocroton molle* from the gills of *Astacopsis serratus*, an Australian freshwater crustacean, and A. S. Pearse (1929) found *Ewingia coenobita* on the gills of the pagurid *Cenobita diogenes* living on the islands south of Florida. This mite is one of the Acaridiae, a group which does not parasitize invertebrates generally. Here the third and fourth pairs of legs in the nymphs and females, which he found, are thickened and have the tarsi modified into powerful hooks for clinging on to the gills. K. Viets (1931) found immature stages of a halacarid, which he named *Astacopsiphagus parasiticus*, on the gills of *Astacopsis serratus*. M. André (1935) reviewed these relationships.

Mollusca

The Mollusca do not appear to be parasitized to any extent. E. A. Brucker (1897) described from the New Zealand *Cryptoconchus porosus*, larvae and nymphs of a halacarid mite *Halixodes chitonis*; Chilton (1883) had previously described a single male of another mite, *Halixodes truncipes*, from the same host. According to H. Vitzthum, they do not appear to be the same species.

Some genera of the Unionicolidae are parasitic on the tissues of bivalves; they bury themselves below the epithelium of the mantle, foot, or the gills, while they ecdyse from one instar to the next; *Unionicola aculeata* (K. Koenike, 1890) lays its eggs below the epithelium of the inhalent siphon, the larvae and nymphs ecdyse in the tissues of the gills, but the active stages live free outside the mollusc. Other species, such as *Unionicola fossulatus* (K. Koenike, 1895), behave in a similar fashion, but the active stages are passed within the mantle cavity.

From the examples of ectoparasitism that have been cited, it can be seen that the mammals and, to a lesser extent, the birds, harbour a complete range of the types of parasites mentioned at the beginning of this chapter.

The lower vertebrates and the invertebrate phyla, however, are only parasitized by such forms as are capable of piercing and sucking up body fluids.

The modifications of structure correlated with the parasitic habit are not very marked. Piercing and sucking mouthparts are found in free-living Trombidiformes, such as *Cheyletus* species, and the length of the chelicerae suggests a similar function in the Uropodina amongst the suborder Parasitiformes. Apart from some modifications of the ambulacral apparatus in connection with clinging to hairs and feathers, dealt with in the section on anatomy, the most striking modifications are the physogastry met with in some of the Trombidiformes and the wholly characteristic feeding apparatus of the ticks. Other groups of mites have become ectoparasitic with relatively little morphological specialization.

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CHAPTER IV

Endoparasitism

SOME few restricted groups of mites have become internal parasites, since they have invaded the respiratory tracts of other animals. This one can envisage as a relatively easy step, not necessarily involving any complex physiological adaptations, nor any great morphological changes. The lungs are of such a structure in vertebrates that, provided the mite can grip the surface, there is an adequate supply of serous fluid, mucus and cellular debris to supply the food required; the humidity is high and oxygen is readily available. The respiratory tract is easily accessible for larvae or adults and though not a suitable place, perhaps, for oviposition this difficulty can be overcome by viviparity. Viviparity is a modification of the life cycle which has been independently acquired in ectoparasitic and commensal mites and in some free-living forms, too.

Among the mammals, two groups in particular are known to serve as hosts for mites living in their respiratory tracts, namely the Primates and the Pinnepedia. The former are parasitized by species of *Pneumonyssus* (see A. C. Oudemans, 1935) and the latter by species of *Halarachne* and *Orthohalarachne*, these mites being modified laelāptids.

Species of *Pneumonyssus* have shortened palps, the sclerotization of the body armour is reduced, and all the legs have empodia and claws. The larvae penetrate into the bronchioles and alveoli, where they complete their development. All stages in the life cycle pierce the lung tissue with the chelicerae, which have a reduced fixed digit. The animals feed by sucking in lymph and, according to R. Deschiens (1951), also ingest cells of the lung epithelium. The reaction of the lung tissue is to endeavour to encapsulate the mites, and this gives rise to little nodules of fibro-connective tissue enclosing the mites and their excreta. Since some of the parasites come to lie under the pleura, the lung surface may show yellowish-white nodules which may be the size of a rice grain; others will occur deeper in the lung tissue. Larger nodules arise, when several mites are in close proximity, by a coalescence of individual nodules. The larvae are produced alive by the females, which remain in the lung tissue, feeding, and, indeed, are too large to make their way along the narrower bronchioles. It is, therefore, thought that the larva is the infective stage of the life cycle.

In section, the nodules show a hollow centre, which may communicate with an alveolus or bronchiole, and which is surrounded by a zone in which there is dilatation of the capillaries and infiltration by histiocytes containing brownish pigment. In this zone fibrous tissue is being formed, and it is mixed with concretions of guanine and other debris. An outer zone also is distinguishable, in which there is less intense infiltration and in which the gnathosoma of the mite is embedded. A nodule of this type normally contains one or two mites. A typical form is *Pneumonyssus simicola* (N. Banks, 1904); it occurs in rhesus monkeys and in *Papio sphinx*.

Pneumonyssus species can occur in mammals other than primates; C. Radford (1938) described the species *procavians* from the hyrax *Procavia capensis*, and R. Deschiens (1951) described the post-mortem appearance of the lungs of a laboratory rabbit which was infected with mites, almost certainly some species of *Pneumonyssus*. In this particular instance, none of the typical nodules were found, but there were haemorrhagic infarcts round the mites, which had flooded the alveoli and finer bronchioles. It seems probable, therefore, that further investigation will reveal *Pneumonyssus* infections in the lungs of other mammals. *Pneumonyssus* may be found in sites other than the actual respiratory tract; the species *dinolti* (A. C. Oudemans, 1935) occurred in the maxillary sinus of a monkey, where it caused hypertrophy and hyperaemia of the lining membrane. *Pneumonyssus caninum* (see W. L. Chandler and D. S. Ruhe, 1940) was found in the frontal sinus of a dog.

Man does not appear to be susceptible to infection by these mites, no cases having so far been recorded. There are, however, recorded cases of normally free-living species being found in the sputum of patients suffering from asthmatic and bronchitic conditions in the tropics. They appear usually to be mites which occur normally on stored cereal or other plant products, and which are possibly inhaled by persons handling these substances. H. F. Carter, G. Wedd and V. St. E. d'Abrera (1944) studied a number of such clinical cases and found mites and their eggs in the sputum. The condition was accompanied by a marked eosinophilia of the blood. Of the mites recorded in this sort of association, *Tarsonemus floricolus* (G. Canestrini and F. Fanzago, 1876) accounts for some 40 per cent and acarids for about 35 per cent; the rest included the genera *Dermatophagoides*, *Sarcoptes* and *Demodex*. Presumably these skin parasites had secondarily invaded the respiratory tract; and, in this connection, it is interesting to note that J. R. Traver (1951) in her account of an infection of the scalp by *Dermatophagoides scheremetewskyi* (A. Bogdanow, 1864) mentions that these mites, when driven from the scalp by medicaments, sometimes invaded the nostrils and that this was accompanied by irritation of the throat, trachea and bronchi.

Various other examples of what might be called chance or casual parasitization have been recorded. A. Castellani (1907) found *Cytodites* (= *Cytoleichus*) *sarcoptoides* (P. Mégnin, 1876) on the omentum of an African. Hope Simpson (1944) found adult mites, eggs and exuvia in a maxillary carcinoma.

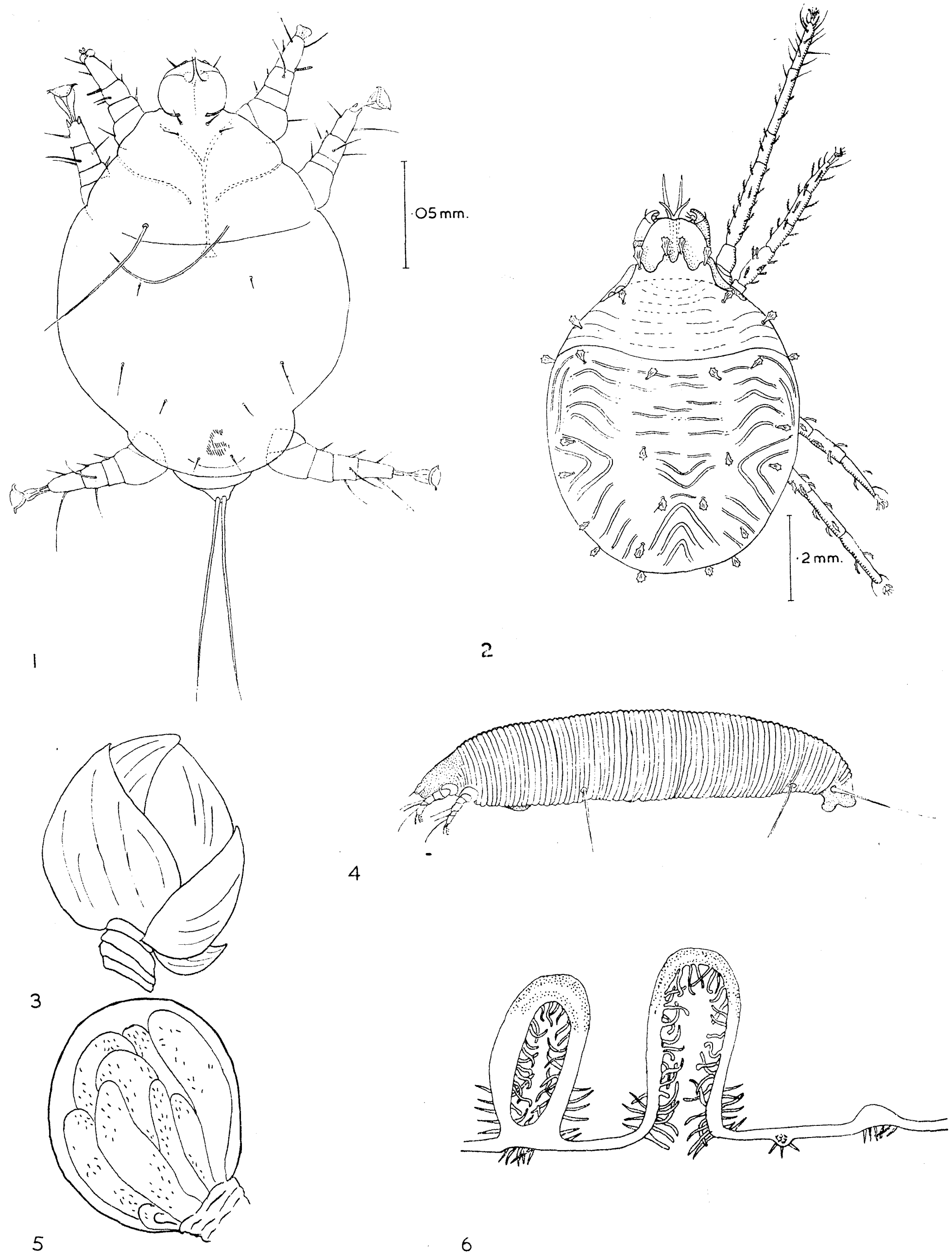

PLATE XXI. **1.** *Locustacarus* sp. from bee's trachea; dorsal view. **2.** *Bryobia praetiosa* (Koch) ♀; dorsal view. **3.** 'Big bud' of blackcurrant; external view. **4.** *Eriophyes ribis* (Westwood); lateral view. **5.** 'Big bud' of blackcurrant; sectional view. **6.** Galls on hedge maple (sections).

Perhaps the most extraordinary example was one mentioned by E. Trouessart (1900). Some 800 live mites and eggs were recovered from the fluid contents of a cyst on the scrotum of a man; Trouessart described the mite as *Histiogaster spermaticus*. As H. Vitzthum (1943) pointed out, it is probably a species of *Histiogaster*, normally occurring in India where the man had lived, which had previously infected an open abscess on the same site.

Mites have frequently been reported as occurring in faeces and urine. In point of fact it is very difficult to exclude the probability of their presence in or on the vessel or instruments used to collect the specimens examined. There is as yet no direct evidence that active mites can live in the bladder or survive passage through the gut. The occurrence of mites in faeces is most probably traceable to the ingestion of food made from infected cereal products.

The only truly endoparasitic mites, apart from *Pneumonyssus*, to be found in mammals are those which occur in the nostrils of the Pinnepedia. They fall into two groups: the genus *Halarachne* is found in the Phocidae, and *Orthohalarachne* in Otariidae and Odobaenidae (see I. M. Newall, 1947). Here, too, the larva is the infective stage. These spread from animal to animal when they congregate on the breeding beaches. The life cycle is modified to the extent that the larvae are produced alive or else hatch as soon as the egg is laid; these larvae give rise directly to adults, no nymphs having been described. Some species may be parthenogenetic, since males have not been found. These mites have the habit of burrowing the whole prosoma into the mucosa and the body is elongate. The females, when anchored into the mucosa in this way, tend to become surrounded by connective tissue. As in *Pneumonyssus*, the fixed digit is reduced, and the remaining motile digit, sharp-pointed. Although they normally imbibe lymph, they may at times ingest blood, too. Various species have been described from a variety of host; *Halarachne halichoeri* (G. Allman, 1847) was described from *Halichoerus grypus* and *Orthohalarachne megellanica* (S. Finnegan, 1934) was found on *Otaria byronia* from the Falkland Islands.

The birds, too, are parasitized by modified laelaptid mites which live in the nares; many of these mites suck blood. They belong to the subfamily Rhinonyssinae. Like the pneumonyssids, they show a reduction of sclerotization and setal development; the chelicerae, however, have a sharp fixed digit and so form an anchor reminiscent of that of the ticks. The stigmata are rotated on to the dorsal surface; presumably a device to keep them free of the mucus layer. As in so many parasitic forms, the life cycle is modified, the females are viviparous and produce nymphs, not larvae. For some species, no males are known, so that parthenogenesis may occur. Several genera are included in this subfamily: *Rhinonyssus nitzschi* (C. Giebel, 1871) was taken from *Caprimolgus europaeus*, *Ptilonyssus nudus* (A. Berlese and E. Trouessart, 1889) from *Passer domesticus*, *Sternostomum rhinoletrum* (E. Trouessart, 1895) from the goose, and *Neonyssus nucifragae* (S. Hirst, 1923) from

Nucifraga caryocatactes. These are the more commonly occurring genera, of which some ten are now listed.

The Acaridiae include two families which parasitize the respiratory tracts of birds, the Cytoditidae with its single genus *Cytodites* (=*Cytoleichus*) (Plate XX, fig. 3) and the genus *Turbinoptes* of the Epidermoptidae. *Cytodites nudus* (F. Vizioli, 1870) lives in the air sacs and lungs of Phasianidae. Unlike the rhinonyssid mites, they do not pierce the lung tissue, but suck the serous fluid from the surface. The mouthparts are modified for this purpose, by fusion of the palps into a rather blunt conical haustellum. These mites are said to cause little inconvenience to the host. The method of transmission is by mites leaving the host and contaminating food or drinking water. This habit does not appear to be restricted to the larvae, since a gravid female has been found in the lung of a two-day-old pheasant chick. *Turbinoptes strandtmanni* was found in the nostrils of the ring-billed gull *Larus delawarensis* by E. M. Boyd (1949), and it is of interest that this genus is in the same family as *Dermatophagoides* mentioned earlier, which also tended to invade the nostrils. The other genera of Epidermoptidae live on or in the skin, and these examples may serve to illustrate how slight is the step from this type of parasitism to an invasion of the respiratory tract.

The genus *Riccardoella* (family Ereynetidae) has been mentioned in connection with the species *limacum* which lives on the mucus in the mantle cavity and on the body surface of pulmonate molluscs; *Riccardoella crassipes* (A. Berlese and E. Trouessart, 1889) was collected from the nasal cavities of sparrows, but has apparently not been recorded since its first discovery.

The reptiles are parasitized by mites similar to the Rhinonyssinae which invade the lungs and air sacs. These mites constitute the Entonyssinae (family Laelaptidae); as well as reduction of sclerotization and setal development, they have well-developed legs with strongly hooked claws for movement over the mucus; the chelicerae of the female are sharply pointed but lack denticles. In the males, the chelicerae are so modified by the spermatophore carrier, that it seems likely that they do not feed. The life cycle is modified by the occurrence of viviparity. *Entonyssus bedfordi* (C. Radford, 1937) and *Ophiopneumicola colubri* (see W. E. Hubbard, 1938) were described from the lungs of snakes, whilst *Pneumophionyssus aristoterisi* (see F. da Fonseca, 1940) was found in the air sacs of *Erythrolamprus aesculapii*.

I have found no records of mites infesting the lungs of amphibians, but in 1952 R. F. Lawrence described *Riccardoella ewesi* in the nasal cavities of the South African *Bufo regularis*, the species being of common occurrence in these toads. There is some suggestion that they may ingest blood, since the gut contained blackish-brown granules of the same appearance as ingested blood in mites known to be blood feeders.

The only other class of animals in which mites live is the Insecta; here, too, the site of infection is the respiratory system. The group of mites concerned is the Tarsonemini, various members of which live in the tracheal trunks of some groups of insects. Probably the most extensively studied of these mites is *Acarapis woodi* (J. Rennie, 1921), which inhabits the tracheae of the honey bee (Plate XX, figs. 4, 5). It is said that there is an age immunity, and that unless the bees become infected during the first week or nine days after emergence, they are immune. The mites enter the anterior thoracic spiracles as adult females and feed by piercing the tracheal wall and sucking blood from the haemocoel. After a few days some half-dozen eggs are laid which hatch in about four days. Adult males are present on the 9th–11th day and females on the 10th–15th day after hatching. All stages of the life cycle feed by piercing the tracheal wall and sucking blood, and this process leads to the development of brown patches on the walls of the tracheae. Apart from the effects of loss of blood, the insect suffers from the blocking of the tracheae by excreta and exuvia, so that its respiratory exchange is diminished. The combined effect is to enfeeble the bee, so that it is unable to fly; infected bees leave the hive and die in the open.

Acarapis is also found on the surface of the body among the 'hairs'. These external forms attach their eggs to the wings. The larvae do not leave the eggs, but only protrude the opisthosomata from the shell. Since it would seem impossible for them to feed in this position, ecdysis to protonymphs must be accomplished on food material derived from the yolk. O. Morgenthaler (1932) claimed to separate two species of *Acarapis* on the ratio of the lengths of the distal segments of leg IV and the idiosoma. He also considered that these species laid their eggs in different positions on the bees, *dorsalis* in the grooves of the dorsal body surface and *externus* between the head and thorax. These species are of very doubtful value, since the idiosomal length varies with the state of nutrition, egg content and the flattening effects of the coverslip.

In the tracheae of Orthoptera and Hymenoptera there are found species of the genus *Locustacarus* (family Podapolipodidae) (Plate XXI, fig. 1); the species *locustae* (H. Ewing, 1932) was found in *Locusta migratorioides* of Central Africa, while *trachealis* (H. Ewing, 1924) occurs in North American insects, such as *Hippiscus apiculatus* and *Arphia carinata*. In these forms the life cycle has become profoundly modified. The eggs give rise to adults directly, but these adults are probably neotenous larvae, having but three pairs of legs and retaining the pair of long posterior setae which are characteristic of larvae in the family.

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CHAPTER V

Mites as Plant Parasites

Many of the mites which are found on plants are predators on plant parasites; there are, however, a limited number of families of mites which have become specialized for piercing plant cells and sucking out their contents. These families all belong to the suborder Trombidiformes which shows a tendency, as a group, towards the development of piercing mouthparts and a suctorial method of feeding.

The Tetranychidae are typical prostigmatic trombids, feeding on the cell content of foliage. The withdrawal of the cell contents results in white patches on the leaves, which later become brown; there is also a tendency for the heavily infected leaves to curl. *Bryobia praetiosa* (C. L. Koch, 1836) (Plate XXI, fig. 2) is the gooseberry mite of Germany; it is very widespread and feeds on a number of other host plants in different parts of its range. In this country, I have found it on *Narcissus* and on Ivy, while in the U.S.A. it has been reported from Alfalfa, Almonds, Clover, Peach, Peas and *Prunus*; it usually attacks the upper surface of the leaves. These races on different host plants (Mathys, 1954) cannot, however, be distinguished by the taxonomist (Pritchard and Baker, 1955; but see Mathys, 1957). This lack of host specificity is a feature of the group, and one plant may be the host of several different species in different parts of its range. The cotton plant in America is parasitized by *Tetranychus telarius* (C. Linnaeus, 1758), in West Africa by *Oligonychus gossypii* (F. Zacher, 1920). The same mite may also be found on different hosts at different times; *Oligonychus pratensis* (N. Banks, 1912) in North Africa moves from date palm to couch grass.

Some genera of the tetranychids can spin silk and cover the foliage with a light web, beneath which the mites live. The genera *Eotetranychus*, *Schizotetranychus* and *Tetranychus* are all said, by D. C. Geijskes (1939), to form a web of this sort. *Tetranychus telarius* overwinters as the adult female in cracks and under loose bark on old trees; this form is brick red. During the summer all stages of the mite are to be found on the foliage of the host plants and these stages range in colour from green with darker spots to carmine, a circumstance which probably led to the description of the green form as a separate species, *bimaculata*, by F. L. Harvey (1893). The summer forms spin a fine web; this species is known as the red spider mite among fruit-growers.

There is another tetranychid known as the fruit tree red spider, *Metatetranychus ulmi* (C. L. Koch, 1836) which does not spin a web and is a serious pest of both soft and top fruit in this country.

The life cycle of *Metatetranychus ulmi* (Koch) was studied by Blair and Groves (1952). Eggs overwinter in a state of diapause, which cannot be broken by rise in temperature, unless the eggs have been previously chilled to temperatures of 1–9° C. for 150–200 days previously (Lees, 1953b); they hatch during April into larvae which begin feeding and produce the first generation of summer forms in about 12 days. After about 3 days from emergence, the females lay eggs which hatch in 11 days to give the larvae of the next generation. Winter eggs may still be hatching when the first generation of summer females have started oviposition. In the course of the year there are five overlapping generations with this short life cycle of about 26 days in all. The fifth generation, which arises in late summer or autumn, produces eggs which enter diapause in the blastoderm stage (Lees, 1955), and it is as these winter eggs that the species exists until the following April.

Blair and Groves found that eggs produced by unfertilized females invariably produced males, but fertilized females produced both males and females. The mite population builds up during the first three summer generations and declines during the fourth and fifth.

The factors involved in the production of the winter eggs were investigated by Lees (1953a), who showed that the dominant factor is the photoperiod. If there is a total day length of upwards of fifteen hours (the threshold of light intensity being 1–2 fc), only summer eggs are produced, with shorter day length diapause eggs. This light factor is normally reinforced by the higher temperatures prevalent at the time of year that this day length occurs, and the nutrient value of the foliage is highest at the same time, and this, too, tends to inhibit diapause.

With shorter day length, lower temperature and ageing foliage, the females of the fourth, and particularly the fifth, generation are induced to lay diapause eggs. This type of life cycle is an adaptation to foliage feeding, in that the emergence of the first generation in any year is delayed until food is available. Should the population build up to high levels and cause extensive damage to the foliage and bruising of the leaves, diapause eggs can be produced at other times. The deutonymph is the sensitive stage.

Tetranychus telarius overwinters as the adult ♀. Under the influence of the factors mentioned above, in late summer and autumn females change from pale green or straw colour to pink, and finally, red. They leave the host plants and enter a state of diapause. In the spring, they return to the host plants, begin to feed, change in colour, and lay the eggs which produce the first summer generation. In areas where the day length shows little, if any, seasonal variation, diapause does not occur; *Oligonychus caffeae* (Nietner, 1861) =*Metatetranychus bioculata* (Wood Mason, 1884) in Assam and Southern India produces non-diapause generations all the year (Lees, 1953b).

A synopsis of the literature on *Metatetranychus* is given by J. R. Groves and A. M. Massee (1951).

Grandjean (1948) considered that the silk gland of web-spinning tetranychids opens on the broad terminal spine of the pedipalpal 'thumb'. Blauvelt (1945) described two groups of glands which opened by a common duct on the rostrum; he called these the silk glands. In other groups of arthropods, such as the Lepidoptera, salivary glands have become modified as silk glands in some cases. The trombid mites are well supplied with salivary glands, the basic arrangement being six paired and one unpaired gland (Sig. Thor, 1903). It is quite feasible that, with restriction of diet to the cell contents of plant foliage, some of these glands should become modified into producers of silk, rather than a fluid saliva.

Among the Pyemotidae (Plate XXII) (Division Tarsonemini, see R. E. Beer, 1954), *Siteroptes* (= *Pediculopsis*) and *Pygmephorus* are the plant equivalents of the genus *Pyemotes*, which is parasitic on insects. The species *graminum* (E. Reuter, 1900) causes white ear in cultivated and wild Graminae, and is said to be a vector of the spores of *Sporotrichum poae*, which causes bud rot in carnations. This species shows the same type of life cycle as *Pyemotes ventricosus*, the female becoming markedly physogastric, while attached to the host plant. The eggs are retained and develop to the adult stage in the enormously enlarged opisthosoma, and the young adults are finally liberated by the breakdown of the maternal body well. The sex ratio is very unequal, there may be only one or two males in a brood of a hundred. Pairing is said to take place to some extent before birth, and virgin females produce haploid males.

Many other tarsonemids are plant parasites, causing various malformations of the host plants. *Tarsonemus fragariae* (H. Zimmermann, 1905, family Tarsonemidae) causes a curling upwards of the leaf margins, and malformation of the young offsets on strawberry plants. The mites overwinter as females on established plants; egg laying begins in the spring and, as the plant begins to produce stolons, mites migrate out along them to the nodes and so come to infect the young plants from the start. The effect is malformation of some leaves which fail to expand, turn brown and drop off; as a result, many young plants die and the survivors produce straggling weak growth. A similar species, *T. pallidus* (N. Banks, 1899) attacks strawberries in North America and also lives on *Antirrhinum*, *Geranium* and *Cyclamen.* In this country it is said that the species *fragariae* lives on *Cyclamen* and *Begonia* in greenhouses. E. W. Baker and G. W. Wharton (1952) regard the two species as synonymous; A. M. Massee (1933a), after a comparison of specimens from America with those occurring in this country, considered Banks' species to be distinct. The species *culmicola* (E. Reuter, 1900) causes silver top in grasses, whilst *Tarsonemus ananas* (H. Tryon, 1898) attacks pineapples in Australia, causing some segments to remain green and go rotten inside, because the mite is a vector of a fungal infection.

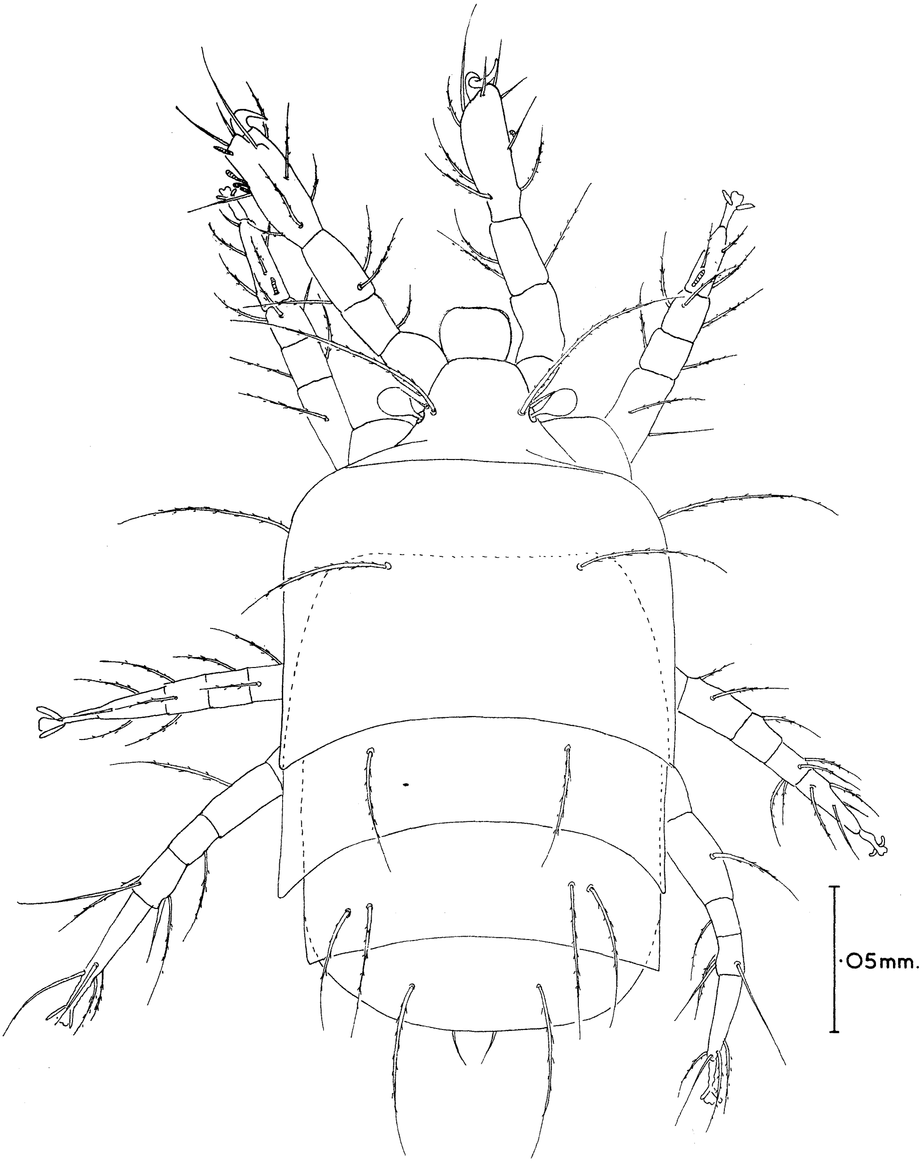

PLATE XXII. *Pygmephorus tarsalis* (Hirst) ♀; dorsal view showing 'segmentation'.

The family Phyllocoptidae includes the so-called rust mites, which produce a roughening and discoloration of the skin of the plant on which they feed. *Phyllocoptruta oleivorus* (W. H. Ashmead, 1879) attacks citrus fruit in California, causing the foliage to become dull and curl. If it attacks the fruit, it causes a silvering of the rind of lemons, but a hardening and darkening of the skin of oranges. *Epitrimerus pirifoliae* (H. H. Keifer, 1938) causes a rusting of the foliage of pear trees and may bring about considerable defoliation. This mite and some other phyllocoptids have a peculiarly modified life cycle, which was followed through by H. H. Keifer (1942) in the case of *Oxypleurites aesculifoliae* (Keifer, 1938), and which has been shown to be similar in *Epitremerus pirifoliae*.

O. aesculifoliae, which causes rust on chestnut leaves, has heteromorphic females which Keifer called deutogynes; the homeomorphic female he called the protogyne. The heteromorphic female was originally described as *Oxypleurites neocarinatus* (H. H. Keifer, 1938). The mites overwinter as the heteromorphic females in crevices on twigs; they become active when the buds begin to grow and, penetrating beneath the outer scales, they begin to feed on the inner bud scales. When the buds have burst and the young leaves expand, these females lay eggs on them. These eggs give rise to the summer generation of males, and females which resemble them are, therefore, called homeomorphic females. As the foliage ages, heteromorphic females appear, leave the foliage and seek crevices on the twigs where they become inactive. Any of the homeomorphic forms still on the leaves perish when these are shed. This type of life cycle is also found in the Hawthorn rust mite, *Calepitrimerus armatus* (A. Nalepa, 1890), and the Elderberry rust mite, *Epitrimerus trilobus* (A. Nalepa, 1890).

The family Phytoptipalpidae (=Pseudoleptidae of A. C. Oudemans) includes several genera of small reddish mites, which pierce plant cells and suck out their contents. *Pseudoleptus floridanus* (N. Banks, 1900) lives under the overlapping leaf bases of the pineapple, and the species *arechalatae* (L. Bruyant, 1911) in the ears of the grass *Distichlis scoparia*. These mites live in colonies and, by force of numbers, may produce ill effects on the host plant. The two species mentioned both have normal life cycles, but according to M. T. Sayed (1942) *Phytoptipalpus paradoxus* (I. Trägårdh, 1904) and other members of the genus have a modified cycle, in that only two immature instars occur between egg and adult, instead of the normal three. This genus also lacks the fourth pair of legs: another indication of a neotenous tendency. E. W. Baker (1948) described a nymphal form *Tenuipalpus eriophyoides*, with an elongated opisthosoma showing annulations. These two tendencies, firstly towards a reduction in leg number, secondly towards an elongation and annulation of the body, give some indication of how a more typical trombid mite could become transformed into an eriophyid.

The families Eriophyidae and Phyllocoptidae are often included in a separate suborder, the Tetrapodili, on account of their having only two pairs of legs in all stages of the life cycle; they would appear to be modified trombids and are best included in the suborder Trombidiformes, as has been done by E. W. Baker and G. W. Wharton (1952).

The eriophyid mites, like the phyllocoptids, are all plant parasites and show a strong tendency to evoke galls or other malformations on the host plant. *Eriophyes lycopersici* (A. M. Massee, 1939) occurs on tomato plants in Morocco and its feeding causes the production of patches of abnormal thick hairs on the stems and leaves. This production of thick and abnormal hairs is a typical reaction to eriophyid infection. These patches of hairs may sink below the general surface to give rise to the so-called dimple gall, such as is found on the underside of the leaves of the white oak and is caused by *Eriophyes querci* (H. Garman, 1883). *Eriophyes vitis* (H. Landois, 1866) causes patches of thick hairs, called erinea, on the underside of vine leaves, a swelling occurring above them on the upper surface. The erineum can, in some cases, sink in very deeply and cause a pouch-like swelling lined with hairs on the upper surface of the leaf (Plate XXI, fig. 6). Pouch galls are caused by *Eriophyes cheriani* (see A. M. Massee, 1933b) on the leaves of *Pongamia glabra* in Southern India, where it is used as a shade tree. If the outgrowth on the upper surface of the leaf is long and narrow, it is called a nail gall, such as those found on lime leaves caused by *Eriophyes tiliae* (H. A. Pagenstecher, 1857). The species *Eriophyes pyri* (H. A. Pagenstecher, 1857), originally a European species, is now spread through North America and Australia. It causes blister-like galls on the upper surface of pear leaves and occasionally on apple leaves, too, the opening of the gall being on the lower surface. The mites pass the winter in the buds and begin to feed before the buds break. The galls are initially red, but become green by midsummer and later turn brown and harden; at this stage the mites have usually left them. These blister galls often contain other species living as inquilines, such as *Epitrimerus piri* (A. Nalepa, 1891).

The galls produced by the host plant in response to infection by eriophyid mites, are characteristic in form for a particular species of mites, just as the insect-induced galls assume specific forms corresponding to what species of insect has caused them. Mite galls differ from insect galls, in that they always have an opening to the exterior, and the interior is a mass of modified hairs, among which the mites feed. Insect galls have only an exit hole and are often of an elaborate structure, showing well-differentiated zones of tissue.

Not all eriophyid mites induce the formation of galls on the host; some members of the family feed in the buds of plants on the developing structures. The infected buds may just dry out, as happens on lilac bushes when they become infected with *Eriophyes lowi* (A. Nalepa, 1890), causing a dwarfing of the shoots and a development of lateral growth. In other cases, the bud reacts by enlarging to give the so-called big bud condition seen on hazels infected with *Eriophyes avellanae* (A. Nalepa, 1889), or blackcurrant bushes where the mite concerned is *Eriophyes ribis* (J. O. Westwood, 1869; see J. Liro and H. Roivainen, 1951). In this case the mites leave the infected buds which dry out in April or May and appear on the foliage. They become scattered by jumping from the plant and being blown about by wind or by clinging to insects. Those that reach another bush live for a time on the foliage, entering new buds as they form. These buds begin to swell and by late summer are big buds (Plate XXI, figs. 3, 5), in which the mites over-winter (A. M. Massee, 1954). The species *avellanae* attacks the flower buds of hazel as well as vegetative ones and causes them to become big buds, which are sterile and like all other big buds do not open.

Another type of deformation is that caused by *Eriophyes populi* (A. Nalepa, 1890), where large irregular masses of buds develop on the twigs. On the willow, three species, described by A. Nalepa, *salicis* (1891), *triradiatus* (1892) and *tetanothrix* (1889), all produce a confusion of slender twigs known as witches' brooms. There is a tendency for the production of slender twigs to be shown by other forms, too; G. Canestrini's species *rudis* (1891) is associated with the witches' broom found in silver birch trees, and infection of hazels by the species *Eriophyes avellanae* is sometimes associated with the production of growths of slender twigs from lateral buds. There is some doubt as to whether the mites are entirely responsible for the production of witches' brooms in trees, since a similar sort of structure occurs on the silver fir and is caused by the fungus *Peridermium elaterium.* It may be that in those cases where mites are involved, they act as vectors of some other fungus infection.

Systematic studies of the Eriophyidae are to be found in the works of H. H. Keifer (1938–46) and A. Nalepa (1898–1924).

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CHAPTER VI

Mites as Vectors

A NUMBER of blood-sucking mites act as vectors of bacterial and virus diseases of their hosts, and may spread these infections to man and his domestic animals. Some free-living species living on plant materials, are likely to be eaten by omnivorous or herbivorous animals; many of these serve as intermediate hosts and vectors of platyhelminth parasites. There is also the possibility of filarial nematodes being transmitted by blood-sucking mites, though this has only been firmly established for *Litomosoides carinii* which is conveyed by *Ornithonyssus bacoti* (S. Hirst, 1913) to cotton rats and other rodents. This was established in 1946 by D. S. Bertram, K. Unsworth and R. M. Gordon, and affords a laboratory method of following a filarial worm through its entire life cycle.

The platyhelminth parasites shown to be spread by mites are all cestodes, the strobilae of which inhabit either ungulates or rodents, and the mites concerned are all of the suborder Sarcoptiformes. C. Joyeux and G. Baer (1945) showed that *Glycyphagas domesticus* (Degeer, 1778) acted as a vector of *Catenotaenia pusilla*, a parasite of rodents. The mite is of common occurrence in rodent nests, and of course both mites and rodents occur together in association with stored cereal products.

The sheep tapeworm *Moniezia expansa* uses mites present in pastures as a vector (H. W. Stunkard, 1937). Recently K. C. Kates and C. E. Runkel (1948) have reviewed the literature and it appears that a wide variety of oribatids serve this purpose. In any given instance, the species involved depends on the mite fauna present, and which of the numerically strong species is capable of swallowing the cestode eggs. The mites so far shown to be suitable include members of the Galumnidae and Oribatulidae.

Other cestodes, *Bertiella studeri* in primates and *Cittotaenia ctenoides* and *C. denticulata* in rodents, are spread by species of Carabodidae in Europe, and in the U.S.S.R. this family of oribatids is a vector of *Anoplocephala perfoliata*—a parasite of horses (E. W. Baker and G. W. Wharton, 1952). Several other families are known to spread various tapeworms of cattle; the Liacaridae, Pelopidae, Ceratozetidae, Notaspididae and Galumnidae all include species which have been shown to be vectors of *Bertiella* or *Cittotaenia* species. This can by no means be considered to be a complete list of the

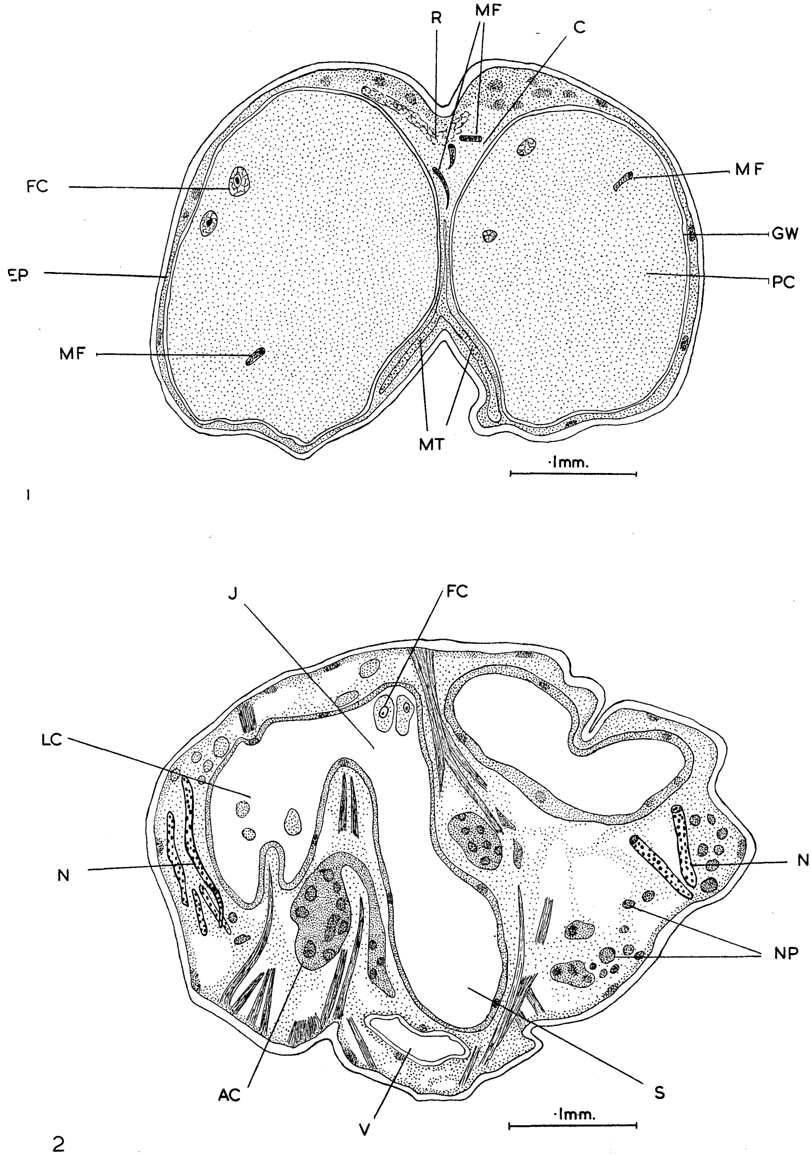

PLATE XXIII. **1.** Transverse section of *Ornithonyssus bacoti* (Hirst) ♀, showing microfilariae. C connective tissue, EP epidermis, FC free cells in the lumen of the gut, GW wall of the gut, MF microfilariae, MT Malpighian tubules collapsed, PC lumen of postdorsal caecum filled with blood, R edge of the rectal wall. **2.** Transverse section of *Ornithonyssus bacoti* (Hirst) ♀, showing infective larvae of *Litomosoides cariniae*. AC accessory glands of the reproductive system, FC free cells in the lumen of the gut, J junction of caeca and stomach; LC anterodorsal caecum, N nematode parasites, NP nuclei of parenchymatous tissue, S stomach, V vagina.

families involved; further investigation will, doubtless, yield other examples of both vectors and parasites.

Among the parasitic nematodes, the filarial worms are commonly spread by blood-sucking arthropods. In the case of *Litomosoides carinii* transmitted by *Ornithonyssus bacoti* mentioned previously, the cycle has been followed in detail (D. S. Bertram *et al.*, 1946). The mite ingests the microfilariae from the peripheral blood-stream (Plate XXIII, fig. 1). These forms, after two ecdyses, and having traversed the gut wall, become the infective larvae lying in the haemocoel of the mite. The infective larva is transmitted to the new host when the mite feeds. How the transference is effected is unknown, for the infective larva is much too big to pass along the channel formed by the mouthparts (Plate XXIII, fig. 2), and, in any case, is not in the salivary glands or gut, which would give it access to the lumen of this channel. It does not appear to be necessary for the rats to ingest the infected mites, as at first sight appears to be the most probable solution to this problem.

Blood-sucking mites play an important role as vectors of protozoan, bacterial and virus infections of vertebrates (E. W. Baker *et al.*, 1956). The causal organism of redwater fever in cattle, *Piroplasma bigemina*, is transmitted in North America by *Boophilus annulatus* (Say, 1821) and by *B. australis* (Fuller, 1899) in South America, Australia, the Philippines and Dutch East Indies. *B. microplus* is a second vector in South America and the West Indies. In East Africa the disease is spread by two species of *Rhipicephalus*, namely *appendiculatus* (Neumann, 1901) and *evertsi* (Neumann, 1897). The infective organism passes from one instar of the tick to the next; adult females transmit it in their eggs to the larvae and nymphs of the next generation, which, in their turn, transmit it to new hosts. A similar disease is caused in Europe by *Babesia bovis* spread among cattle by *Ixodes ricinus* (Linnaeus, 1758). Here again there can be transovarial passage of the organism from one generation of ticks to the next. In eastern and south-eastern Europe sheep are infected with *B. motusi* spread by *Rhipicephalus bursa* (Canestrini and Fanzago, 1887), a one-host tick, the passage being from egg to larva to adult and back to a sheep. *Dermacentor reticulatus* (Fabricius, 1794) is the vector of *B. caballi* to horses over the same area and the Caucasus.

The biliary fever of horses occurring in southern Europe, Africa, Asia and South America is caused by *Babesia equis*. In South Africa the vector is *Rhipicephalus evertsi*. Malignant jaundice in dogs is caused in Europe by *Babesia canis* spread by *Dermacentor reticulatus*. In U.S.A., Asia and North Africa, the vector is *Rhipicephalus sanguineus* (Latreille, 1806), while in South Africa *Haemalastor leachi* (Audouin, 1826) is implicated.

Anaplasmosis of cattle, in which small coccus-like bodies are found at the periphery of red cells, has a wide variety of vectors among ticks. Restricted to cattle, it is spread in North America and South Africa by *Boophilus annulatus* (Say, 1821), *B. microplus* and *B. decoloratus* (Koch, 1844), *Dermacentor andersoni* (Stiles, 1908) and *D. variabilis* (Say, 1821), *Haemalastor lusitanicum*

(Koch, 1844), *Ixodes ricinus*, *I. scapularis* (Say, 1821), *Rhipicephalus sanguineus* and *R. bursa*, *Dermacentor occidentalis* (Marx, 1892) and *D. albipictus* (Packard, 1869). It appears that the micro-organism ingested by the tick undergoes no transovarial transmission (R. Matheson, 1950).

Along the coastal strip of East Africa, *Theileria parva* causes East Coast or African fever in man. This protozoan undergoes schizogamy in the spleen and lymph nodes and has a phase inhabiting the red cells. It is spread by *Rhipicephalus appendiculatus* (Neumann, 1901) which ingest the stage inhabiting the red cells. In the tick a complex cycle of reproduction is said to take place, and finally infective forms appear in the salivary glands of the ticks. There is no transovarial passage from tick to eggs.

Among the Haemogregarines, *Karyolysus lacertarum* is transmitted from lizard to lizard by *Liponyssus saurarum* (Oudemans, 1901), in which the protozoan undergoes sexual reproduction followed by sporogamy. The sporoblasts enter the mite's eggs and so reach the next generation, where they are found in the gut epithelium. The faeces of infected mites, and perhaps the mites themselves, may be ingested by lizards. Infection by ingestion of infected mites is the method of dissemination of *Hepatozoon muris*. In this instance the protozoa are ingested first by the rodent parasite *Laelaps echidninus* (Berlese, 1887), and sexual reproduction and sporblast formation occur in the mite. *Trypanosoma cruzi* will produce crithridial bodies in the gut epithelium of the tick *Ornithodorus moubata* (Murray, 1877), or reduviid bugs. Infection of a new host is by scratching the faeces into the skin or by ingestion, not by the tick itself.

The spirochaetes of relapsing fever, *Treponema* sp., have vectors which include, as well as lice, several tick species. *T. duttoni* which causes this fever in West Africa is spread by *Ornithodorus moubata*. There can be transovarial transmission from one generation of ticks to another (R. Geigy, 1951–6) up to the third generation. In North America *O. turicata* (Dugès, 1876), *O. parkeri* (Cooley, 1936) and *O. hermsi* (Wheeler, 1935) are all vectors of this disease; in Central and South America it is spread by *O. talajae* (Guérin Meneville, 1849) and *O. rudis* (Karsch, 1880). The Spirochaeta are shed in the fluid eliminated from the coxal glands and anus of *O. moubata* while it feeds; in the case of *O. turicata*, transmission is by the bite. Other animals, such as rodents, are susceptible and many form a reservoir of the infective organism. Davis (U.S. public health reports, 1943) thinks that the ticks themselves are the principal reservoir.

Fowl spirochaetosis (*Spirochaeta gallinarum*) is spread by *Argas persicus* (Oken, 1818) in India, Australia, Brazil, Egypt, the Sudan, Germany and Transcaucasus, and Louping Ill of sheep is transmitted by *Ixodes ricinus* (Linnaeus, 1758).

Tularemia, a disease of rabbits and hares, is caused by *Pasturella tularensis*. A. L. Burroughs *et al.* (1945) showed that there are numerous natural reservoirs, including birds, insectivores, rodents, carnivores and ungulates.

Transmission to man is by contact with infected animals, mainly rabbits; *Dermacentor andersoni* (Stiles, 1908) and *Haemaphysalis leporis palustris* (Packard, 1869) can transmit it, as can the deerfly *Chrysops discalis*. These vectors are mainly important in keeping up the natural reservoirs.

Rickettsial bodies are also transmitted by mites. *Dermacentor venustus* (Banks, 1908), an ixodid tick, was shown as early as 1906 to be concerned in the spread of Rocky Mountain spotted fever, the causal organism of which was shown by S. B. Wolbach (1919) to be a *Rickettsia*. This occurs mainly in small mammals, man being the only susceptible large animal. In U.S.A. *Dermacentor variabilis* (Say, 1821) and in South America *Amblyomma cajennensis* (Fabricius, 1787) are vectors. The forms which develop in the tissues of these ticks, including the salivary glands and ovaries, are large lanceolate bodies. Various other species of ticks, *Ornithodorus parkeri* (Cooley, 1936), *Dermacentor occidentalis* (Marx, 1892), *Rhipicephalus sanguineus* (Latrielle, 1806) and *Haemaphysalis leporis palustris* (Packard, 1869), can transmit the disease from rodent to rodent and are therefore important in maintaining the natural reservoirs of the disease.

Q fever of Queensland and Nine mile fever of parts of North America are caused by *Rickettsia burneti*. The main reservoir is the bandicoot rat, but all species of bush-living mammals are susceptible. *Haemaphysalis humerosa* (Warburton and Nuttall, 1909) from a bandicoot was found to contain the infective organism, but this tick does not bite man and so can only be a vector among the reservoir hosts. *Rhipicephalus sanguineus* and *Ixodes holocyclus* (Neumann, 1899) are potential vectors to man. In North America, *Dermacentor andersoni* (Stiles, 1908), *D. occidentalis* and *Amblyomma americanum* (Linnaeus, 1758) have been shown to carry the infective organism. The rickettsiae are in the gut wall and the faecal waste is heavily infected and dangerous to broken or injured skin. They may also enter by the bite.

It might be thought that infection of female ticks by male ticks infected by spirochaetes such as *T. duttoni* might occur, since the spirochaetes are known to penetrate a great many of the host tissues. R. Geigy (1953) showed that in *Ornithodorus moubata* (Murray, 1877), where it is true that the spirochaete invades the testes, there is no transmission to uninfected females which pair with infected males.

Another effect of ticks on man, particularly young children, is the induction of tick paralysis. This is not due to an infective organism, but to the tick itself. Starting with motor uncoordination, it spreads up the trunk and, should the respiratory mechanism become involved, may end fatally. On removal of the tick, recovery is very rapid. In North America *Dermacentor andersoni* (Stiles, 1908) and *D. variabilis* (Say, 1821) are known to produce this effect. The disease also affects sheep, cattle and dogs. Species of *Ixodes* may produce similar results. It is said that the peculiar ascending paralysis can be confused with poliomyelitis.

Tsutsugamushi disease of the Japanese islands is caused by *Rickettsia* *niponica*, and occurs with different degrees of virulence in Papua, New Guinea, Java, Sumatra, Formosa, Indochina, Malaya and Burma. In Japan, the average mortality rate is 40 per cent, in Formosa 10 per cent. The disease has been variously called Scrub Typhus, Pseudotyphus and Rural Fever. In Japan, the most important vector is *Trombicula akamushi* (L. Brumpt, 1913) and from India, through the islands to Australia, it is *Trombicula delienus* (E. Walch, 1923). Other trombiculid larvae have also been shown to be capable of acting as vectors, for example *Schöngastia blastowei* (C. E. Gunther, 1939) in New Guinea. These larvae all normally feed on small rodents, which are the normal hosts of the *Rickettsia niponica*, and, therefore, act as reservoirs of the disease.

Rickettsia akari which normally lives in mice causes, in man, Rickettsial pox and the vector can be a blood-sucking mite, such as *Allodermanyssus sanguineus* (S. Hirst, 1914); C. B. Philip and L. F. Hughes (1948) showed that *Ornithonyssus bacoti* (S. Hirst, 1913) could transmit the infection from mouse to mouse, and so is another possible vector. The outbreak of Rickettsial pox in New York in 1946 was transmitted by *Allodermanyssus sanguineus*, which was plentiful in the mouse-infested tenements, where the disease occurred.

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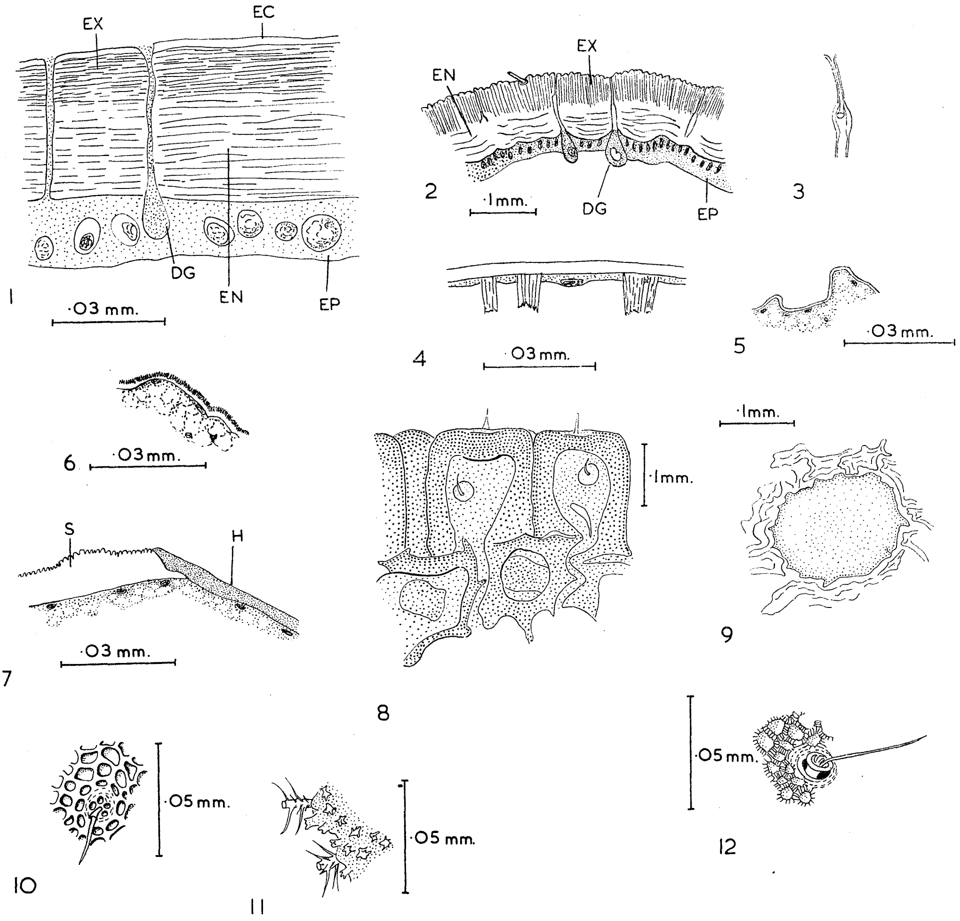

PLATE XXIV. **1.** *Holothyrus gervaisi* (Thon). T.S. cuticle. **2.** *Ixodes ricinus* (Linné). T.S. soft cuticle. DG dermal gland, EC epicuticle, EN endocuticle, EP epidermis, EX exocuticle. **3.** Detail of a duct of a dermal gland in fig. 2. **4.** *Allothrombium fuliginosum* (Hermann). T.S. of the dorsal plate to show lack of distinct endocuticle. **5.** *Acarus siro* (Linné) (= *Tyroglyphus farinae*). T.S. cuticle from opisthosoma. **6.** *Cheyletus munroi* (Hughes). T.S. soft cuticle from opisthosoma. **7.** *Ornithonyssus bacoti* (Hirst). T.S. cuticle of two types. S soft cuticle with folded surface, H brown sclerotized cuticle, lacking endocuticle. **8.** *Argas persicus* (Oken). Integument from the posterior dorsal border of a female. **9.** *Argas persicus* (Oken). Individual fossette from a female. **10.** *Trachytes* sp. Sculptured cuticle from the dorsal surface. **11.** *Ctenoglyphus plumiger* (Koch). Tubercles of the cuticle. **12.** *Labidostoma luteum* (Kramer). The integument of the scapular region.

CHAPTER VII

The Cuticle

As in all arthropods, the exoskeleton is secreted by the epidermis and becomes differentiated into hard sclerotized regions forming the limb segments or body plates, and softer flexible arthrodial membranes. In the main, it would appear to be differentiated into layers comparable with those of the insects, wherever substantial sclerotization occurs. The various layers have been given names, and their homologies with the insect exoskeleton appear to be as follows:

Mite	*Insect*	*Remarks*
Hypostracum	Endocuticle	Takes up basic dyes
Ectostracum	Exocuticle	Takes up acid dyes
Epiostracum	Epicuticle	Polyphenol and cuticulin
Tectostracum		Wax and cement unstainable

The accounts in the literature of exoskeletal structure are summarized by H. Vitzthum (1943) and indicate a considerable variation, both of structure and of the interpretation placed upon it.

It has been shown by M. Pryor (1940a and b, 1947) and others, that the hardening of the exocuticle to give rise to sclerotized regions, is due to orthoquinone tanning of proteins. This tanned protein permeates the chitin of the exocuticle to greater or less degree, conferring upon it varying degrees of horniness. Quinone tanning of protein is accompanied by a darkening in colour. In the Acari, the body may present extensive areas of the opisthosoma where the exocuticle is white, for example the ornithonyssids and female *Ixodes*. Sectioning shows that this paleness is not due to thinness of the exocuticle, which in fact may be thicker than the brown sclerotized regions of the skeleton. It would, therefore, seem that there is present here some other form of exoskeletal substance. In the case of the examples quoted, the opisthosoma undergoes considerable distension after feeding, together with change of contour from flattened to rounded. The exoskeleton must, therefore, be much more pliable than quinone-tanned scleroprotein, and is probably extensible, too. Working on the eggshells of a tetranychid, J. W. L. Beament (1951) came to the conclusion that they included a sulphur-tanned keratin-like substance. Sulphur-containing substances have been found in silkworm and other insect eggshells (A. Tichomiroff, 1885). Sulphur-tanned protein, like keratin, is white in colour and flexible. The quinone-tanned proteins of insectan cuticles are dark and much more rigid and, according to R. H. Hackman (1953), contain no sulphur. Personal observations on the exoskeletons of tyroglyphid mites, whose bodies are largely covered by the white type of cuticle, have shown that it contains some 3–4 per cent of sulphur. Chromatographic analysis of hydrolysates of these skeletons, show that the sulphur is not present in the form of cysteine, as it is in keratin. Presumably we are here concerned with some other type of sulphur tanning, probably due to the preferential reaction of quinones and sulphydril groups.

The epiostracum, when present, in all probability represents the cuticulin layer of insects, and the tectostracum, the water-proofing wax plus cement. These outer layers are often finely folded or sculptured on the surface of the exocuticle (Plate XXIV, figs. 10, 12), giving a wrinkled appearance to the soft parts of the body. This is particularly well marked in the epizoic acarids. In many instances this wrinkling has been reported as absent, but this may have been due to faulty observation, since these layers are very tenuous and do not stain.

The endocuticle, as in arthropods generally, is mainly of chitin and gives a chitosan reaction. It may, however, be absent as a discrete layer, particularly where sclerotization of the body is heavy, as it is in the dorsal plates of mesostigmatic mites. It also appears to be reduced to small areas around the 'hair' bases of many acarid mites. In such forms as the holothyroids, where a heavy skeleton is developed over the whole body surface of these very large mites, both endocuticle and exocuticle are well differentiated (Plate XXIV, fig. 1). W. Winkler (1888), working on *Pergamasus crassipes* (Linnaeus, 1758), distinguished an endo- and an exocuticle on the soft parts of the body, and this agrees with E. Steding's (1924) account for *Halarachne*, I failed to find these layers in *Ornithonyssus bacoti* (Hirst, 1913) (Plate XXIV, fig. 7). In the ixodid ticks, the scutum or podosomatal plate of the female shows a distinct endocuticle pierced by bunches of pore canals, which are said to correspond to the epidermal cells; the exocuticle is pierced by pore canals, closed externally by the epicuticle (M. Rüser, 1933; G. Frick, 1936). The soft parts of the body show a well-differentiated endo- and exocuticle, both pierced by pore canals and the ducts of dermal glands, and covered by a finely wrinkled epicuticle (Plate XXIV, fig. 2). In the argasid ticks, the body is covered by a soft cuticle of similar structure (Plate XXIV, fig. 8), in which are set small sclerotized platelets for muscle attachment (Plate XXIV, fig. 9); these lack the endocuticle, as do the seta-bearing scutellae.

The Trombidiformes, whose structure has been investigated extensively by Sig Thor (1903), exhibit four main types of exoskeletal structure on the body. In *Lebertia* the body is covered by a thick soft integument, differentiated into the two primary layers, of which the exocuticle is the thicker. Both layers are penetrated by spirally twisted canals, which are, presumably, the ducts of dermal glands. The whole is covered by an epicuticle. In *Leptus* and *Linopodes*, the endocuticle is missing, and a stratified exocuticle lies directly on the epidermis (Plate XXIV, fig. 4); *Erythraeus* shows the folding or ridging of the epicuticle and the outer surface of the exocuticle, and this is even more marked in the Tydeidae and Cheyletidae (Plate XXIV, fig. 6), where the ridges may be marked by punctate depressions along their length. In *Trombidium*, the thin exocuticle appears to be divided into polygonal areas, thought by Sig Thor to correspond to the epidermal cells. He also considered that *Calyptostoma* has a unique integument, in that the layer in contact with the epidermis contains fibrils irregularly twisted round one another; he called this the fibrillostracum. Above this lies the exocuticle, in which are sunk the setal bases, joined to one another by radiating bundles of fine fibrils. The Tetrapodili have an integument which can only be distinguished as a layer lying on the epidermis, and thickened over the elongated opisthosoma in a series of bands; this gives an appearance of pseudosegmentation to these mites (Plate XXI, fig. 4). Nothing is known of the intimate structure of the exoskeleton.

The Sarcoptiformes are typically soft bodied only in the Acaridiae, the Oribatei being well armoured in the adult stage. The Acaridae are the only family whose integument has been described. Here a thin exocuticle lies directly on the epidermis which, except at times of ecdysis, is a thin meshwork of branched cells. In the region of the body plates, if any, it is thicker and, in surface view, appears porose, because of the existence of perpendicular pore canals. The whole surface is covered by a thin epicuticle. A distinct chitinous endocuticle is generally missing (Plate XXIV, fig. 5), except where the exocuticle is thickened to form the ring-shaped sockets of sensory setae (Plate XXIV, fig. 11). In some of the epizoites on birds, there are epidermal extensions beyond the posterior end of the body; these produce an integumentary layer, giving the flap-like extensions seen in several genera of the Proctophyllodidae. These have nothing to do with the leaf-like 'hairs' which sometimes occur in a similar position. In some of these epizoic forms, plates of what appears to be the normal brownish sclerotized exocuticle, appear on the body; for example, in *Proctophyllodes* and *Trouessartia*.

The thick and hard plating of the Oribatei is produced by a well-developed epidermis, which very often has a very uneven outer surface. The exoskeletal layers mould themselves to this, and produce a much-sculptured effect. The exoskeleton appears to consist of exocuticle, entirely covered by a thin epicuticle; this closes the outer ends of the pore canals, which penetrate the exocuticle. Outgrowths of the epidermis, in such forms as *Notaspis*, *Pelops*, *Galumna*, etc., produce the lamellae and translamellae (Plate XXXIV, figs. 2, 3), and the narrower shoulder seams. Epidermal glands in some oribatids, *Pelops* and *Tectocepheus* for example, produce sticky exudations to which particles of dirt adhere, giving a false body covering.

The skeleton of the appendages, in all the acarine groups, seems to lack a clearly differentiated endocuticle. The bases in which setae are set, is made from the exocuticle and epicuticle which sinks down into the endocuticle, if it is present. The setae appear to be structures made of the same substance as the exocuticle; they are dealt with more fully in a consideration of sensory organs.

The cuticle may remain capable of growth even after a mite is well established in an instar; this was demonstrated by A. D. Lees (1952) in the female of *Ixodes ricinus* (Linnaeus, 1758). In this tick, feeding takes place in two phases after attachment to the host. During the first phase, which lasts about a week, blood is taken in slowly, digested and absorbed, the gut remaining virtually empty. On the inner side of the cuticle, a new layer, some 45µ thick, is added. The outer cuticle retains its original thickness despite an increase in surface area due to stretching caused by the new growth, so it too must grow; and in fact its weight increases considerably from 0·6 mg. to 5·3 mg. The total thickness of the cuticle is now some 100µ. During the second phase of feeding, which occupies a day, blood is ingested rapidly and the gut distended, the cuticle is stretched and its thickness reduced by about 50 per cent. During the first phase, the epidermal cells are hypertrophied and show histological signs of secretory activity.

All stages of all ixodid ticks, it is said, show these changes of cuticle during feeding, except, perhaps, the larvae and nymphs of *Haemaphysalis inermis* (Birula, 1895). In argasid ticks this peculiar behaviour of the cuticle is shown only by the larvae, which feed slowly. A. D. Lees considers that this cuticular adaptation has allowed the ixodids to indulge in one very large blood meal in each instar and so reduce the number of instars without reducing fecundity. One probable disadvantage is that long attachment to the host may result in the tick dropping off in some unfavourable locality. Lees considers the whole of the cuticle of the ticks to be endocuticle. The fact that the soft parts of the cuticle can be differentiated by staining reactions into an outer and inner region, and that these layers are physically separable on dissection is, I think, justification for regarding them as an exocuticle and endocuticle (cf. table at the beginning of this chapter). The hard parts of the skeleton which are sclerotized, I regard unequivocally as exoskeletal; A. G. Richards (1951) defines the exocuticle as the part of the procuticle which 'becomes hardened and darkened by sclerotization, giving an outer dark exocuticle'.

SEGMENTATION

The modification of primary segmentation is extreme in the Acari and embryological knowledge is very limited, therefore it is not possible at present to homologize the segmentation of the Acari with that of other arachnid groups. In all probability, as in the scorpions and spiders, there is a precheliceral segment which, together with the cephalic lobes and the segments bearing the chelicerae and pedipalpal limbs, constitutes the gnathosoma. Then follows the body region bearing the four pairs of walking legs, which may be called the podosoma. The podosoma is, in a great many cases, subdivided by a dorsal groove between legs II and III (Plate VII, fig. 2), into an anterior and posterior half. In other arachnids, there is a similar groove behind the fourth pair of legs, or else the body is constricted at this point. Thus the subdivision of the body up to the last pair of legs, is peculiar to the Acari as a group. The whole of this region, which is called the prosoma, is in all cases divisible into a distinct gnathosoma and a podosoma, the podosoma being, in many cases, further divided into a propodosoma and a metapodosoma. Each of the latter tagmata bears two pairs of legs and presumably corresponds to two segments. The tergites of the propodosoma usually fuse early to give a propodosomatal shield or plates. The sterna of the prosomatal region were called by C. Börner (1903):

Protosternum = cheliceral segment
Deutosternum = pedipalpal segment
Tritosternum = leg segment I
Tetrasternum = leg segment II
Pentasternum = leg segment III
Metasternum = leg segment IV

The tergite, deutosternum and pedipalpal coxae of the pedipalpal segment in the Parasitiformes, form the ring of the basis capituli of the gnathosoma. That group shows the structure very clearly, but the basic skeleton of the gnathosoma in the other suborders includes the same elements. The region of the body lying behind the fourth pair of legs, Börner called the opisthosoma. In the older literature, the terms cephalothorax and abdomen are met with, but seem wholly unsuitable; for example in the works of E. Korschelt and K. Heider (1890), J. Wagner (1892), N. Banks (1915), S. Hirst (1917). In the primitive Arachnida, the genital segment lies at the anterior end of the opisthosoma, a pregenital segment between it and the fourth pair of legs. In the Acari, the position of the genital opening, though on the ventral surface, is variable, and may not be the same in the two sexes of the same species. If the scorpions are regarded as giving some guide to the primitive condition, the opisthosoma consists of twelve segments, which in the case of the scorpions, is subdivisible into a pre- and post-abdomen. The Notostigmata give the appearance of having nine opisthosomatic segments. The Tarsonemini show traces of segmentation, some consider, the dorsal surface of the opisthosoma being covered by small tergite-like shields, which tend to overlay one another considerably (Plate XXII); they may also extend round the sides and on to the ventral surface. A. C. Oudemans (1886) gives the number of such sclerites as four in *Tarsonemus*, *Avrosia* and *Acarapis*; H. Vitzthum (1943) as four in *Resinacarus*, *Scutacarus*, *Imparipes* and *Microdispodides*, and seven in *Pyemotes*. These sclerites are hysterosomatal; that is, they include a sclerite corresponding to the metapodosoma (legs III and IV). After deducting this, we are left with an opisthosoma which varies from two to six segments. Thus, although such sclerites, when they occur, may represent various combinations of original tergites, they no longer afford a guide to the number of original segments.

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CHAPTER VIII

The Exoskeleton and Arrangement of the Body Sclerites

THE primitive arrangement of tergite, sternite and lateral pleurites of the arthropod, is not met with in the Acari. Fusion of the plates or their modification following the development of a muscular system, which has lost most of its original metamery, has led to the development of an exoskeleton which shows little trace of segmentation. The attachments of muscles have, in many places, produced either the pits seen on the bodies of trombids, or the sclerotized platelets found in the integuments of argasid ticks (Plate XXIV, fig. 9). The expansion of plates already existing, may be brought about by the incorporation of enlarged bases of sensory setae, or these may form subsidiary but independent platelets, as is seen in many Acaridiae.

In the Holothyroidea there is a general hardening of the integument into a dorsal (carapace of Thon) and a ventral shield (plastron of Thon) (Plate II). The dorsal plate overhangs the ventral one, and is attached to it by a thin extensible strip of exoskeleton. The larval condition is not known, but nymphs and adults are similar. In all stages, the anus lies in an oval space, its opening guarded by a pair of lateral valves. The genital opening appears in the adult between coxae IV; in the male, it is a transverse slit in the middle of a thinner area of the plate and it is closed by a pair of transverse valves (Plate II). In the female, the genital opening extends from the middle of the opisthosoma to the level of coxa III; it lies inside a thickened ring of chitin and is closed by four valves, of which the one articulated posteriorly is by far the largest. This valvular mechanism cannot be homologized with the valve mechanism found in the Mesostigmata. Both dorsal and ventral shields are covered with short bristles, which are more numerous dorsally. Unfortunately nothing is known of the muscular system, except the fact that dorso-ventral musculature is present.

In the ticks, the exoskeleton is better developed in the ixodids than in the argasids. In the larval ixodids (Plate XIX, fig. 1), there is a propodosomatal shield, probably equivalent to the fused tergites of the first two leg-bearing segments, called the scutum. In the female, the body behind this remains

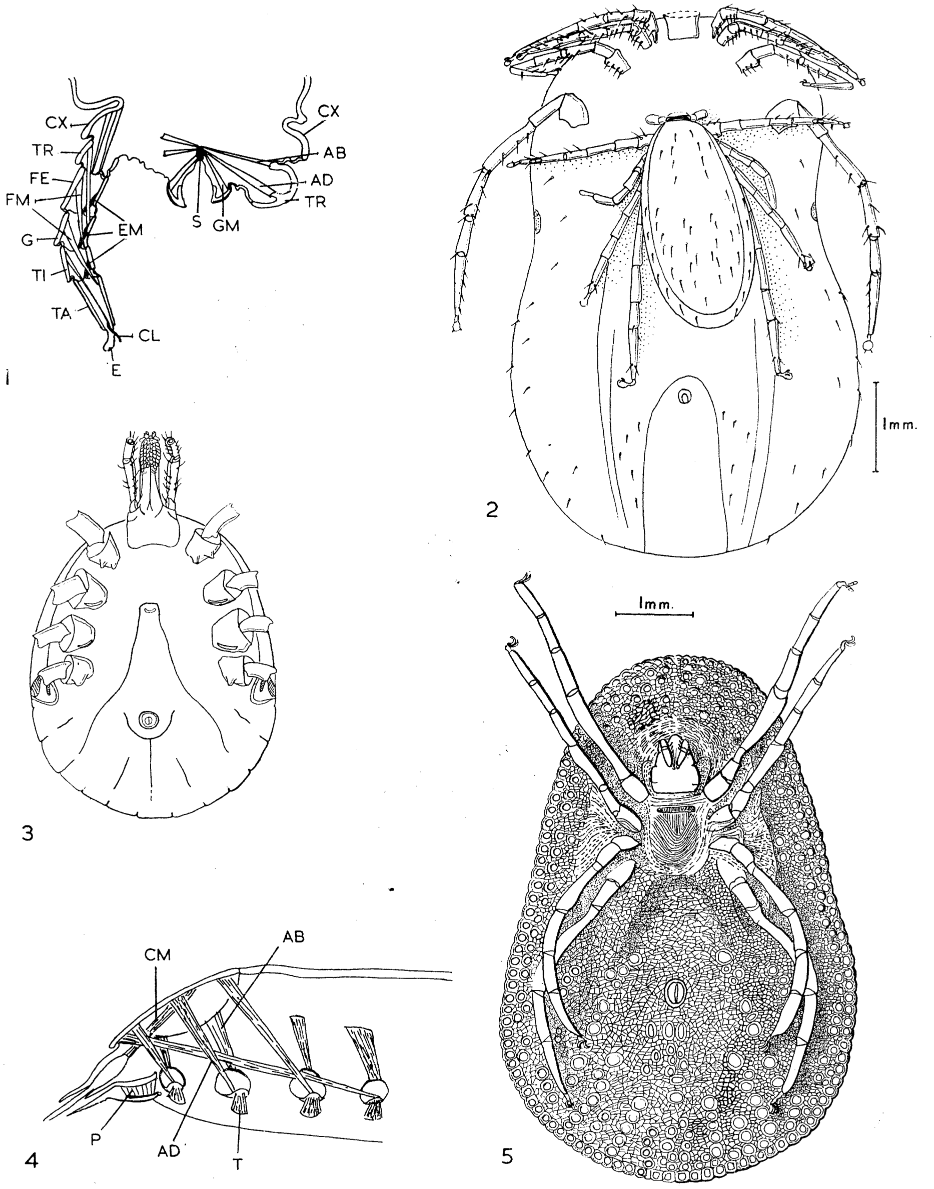


PLATE XXV. **1.** Diagram of the typical leg musculature. AB abductor of trochanter, AD adductor of trochanter, CL claw, CX coxa, E empodial sucker, EM extensor muscles, FE femur, FM flexor muscles, G genu, GM muscles of genital valves, S sternum, TA tarsus, TI tibia, TR trochanter. **2.** *Ixodes ricinus* (Linné); male in coitu. **3.** *Amblyomma hebraeum* (Koch) ♀, ventral view; to illustrate metastriate condition. **4.** *Ixodes ricinus* (Linné); diagram of the anterior musculature, AB abductor muscle, AD adductor muscle, CM cheliceral muscle, P pharyngeal dilators, T tensor muscle. **5.** *Argas persicus* (Oken) ♀, ventral view; a typical argasid tick.

soft, though grooves due to muscle attachment mark off an area, the alloscutum. In the male (Plate XXV, fig. 2), the alloscutal area hardens and fuses to the scutum, to give rise to a conscutum. In some species of *Haemalastor*, a groove separates the scutum and alloscutum. Such extensive hardening would interfere, in the female, with the intake of food and production of eggs.

Ventrally, the male develops a pregenital shield, a large ventral plate behind the genital opening and an anal plate, in the anterior part of which lies the anus. The anal plate is flanked by a pair of adanals. In the Metastriata (Plate XXV, fig. 3), the ventral surface is subdivided by grooves and strong sclerotization occurs mainly towards the posterior end of the body. The anus lies further forwards than in the Prostriata and the single anal plate is lost, the anus being flanked by a pair of plates; lateral to these lie a pair of adanals. Posteriorly, one or two pairs of very small subanal plates may be present. P. Schulze (1932) has used these plates to link ticks to the fossil Anthracomarti.

In the ixodids, the dorso-ventral musculature has a marked effect on the exoskeleton. On the scutum there is a groove on either side of the mid-line, the cervical groove, and more laterally, a pair of scuto-lateral grooves. On the alloscutum, there is a median groove and a pair of anterior and posterior paramedian grooves. Grooves corresponding to the alloscutal ones are found on the ventral surface. Confined to the alloscutum are paired anterior and posterior lateral grooves. From the grooves on the alloscutum, except the lateral ones, dorso-ventral muscles run to their corresponding grooves on the ventral surface, and form sheets of muscle between the caeca of the gut.

In the ixodids the grooves on the scutum mark the attachment of muscles from the coxae of the legs (Plate XXV, fig. 4). Only leg I has a movable coxa, its adductor having its origin in the cervical groove and its abductor in the lateral scutal groove. Similar muscles run to coxae II and III, but to coxa IV a long oblique muscle runs from the base of the gnathosoma. Shorter muscles run from all the coxae to the lateral grooves on the ventral body wall. Since three of the four coxae are not movable, this system of muscles presumably serves to brace the anterior part of the body. The muscular system of the ixodids has been investigated most fully by M. Rüser (1933).

The flexor muscles of the gnathosoma have their origin on the hind edge of the scutum, and the levators on the middle part of the cervical grooves, while the retractor muscles of the chelicerae originate on the posterior part of the scutum.

In the argasids, the musculature which is essentially similar, has its origin on small individual platelets (Plate XXV, fig. 5), the larger of which are arranged in longitudinal rows. The dorso-ventral muscles do not appear to form sheets between the gut caeca, except in *Ornithodorus*. The extensive dorso-ventral musculature of the ticks, is presumably related to the fact that

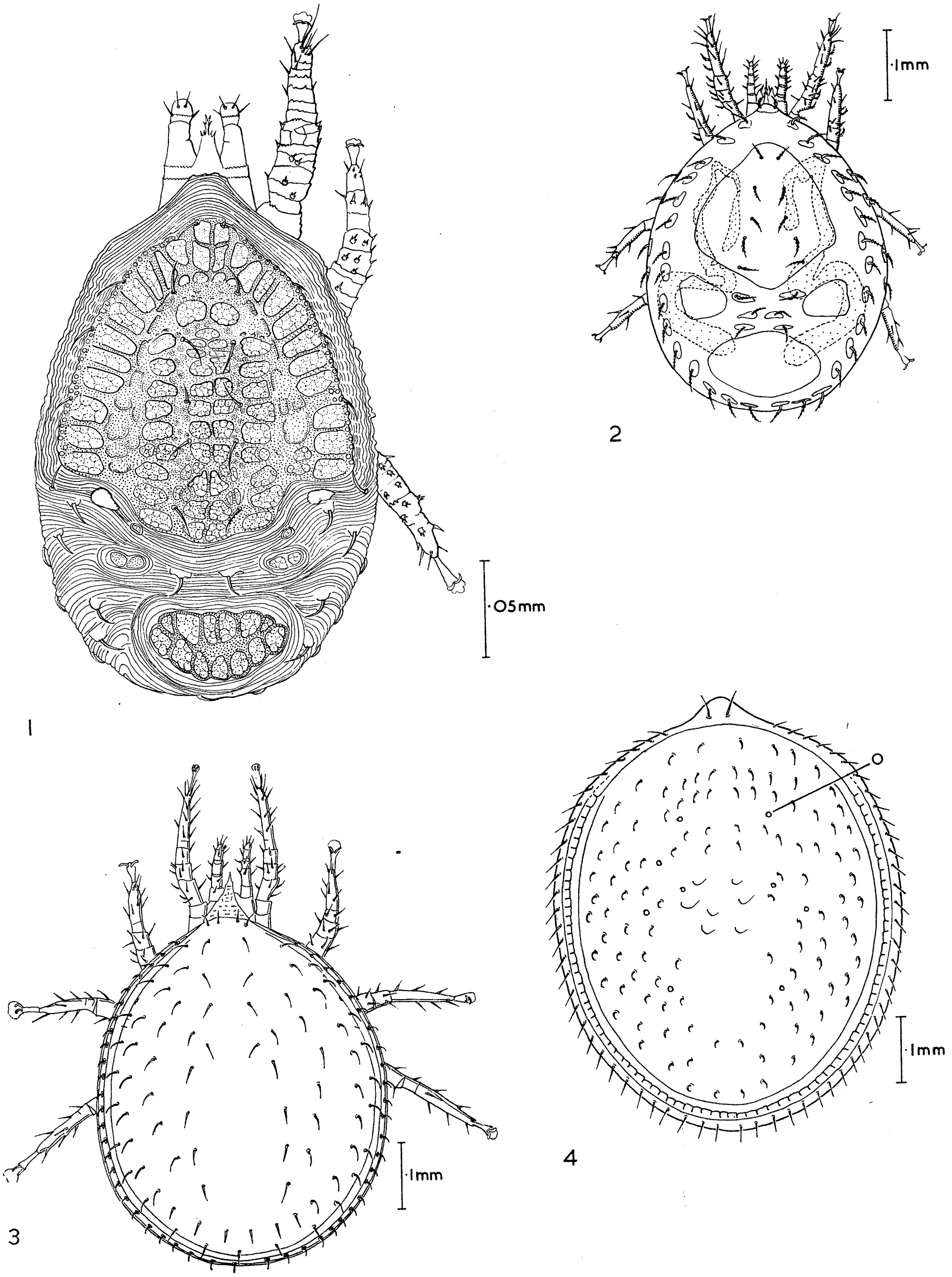


PLATE XXVI. **1.** *Leiodinychus* sp.; dorsal view of larva. **2.** *Leiodinychus krameri* (Canestrini); dorsal view of protonymph. **3.** *Leiodinychus krameri* (Canestrini); dorsal view of deutonymph. **4.** *Leiodinychus krameri* (Canestrini); dorsal view of male. o openings of glands.

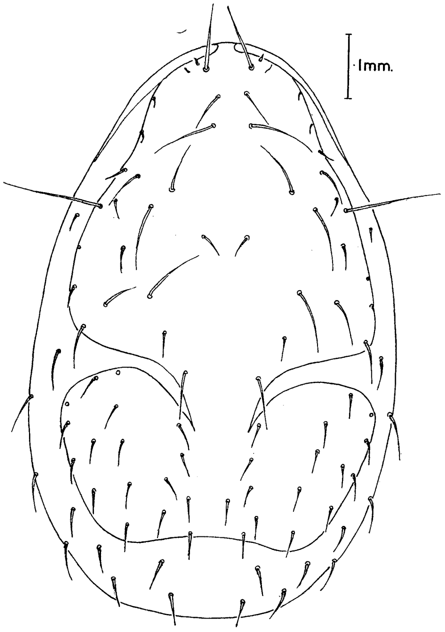
they lack the longitudinal muscles found in practically all other Acari, and use this means to retain the general body shape. Contraction of the dorso-ventral muscles during egg-laying, may also be an important function.

The Mesostigmata generally show an enlargement of the anterior dorsal shield, so that it covers all the leg-bearing segments in all stages of the life history, and presumably corresponds to four fused tergites. Endoparasites, such as *Pneumonyssus* and *Halarachne*, lack this plate. During the ecdysis from larva to nymph, the pygidial shield enlarges and between it and the podosomatal shield, a number of interscutal platelets arise, to which dorso-ventral muscles are attached (Plate XXVI, figs. 1, 2). The arrangement of these platelets is used by systematists.

In the Mesostigmata, the interscutal plates become added to the pygidial plate in the deutonymph (Plate XXVI, fig. 3), the dorsal surface being covered by two large plates—the podosomatal or notocephalon and opisthosomatal or notogaster. These invariably fuse in the Uropodina (Plate XXVI, fig. 3), and similar fusion is shown by *Hypoaspis* deutonymphs, though usually it only takes place in the adult in the majority of gamasids. In males of *Parasitus*, the plates are still clearly defined, and a deep cleft on either side occurs in both sexes of *Veigaia* (Plate XXVII, fig. 1). *Eugamasus* shows a line of demarcation, but the fusion is complete in *Pergamasus* (Plate XXVII, cf. figs. 2, 3). The female normally shows less degree of fusion than the male (Plate XXVII, fig. 4); this is possibly connected with the need for greater plasticity during egg laying, although in *Holoparasitus* the dorsal shield shows a contact with the ventral one. Presumably such forms as the Rhodacaridae, with separate podosomatal and pygidial shield in which the interscutal elements are still discernible, are the most primitive; the female of *Liroaspis* has separate interscutal elements.

In the laelaptids sensu latu, similar fusions have occurred to give a single plate as in *Ornithonyssus*, though the extent of this may be reduced in parasitic forms. In *Ornithonyssus*, the hind part of the shield is reduced. In *Ophionyssus* and *Neonyssus* there are two separate shields, the pygidial being small and well separated from the podosomatal.

In the larvae of the Mesostigmata, on the ventral surface there are four pairs of setae in the sternal region. The sclerotized sternal plate usually extends from just behind the first pair to midway between the third and fourth pairs (Plate XXVIII, fig. 1). The anus is surrounded by an anal plate, carrying two adanal and one postanal setae. In the protonymph, the fourth pair of legs have appeared external to the fourth pair of sternal setae, and anteriorly the sclerotized sternum now includes the first sternal setae (Plate XXVIII, fig. 2). The deutonymph commonly carries all four pairs of sternal setae on the sternal plate (Plate XXVIII, fig. 3). In the adult female, additional sclerotization occurs on the ventral surface. Basically, this includes an epigynial plate covering the genital opening, which is in the region of coxae IV primitively, and a ventral plate between this and the anal plate



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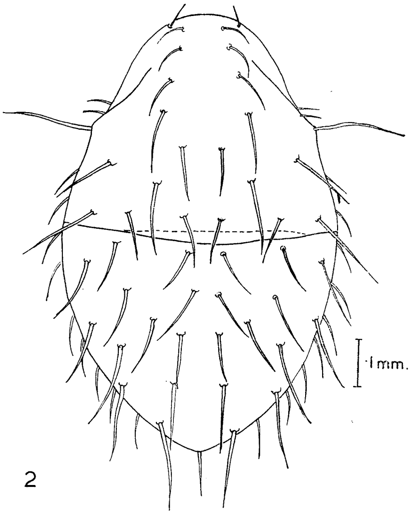

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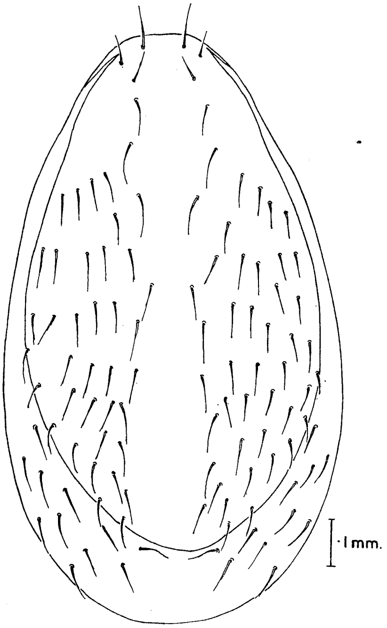

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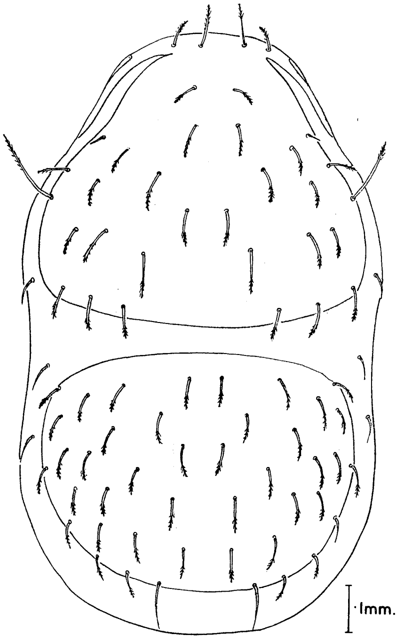

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(Plate XXVIII, fig. 4). The ventral plate is fused, either to the anal to give a ventrianal plate, or to the epigynial to give a genitoventral plate (Plate XXIX, fig. 2). The fourth pair of sternal setae is now usually carried on separate platelets, the metasternal plates (Plate XXIX, fig. 2). The genital setae (5), which make their appearance in the deutonymph, may or may not be carried on the epigynial plate of the adult. Behind coxae IV are a pair of inguinal plates, corresponding to the dorsal interscutal plates; dorso-ventral muscles run from one to the other. These plates, if expanded, are called metapodal plates, for example, in *Eulaelaps stabularis* (Koch, 1839) (Plate XXIX, fig. 2). External to the coxae, with their apices between them, a series of triangular parapodal or exopodal plates arise and, in a corresponding internal position, the endopodal plates (Plate XI, fig. 2). The endopodal plates may become fused with each other, or with the sternum. The most anterior pair of endopodal plates lies between legs I and the pedipalps, and if remaining separate, these are called jugularia (Plate XI, fig. 2). They may fuse to give a transverse plate in *Pergamasus decipiens* (Berlese, 1903), or become each subdivided into two, for example in *Pergamasus hamatus* (Koch, 1839).

In the male, the genital opening is in the middle of the sternal plate, in the Trachytina and Uropodina protected by a flap from in front (Plate XXIX, fig. 4); in the other Mesostigmata, the opening is under the anterior edge of the sternum (Plate XXIX, fig. 3). The opisthosoma is covered in the adult male, either by a complete sclerotization, or by a ventrianal plate which meets the elongated sternum posterior to leg IV.

From the deutonymph onwards, the spiracle on each side opens into a groove or a tube, the peritreme (Plate XXIX, figs. 2, 3), carried by a long narrow plate—the peritrematal plate—lying on the lateral body wall above the parapodal plates. The peritrematal plate may fuse with neighbouring plates; in parasitic forms it tends to be reduced.

I. Trägårdh, in his long series of papers on the phylogeny of the Mesostigmata (1912–50), was of the opinion that the relationships of the various groups of mesostigmatic mites could be traced through the morphology of the female sterni-genital region. He considered that the four pairs of sternal setae each originally stood on a coxal plate in the body wall, having associated with it a 'pore' posterior to its base. By a consideration of the four pairs of setae and their associated 'pores', he traced the various complicated ways in which the sternal elements, the epigynial plate, the ventral plate and sclerotization of the dorsal wall of the genital invagination may come into relationship with one another. These views are summarized diagrammatically (Plate XXX, figs. 1 to 11, 13 to 16). He restricts the term jugularia to

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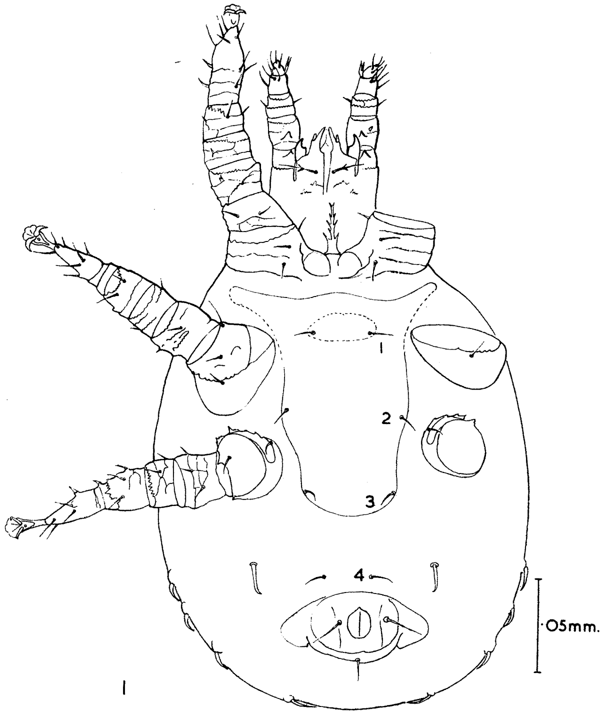
PLATE XXVII. **1.** *Veigaia cervus* (Kramer) ♀; dorsal view. **2.** *Eugamasus cornutus* (Canestrini) ♂; dorsal view. **3.** *Pergamasus crassipes* (Linné) ♀; dorsal view. **4.** *Eugamasus magnus* (Kramer) ♀; dorsal view.



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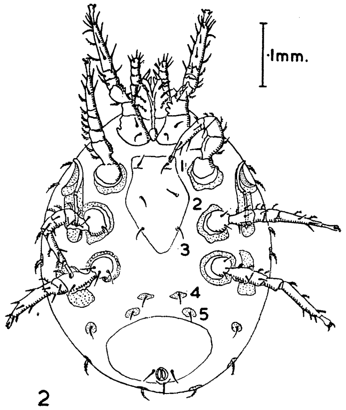

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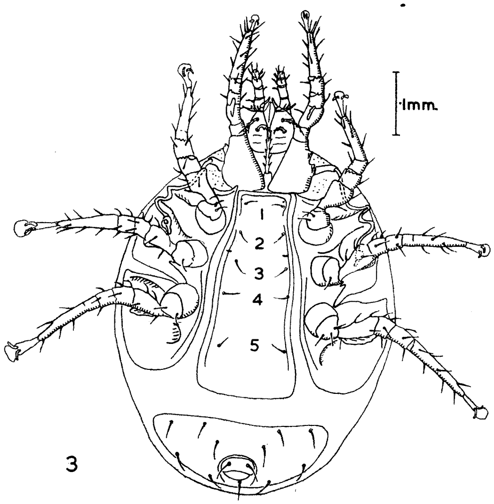

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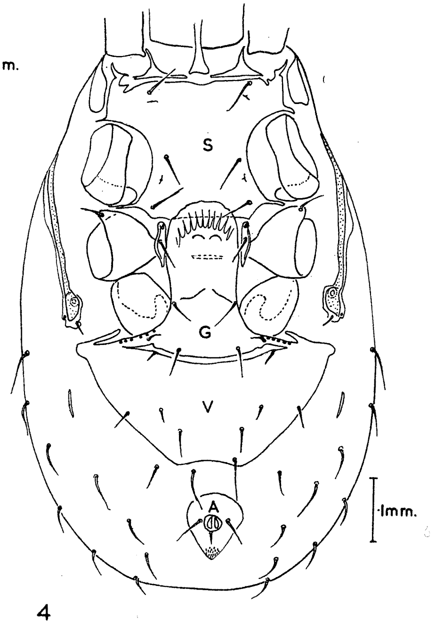

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separate platelets carrying sternal setae I, and the epigynial plate to such forms as carry the genital setae on it.

H. Vitzthum (1943) considers that the plates have arisen by extension of setal bases. If the tritosternum, very constant in appearance like the sternal setae, is considered to represent the sternum elements of the segment behind the pedipalps, that is the segment of leg I, then, including the four pairs of sternal setae, there would seem to be five segments corresponding to four pairs of legs. Furthermore, the first sternal setae are level with leg II, and not I, in the vast majority of forms, and leg I is articulated to the body in front of the anterior edge of the sternum: so that Trägårdh's premise is open to criticism.

J. Camin and F. E. Gorirossi (1955) have modified Trägårdh's system, having re-examined the various species on which it was built. Their conclusions are that the Mesostigmata early dichotomized into a branch with a single genital operculum, the Monogynaspida leading to the Uropodina, Gamasina and Liroaspina, and a branch with a three-valved genital opening, the Trigynaspida, including the Cercomegistina, and Antennophorina (Plate XXX, figs. 12, 17, 18). Trägårdh, on the other hand, split the group into the Agynaspida, in which the epigynial shield was primitively missing, in his opinion, and the Eugynaspida, which possessed an epigynial shield as an anterior outgrowth of the ventral, separated off usually by a suture to give greater flexibility; the epigynial plate might also be flanked by lateral plates, also anterior extensions of the ventral plate. In the former group, he placed *Liroaspis*, *Microsejus* and *Megisthanus*; all other species he considered to be eugynaspid. There is, thus, a fundamental divergence of opinion as to the relationships of the various types of mesostigmatic mites.

In effect, we are here dealing with the end products of long evolutionary histories and, in the absence of the direct evidence of fossil forms, and with a complete absence of embryological knowledge of the forms concerned, coupled with the fact that the mite fauna is very incompletely known, it is evident that the phylogenetic trees are certain to be largely illusory. In point of fact, there is yet another way in which the various types of sterni-genital region could arise.

Both Trägårdh and Camin and Gorirossi have ignored the nymphae, plates lying beneath the epigynial plate and figured by Berlese (Plate XXX, figs. 19, 20) and these may have played a significant part in the evolution of the sterni-genital regions. In primitive arachnids, the genital opening is usually considered to have been in the membrane behind the pregenital segment, which lies immediately behind leg IV. There is no reason to suppose

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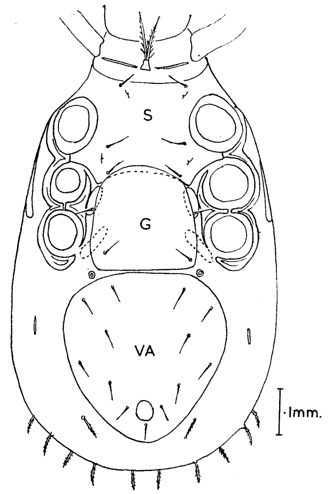
PLATE XXVIII. **1.** *Leiodinychus* sp. larva; ventral view. **2.** *Leiodinychus krameri* (Canestrini) protonymph; ventral view. **3.** *Leiodinychus krameri* (Canestrini) deutonymph; ventral view. 1–5 elements progressively incorporated in the sternal plate. **4.** *Veigaia cervus* (Kramer) ♀; ventral view. A anal plate, G genital plate, S sternal plate, V ventral plate.



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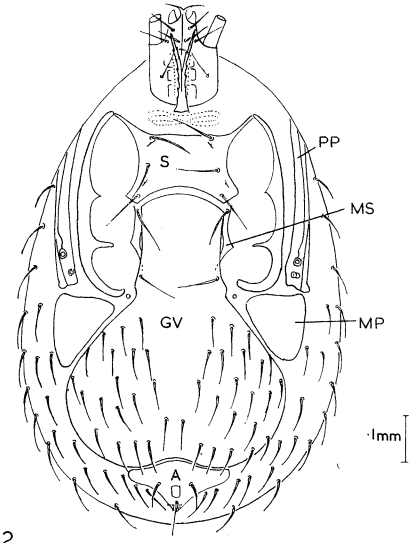

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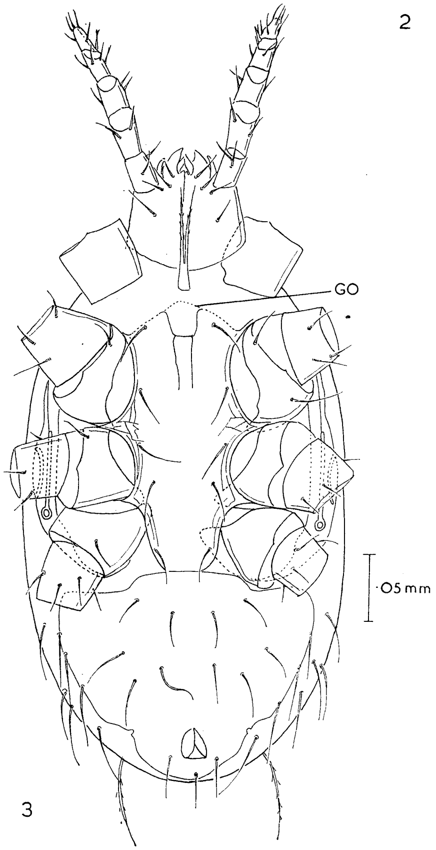

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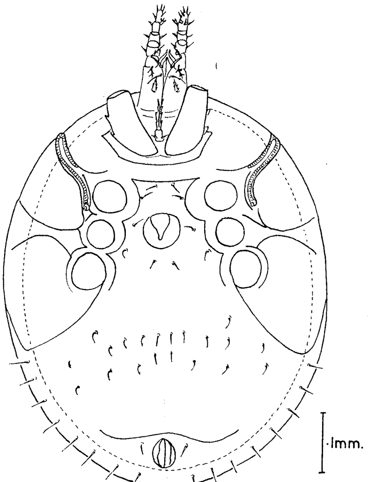

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that the acarine ancestor differed in this respect, since the genital opening frequently lies in the neighbourhood of the fourth coxae. In the scorpions, the genital opening is covered by a flap or operculum carried by the post-genital sternite. It is not unreasonable to suppose that this flap may have been present as an anterior extension of a ventral plate, formed by fusion of the opisthosomatic segments in the primitive Mesostigmata. Growth of this operculum, coupled with the necessity for a wide opening to allow egress of a relatively big egg, might well lead to the division of the pregenital sternite into two; we should then have the primitive three-valved condition postulated for the Trigynaspida by Camin and Gorirossi (1955). Enlargement of the genital operculum or epigynial plate, so that it overlay the divided pregenital sternite, would give the condition seen in *Pergamasus*, in which a trigynaspid condition exists, but in which the antero-lateral valves are the two metasternal plates, carrying the fourth sternal setae (Plate IV, fig. 2); the divided pregenital sternite beneath the epigynial plate being the nymphae of Berlese. Such a condition would be a starting-point for the monogynaspid branch of Camin and Gorirossi, and lead, in the way Trägårdh so carefully illustrated, to the Trachytina and Uropodina. If, on the other hand, the two plates derived from the pregenital sternite, that is the 'Nymphae' enlarged at the expense of the epigynial plate, we should arrive at a form like *Diplogynium.*

In the dorsal wall of the vaginal invagination are sclerites which have muscle attachments on to the sternum, and which, curving round the lateral walls of the vagina, articulate with the valves (claviform sclerites of Camin and Gorirossi). Reduction of the ventral armature following an anterior extension, such as is seen in *Diplogynium*, would expose the dorsal wall of the vaginal invagination, and increase in the initial sclerotization would give rise to the median plate of Trägårdh, or the sternigynial plate of Camin and Gorirossi, in such forms as *Klinckowstroemia.* The ways in which the various types of armature could be derived, on this theoretical basis, are summarized in figures 21 to 26, of Plate XXX.

If one regards the early acarine form as one which had poorly developed sclerotization, then the existing plates may well have arisen from fusions of setal bases and such existing segmental sclerites as there were, as H. Vitzthum (1943) suggests. In this case, the various types of sterni-genital pattern may each have arisen independently, and any phylogenetic significance be quite illusory. It is well to remember in this respect, that there are very large gaps in our knowledge of the mite fauna of the tropics, and forms may well be

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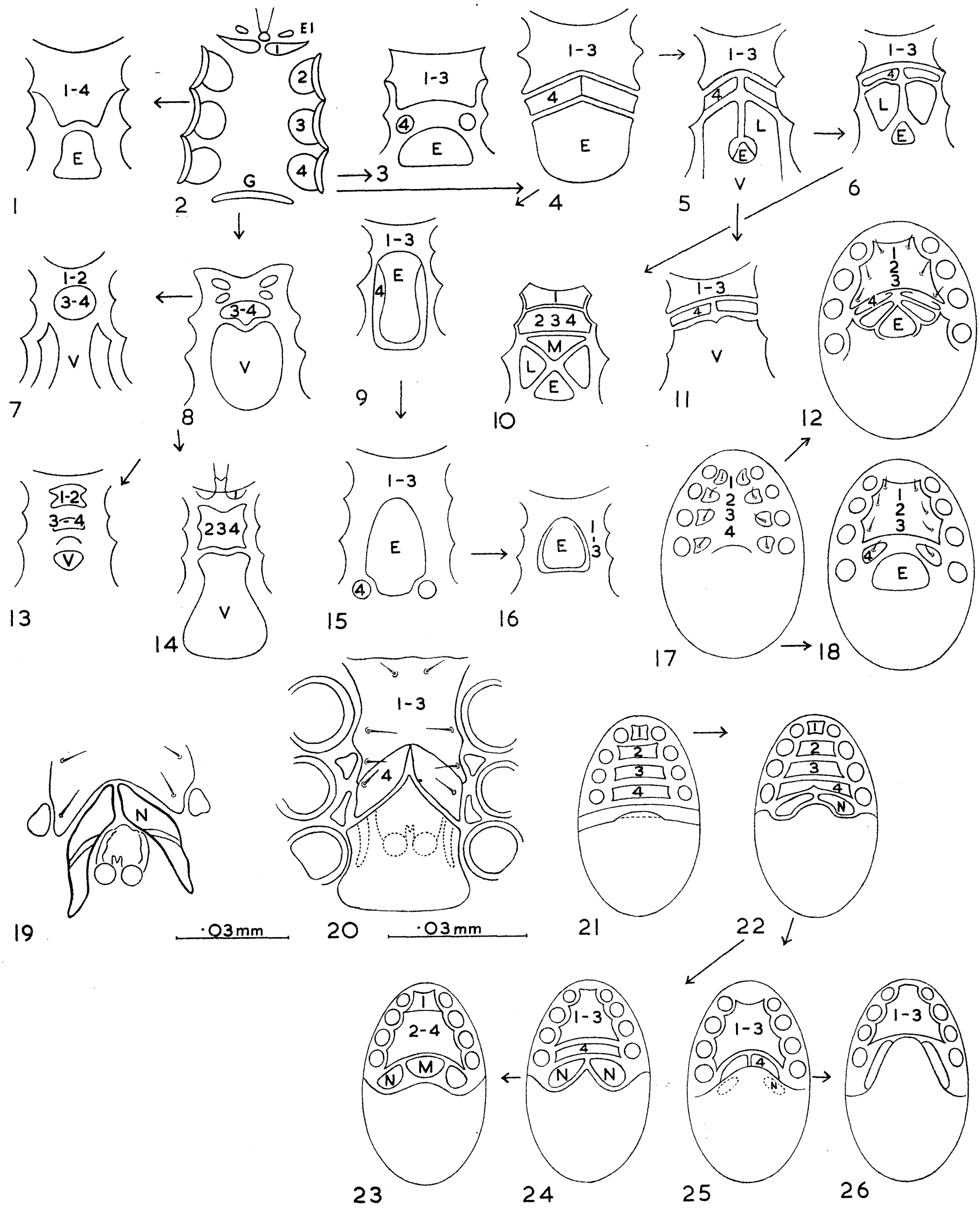
PLATE XXIX. **1.** *Macrocheles* sp. ♀; ventral view. S sternal plate, G genital plate, VA ventrianal plate. **2.** *Eulaelaps stabularis* (Koch) ♀; ventral view. A anal plate, GV genitoventral plate, MP metopodal plate, MS metasternal plate, PP peritrematal plate. **3.** *Blattiosocius tineivorus* (Oudemans) ♂; ventral view. GO genital opening. **4.** *Leiodinychus krameri* (Canestrini) ♂; ventral view.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found which do not conform at all to any of the existing schemes, none of which is founded on incontrovertible evidence. It must, however, be agreed that Carnin and Gorirossi's criticism of the agynaspid group of Trägårdh was well founded. As they pointed out, *Liroaspis* and *Megisthanis* both have genital openings well forward between legs II and III, not a primitive character, and *Microsejus* shows every sign of a reduction of sclerotization.

The anal plate carrying the three anal setae, can extend forwards, carrying additional setae from the soft part of the opisthosoma, anterior to the anus. It is then called a ventri-anal plate. It may lose its posterior seta, as seen in the Uropodina, Trachytina, Celaenopsina, etc. When the seta is present, the posterior margin of the anal plate is marked by a band of fine pores, whose function is unknown.

The musculature of the Mesostigmata, in so far as it is known, does not appear to have as direct an effect on the exoskeleton as in the ticks. In the opisthosoma, apart from the dorso-ventral muscles running from the interscutal plates to the inguinals, there are dorso-ventral muscles running from the pygidial plate to the anal plate. Their contraction appears to bring about the opening of the anus and the compression of the hind gut simultaneously. The other dorso-ventral muscles are incomplete, for in the podosoma, there is present an endosternite (Plate XLVII, fig. 2). This structure is of similar material to that of the muscle tendons, and forms a horizontal plate beneath the anterior caeca of the stomach. Muscles run from the podosomatal plate on to its dorsal surface; to its edges and ventral surface are attached the origins of the muscles operating the movable coxae. Tensor muscles from the lateral body wall also run on to the edge of the endosternite, while to its anterior border, in laelaptids generally, are attached the flexors of the gnathosoma. In the Parasitidae, these muscles run on to the podosomatal shield. This shield also carries the levators of the gnathosoma, and the retractors of the chelicerae. There is a tendency, in forms which can protract and retract the chelicerae, for the origin of these muscles to lie more posterior, so that in the Uropodina they lie far back in the body, level with the anal region.

In *Laelaps echidninus* (A. Berlese, 1887) (see J. Stanley, 1931) and in *Ornithonyssus bacoti* (S. Hirst, 1913) (see T. E. Hughes, 1949), there are

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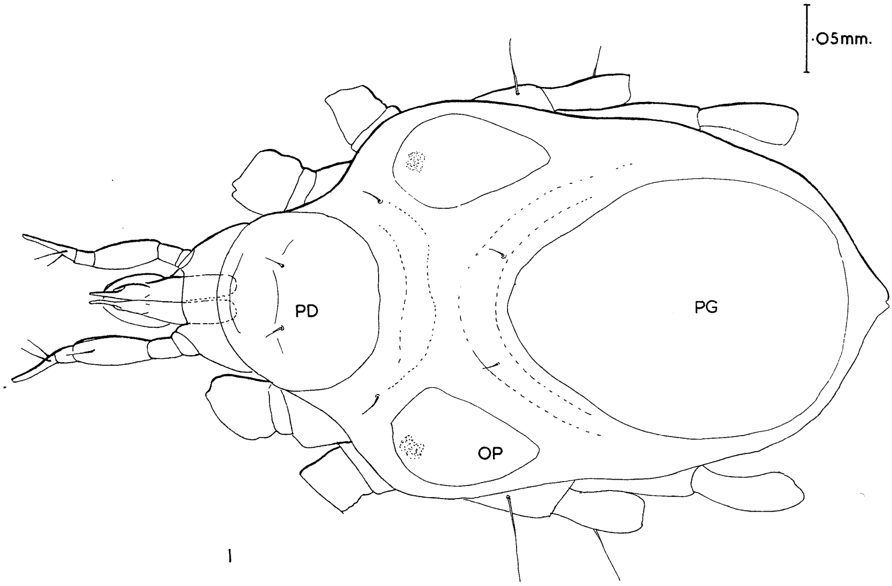
PLATE XXX. Ventral plates of Mesostigmata. **1.** *Gamasellus.* **2.** Primitive arrangement, after Trägårdh. **3.** *Macrocheles.* **4.** *Pergamasus.* **5.** *Euzercon.* **6.** *Diplogynium.* **7.** *Megisthanus.* **8.** *Liroaspina.* **9.** *Trachytes.* **10.** *Klinkowstroemia.* **11.** *Caelenopsis.* **12.** Trigynaspid of Camin & Gorirossi. **13.** *Macrosejus.* **14.** *Epicrius.* **15.** Polyaspina. **16.** *Uropoda.* **17.** Primitive type of Camin & Gorirossi. **18.** Monogynaspid type of Camin & Gorirossi. **19.** *Pergamasus crassipes* (Linné); with eipgynial plate removed. **20.** *Pergamasus crassipes* (Linné); with epigynial plate complete. **21.** Primitive condition—Hughes. **22.** Establishment of Nymphae. **23.** Condition leading to *Klinkowstroemia.* **24.** *Diplogynium* condition. **25.** Gamasid condition. **26.** *Trachytes*-like condition. 1–4 sternal plates, E epigynium, G genital opening, L lateral plate, M median sclerotization of vaginal wall, N nymphae, V ventral plate.



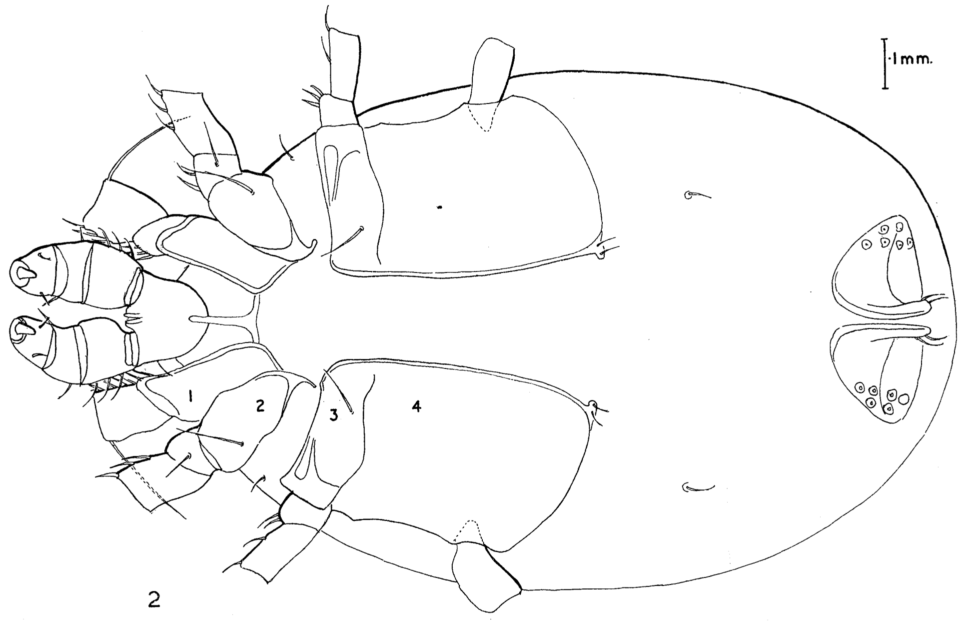


PLATE XXXI. **1.** *Copidognathus fabricius* (Lohmann) ♀; dorsal view. OP ocular plate, PD propodosomatal plate, PG posterior dorsal or pygidial plate. **2.** *Unionicola crassipes* (Müller) ♀; ventral view. 1, 2, 3, 4 the four coxal plates incorporated in the body wall.

muscles which run from the base of the labrum epipharynx to the cheliceral sheaths, where they join the basal joint of the chelicerae. These muscles may act as protractors of the chelicerae (T. E. Hughes, 1949). F. E. Gorirossi (1950) is of the opinion that they originate on the subcheliceral plate and operate the labrum epipharynx (Plate XL, fig. 1).

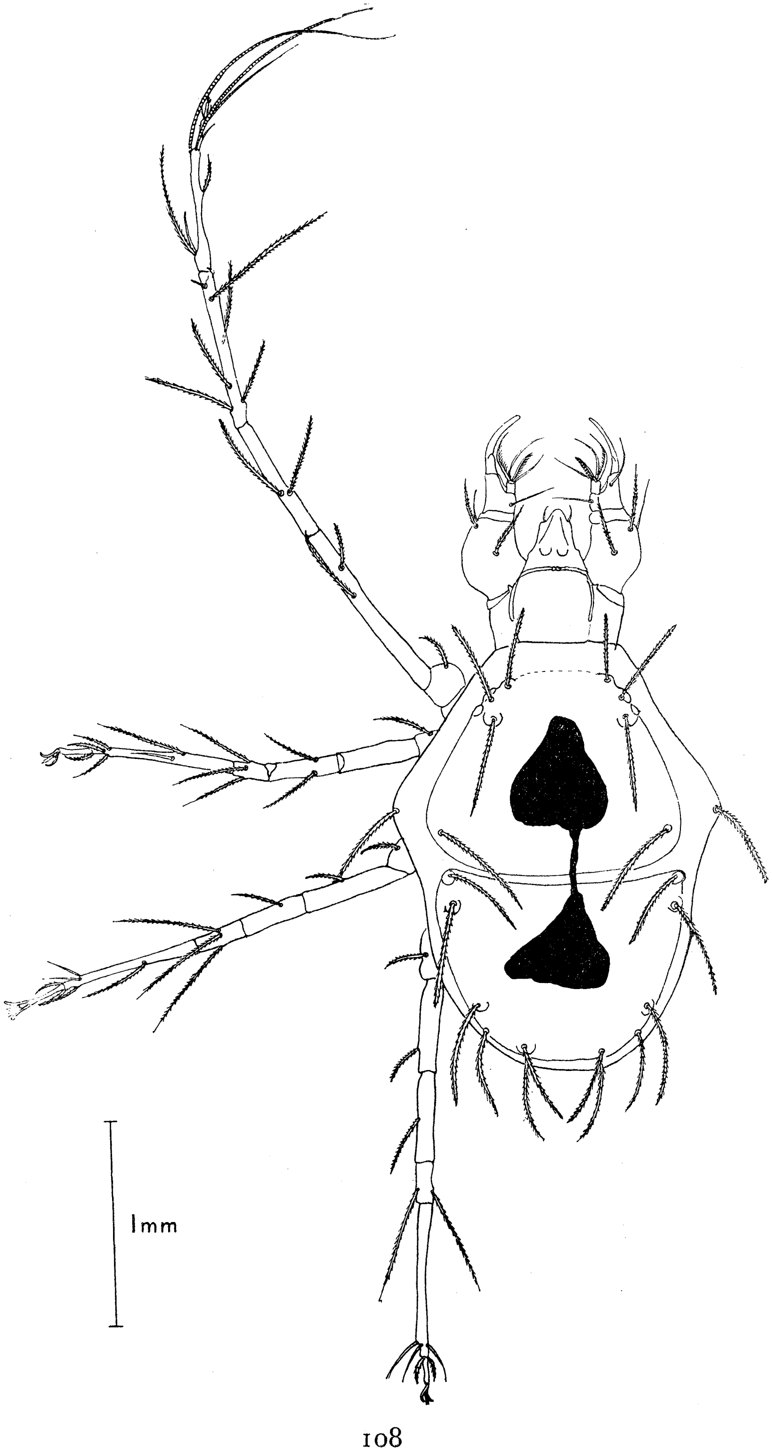
In the Mesostigmata, there is a well-developed system of longitudinal muscles, which originate dorso-laterally on the body wall above coxa I, often producing a definite depression in the body outline. The strands of muscle run backwards and downwards obliquely, and are inserted on the posterior ventral walls of the opisthosoma. Their function seems to be that of tensors, supporting the opisthosoma; a function which, in a fully gorged or egg-carrying female, is a very necessary one.

The Trombidiformes show a great diversity of body plates, which it is not possible to reduce to a common plan. There has been, in terrestrial forms, a reduction of the dorsal plating, which has been followed in the hydrachnellids by a secondary development of plates. The Raphignathidae show the presence of a propodosomatal plate, a pygidial plate and, laterally in the space between them, two occular plates. This may be a primitive pattern, since it is shown by all the Halacaridae, with variations as to the size of the occular plates (Plate XXXI, fig. 1); *Tectopenthalodes* also shows this four-plated arrangement of the dorsal surface.

Ventrally, the plating is derived to a great extent from the coxal surfaces. The coxae are sunk into the body, and their ventral surfaces form coxal plates, separated by apodemes. This state of having four separate coxal plates on each side (Plate XXXI, fig. 2) of the podosoma is seen in many species of *Rhombognathus* and *Cheyletus*. The coxal plates of legs I and II tend to fuse, as do those of III and IV, giving two plates on either side of the podosoma, and this may be further reduced by the anterior pair meeting and fusing in the mid-line, as in *Cunaxa* (anterior epimeral plate of Viets). Posterior to these coxal plates, there is a genital plate as in *Rhombognathus*, but this is frequently enlarged to form a genitoanal, as in Nicoletiellidae. Thus there are four ventral plates, common anterior coxal, coxal III and IV of each side and genitoanal, corresponding to the four dorsal plates. These plates may enlarge, meet and fuse as in *Bonzia* among the cunaxids.

In the main, the Eleutherengona show a reduction of plating and have a soft integument covering the dorsal surface, as in the Eupodidae and Rhagidiidae, etc.; and the ventral plating is then reduced to that associated with the coxal surfaces. Where plating is developed, as in the halacarids (Plate XXXI, fig. 1), it tends always towards the four dorsal and four ventral plates.

In the Eleutherengona, secondary development of dorsal plating may occur. For example, in *Cheyletiella parasitivorax* (P. Mégnin, 1878) there is a propodosomatal shield; in *Cheletomorpha* (Plate XXXII) this shield extends back to between legs III and IV and is followed by a post-dorsal plate,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while in *Cheyletia* and *Cheyletus* there is a propodosomatal and hysterosomatal shield.

In the adult Trombidiidae, there is a system of eight pairs of dorso-ventral muscles running obliquely downwards and forwards, their attachments to the dorsal surface showing a slight depression. This number may become reduced, so that in most hydrachnellids, there are four pairs of dorso-ventral muscles. Where there is a dorsal plate and a ventral plate which curves up the body sides, the dorso-ventral muscles are far out to the sides of the body and serve to pull the plates together. In *Frontipoda*, where the dorsal plate is reduced and the ventral plate carried far dorsally, the two middle pairs of dorso-ventral muscles have their insertions far up this plate. They thus come to lie horizontally and pull the two sides of the ventral plate together. Larval Trombidiidae differ from the adult in that there exists a system of longitudinal muscles in the hysterosoma. These muscles have a segmental appearance and dorso-ventral musculature is lacking.

The Parasitengona show this tendency for reduction of plating even more strongly. The Trombidiidae have the dorsal armour reduced to the propodosomatal shield (Plate XXXIII, fig. 1) in the larva, together with a number of small platelets, usually associated with setae, as in *Allothrombium.* In the adults the propodosomatal shield is reduced to a crista metopica, the details of which are of systematic importance, while the rest of the dorsal surface is unplated. In the hydrachnellids, there may be extensive armour developed, but it is all of a secondary nature and very diverse in form.

The crista metopica (Plate XXXIII, figs. 2, 3, 4) represents a reduced propodosomatal shield, and includes one or two soft areas, in which are set one or two pairs of pseudostigmatic organs or trichobothria. Only in a few cases do these stand outside the crista, and, where no crista is present, as in Rhagidiidae, Eupodidae, Penthaleidae and Anystidae, there is a swollen area carrying two pseudostigmatic organs, the epivertex. There is seen the same tendency to reduce the plate in hydrachnellids. Emargination from behind has almost split the plate into two in *Diplohydrachna cruenta* (O. F. Müller, 1776), while in *Rhabdohydrachna* only two small strips are left, and in *Hydrodroma* only the larva carries a rudiment of it. In the Thyasidae, the plate is lost but around the median eye or frontal organ stand four pairs of setae, of which two pairs are pseudostigmatic organs. The other two pairs have platelet bases, the pre- and post-frontals of O. Lundblad. Muscle attachment gives rise to other plates. These, K. Viets considered, would primitively have the arrangement as seen in *Panisellus* (Plate XXXIII, fig. 5), five pairs of dorsocentralia and, more laterally, four pairs of dorsolateralia. Between the dorsocentralia and dorsolateralia are a row of six setae, dorsoglandularia, and more laterally, four lateroglandularia. The

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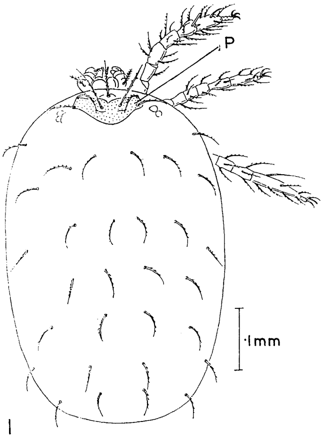
PLATE XXXII. *Cheletomorpha lepidoptorum* (Shaw) ♀; dorsal view, to show the greatly elongated leg I used as a sensory appendage.



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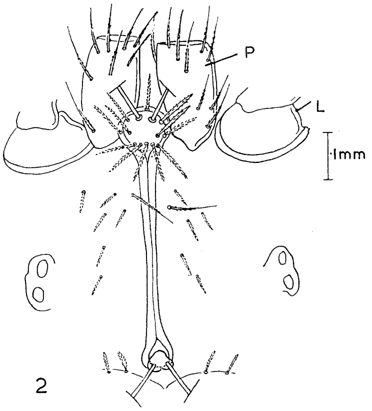

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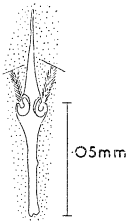

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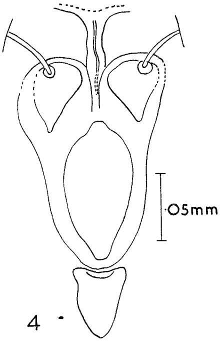

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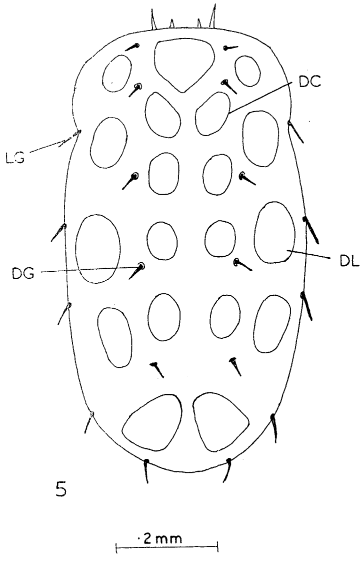

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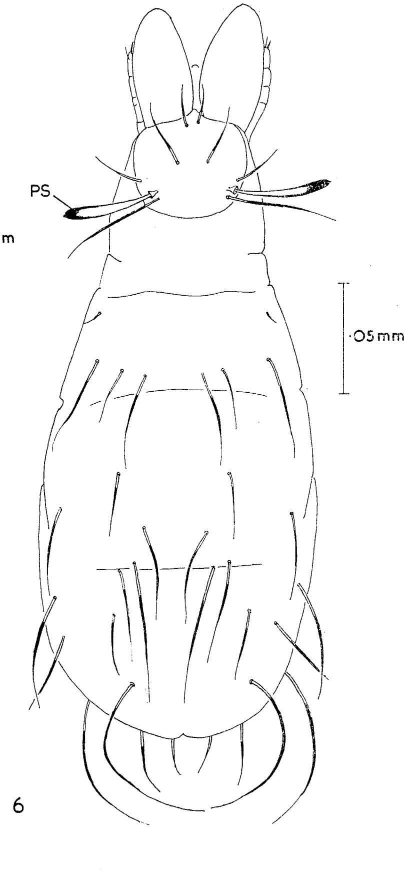

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pre- and post-frontals extend to join the chitinization over the eye and so form an anterior shield. Fusion of the other platelets to give a dorsal shield, pierced by the glandularia, is seen in *Thyopsis*, while in the Hydrovolziidae the manner of fusion leads to a similarity with the halacarids.

Ventrally the coxal plates are strongly developed in the hydrachnellids (Plate XXXI, fig. 2), and the development of a genital plate leads to the whole ventral surface becoming hardened. This ventral plating can extend upwards over the sides of the body, so that, in the absence of dorsal plates, it may almost cover the body, for example, in *Frontipoda*.

The Sarcoptiformes show a considerable divergence between the Oribatei and Acaridiae, the former tending to be heavily armoured, the latter soft-bodied on the whole, though the heteromorphic deutonymph may be heavily sclerotized. In the adults, there is a tendency for those epizoic on birds to develop a fairly well-formed plating and in these forms the original propodosomatal shield may be extended by the incorporation of setal bases, and the pygidial shield may be extended to cover the whole of the hysterosoma (Plate XV, fig. 1); on the other hand, the pygidial plate may remain small, as in *Pterolichus obtusus* (C. Robin, 1868), and a separate post-dorsal plate usually develops. In free-living forms, a dorsal propodosomatal shield is present, reduced to a narrow median strip in the Glycyphagidae, which is comparable to the crista metopica of the Trombidiformes (Plate XXXIII, fig. 3). In many of the epizoic forms, for example *Proctophyllodes*, *Joubertia*, etc., there are posterior extensions of the hysterosomatal plates, like the lateral pteromorphae of oribatids.

In the Oribatei, the immature stages have a soft or leathery integument, largely retained by the Palaeacaridae (Plate XXXIII, fig. 6), without any clearly defined propodosomatal shield. During the ecdysis to the adult stage, dorsal plates are usually developed. These remain separate in the Apyctima, but fuse in the Pyctima (Plate XXXIV, figs. 1, 3). A peculiarity of the oribatids is a tendency for the plates to project from the body; such projections have been characterized by F. Grandjean (1933 and 1934) as tecta or limbi, according to whether they contain a part of the epidermis in the former case, or are the thickened chitinous edges of a plate in the latter (Plate XXXIV, fig. 4). Limbi, therefore, tend to occur at the edges of body plates, like the genital or anal valves; such thickened edges are, in point of fact, by no means limited to this group, but also occur as the anal valves of Acaridiae and the antero-dorsal plate of some Mesostigmata. Setae, which

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PLATE XXXIII. **1.** *Trombicula autumnalis* (Shaw) larva; dorsal view. P propodosomatal shield. **2.** *Erythraeus regalis* (Koch); crista metopica. L leg I, P base of pedipalp. **3.** *Glycyphagus ornatus* (Kramer) ♂; crista metopica. **4.** *Allothrombium fuliginosum* (Hermann); crista metopica. **5.** *Panisellus thienemanni* (Viets); diagram of dorsal plates and glandularia. DC dorsal centralia, DG dorsal glandularia, DL dorsal lateralia, LG lateral glandularia. **6.** *Aphelacarus acarinus* (Berlese); dorsal view. PS pseudostigmatic organ. The legs have been removed.

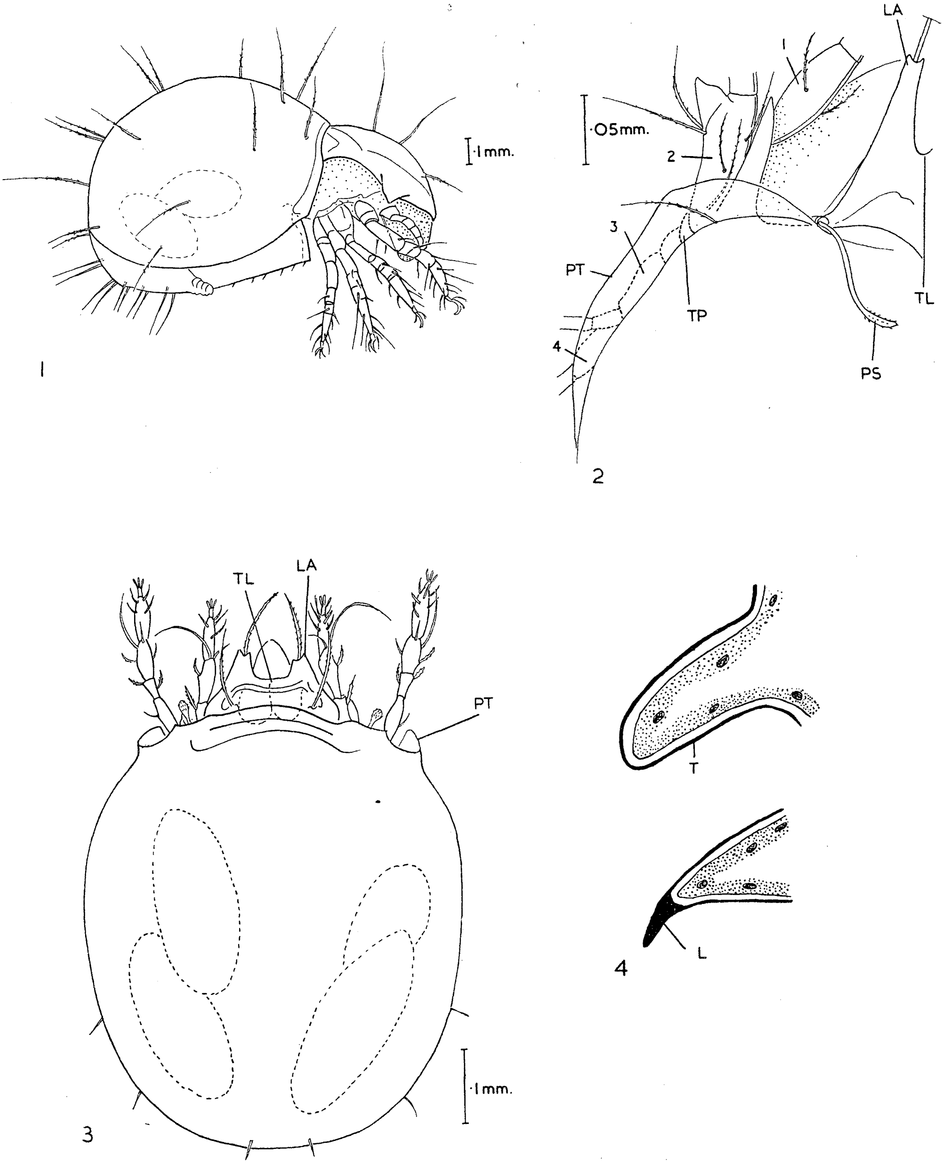

PLATE XXXIV. **1.** *Phthiracarus* sp. ♀; lateral view. **2.** Oribatid pteromorphs. 1–4 bases of limbs, PT pteromorph, LA lamella, TL trans-lamella, TP tectopedium. **3.** *Trichoribates trimaculatus* (Koch) ♀; dorsal view. **4.** Diagrams of Tectum and Limbus.

are carried near the edges of such plates, remain in contact with the hypodermis and nervous system, through canals which perforate the chitin.

The tecta form flaps of the body surface which overhang the legs and rostrum and give rise to lamellae and pteromorphae (Plate XXXIV, fig. 2). The lamellae are flaps, which may arise near the setae scapulares externae and run forwards and inwards to the lamellar seta. The anterior ends of the lamellae may meet, as in *Notaspis*, etc., or they may be connected by a transverse fold (translamella), for example *Gustavia*, etc. The pteromorphae arise from the notogaster and encircle the posterior part of the podosoma, covering the sides of the body and the posterior two pairs of legs in the Galumnidae, Pelopidae, etc.; C. Willmann (1931) excluded from the pteromorphae, the smaller outgrowths which extend from the shoulder angles, such as occur in the Lohmanniidae. He was here following A. D. Michael's (1883) division of the Aptyctima into Pterogasterina and Apterogasterina. There is considerable variation in size of such outgrowths within individual genera and, therefore, it is probable that F. Grandjean's contention that these are all pteromorphae is anatomically sounder.

These pteromorphae have protoplasmic extensions of the hypodermal cells, lying at their bases between the upper and lower chitinous surfaces, and they often carry setae which are similar to those on the notogaster. When big pteromorphae are present, they can usually be depressed by special muscles whose origin is a wide one on the hysterosoma, the fibres converging on a point in the middle of the pteromorph; recovery is presumably by elasticity.

Associated with the exoskeleton are dermal glands. The actual knowledge of these is very scanty. None have been previously described in the Notostigmata or Holothyroidea, though in the latter group they certainly exist (Plate XXIV, fig. 1). In the Parasitiformes, the ticks possess dermal glands scattered over the soft parts of the body (Plate XXIV, figs. 2, 3); P. Sculze's (1942) assertion that they are lacking in the argasids is, according to A. D. Lees (1947), incorrect. P. Schulze (1942) and S. Yalvac (1939) regarded these structures as sensory organs with additional glandular functions, although the sensory function of these organs has never been demonstrated. In ixodids the layers of the epicuticle are cuticulin, polyphenol and wax; all these layers are secreted by the epidermis, and the dermal glands 'appear to add nothing of structural significance to the substance of the cuticle' (A. D. Lees, 1947). In argasids, there is an additional cement layer outside the wax and in *Ornithodorus moubata* (Murray, 1877), these glands are congregated round the tubercles. The yellow greasy substance secreted by the dermal glands of *Ixodes ricinus* (Linnaeus, 1758) is considered by H. Falke (1931) and S. Yalvac (1939) to be a waterproofing material; A. D. Lees (1947) is not of this opinion, since it is insoluble in chloroform, while whatever provides the waterproofing, is soluble in chloroform; it may be a product of digestion of red cell envelopes (T. E. Hughes, 1954). In *Dermacentor andersoni* (Stiles, 1908) there are two types of gland: a large type with a wide duct, sensillium sagittiforme, and a smaller type, sensillium hasteforme. The larger type secretes the yellow grease, the smaller reaches a maximum size by the end of engorgement and, after the tick has left its host, it undergoes rapid involution, its nuclei remaining round the duct. After the cuticle is freed from the epidermis, these nuclei form a third type of gland—multinucleate—which attains a maximum before, and dwindles after, the shedding of the moulting fluid.

In the Mesostigmata, the Uropodina show symmetrical pores on the dorsal surface, which are probably the openings of dermal glands (Plate XXVI, fig. 4). Paired vesicles occur behind the last leg laterally in some gamasids and *Eulaelaps stabularis* (C. L. Koch, 1839) has one pair, *Euhaemogamasus horridus* (A. D. Michael, 1892) two pairs. Similar vesicles are found in *Urotrachytes*. These vesicles contain, it is said, a yellow oily fluid which may have some function in coating the cuticle.

In the Trombidiformes, the hydrachnellids have well-developed glands, associated with setae and platelets, the various rows of glandularia already mentioned. The glands are groups of cells discharging into a common duct; Sig Thor (1902) distinguished hard and soft glands, the hard ones having a network of chitin round them. U. Schmidt (1935) failed to find this chitin histochemically. The appearance may be due to a connective tissue sheath, such as is found round the glands of *Hydrodroma*, which contains elongated nuclei suggestive of the presence of muscle cells.

The male of *Arrenurus* has the posterior part of the body modified to a kind of tail carrying the last two pairs of dorsal, ventral and lateral glandularia (Plate VI, fig. 3). The last dorsal pair becomes greatly enlarged to form a cement gland, used in coition. Nothing is known of the general function of this extensive glandular equipment of the hydrachnellids.

Most Acaridiae (Plate VII, fig. 2) and all Oribatei have a pair of vesicular organs behind leg IV; these are said to be oil glands, though previously they have been described as eyes. The areae porosae of oribatids with pteromorphae may also be the openings of dermal glands.

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CHAPTER IX

Sensory Organs and the Central Nervous System

SENSORY ORGANS

In addition to glands, the epidermis is responsible for the production of exteroceptor sensory organs which take the form of setae primitively, though the setal form may be considerably modified. In the Trombidiformes and Sarcoptiformes, certain setal structures contain chitin which is birefringent, other setae are not birefringent. The Parasitiformes and Holothyroidea produce only isotropic or non-birefringent chitin. On these grounds, F. Grandjean (1935a) has proposed a division of the Acari into Actinochitinosi (with birefringent chitin) and Anactinochitinosi. He has also distinguished a number of different types of sensory structure in the Actinochitinosi, which, of course, cannot be recognized in the Anactinochitinosi.

True setae occur in all mites and have no protoplasmic core, the sensory cell being stimulated, presumably, by passive movements of the seta, at whose base it is situated. In the Sarcoptiformes and Trombidiformes, they have a core of actinochitin covered by ordinary isotropic chitin and, where setae are feathered or blade-like, this is due to modifications of the outer cover. The actinochitin core may contain cavities filled with some substance of an unknown nature. On this basis, the cheliceral digits and tarsal claws are regarded as being derived from setal structures, on account of their birefringence.

By modification of the true seta, a structure called an acanthodion (Plate XXXVI, fig. 4) arises. In this, the actinochitin core is hollow and contains a protoplasmic extension of the sensory cell. Acanthodia are restricted to the tarsi and occur on the palpal tarsus, leg I, sometimes leg II, never leg III or IV. Several acanthodia can arise from one socket. If the setae are regarded as being tactile in function, these structures with their protoplasmic core, are probably chemoreceptors. The solenidion (Plate XXXVI, fig. 5) is a similar kind of structure, but contains no actinochitin; it is usually blunt-ended and contains a short protoplasmic extension of the sensory cell lying at its base. The surface is smooth and may be blade-shaped. Solenidia occur dorsally or ventro-laterally on the genu, tibia and tarsi of

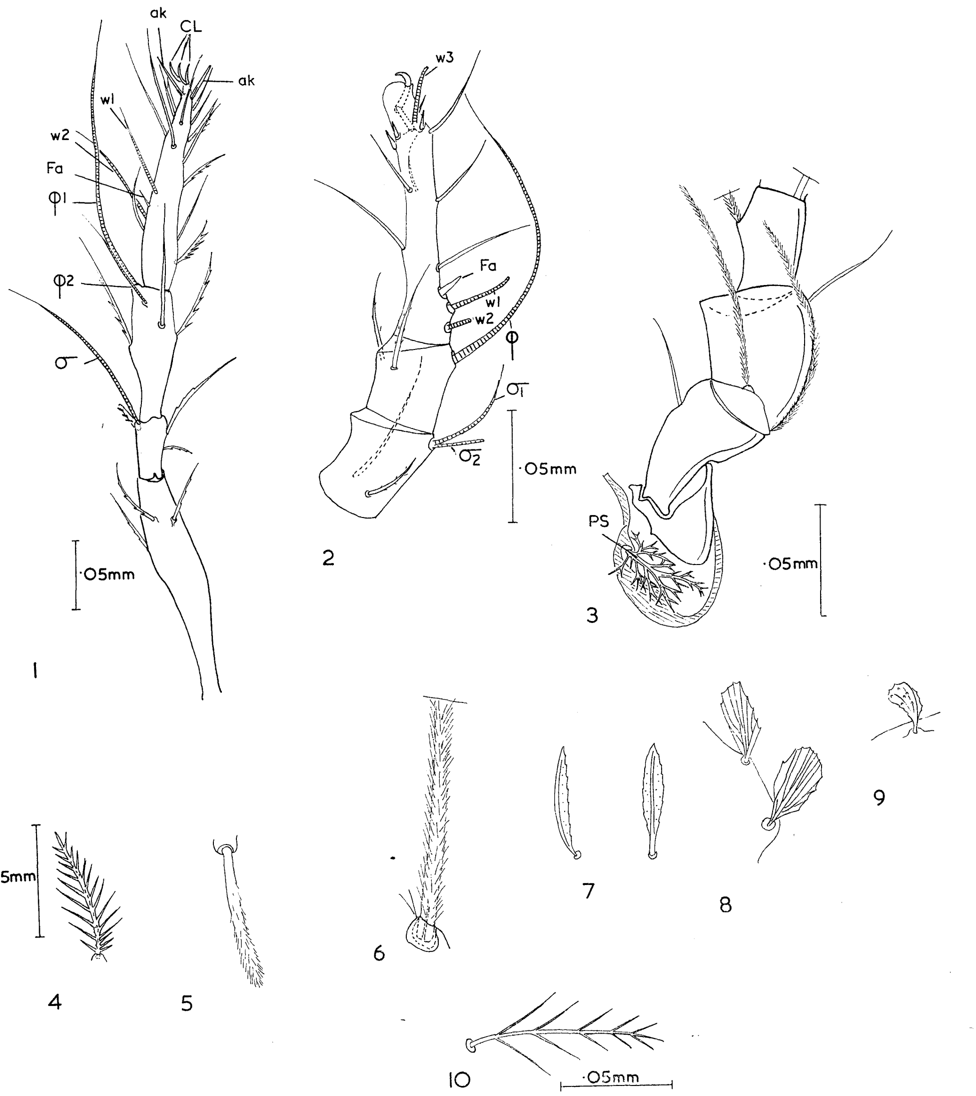


PLATE XXXV. **1.** *Ceratoppia bipilis* (Hermann); lateral view of left leg I. CL claws. The setae, genu, tibia and tarsus are lettered according to Grandjean's system. AK acanthoids, FA famulus, φ, σ_1, σ_2, ω_1, ω_2, ω_3 solenidia. **2.** *Tyrophagus tenuiclavus* (Zachvatkin); lateral view of left leg I. Letters as in fig. 1. **3.** *Glycyphagus michaeli* (Oudemans) ♀; supra coxal seta and base of left leg I. PS supra coxal seta. **4.** *Ctenoglyphus plumiger* (Koch) ♀; lateral seta. **5.** *Eugamasus magnus* (Kramer); terminal seta. **6.** *Glycyphagus destructor* (Schrank); base of dorsal seta. **7.** *Kleemania plumosus* (Oudemans); dorsal seta. **8.** *Cheyletia* sp.; fan-shaped seta at edge of dorsal plate. **9.** *Bryobia praetiosa* (Koch); terminal seta. **10.** *Allothrombium fuliginosum* (Hermann); leg seta.

palps and legs (Plate XXXV, figs. 1, 2). Usually solenidia arise from a common socket with a true seta. The sensory club (of A. A. Zachvatkin) on tarsus I of acarids is a solenidion, and so are the podosomatal 'Brüststeile' of the acarid larva. It has been suggested that these 'Brüststeile' are concerned with breaking the eggshell. The larva has three pairs of legs folded over the ventral surface and covering these structures, so that, apart from their own intimate structure, this interpretation of their function seems untenable (T. E. Hughes, 1950).

Associated with a solenidion on tarsus I of the oribatids is a structure called, by F. Grandjean (1935b), the famulus (Plate XXXVI, fig. 10). It has an actinochitin core, which is hollow and filled with protoplasm, and its surface may appear to be ringed; it always arises from a pit. H. Vitzthum (1943) regards the 'tentacle organs' of C. Willmann, found in *Rhagidia* and *Nicoletiella*, as famuli on the dorsal surface of tarsi I and II. The seta associated with the club-shaped organ (of A. A. Zachvatkin, 1941) of acarids would appear to be the corresponding structure in the Acaridiae (Plate XXXV, fig. 2).

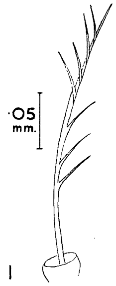
The body surface also carries setae (Plate XXXV, figs. 4 to 10) which, in the Acaridiae and Eleutherengona, consist usually of seven sets of pairs of setae. On the propodosoma are the internal and external vertical setae, and the internal and external scapula setae. On the hysterosoma there are five rows of setae—humerals, dorsals, lumbars and sacrals, each row having an internal and external seta on each side, and finally a pair of clunales. The nomenclature of these setae is varied and the accompanying table equates the terms of numerous authors.

NAMES OF SETAE AND THEIR SYNONYMS

Setae of the Idiosoma

A. C. Oudemans' or A. A. Zachvatkin's (1941) nomenclature	H. H. J. Nesbitt's (1945) nomenclature
Internal vertical	Rostral
External vertical	Cervical
External scapular	Outer proporosomatal
Internal scapular	Inner propodosomatal
External humeral	Outer humeral
Internal humeral	Middle humeral
Ventral	Inferior humeral
First dorsal	Inner humeral
Second dorsal	First lumbar
Third dorsal	Third lumbar
Fourth dorsal	Inner submargina
Anterior lateral	Second lumbar
Posterior lateral	Outer submarginal
External posterior	Middle submarginal
Internal posterior	Marginal
Coxal	Anterior and posterior interepimerals
Genitals	Anterior, middle and posterior paragenitals

Sensory Organs and the Central Nervous System



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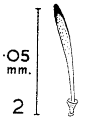

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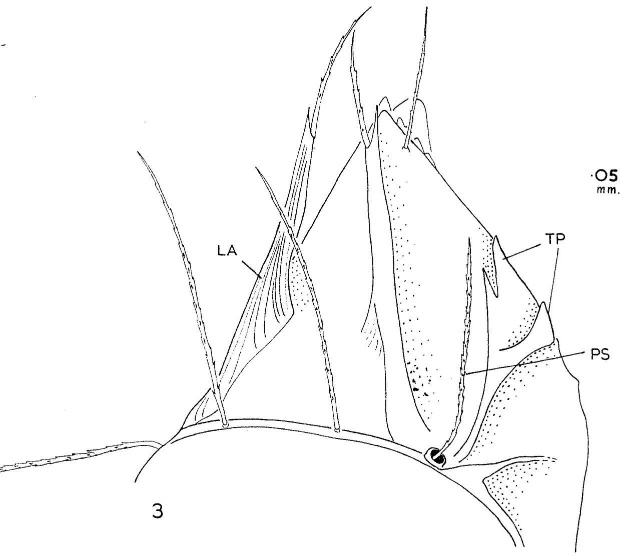

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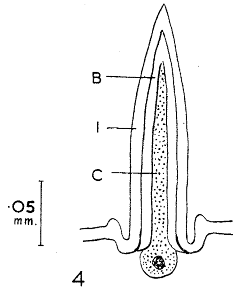

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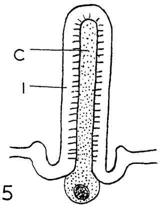

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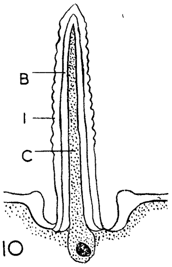

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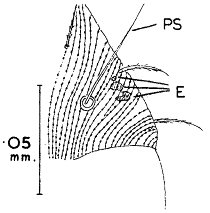

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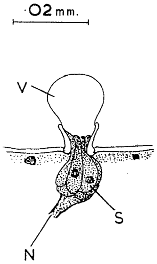

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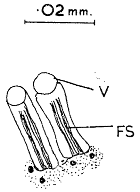

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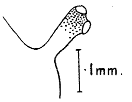

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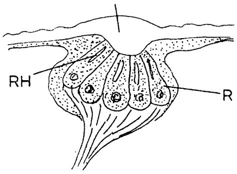

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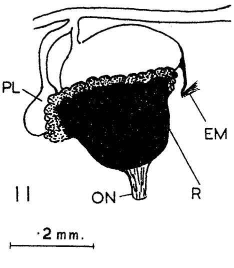

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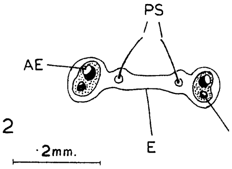

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Setae of Legs

Zachvatkin's nomenclature	Grandjean's (1935b) nomenclature	Nesbitt's nomenclature
A, α	Solenidion, ω_1	Macrosense seta
B, β	Famulus, ϵ	Microsense seta
C, γ	Solenidion, ω_2	Subbasal
D, δ	aa	Parasubbasal
E, ϵ	ba	Dorsal median
	wa	Ventral median
	s	Ventral terminal
	la	Median
	ra	Lateral
	u and v	Inner ventral terminal spinules
	p and q	Outer ventral terminal spinules
	Solenidion ω_3	Caruncular
	f	Medial terminal
	e	Second dorsal terminal
	d	First dorsal terminal
	ϕ	Dorsal tibial
External genual	Solenidion, σ^{1}	
Internal genual	Solenidion, σ^{11}	

Supra coxal setae arise above coxa I (Plate XXXV, fig. 3) in the Sarcoptiformes and many Eleutherengona. These setae become branched and flattened in many Acaridiae and lie at the posterior end of the podocephalic canal. A supra coxal seta above the pedipalpal coxa occurs in some of the Trombidiformes and Sarcoptiformes and was called, by F. Grandjean, the laterolabial. The nomenclature of the body setae has diverged between Acaridiae and Oribatei. H. Vitzthum (1943) gives the following homologies:

Acaridiae *Oribatei*
Internal vertical = lamellar seta
External vertical = rostral seta = nuchal seta
= cervical seta
Supra coxal I = exostigmatal seta (pseudostigmatic)
Internal scapula = interlamellar seta
External scapula = pseudostigmatic seta

PLATE XXXVI. **1.** *Hypocthonius rufulus* (Koch) ♀; left pseudostigmatic organ. **2.** *Aphelacarus acarinus* (Berlese); right pseudostigmatic organ. **3.** *Ceratoppia bipilis* (Hermann) ♀; dorsolateral view of propodosoma. LA lamella, PS pseudostigmatic organ, TP tectopedia. **4.** Acanthodion. **5.** Solenidion, radial canaliculi into its walls. **6.** *Tydeus interruptus* (Sig Thor); eye and pseudostigmatic organ. **7.** Erechthaestheton of *Protzia* sp. N nerve, V vesicle, S sensory cells. **8.** Erechthaestheton ('genital suckers') of *Acarus siro* (Linné). FS sensory fibrils, V vesicle. **9.** *Allothrombium fuliginosum* (Hermann); right eye. **10.** Famulus. B birefringent actinochitin, I isotopic ordinary chitin, C cytoplasmic contents. **11.** *Piona* sp.; double eye. EM eye muscle, ON optic nerve to cerebral ganglion, PL posterior lens, R retina. **12.** *Eylais hamata* (Koenike); eyes connected by an eye plate or 'augenbrille'. AE anterior eye, E 'Augenbrille', PE posterior eye, PS pseudostigmatic organ. **13.** The Eylais type of eye. L lens, R retina, RH rhabdome.

All these types of seta are the product of trichogenous cells in the epidermis, which usually approaches closer to the surface at the base of the seta. The seta normally arises from the bottom of a depression in the integument, which has a thickened rim-like edge. In the Parasitiformes there can be made out a pattern of dorsal setae in the deutonymphs, which often becomes obscured in the adults by the development of numbers of additional setae. Pointing forwards from the anterior end of the propodosomatal shield is a pair of vertical setae; there are also laterally pointing smooth 'hairs', one pair in the Parasitidae, two pairs in the Laelaptidae. Setae humerales point sideways from the edge of the shield and between these, setae scapulares; behind them lie the setae medianae and on the hind end of the opisthosomatic shield, the setae posteriores. In adults the condition is usually obscured by the development of numerous other setae. Such 'hairs' on the body may assume elaborate forms of feathering (Plate XXXV, fig. 4); for example, in *Ctenoglyphus* (Sarcoptiformes), the entire body is fringed by elaborate ctenose setae (Plate VIII, fig. 2). Specialized 'hair' structures also occur on the body. The 'poil bothrionique' of F. Grandjean, like the famulus, has a hollow actinochitin core filled with protoplasm, the outer chitin sometimes being feathered. Such setae arise from cup-like depressions in the integument. The pseudostigmatic organs of Trombidiformes and Oribatei are typical (Plate XXXVI, figs. 1, 2, 3). They also sometimes occur on the legs; for example, on the palp tarsus of *Bdella*, and the dorsal seta on tarsus I and II of *Trachymolgus*. The pseudostigma were so called by A. D. Michael (1883), H. Nicolet (1855) having taken them to be spiracles—reduced or absent in aquatic forms; they are well developed in all the Endeostigmata and Prostigmata, and in the Oribatei, appear as a pair of pits covered by membranes which are pierced by a pair of long setae (Plate XXXVI, figs. 3, 6), each of which arises from the bottom of one of the pits. In the higher Oribatei, the edges of the pits are raised to give a cup-like effect (Plate XXXVI, fig. 3). The setae are usually smooth at the base but feathered distally, but in the Trombidiinae they are club-shaped. The usual single pair is duplicated in the Johnstonianinae, Erythraeidae and Thyasidae. The function of these pseudostigmatic 'hairs' is not known, but it may be assumed that they serve in the detection of stimuli not present in water. The Acaridiae, however, do not possess these structures as such, but the external scapula setae correspond in position to them.

Sensory structures of the hydrachnellids, termed by K. Thon (1900) Erechthaestheta (Plate XXXVI, figs. 7, 8), are of widespread occurrence, associated with the genital region. Such an organ consists, essentially, of a group of cells sunk below the epidermis. These cells send processes upwards through a hole in the integument into a very thin vesicle of the integument, which is joined to the general surface by a thickened ring; the vesicle was called the Erechthopoma by Thon. The vesicle may be flattened down, as in *Piona*, and the structures distributed over the general integument, as in

Eylais. By enlargement of the spherical vesicle and elaboration of the ring at its base, the structure can come to resemble an acorn in its cup, as in *Protzia* (Plate XXXVI, fig. 7). They may be small and numerous in the genital region, for example *Arrenurus*, or larger and less numerous. Similar structures associated with the genital region are found in the Trombidiformes, in the Trombidiidae, female Anystinae, Bdellidae, Cunaxidae, and marine Halacaridae. In *Labidostoma*, Rhagidiidae, Eupodidae, Penthalodidae, Penthaleidae and Erynetidae, there are only two pairs. In the Tydeidae, Tetranychidae, Stigmaeidae, Cheyletidae, Pterygosomidae, Raphygnathidae, the marine hydrachnellids, Pseudoleptidae, Cryptognathidae, Speleognathidae and Tetrapodili, they are not present. Among the Sarcoptiformes, the Oribatei have three pairs and the Acaridiae two pairs associated with the genital opening (Plate XXXVI, fig. 8), though they may be confined to the female.

Such organs have been variously described as genital feelers, or genital suckers. H. Vitzthum (1943) points out they are, in point of fact, sensory organs, probably modified solenidia. This view was also expressed by A. M. and T. E. Hughes (1938) concerning those organs in *Glycyphagus domesticus* (Degeer, 1771), where a rich nerve supply is traceable. L. Halik (1929), by intravital staining of water mites, showed them to be similar to the chemoreceptors of freshwater Crustacea, for example *Daphnia*; and Hannah Schulze (1922) observed female acarids to open the genital valves and apply these organs to the substrate. It is to be assumed that they are employed in the selection of suitable sites for egg-laying. Where they occur in the male, they may well serve some purpose during coition.

There also occur on the integument small scar-like marks (Ringeljes linsominge organen of Oudemans, fissures and cupules of Grandjean, pori repugnatori of Berlese, Spaltorganen of Vitzthum). They appear as slit or cup-shaped depressions in the integument and a short duct has been described as running inwards from each depression. F. Grandjean (1951) considers that the primitive arachnid had a transverse row of such slits on each sternite and tergite, and most gamasids have three pairs in the sternum and a varying number in the dorsal shield, whilst the Acaridiae and Eleutherengona have fewer. They are assumed to be sensory organs, but no nervous supply has ever been traced to them and, in my opinion, their sensory function is very doubtful. Sections do not reveal any sensory or glandular structures in the region where they occur on the sternite of gamasids. I am of the opinion that they are muscle attachments and that the 'duct' is the tendon; they have the same appearance as the phragma of insects which are known to be muscle attachments. Some of them may be stress-sensitive organs, like the lyriform organs of spiders.

Other doubtful sensory organs which have been described are the saggitiform, hastiform, and lantern-shaped sense organs described by P. Schulze (1942) and J. Dinnick and F. Zumpt (1949) in larval ticks. These structures have also been described as stigma, but this is certainly incorrect. They are said to be glandular-cum-sensory organs. Their glandular function has been shown by A. D. Lees (1947), their sensory nature has never been demonstrated; J. Dinnick and F. Zumpt's (1949) description was from whole mounts in Berlese fluid; in section I have been unable to trace any nervous connections and consider A. D. Lees' interpretation the most probable.

The eyes of the Acari, when present, are never faceted. Ixodei and the majority of the Endeostigmata carry an eye on either side, the majority of the Parasitengona have two pairs, and a median eye is added in most halacarids and many hydrachnellids. Where two pairs are present, they may be very close together, as in many hydrachnellids, while in *Allothrombium* they are on a movable stalk (Plate XXXVI, fig. 9). Eyes are rarely present in the Sarcoptiformes, although *Carpoglyphus* has a single pair of eyes above coxa I. The hypopial deutonymphs of *Calvolia* have eye spots near the tip of the propodosoma and in *Histiogaster* these lie above leg I, with the cornea surmounted by a bristle. A. Berlese (1910) describes a median eye in front of the lamellar setae and paired eyes in front of the pseudostigmatic organs of *Heterochthonius gibbus*. These eyes all consist of a 'lens', differentiated in the integument and backed by brownish-black pigment.

In *Haemalastor clypeolatus* (L. G. Neumann, 1899), the lens is differentiated as a golden-red area on each side of the scutum in the female; below this the hypodermis is in the form of clear vitreous cells which, according to Bonet, secrete the cornea. The retinal cells, presumably delaminated from the epidermis, lie below this vitreous layer and are connected to the supraoesophageal nerve mass by fibres. A somewhat similar state of affairs was recorded by A. D. Michael (1896) for the eyes of *Neomolgus littoralis* (Linnaeus, 1758).

In the halacarids, the lateral eyes lie under the occular plates which are transparent above them and may bulge slightly (Plate XXXI, fig. 1); the median eye lies below the dorsal plate, which is not differentiated above the eye. The lateral eye has a spherical lens which is in contact with the retinal cells, the whole eye being surrounded by pigment; the vitreous cells are missing, but the retinal cells each contain a rhabdome, which tapers towards the centre of the circle formed by the retinal cells.

The hydrachnellids have two pairs of lateral eyes and a median eye, often called the frontal organ. When the lateral eyes of a side are close together, they are often enclosed in a common chitinous capsule which projects above the surface. If, in addition, they lie near the mid-line, the capsules are joined by a transverse ridge (the 'Augenbrille' of Haller) (Plate XXXVI, fig. 12). This group exhibits eyes of two types; the simpler one is that in which the lens is a differentiated part of the general integument (Plate XXXVI, fig. 13) (*Eylais*, *Hydrodroma*, *Hydrochoreutes*). In this type of eye, where two are enclosed in a capsule, it is open below like an inverted cup, in whose bottom are differentiated two lenses in the plane of the integument. In *Piona*, *Limnesia*, *Hygrobates*, *Unionicola* and *Arrenurus* the whole eye is sunk beneath the integument; the anterior cornea is joined to the integument by a strip of chitin, to which two muscles are attached, and therefore it is movable. If the posterior eye of that side is joined to it, the two will be movable together (*Limnesia* and *Piona*). In the eyes of these hydrachnellids, vitreous cells are wanting and the lens is in direct contact with the retinal cells, which contain rhabdomes. The median eye consists of a club-shaped group of retinal cells, which contain a dark violet pigment. These cells are in contact with an integumentary lens.

It has been mentioned, in connection with the legs, that leg I may serve a sensory function and cease to be a locomotory organ in some cases. Special sensory apparatus is therefore often developed on this pair of legs. The most fully investigated structure in this respect is Haller's organ in the ticks. This structure, though varied in form in the different groups, has a basic pattern which has been clarified by P. Schulze (1941). In *Eschatocephalus vespertilionis* (C. L. Koch, 1844) tarsus I carries dorsally an elongated groove, which carries in its distal half, a number of sensory bristles and proximally, five curved (sickle-shaped) setae (Plate XXXVII, fig. 1), of which the most posterior is the largest; distal to the groove there is a clump of long setae and proximal to it, a rather scattered clump. The nymphal structure resembles the adult's but in the larvae, the sickle-shaped setae are only slightly curved. In *Ixodes unicavatus* (Neumann, 1908) the setae in the posterior part of the canal are sickle-shaped and delimited by a ridge from the anterior part, which has three long and one shorter seta; *I. uriae* (White, 1852) shows a thickening which dips down into the tarsus. In the other Prostriata, the posterior part of the trough is converted into a capsule by the extension of the anterior and posterior boundary walls as a very thin cover, which leaves only a small circular opening dorsally. The sensillae within this capsule are mostly only slightly curved, thin-walled and blunt-ended setae of the chemoreceptor type. In *I. ricinus* (Linnaeus, 1758) (Plate XXXVII, fig. 2), for example, one seta, the 'Signalhaar' of P. Schulze (1941), projects through the opening of the capsule, is a larger and straighter structure than the other capsular setae, and arises dorsally. On the other hand, in *I. hexagonus* (Leach, 1815) the dorsal seta, or Sickelhaar of P. Schulze, is at first straight and then bends downwards to lie below the opening. The Prostriata are subdivided into two groups by Schulze according to whether the capsule is complete, the Thecorhina, or incomplete, the Plynorhina.

In the Metastriata the anterior trough is reduced and preceded by a thick ridge of chitin, the capsule is also bounded posteriorly by dark chitin. The capsular form is different in the two groups Amblyommidae and Hyalommidae. In the first, it forms one or two vesicles, and contains chemoreceptors and occasionally, a signal seta; in the second, no such vesicle is formed, and the setae are fused into a massive 'Haarberg'. In the argasids, the trough is also reduced and, though in the larva the capsule follows the usual plan, in the adult it is sunk into the tarsus.

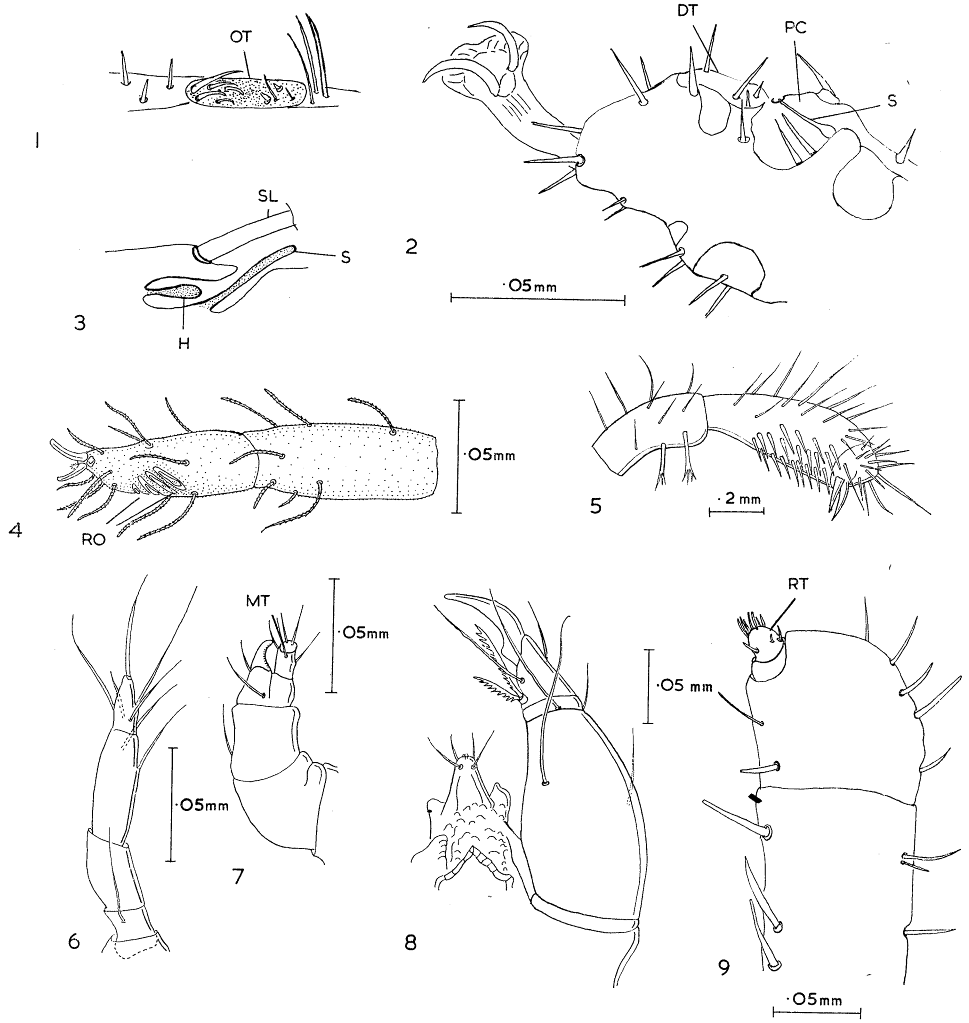


PLATE XXXVII. **1.** *Eschatocephalus vespertilionis* (Koch); diagram of Hallers organ. OT open trough. **2.** *Ixodes ricinus* (Linné); Hallers organ on tarsus I. DT distal trough, PC proximal capsule, S signal hair. **3.** *Opilioacarus* sp.; diagram of sensory pit on tarsus I. H short blade-shaped hair in pit, S signal hair, SL long seta proximal to pit. **4.** *Rhagidia gelida* (Thorell); dorsolateral view of right tarsus I. RO rhagidial organ. **5.** *Holothyrus coccinella* (Gervais); ventral view of terminal joints of left pedipalps. **6.** *Labidostoma luteum* (Kramer); ventral view of left pedipalp. **7.** *Bryobia praetiosa* (Koch) ♀; ventral view of right pedipalp. MT modified tarsus. **8.** *Cheyletus munroi* (Hughes); ventral view of pedipalp. **9.** *Ixodes ricinus* (Linné); ventral view of right pedipalp of ♀. RT reduced tarsus.

G. I. Haller (1881) considered the organ to be stimulated by gravity. The presence of a tallowy secretion or of refringent granules on the setae, has been repeatedly reported and P. Schulze does not dismiss altogether the idea of a gravitational response. As A. D. Lees (1948) described, the unfed adult frequently quests with the first pair of legs, and he considered that the capsular region is olfactory in function, whilst the trough region is sensitive to changes in the humidity. R. Totze (1933) showed this organ to be sensitive to dilutions of butyric acid.

In other groups of Acari, tarsus I also carries special sensory structures. In the Notostigmata a pit sinks in obliquely backwards from the dorsal surface of tarsus I and communicates with a cavity, the cavity contains a blade-shaped seta, which does not emerge into the pit (Plate XXXVII, fig. 3). In Rhagidiidae, C. Willmann (1934 and 1953) and Sig Thor (1934a) found what they called the rhagidial organ on tarsi I and II (Plate XXXVII, fig. 4). A. C. Oudemans (1915) had previously seen it on tarsus II. It consists of a series of up to six parallel grooves leading into pits, each with a ragged border. Above each hole lies a long solenidion ('Schluppenhaar' of Willmann).

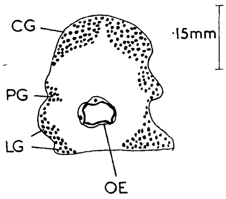
Sig Thor (1934b) described a similar but simpler organ on tarsus I and II of *Penthaleus* and called it the 'penthaleus organ'. Organs consisting of one or two shallow pits, over each of which lies a solenidion, are found in Tydeidae, Eupodidae and Erythraeidae.

The Mesostigmata show a collection of solenidia and setae near the end of tarsus I, and frequently carry the legs in the air (Uropodina), or tap the substrate with them (Gamasides). The Acaridiae show a large solenidion on the dorsal surface of tarsi I and II in all stages of the life history. These structures may in all cases be chemoreceptors and perhaps olfactory in function.

Special sensory mechanisms are also present on the palps (Plate XXXVII, figs. 6, 7, 8). In the Holothyroidea the dorsal surface of the palpal tarsus is covered by thick bristles (Plate XXXVII, fig. 5), innervated by a mass of cells which fills the tarsus. A group of chemoreceptors lies ventrally on the remains of the tarsus at the tip of the palps in the ticks, similarly innervated by a mass of large sensory cells (Plate XXXVII, fig. 9). The Mesostigmata have a forked seta at the base of the palpal tarsus, which may also have a sensory function, though it is considered by F. Grandjean (1954) to be the true claw of the palp. This view seems quite untenable.

THE CENTRAL NERVOUS SYSTEM

The loss of segmentation which characterizes the Acari, is nowhere more clearly seen than in the anatomy of the central nervous system. In place of the typical cerebral ganglia, circumoesophageal commissures and ventral segmentally ganglionated chain of the great majority of Arthropoda, we find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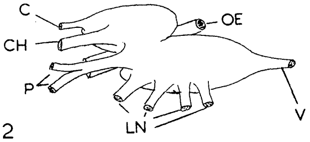
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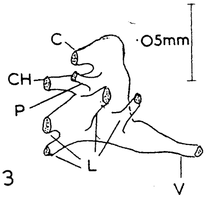
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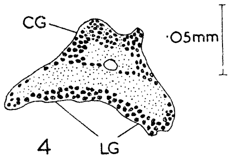
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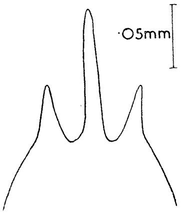
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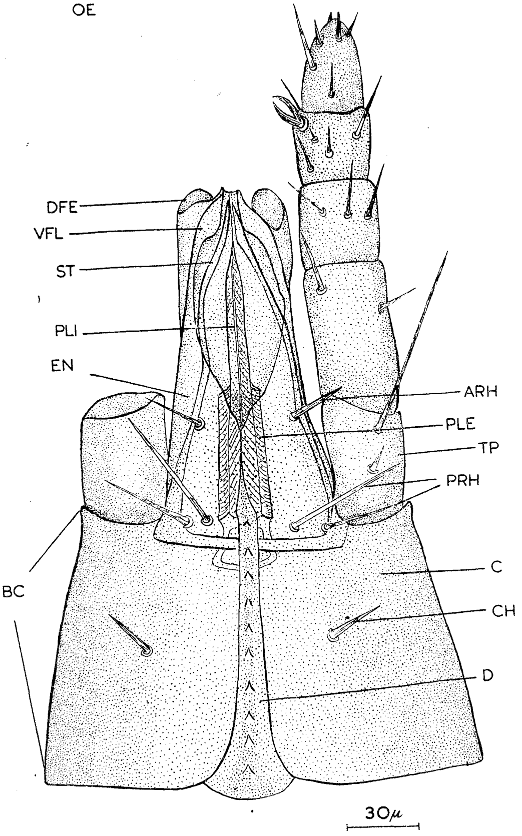
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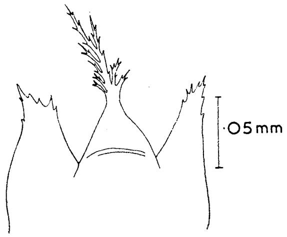
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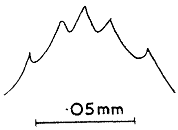
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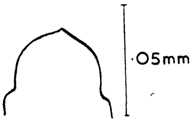
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in this group a solid mass of nervous tissue pierced by the oesophagus. This mass of tissue is divisible into a part lying dorsal to the oesophagus and a ventral lobe; lateral commissures are not distinguishable as such. The loss of the commissures is due to the narrowness of the oesophagus, and the tendency shown by the ganglia concerned with the cheliceral and pedipalpal appendages to migrate dorsally. Although the relative shapes of these two parts of the 'brain' may vary from group to group, they are present in all the Acari. The Holothyroidea differ slightly from the rest of the Acari in having antero-ventrally, on the suboesophageal nerve mass, a pair of outgrowths, the corpora pedunculata (mushroom-shaped bodies of Thon). In the immature stages, especially the larvae, the central nervous system occupies a relatively larger space than it does in the adults, and extends back into the region of the third pair of legs.

The brain is invested by a thin connective tissue sheath, beneath which lies a layer of ganglion cells, which do not form a uniform peripheral layer. They project inwards at certain points into the central fibrous part of the brain, and so come to delimit the boundaries of the individual ganglia which together make up the whole structure (Plate XXXVIII, fig. 1).

Among the Parasitiformes the tick's brain, owing to its greater size, has been worked out in some detail. The supraoesophageal mass consists of paired cerebral ganglia fused in the mid-line and, anterior and ventral to these, the pair of ganglia belonging to the cheliceral segment. From the first arise, in ixodid ticks, the optic nerves; in argasids (e.g. *Argas persicus* (Oken, 1818)), which lack eyes, L. E. Robinson and J. Davidson (1913) found no nerves, though it is probable that the sensory setae of the antero-dorsal region are always innervated from these ganglia (Plate XXXVIII, fig. 2). Where areae porosae are present, nerves run to them from the cerebral ganglia and break up into fibres, each of which ends in a cell, with a fine process projecting into one of the pores. The cheliceral nerves arise from the dorsal sides of the cheliceral ganglia; they supply both the muscles

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PLATE XXXVIII. **1.** *Acarus siro* (Linné) (= *Tyroglyphus farinae*); T.S. of central nervous system. CG cerebral + cheliceral ganglia. LG ganglia of legs I and II, OE oesophagus, PG pedipalpal ganglion. **2.** Mesostigmatic central nervous system. C nerve from labrum and epipharynx, CH cheliceral nerve, LN nerves to the legs, OE oesophagus, P pedipalpal nerve, V 'visceral' nerve to opisthosoma. **3.** *Acarus siro* (Linné); central nervous system. C cerebral ganglion and nerve to labrum, CH cheliceral nerve, L nerves to legs, P pedipalpal nerve, V 'visceral' nerve to opisthosoma. **4.** *Ornithonyssus bacoti* (Hirst); T.S. of central nervous system. CG cerebral + cheliceral ganglia, LG ganglia of the propodosoma. **5.** *Eugamasus magnus* (Kramer) ♀; epistome. **6.** *Ornithonyssus bacoti* (Hirst) ♀; ventral view of gnathosoma. ARH anterior rostral seta, BC basis capituli, C coxa of pedipalp, CH capitular seta, D deutosternum, DFE dorsal flap of endite (mala externa), EN endite of pedipalp, PLE paralabrum externum, PLI paralabrum internum, PRH posterior rostral seta, ST stylus, TP trochanter of palp, VFL ventral flap of endite (mala interna). **7.** *Veigaia cervus* (Kramer) ♀; epistome. **8.** *Pergamasus crassipes* (Linné) ♀; epistome. **9.** *Kleemania plumosus* (Oudemans) ♀; epistome.

within the chelicerae and the retractor muscles of the chelicerae. The pedipalpal ganglia lie level with the entry of the oesophagus into the brain in ixodids; in *Argas persicus* they are apparently somewhat lower and are joined to the cerebral ganglia by short but wide commissures, which lie on either side of the oesophagus. The pedipalpal nerves innervate, not only the palps, but the pharyngeal musculature as well, so that they must be mixed nerves containing both motor and sensory fibres. The suboesophageal nerve mass includes the four pairs of ganglia associated with the leg-bearing segments. From these ganglia, nerve trunks arise which divide into two, one branch supplying the muscles attached to the coxae, the other branch passing into the leg. Behind and between the fourth pair of pedal ganglia, lie the so-called 'splanchnic' ganglia, of which there may be four pairs; two pairs were described in *Argus persicus* (Oken, 1818). From these ganglia, two or more nerve trunks pass back to innervate the genital system, the gut and the body musculature of the opisthosoma (Plate XXXVIII, fig. 2). L. E. Robinson and J. Davidson (1913) were of the opinion that the variability from species to species of the number of these nerves, had led H. A. Pagenstecher (1862) to give four pairs of 'splanchnic ganglia', instead of two. These ganglia would seem to be the ganglia of some of the opisthosomatal segments, so that the term splanchnic is not a particularly happy choice of name. In the ticks, the brain lies within a blood space, a continuation of which surrounds each of the main nerve trunks.

The Mesostigmata show some slight variation of arrangement from the ticks. An unpaired nerve ('Zungennerve' of W. Winkler, 1888) leaves the fused cerebral ganglia and is distributed to the labrum, epipharynx and dorsal pharyngeal musculature. No such nerve has been described in the ticks, where the labial and epipharyngeal development is less. From the cerebral ganglia a pair of fine nerves lead up to the vertical setae.

The cheliceral ganglia have migrated forward above the level of the oesophagus, and from them arise the nerve trunks of the cheliceral segment. H. Vitzthum (1943) considers that the motor components of these nerves are derived from the suboesophageal part of the system. Taking into consideration the segmental origin of the whole system, this view does not recommend itself. Commissures join the cheliceral ganglia to the pedipalpal pair, which lie at the antero-dorsal end of the suboesophageal lobe. The nerve trunks associated with this pair of ganglia serve the palps and the pharyngeal musculature, and have trunks which pass along the hypostome to the rostral setae. The rest of the ventral lobe is composed of the four pairs of pedal ganglia and the 'splanchnic' ganglia.

The pedal nerves supply not only the legs with motor and sensory branches, but also the body musculature in their region. From the 'splanchnic' ganglia, of which there are probably two pairs, arise two pairs of splanchnic trunks, which innervate the gut and genital system and any opisthosomatal musculature. The innervation of the sensory mechanism of the opisthosoma is not known in the Mesostigmata.

The Trombidiformes show an essentially similar overall plan. The median nerve arising from the cerebral ganglia has been described in several genera and is probably present in all; it supplies the dorsal pharyngeal musculature. In such forms as possess eyes, these are innervated from the cerebral ganglia, as is the frontal organ, where present. The cheliceral ganglia lie ventral and lateral to the cerebral ganglia, so that the whole supraoesophageal mass is more high and pyramid-shaped than in the Mesostigmata. The cheliceral nerves arise antero-laterally from the mass level with the oesophagus.

The pedipalpal nerves arise from ganglia lying level with, or below, the oesophagus and supply the palps (A. D. Michael, 1895; H. B. Henking, 1882; H. Thomae, 1925). The four pairs of nerves to the legs each divide into two, one branch innervating the muscles associated with the coxa, the other running into the leg to muscles and sensory setae. The splanchnic nerves arise as a pair of stout trunks from the hind end of the ventral lobe, and give off branches to the genital sense organs, if such are present. In the Prostigmata (Sig Thor, 1904), a network of nerve fibres has been described below the epidermis, connecting with sensory cells at the bases of the setae; such a network has not been described in other groups. In the Tetrapodili, the central nervous system is displaced backwards into the opisthosoma, and the reduction in the number of legs leads to a diminution in size of the ventral lobe. The two nerves to the genital region arise ventrally from the ventral lobe, and from its posterior border, a pair of splanchnic nerves run back to the gut.

The Sarcoptiformes show a similar arrangement of the central nervous system to the Acari in general (Plate XXXVIII, fig. 3). The cerebral and cheliceral ganglia form the dorsal region and lie well forward in the propodosoma. The pedipalpal ganglia lie level with the oesophagus. The ventral lobe extends back beyond the dorsal lobe, and includes the ganglia of the leg-bearing segments and, in *Acarus siro* (Linnaeus, 1758) (=*Tyroglyphus farinae*) and *Glycyphagus domesticus* (Degeer, 1771), one pair of splanchnic ganglia. The splanchnic nerves have branches which innervate the genital sensory organs in the females of the species.

H. Vitzthum (1943), in his discussion of the central nervous system of the Acari, spoke as though the dorsal mass is sensory and the ventral mass motor in function and termed them the supra- and suboesophageal ganglia. He evidently considered that fibre tracts within the central nervous system passed from one to the other to supply the main nerve trunks with sensory and motor components. Sections of the central nervous system of Mesostigmata (Plate XXXVIII, fig. 4), Trombidiformes and Sarcoptiformes do not support this idea. They show that the nervous mass is divisible into paired ganglionic masses as in the ticks. The presumption is that each of the main divisions, dorsal and ventral lobes, consists of a number of originally segmental elements fused together. In point of fact, the paired ganglia of the segments bearing appendages, are still discernible, as are a pair of cerebral ganglia. The 'splanchnic' ganglia which presumably represent the condensed ganglia of the opisthosoma, seem to comprise, at the most, two pairs in ticks and in Sarcoptiformes, one pair. The structure of this part of the nervous system is, therefore, of no help in determining the original number of segments in the opisthosoma, since in the few cases where the embryonic development has been worked out, there appears no alteration in the number of ganglia; indeed, in *Acarus siro* (= *Tyroglyphus farinae*) (T. E. Hughes, 1950) the central nervous system differentiates in its definitive form, even in the early stages. A noticeable feature of the nerve trunks which run between the central nervous system and the various appendages, is the large number of conspicuous nuclei that occur along them.

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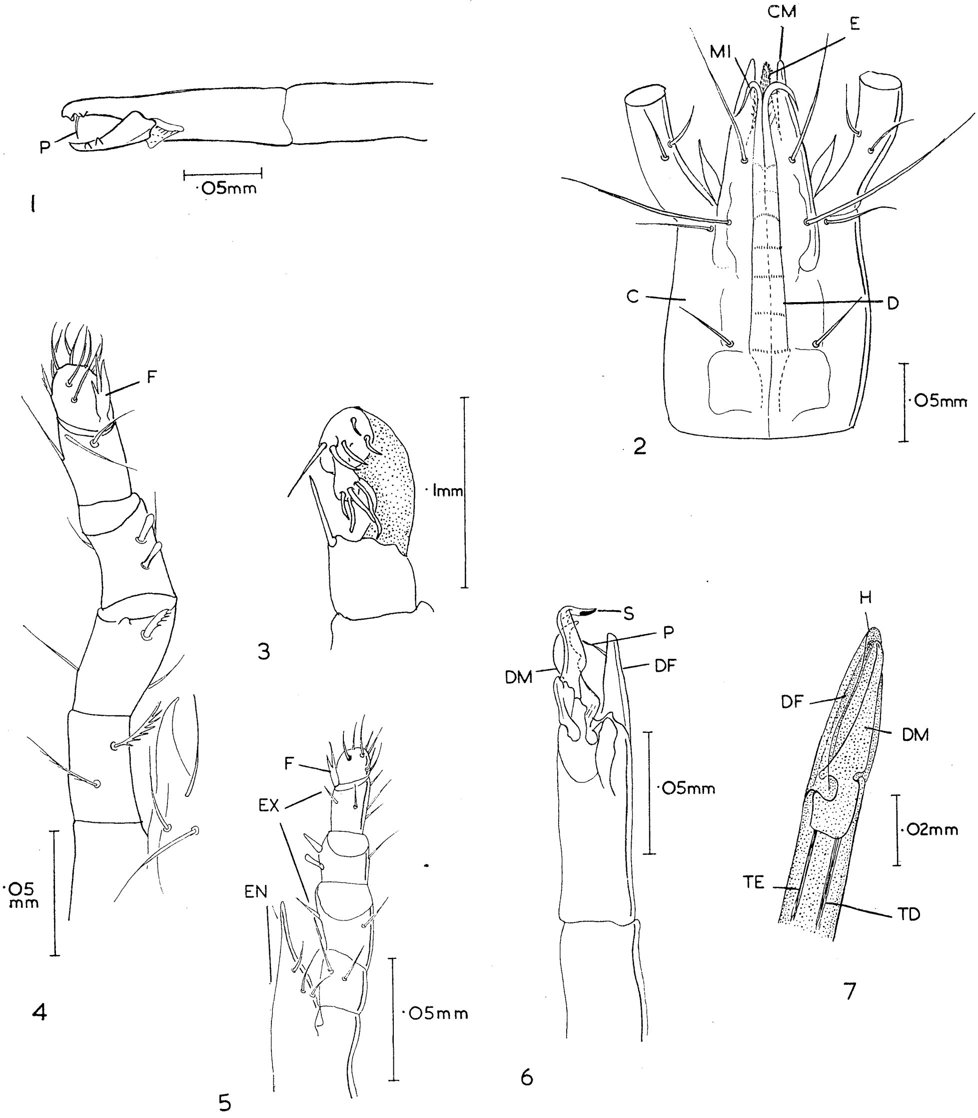


PLATE XXXIX. **1.** *Haemogamasus pontiger* (Berlese) ♀; lateral view of right chelicera. P pilus denticularis. **2.** *Macrocheles matrius* (Hull) ♀; ventral view of gnathosoma. C coxa of pedipalp, CM corniculi maxillaris, D deutosternum, E epipharynx, MI mala interna. **3.** *Heterozercon* sp.; right palp in ventral view. **4.** *Eugamasus butleri* (Hughes); deutonymph, ventral view of right palp. F three-pronged forked 'hair'. **5.** *Garmania domestica* (Oudemans) ♀; ventral view of left pedipalp. EN endite of pedipalp, EX exite of pedipalp, i.e. the palp, F two-pronged forked 'hair'. **6.** *Haemolaelaps casalis* (Berlese) ♂; ventral view of chelicera. DF digitus fixus, DM digitus mobilis, P pilus, S spermatophore carrier. **7.** *Ornithonyssus bacoti* (Hirst) ♀; chelicera. H hood, TD depressor tendon of digitus mobilis, TE elevator tendon of digitus mobilis. Other letters as in fig. 6.

CHAPTER X

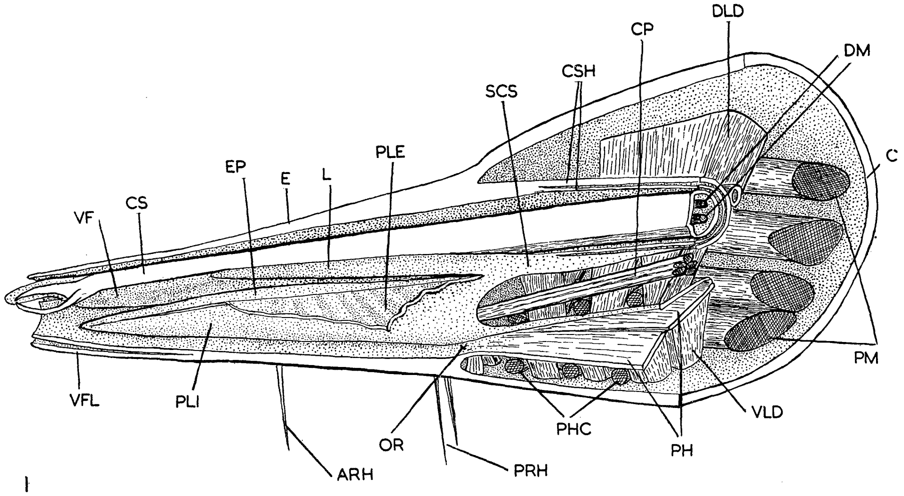
The Gnathosoma and the Appendages

THE GNATHOSOMA

The Acari have a definite anterior body region, consisting of at least three segments fused together, a precheliceral, a cheliceral, and a pedipalpal segment. This gnathosoma is movable on the rest of the body and is well sclerotized; often it is retractile to a greater or less extent within the anterior part of the podosoma, and the cavity into which it may be retracted is called the camerostome. The gnathosomal roof consists of the fused tergites of the segments concerned, and may project forwards as a lobe, usually called the epistome (Plate XXXVIII, figs. 5, 7, 8, 9). As R. E. Snodgrass (1948) points out, the epistome is not comparable to that of insects and he terms it the tectum capituli. It lies above the chelicerae, which have migrated to a position dorsal to the oral opening. The cheliceral appendages are uniramous and in the adult consist, in the great majority of mites, of three segments. Each of the pedipalpal appendages consists of a coxa directed forwards, which bears primitively two rami; the outer ramus, or exite, being the palp, the endite or inner ramus forming, with its fellow and an anterior prolongation of the pedipalpal sternite, a lower lip or labium of greater or less complexity. The palp consists of five segments initially. The pedipalpal coxae form a great part of the gnathosomal skeleton, becoming fused with the roof and ventral elements of the gnathosomal segments (Plate XXXVIII, fig. 6).

The chelae arise by a dorsal projection of the tibia forming the digitus fixus (Plate XXXIX, fig. 1), the digitus mobilis being the tarsal joint, this type of chela working in a vertical plane. Presumably the tibia articulates with the cheliceral base, the homologies of which are doubtful; it is in this basal joint that the muscles operating the digitus mobilis lie. Both jaws of the chelae are denticulate in simple forms, but there occurs within all the major groups a tendency to loss of denticulation and reduction to a simple stylet form, wherever the food is of a fluid nature.

The pedipalpal palp originally consisted of five free joints beyond the coxa (Plate XXXVIII, fig. 6, and Plate XXXIX, fig. 4), the trochanter is short, the femur usually widens distally, the genu is small and both tibia and tarsus are present, the latter even sometimes carrying a small claw—like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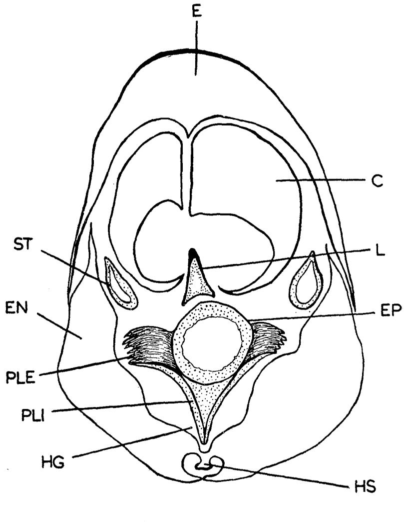
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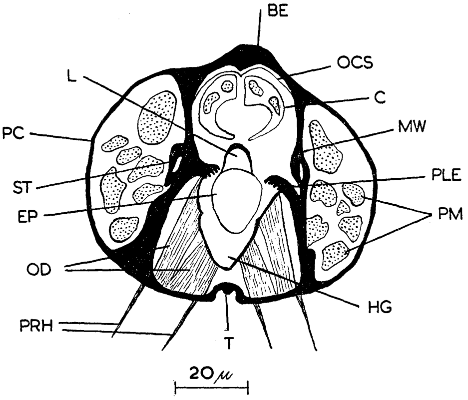
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those of the walking legs (Notostigmata). This type of palp becomes greatly modified in all the major groups, such modification generally involving loss of segments. The endite (Plate XXXIX, fig. 5) shows a tendency to fuse with its fellow in the mid-ventral line and to lie with its free edge directed obliquely upwards and outwards, thus forming a shallow trough below the oral opening. The endites referred to as maxillae by many authors, are frequently subdivided at the distal ends, which may remain free, into lobes of considerable complexity. Such lobes are the malae internae and externae (Plate XXXIX, fig. 2).

The segmentation of the gnathosoma is so lost by fusion, and the embryological knowledge is so scanty, that its structure is largely conjectural. The sterna of the segments involved were termed by C. Börner (1902), the prosternum of the cheliceral segment and the deutosternum of the pedipalpal segment. The tergites are never distinguishable and any arguments, such as those of E. Reuter (1909), based on the positions of transverse rows of setae do not seem reliable, since the number of such setal rows varies. In the Acari the prosternum is not recognizable. The deutosternum is often present as a small chitinous plate between the coxae of the pedipalps, it frequently projects forwards to unite with the pedipalpal endites, the whole structure being termed a hypostome by some authors.

In the Parasitiformes, among the Mesostigmata the pedipalpal coxae are enlarged, and form the greater part of the gnathosomal skeleton or basis capituli (Plate XL, fig. 3), the original roofing projecting as an epistome above the chelicerae. The form of this epistome is made use of by systematists (Plate XXXVIII, figs. 5, 7, 8, 9). It is lanceolate in the Uropodina and Iphidinae, 3–5 lobed in the majority of Parasitidae, bilobed in Macrochelidae and bears a jagged terminal point in the Haemogamasidae. The lateral walls of the gnathosoma are formed by the external walls of the coxae, which dorsally fuse with the roof of the gnathosoma. The coxae extend ventrally, but do not meet in the mid-line, being separated by a narrow structure which probably represents the deutosternum (Plate XL, fig. 3). In the

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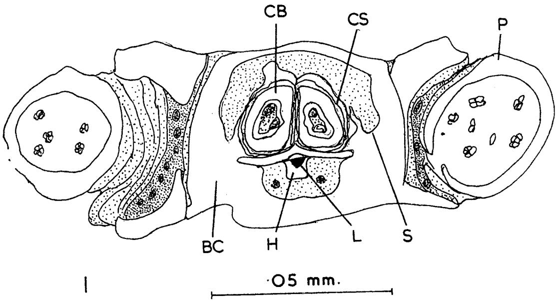
PLATE XL. **1.** *Ornithonyssus bacoti* (Hirst); diagram of structure of the gnathosoma. ARH anterior rostral seta, C wall of basis capituli, CP cheliceral protractor muscles, CS cheliceral shaft, CSH cheliceral sheaths, DLD dorsolateral dilator muscles, DM muscles operating digitus mobilis of chelae, E epistome, EP epipharynx, L labrum, OR oral opening, PH pharynx, PHC pharyngeal constrictors, PLE paralabrum externum, PLI paralabrum internum, PM palpal muscles, PRH posterior rostral setae, SCS subcheliceral shelf, VF ventrolateral flange of chela, VFL ventral fold of endite of pedipalp (mala interna), VLD ventrolateral dilator muscles. **2.** *Ornithonyssus bacoti* (Hirst); T.S. rostrum. C chela, HG hypostomal groove, HS anterior prolongation of hypostome, other letters as in fig. 1. **3.** *Ornithonyssus bacoti* (Hirst); T.S. gnathosoma at level of posterior rostral setae. BE base of epistome, MW mesial wall of coxa of pedipalp, OCS outer cheliceral sheath, OD oral dilators, PC wall of pedipalpal coxa, PLE postlateral wall of paralabrum externum, where it joins the mesial wall of the coxa, T anterior tooth of deutosternum. Other letters as in figs. 1 and 2.



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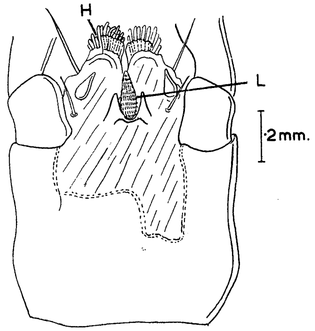

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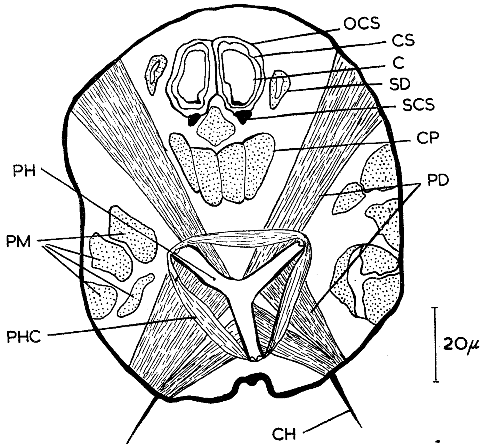

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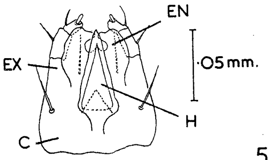

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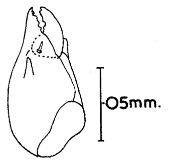

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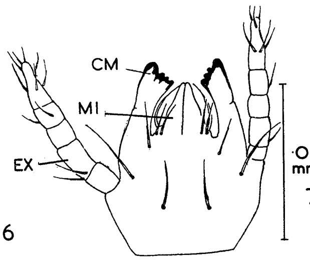

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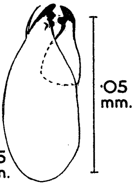

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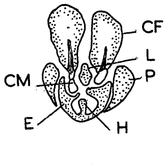

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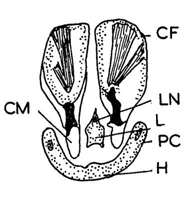

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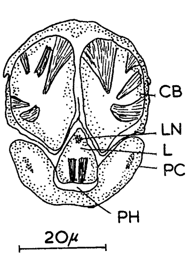

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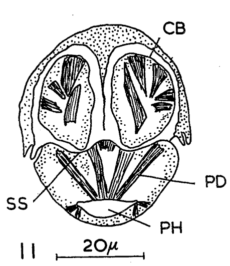

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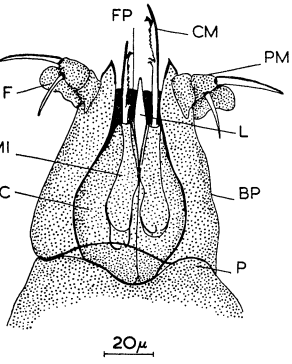
absence of embryological evidence, it is not possible to evaluate this region accurately. The coxae carry, in this region, the paired capitular or coxal setae. The mesial walls of the coxae, at the level of the mouth, are joined to each other by a stout chitinous plate, the subcheliceral shelf. This, as R. E. Snodgrass (1948) has pointed out, is the real epistome homologous with that of insects, since it carries some, at any rate, of the dorsal dilator muscles of the pharynx. Above the subcheliceral shelf, the mesial walls of the coxae are thin and form a sheath round the basal part of the chelicerae. These sheaths become much more marked in forms with retractile chelicerae. The palps are exites of the pedipalpal limb and are attached antero-ventrally to the coxae by movable trochanters. The Uropodina and Gamasides have the primitive arrangement of palpal joints. In the Heterozerconidae the tarsus tends to be directed ventrally (Plate XXXIX, fig. 3). In the Gamasides, there is a forked seta at the base of the tarsus on the ventral side. The root of this seta may be covered by the overlap of the tibial joint, or it may even arise from the tibia. This seta is three-pronged in the Parasitidae and two-pronged in others (Plate XXXIX, fig. 4).

Internal to the palp, there arises from each coxa, a lobe which carries three setae, here referred to as rostral setae, but more frequently called maxillary, since this endite of the pedipalp is called a maxilla by many authors. Anterior to these setae, the endite may divide into a mala interna and a mala externa, which very often carries at its tip a chitinous point, the corniculus maxillaris.

The hypostome formed by these lobes, together with any elongation of the deutosternum, and the epistome, together tend to enclose the cheliceral bases, and in many forms, such as *Dermanyssus* and *Ornithonyssus*, this gives rise to a rostrum within which the chelicerae are retractile (Plate XL, figs. 1 to 3). In forms where the food is of a fluid nature, the corniculi and malae internae become reduced to small flaps ('Lappiger Anhang' of Börner). This is the case in myrmecophilous and parasitic species.

PLATE XLI. **1.** *Ixodes hexagonus* (Leach); T.S. gnathosoma. BC basis capituli, CB cheliceral basal joint, CS cheliceral sheath, H hypostomal gutter, L labrum, P palp trochanter, S softer unsclerotized cuticle. **2.** *Holothyrus coccinella* (Gervais) ♂; dorsal view of gnathosoma. H hypostome, L labrum. **3.** *Ornithonyssus bacoti* (Hirst); T.S. gnathosoma through the pharynx. C chelicera, CH capitular seta, CP cheliceral protractor muscles, CS cone sheath, OCS outer cheliceral sheath, PD pharyngeal dilator, PH pharynx, PHC pharyngeal constrictors, PM palpal muscle, SCS apodema of subcheliceral shelf, SD salivary duct. **4.** *Acarus siro* (Linné); dorsal view of hypostome, the chelicerae having been removed. C coxa of pedipalp, EN endite of pedipalp, EX exite of pedipalp or the palp, H hypostome. **5.** *Acarus siro* (Linné); internal view of right chelicera. **6.** *Aphelacarus acarinus* (Berlese); ventral view of hypostome. CM caeca maxillaris (mala externa), MI mala interna. **7.** *Aphelacarus acarinus* (Berlese); internal view of right chelicera. **8, 9, 10, 11.** Progressive sections from the tip of the chelicerae towards the pharynx of *Acarus siro* (Linné); CB basal joint of chelicera, CF digitus fixus of chelicera, CM digitus mobilis, E endite of pedipalp, P exite or palp, H hypostome, L labrum, LN labral nerve, PC palpal coxa, PD pharyngeal dilator muscles, PH pharynx, SS subcheliceral shelf.



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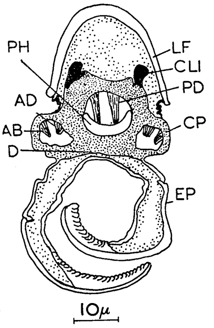

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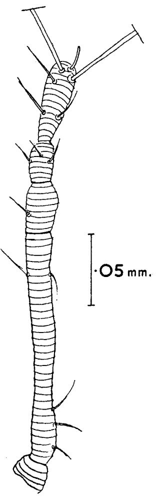

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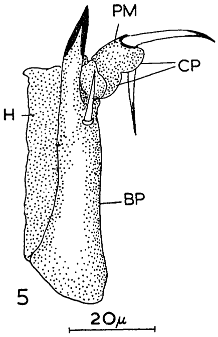

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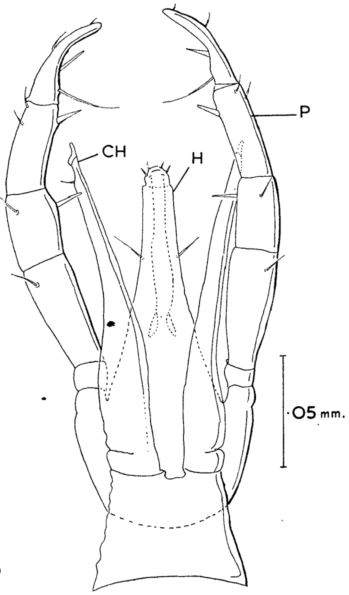

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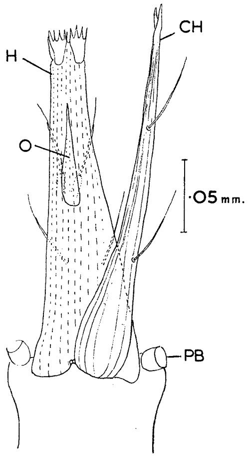

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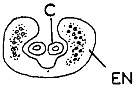

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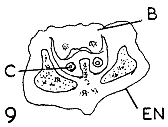

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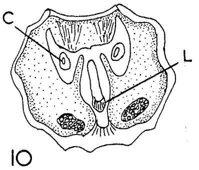

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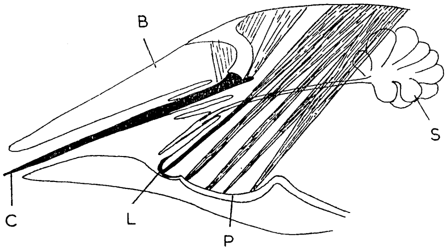
The mouth is bounded above by a labrum, which is carried on the anterior edge of the subcheliceral plate. Below this there may lie another median structure, the epipharynx, a prolongation of the dorsal wall of the pharynx. The labrum may be flanked on either side by paralabra (Plate XL, fig. 2). Arising from the mesial wall of the pedipalpal coxae at the level of the mouth, there are a pair of styles at whose bases the ducts of the salivary glands may open, or these ducts may be carried to their tips. In the Macrochelidae these styles are reduplicated, the outer pair being the shorter. The epipharynx in general is fringed along its lateral edges, and in parasitic forms, such as *Ornithonyssus*, it may exceed the labrum in length. In such forms, it serves to direct blood into the gutter formed by the hypostome, and so into the mouth. Because of their dorsal migration, the chelicerae lie above the labrum and below the epistome. Frequently they are protractile, and when at rest, penetrate deeply into the body, carrying the integuments back with them as an eversible sheath.

The form of the chelicera may be modified in the male Gamasides, by the development of a structure, used for the transference of spermatophores on the digitus mobilis (Plate XXXIX, fig. 6). In *Parasitus bombophilus* (H. Vitzthum, 1930), there is an oblique groove on the outside running from above, near its base, downwards towards the ventral edge. The groove has apparently become deeper and subdivided the digit, in such forms as *Halolaelaps*, *Parasitus* and *Eugamasus*, where a loop occurs attached at both ends to the digit. The anterior junction is broken in *Gamasolaelaps* to give a freely projecting spermatophore carrier, which can exceed the cheliceral shear in length, for example, *Gymnolaelaps myrmophilus* (see A. D. Michael, 1891), or even become very long and curled as in *Platyseius mollicomus* (A. Berlese, 1916).

Ectoparasitism leads to loss of teeth and slender cheliceral shears in such forms as *Ornithonyssus* (Plate XXXIX, fig. 7). There, too, the chelicerae are

PLATE XLII. **1.** *Histiostoma* (= *Anoetus*) *sapromyzarum* (Dufour); dorsal view of gnathosoma. BC basal joint of chelicera, BP basal segment of pedipalp, CM digitus mobilis, CMI base of digitus mobilis within the basal joint of the chelicera, FP floor of preoral cavity, L labrum, MF chitinous flange on terminal segment of palp, P anterior end of the podosoma, PM movable segment of the palp. **2.** *Listrophorus leukarti* (Pagenstecher); T.S. gnathosoma at the level of the mouth. AB abductor of endite, AD adductor of endite, D deutosternum, CP coxa of pedipalp, C chelicera, CLI prolongation of the dorsal wall of coxa I, EP endite of pedipalp, LF lateral flange of gnathosomatal wall, PD anterior pharyngeal dilators, PH pharynx. **3.** *Histiostoma sapromyzarum* (Dufour); internal view of right chelicera. **4.** *Spinibdella* sp.; dorsal view of left pedipalp. **5.** *Histiostoma sapromyzarum* (Dufour); dorsal view of pedipalp. BP basal segment, CP chitinous plates, H floor of prebuccal cavity, PM movable terminal segment. **6.** *Cunaxa setirostris* (Hermann); dorsal view of gnathosoma. CH chelicera, H hypostome and endites of pedipalp, P palp. **7.** *Spinibdella* sp. ♀; dorsal view of gnathosoma. O oral opening, PB basal joint of palp, other letters as in fig. 5. **8, 9, 10.** *Cheyletus eruditus* (Schrank); successive transverse sections through the rostrum. B basal joint of chelicera, C cheliceral stylets, EN endite of pedipalp, L labrum.

The Gnathosoma and the Appendages



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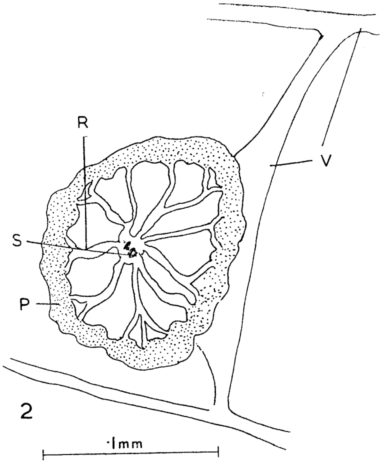

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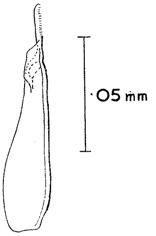

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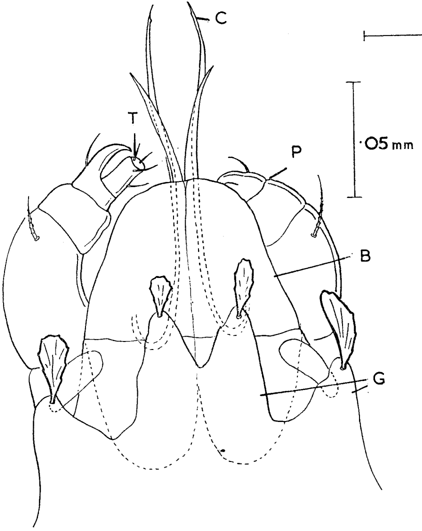

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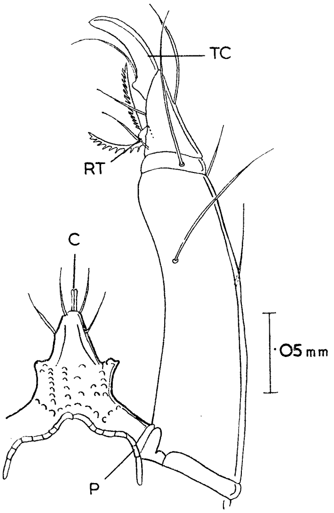

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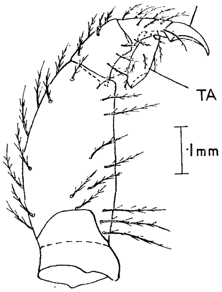

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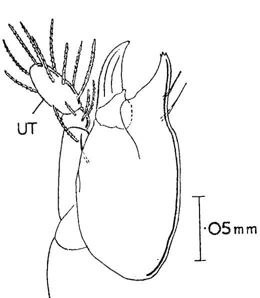

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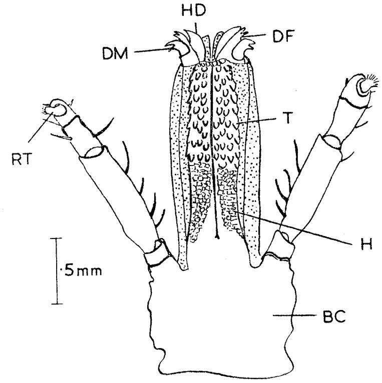

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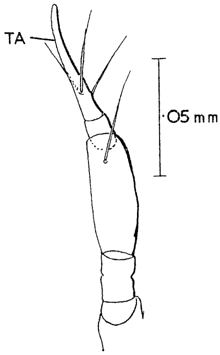

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hollowed out on their mesial surfaces, so that together they form a tube which functions as an extension of the pre-oral canal, opening post-ventrally into the hypostomal gutter. When the chelicerae are protruded, they are thus able to serve as a feeding tube up which blood can be drawn. In *Dermanyssus* the digitus fixus is reduced and the chelicerae are stylet-like. The reduction of the digitus fixus also occurs in many myrmecophilous forms, for example, *Myrmonyssus brachiatus* (A. Berlese, 1903). Endoparasitism leads to profound modifications of the digits, so that in such forms as *Halarachne* little trace of the shear structure remains.

In the Gamasides, the tibia bears ventrally at the articulation of the digitus mobilis, a row of stiff bristles which project forwards over the joint. These bristles may be gathered on to a slight bump as a fan-shaped tuft, which may be duplicated in *Macrochelidae.*

In the Ixodei, this complicated arrangement of mouth parts has to some extent been simplified. There is the usual cylindrical basis capituli, to which the palp is attached antero-ventrally. The pedipalpal coxae extend further ventrally and meet in the mid-line, except where a small triangular plate (which represents the deutosternum) lies anteriorly. There is no epistome, and so the chelicerae are exposed dorsally. About their entry into the gnathosoma, are two short external cheliceral sheaths, which are derived from the anterior edge of the roof of the basis capituli. Anteriorly, these sheaths are reflected inwards and are continuous with the cheliceral sheaths. Below the chelicerae in the mid-line, there lies a stylet-like organ, which is shorter than the labrum of the Mesostigmata (Plate XL, fig. 1). S. K. Sen (1934) considered this to be an anterior prolongation of the pharynx, open at its tip and used as a tube in feeding. This was accepted by Vitzthum (1943). It was not confirmed by D. S. Bertram (1939), who considered it to be homologous with the labrum, or labrum and epipharynx of other Acari. D. R. Arthur (1946) is of the same opinion as Bertram. Moreover, he has shown that in *I. ricinus* (Linnaeus, 1758) and *I. hexagonus* (Leach, 1815), this stylet lies at its base in the middle of a thin chitinous sheet, which stretches across the hypostomal gutter and corresponds, in position, to the much more

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PLATE XLIII. **1.** Trombid; diagram of pharyngeal pump. B basal joint of chelicera, C stylet of chelicera, L labrum, P pharynx, S salivary gland. **2.** Erythraeid larva; cytostome on the hind wing of a locust. P peripheral canal, R radial canal, S stylets, V venation of host's wing. **3.** *Copidognathus fabricii* (Lohmann); dorsal view of left chelicera of a ♀. **4.** *Allothrombium fuliginosum* (Hermann); internal view of left palp. TA tarsus, TI tibial claw. **5.** *Bryobia praetiosa* (Koch); dorsal view of gnathosoma. B basal joint of chelicera (cheliceral plate), C stylets of chelicerae lying below endites of the pedipalp, G gnathosoma, P palp. **6.** *Cheyletus munroi* (Hughes); dorsal view of right pedipalp. C stylets of chelicera, P peritreme, RT reduced tarsus, TC tibial claw. **7.** *Rhagidia gelida* (Thorell); dorsolateral view of left chelicera and palp. UT unmodified tarsus. **8.** *Amblyomma variegatum* (Fabricius); ventral view of gnathosoma. BC basis capituli, DF digitus fixus, DM digitus mobilis, H hypostome, HD hood of chela, RT reduced palp tarsus, T teeth on hypostome. **9.** *Copidognathus fabricii* (Lohmann); dorsal view of palp. TA elongated tarsus.

elaborate paralabra of the Mesostigmata (Plate XLI, fig. 1). Below the stylet's base, the mouth opens and is continuous with the hypostomal gutter ('Blutrinner' of Schulze), which lies along the dorsal surface of the hypostome in the mid-line (Plate XLI, fig. 1).

The hypostome or clava appears to be of paired origin, without any median prolongation of the deutosternum. Terminally, there is often an indentation and a line along the mid-ventral surface. At its base, it is provided with bilaterally symmetrical muscles which can move the two halves, as if they were hinged along the mid-line. The outward pressure exerted by these muscles, coupled with the teeth on the ventral surface of the hypostome, is a major factor in anchoring the tick to its host. Thus the hypostome here corresponds to the endites of the pedipalpal limb (Plate XLIII, fig. 8). There is no separate epipharynx in the ticks, but below the base of the labrum, a swollen vesicle operative in opening and closing the mouth (D. S. Bertram, 1939) may represent its base, which in such forms as *Ornithonyssus* serves the same purpose (T. E. Hughes, 1949). There are no paired styles, the salivary ducts open into a pocket or salivarium above the labrum. In the argasids, the whole gnathosoma is retractile within a deep camerostome and so is not visible from above.

In ticks, the palpal tarsus comes to be directed downwards and to articulate on the ventral side of the tibia (Plate XLIII, fig. 8). The palpal trochanter is sunken deeply into the palparium of the coxa and so lost. In *Ceratixodes* and *Lepidixodes*, the inner surface of the palp is concave and the two palps ensheath the hypostome.

The chelicerae are difficult to homologize with those of other Acari. In the first place the shear operates in a horizontal plane. The digitus externus moves away from the digitus internus, and on both digits the teeth are external. Both digits are movable and a membranous sheath, arising from the basal joint, may extend forwards along the digitus internus and, to some extent, over the base of the digitus externus. The function of these chelicerae seems to be cutting the host tissues, so that the toothed hypostome may be inserted. In A. C. Oudemans' (1906) view the sheath is derived from the digitus fixus of other forms, since in trombids this digit is sometimes reduced to a scale-like structure, the digitus internus being the equivalent of the digitus mobilis of the Mesostigmata and the digitus externus, a new structure. On the other hand, since the digitus fixus of the Notostigmata and Mesostigmata show two indentations considered to be sensory, and there are two pore-like pits on the digitus internus, F. Grandjean (1931) homologizes these two structures. These chelicerae slide over the shelf formed by the hypostome.

In the Holothyroidea, the pedipalpal coxae extend far into the ventral surface of the gnathosoma, so that the deutosternum is long and narrow as in the Mesostigmata; dorsally, they are united with the roof of the gnathosoma, which is thrown forwards as an epistome above the bases of the chelicerae, which are ensheathed and penetrate deeply into the body. The mesial walls of the coxae are joined by a subcheliceral shelf, which carries the dorsal dilators of the pharynx. Anteriorly, the subcheliceral shelf carries a labrum of a unique form. This structure is swollen and curved down over the mouth, its surface is covered with downwardly directed chitinous teeth and its interior filled by radial muscles. This constitutes the Radular organ of K. Thon (1905). It is presumably used to rasp the food, held by the chelate chelicerae (Plate XLI, fig. 2). These chelicerae, according to K. Thon (1905), are five segmented, but only two joints have arthrodial membranes so that, as R. E. Snodgrass (1948) has pointed out, they are really three segmented, as in other Acari. The palps are five segmented and the short tarsus, according to H. Vitzthum (1943), carries a paired ventral claw. The endites of the pedipalpal segment are fused in the median line, and end in two flaps anteriorly: an inner thin lobe and an outer tooth-like one, which would seem equivalent to the malae internae and externae respectively.

The Notostigmata, according to R. E. Snodgrass, show an early stage in the development of the acarine gnathosoma, though in no sense a primitive one. The roof of the gnathosoma fuses laterally with the coxae of the pedipalpal appendages, but is not thrown forwards at all; the three segmented chelate chelicerae are thus plainly visible from above. Beneath the chelicera, a substantial subcheliceral plate joins the coxal walls; ventrally, the coxae are separated by a narrow deutosternum. The endites of the palpal appendages appear to be subdivided into an outer denticulate lobe ('organe muscullaire' of F. Grandjean), and an inner toothed lobe ('organe de With' of Grandjean). The palp has five free joints and terminates in a paired claw. The labrum is swollen and toothed and overhangs the mouth and is flanked by, what are most probably, swollen paralabra. These lobes are said to act as a closure mechanism for the oral opening (F. Grandjean, 1931).

Internally, the gnathosoma of all Acari contains a suctorial pharynx and its musculature, the musculature operating the palps, and is traversed by the retractor muscles of the chelicerae, if these are retractile. The ducts of the salivary glands also pass through the basis capituli to open near the oral opening, in forms where the morphology is known. In all the forms being considered, the shape of the pharynx is essentially similar. When contracted it presents, in transverse section, the appearance of a three-pointed star with one arm directed downwards to the mid-ventral line; when dilated, it has the appearance of an inverted triangle (Plate XLI, fig. 3). Each wall consists of two long chitinous plates, jointed to each other along the mid-line of the wall and to similar plates at the angles of the pharynx. These plates can be pulled outwards by the contraction of the dilator muscles, which originate on the ventro-lateral walls of the basis capituli and the subcheliceral plate; some of the posterior dorsal dilators originate on the dorso-lateral walls of the basis capituli. Constrictor muscles encircle the pharynx between the dilator insertions, running from angle to angle (Plate XLI, fig. 3). In the ticks and in such Mesostigmata as have been investigated, the closure of the oral opening, which leads directly into the pharynx, is by the collapse of the anterior end of the pharynx against the swollen base of the epipharynx.

Arising within the base of the epipharynx, there is, in *Ornithonyssus bacoti* (S. Hirst, 1913) and in *Laelaps echidninus* (A. Berlese, 1887), a group of muscles which pass obliquely upwards and backwards to an insertion on the cheliceral shafts, where these merge with their sheaths. J. Stanley (1931), who first described these muscles, regarded them as dorsal dilators of the pharynx corresponding to the most anterior ventro-lateral pair, but was doubtful of their function. T. E. Hughes (1949) suggested that they are really cheliceral protractors and also depress the epipharynx and labrum during feeding (Plate XL, fig. 1, and Plate XLI, fig. 3). This view was not supported by F. Gorirossi (1950), who considered their insertion, in *Ornithonyssus*, to be on the subcheliceral shelf, and their function, the movements of the epipharynx and labrum.

No such muscle group is present in the ticks, so far as is known, but K. Thon (1905) figures a similar muscle group passing obliquely upwards and back from the base of the Radular organ in *Holothyrus*. Their contraction would pull this organ downwards.

In the Sarcoptiformes, the gnathosoma is much simpler in the majority of forms. There is no forward projection of the roof of the gnathosoma, so that the chelicerae are exposed dorsally. There is usually a short projection above the oral opening, the labrum; this is not visible, except in dissected specimens or in sections (Plate XLI, figs. 8 to 11), since it is hidden by the basal joints of the chelicerae (T. E. Hughes, 1953). The roof of the gnathosoma is formed from the dorsal plate fused to the pedipalpal coxae. A subcheliceral plate joins the mesial walls of the coxae. Ventrally, the coxae are fused with the deutosternum, the presence of the coxae being indicated by a pair of setae in the Acaridiae and majority of Oribatei. This region is called the labium by Michael, Oudemans and Grandjean (Plate XLI, fig. 4). The endites of the pedipalpal limbs continue this labium forwards for a short distance ('lingula' of E. Claparède and I. Trägårdh, 'langue' of F. Grandjean). In the Oribatei, it is formed of two symmetrical halves, lying primitively in the plane of the labium, and each carrying at least one seta. The coxae also bear a pair of oblique hairless lobes on either side of the mouth ('caeca maxillaris' of Grandjean) (Plate XLI, fig. 6); in the Oribatei their free edges are denticulate. In such forms as have stylet-like or feeble chelicerae, these lobes are often extended dorsally to meet each other, and so form a short conical tube ('Haustellum' of Berlese).

In some of the Acaridiae, the flaps undergo considerable modification. In some Anoetidae they are expanded to meet above the chelicerae (Plate XLII, fig. 1). In *Listrophorus*, they are enlarged and curved towards the mid-ventral line (Plate XLII, fig. 2), so that their roughened inner surfaces clasp the hair on which the animal runs (T. E. Hughes, 1954). In epizoic forms on birds' feathers, they frequently become expanded, too, but never to the extent seen in *Listrophorus*.

The pedipalpal palp in many Oribatei is of five segments, for example, Acaronychidae and Parhypochthoniidae, while some species of *Oribotritia* have five, others three. In the Acaridiae, there are usually said to be two free joints and the trochanter is said to be sunk into the palparium in the coxa. There is, in addition, an excentric knob which may represent the tarsus. In species of *Histiostoma*, the palp is widened in the dorso-ventral direction and its free end is fringed (Plate XLII, fig. 5). During feeding, there is a very rapid movement of these palps, which appear to whisk the almost fluid food into the preoral cavity (T. E. Hughes, 1953). In some forms, the palp is lost, for example *Creutzeria*. The chelicerae are typically stout and chelate (Plate XLI, figs. 5 and 7), but in forms which have adopted a habit of feeding on soft, or semifluid, food they become thinner; there is also reduction of the chelae in *Pelops*, *Suctobelba*, and numerous other genera. In the *Anoetidae*, *Linobiidae* and the Oribatei, *Gustavia* and *Galumnella* the digitus mobilis is lost, the digitus fixus elongated and denticulate on its ventral surface. In *Cederhjelmia* the digitus mobilis is denticulate on the surface away from the digitus fixus.

In the Sarcoptiformes the gnathosoma contains a pharynx of quite a different pattern to that previously described (A. D. Michael, 1901). The pharynx is crescentic in transverse section with the concavity lying upwards. It consists of two curved walls lying one within the other and joined along their edges (Plate XLI, figs. 10, 11). The lower wall is attached laterally and mid-ventrally to the wall of the gnathosoma. The upper wall can be raised by paired dilator muscles, which have their origin on the subcheliceral plate, and their insertions along the middle of the upper wall. Constrictor muscles run from edge to edge of the pharynx, across its upper side, between the dilators. By rhythmic action of these muscles, food can be squeezed along the pharynx into the oesophagus.

The salivary glands open, in such cases where the anatomy is known, into the roof of the buccal space, that is, at the sides of the labrum in the same position as in many Mesostigmata; in some forms, the two ducts may unite before they open by a common median pore. F. Lönnfors' (1930) contention that, in *Carpoglyphus lactis* (Linnaeus, 1758) and in various epizoic forms from birds, the salivary glands open above coxa I and that no glands open anteriorly, does not seem feasible for such forms as acarids and others, which take relatively dry food broken up by the chelicerae. It is difficult to understand how such a pabulum could be squeezed along the pharynx and the long narrow oesophagus without some form of lubrication.

The Trombidiformes show a great degree of variation in the gnathosoma, with a tendency to extreme fusion of its parts. In the Eupodidae, Penthalodidae, Penthaleidae, Rhagidiidae (Plate XLIII, fig. 7), Pachygnathidae and Cunaxidae, the chelicerae remain chelate, if only feebly so. The roof of the gnathosoma joins the coxae of the pedipalps, but does not extend forwards. Thus, as in the Sarcoptiformes, the chelicerae are visible from above (Plate XLII, fig. 6). Below the chelicerae, lies a structure usually called a rostrum, which often carries the oral opening near its tip. It is composed of the distal parts of the pedipalpal coxae and the pedipalpal endites. Ventrally, the coxae are fused to a narrow deutosternum. The rostrum is thus equivalent to the hypostome of the Mesostigmata. In *Rhagidia* this is clearly so, the rostrum is a trough, formed by the endites being fused in the mid-ventral line and continuing the ventral wall of the gnathosoma, without clear demarcation between. There is a subcheliceral plate, but only in *Speleorchestes* and *Nanorchestes* does it carry a freely projecting labrum in the mid-line.

The specialization among the Trombidiformes for a sucking method of feeding, reaches its highest development in the larvae of Parasitengona and in the adults of such forms as Erythraeidae, Cheyletidae and Tetranychidae. Here the chelicerae are stylet-like and the endites of the pedipalpal limbs are carried up and fused above them (Plate XLII, figs. 8, 9, 10). The basal parts of the chelicerae are generally considered to have fused together to form a stout structure, the cheliceral plate (H. Vitzthum), mandibular plate (other authors), or stylophore (Snodgrass). The stylets are considered to be the two more distal parts of the chelicerae, they curve upwards proximally and are attached to the cheliceral plate on its ventral surface, being inserted into depressions there. They are protruded by muscles, but apparently withdrawn by the effects of their own elasticity. The cheliceral plate fuses with the endites of the pedipalps proximally and this creates a closed food channel pre-orally, into which the labrum projects dorsally. This formation of the rostrum is quite dissimilar to that found in the Mesostigmata, and is associated with a different type of pharyngeal pump. In both *Tetranychus* and *Cheyletus* the pharynx is much shortened and cup-shaped. The dorsal wall projects into the hemispherical ventral wall, and the dilator muscles form a compact group, whose origin is on the subcheliceral shelf, and whose insertion is on the flexible dorsal wall of the pharynx. The axis of this cup is directed obliquely downwards and forwards (Plate XLIII, fig. 1). From the dorsal wall anteriorly, the labrum projects obliquely into the pre-oral tube, formed by the fusion of the basal parts of the cheliceral and the pedipalpal endites. From this labrum, a muscle runs obliquely up and back to the subcheliceral shelf. If the contraction and relaxation of this muscle is slightly in advance of those operating the pharyngeal roof, a valved diaphragm pump would result, capable of pumping fluid food from the opening at the end of the rostrum, along the narrow oesophagus, which opens from the posterior side of the pharyngeal cup. In *Tetranychus* it is said (W. Blauvelt, 1945), that this pump can be watched in operation.

The larvae of the Parasitengona were described as having an additional feeding structure: a tubular organ inserted into the wound made by the chelicerae and, presumably, an extension of the pharynx. The length of this organ often exceeds the body length in *Trombicula.* It was called a tongue (E. Trouessart, 1897), but has been shown, by M. André (1927), to be a product of the host's tissues, in response to the saliva injected by the larva (Plate XLIII, fig. 2). The structure, renamed a cytostome, has been reported more recently by B. M. Jones (1950).

The form of stylet chelicera varies slightly. In most trombids the digitus fixus is lost, being reduced to a transparent scale-like object above the mobile digit in Trombidiidae, Anystidae and Pseudocheylidae. The digitus mobilis is curved and saw-toothed in the majority of Eleutherengona, Trombidiidae and hydrachnellids (Plate XLIII, fig. 3), straight and long in Erythraeidae and hydrachnids. In the Stigmaeidae, the chelae are needle-like and, by loss of the digitus fixus too, a needle-like digitus mobilis is left, the condition seen in the Tetranychidae, Tetrapodili, Pseudoleptidae, Cheyletidae, Demodicidae and Tarsonemini. In these forms, the cheliceral bases have fused to form the cheliceral plate (Plate XLIII, fig. 5).

The palpal part of the pedipalp (Plate XLIII, fig. 7) also becomes considerably modified in many of the Trombidiformes. It can become chelate in either of two ways. In the Eylaidae among the hydrachnellids, the tarsus is terminal as in *Copidognathus* (Plate XLIII, fig. 9); in the others, for example, Arrenuridae, the tibia projects ventral to the tarsus as a fixed digit; on the other hand in the Thyasidae it forms a dorsal fixed digit; in both cases a chelate form results (Plate XLIII, fig. 5), which is raptorial. The tarsus may lose its mobility, becoming fixed in a downwardly directed position, as in the Trombidiidae and Erythraeidae (Plate XLIII, fig. 4). In the Teneriffidae and Cheyletidae, the tarsus is reduced to a mere vestige and the tibial claw well developed to a stout conical process (Plate XLIII, fig. 6). In Tetranychidae, the tibial claw is reduced and the tarsus terminal. Reduction in the number of palpal joints is seen in the Tetrapodili, where only two free joints persist.

The Bdellidae show a modification of the gnathosoma peculiar to themselves, and characterized by a long conus buccalis. The endites of the pedipalps reach up to the ends of the chelicerae, which are feebly chelate. These endites are fused, probably, to a long extension of the deutosternum, since between the tips of the endites is a thin median lobe. Each endite bears inside at its tip, a fringed lobe. The long chelicerae lie in the trough thus formed. The Bdellidae thus come to have a snouted appearance like a weevil (Plate XLII, fig. 7). The palp is also modified, the tarsus and femur being elongated, the other joints short, so that the palp is bent in the middle.

THE LEGS

In the larval stages, three pairs of legs are present, except in the Tetrapodili, which have two pairs at all stages. The larvae of Notostigmata and Holothyroidea are undescribed. In the nymphal and adult stages, four pairs are present, articulated in various ways with the podosoma.

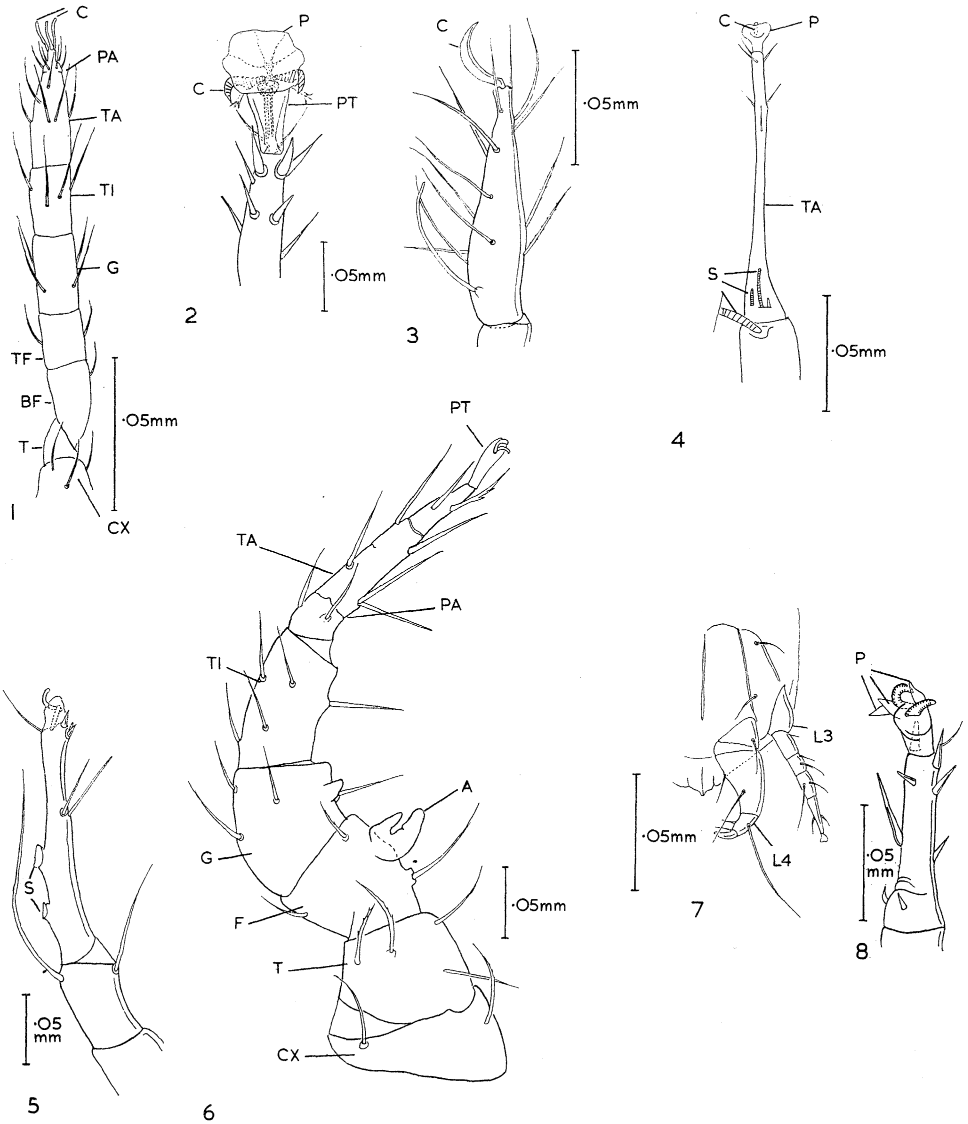

PLATE XLIV. **1.** *Aphelacarus acarinus* (Berlese); ventral view of left leg I. BF basifemur, C claws, CX coxa not sunk into the body, G genu, PA pseudoarticulation on tarsus, T trochanter, TA tarsus, TF telofemur, TI tibia. **2.** *Macrocheles matrius* (Hull); ventral view of left ambulacrum II. C claw, P pulvillus, PT pretarsus. **3.** *Hypochthonius rufulus* (Koch); dorsolateral view of left leg I. C claw. **4.** *Glycyphagus ornatus* (Kramer) ♂; dorsal view of tarsus I of left leg. S solenidia, other letters as in fig. 1. **5.** *Tyrophagus tenuiclavus* (Zachvatkin); lateral view of right leg IV of ♂. S suckers used in coition. **6.** *Eugamasus butleri* (Hughes) ♂; lateral view of right leg IV. A apophyses, other letters as in figs. 1 and 2. **7.** *Tarsonemus* sp. ♂; ventral view to show enlarged leg IV. L 3 leg III, L 4 leg IV. **8.** *Trachytes* sp. ♀; dorsal view of distal end of tarsus III. P lobes of pulvillus.

The Legs

The primitive number of segments in the leg would appear to be six: coxa, trochanter, femur, genu, tibia and tarsus (Plate XLIV, fig. 6), movably jointed to each other by arthrodial membranes. This number may be increased by the subdivision of the femur into basi- and telofemur (Plate XLIV, fig. 1), as in some of the oribatids, e.g. *Palaeacarus*, *Acaronychus*, *Arthronothrus*, *Aphelacarus*, giving seven movable joints. In the Parasitengona, among the Trombidiformes, the Tromdibiidae, Erythraeidae and many Hydrachnellids have divided femora. In the Eleutherengona, pseudoarticulations are present in Rhagidiidae and on femur IV of the Eupodidae, and in the majority of Anystidae and the Halacaridae, there is a true subdivision of the femora, at any rate in the adults. In Parasitiformes the presence of pseudoarticulations on the femora is very common, but true subdivision does not occur.

Another means by which the number of segments may be increased, is the subdivision of the tarsal joint; in the Erythracarinae there is a progressive division of the tarsus into a basitarsus, which is quite long, and a number of distal segments, one in *Chaussieria* to *Tarsotomus* where tarsi I, II, III, and IV have respectively seven, eleven, fourteen and eighteen segments. In the Notostigmata also, a movable joint occurs, subdividing the tarsus into two. This group is peculiar in showing, also, subdivisions of the trochanter on leg III and IV of the adult. Pseudoarticulations are common among the Mesostigmata (Plate XLIV, fig. 6) and grooves on the very long leg I of *Linopodes* (Prostigmata) simulate joints.

The number of limb segments is also frequently reduced by fusion of segments, and particularly by incorporation of the coxae into the ventral surface of the podosoma. In the Notostigmata, Holothyroidea and Mesostigmata, the coxae are movable, but show a slight tendency, in many Mesostigmata to sink into the body surface. In Ixodides, coxa I is said to be slightly mov able, but coxae II, III and IV are proximally sunk beneath the ventra surface, and quite immovable; the covered part is referred to as a subcoxa by P. Schulze (1932). In the whole of the Trombidiformes and all the Sarcoptiformes, except the primitive oribatids already referred to, the coxae are incorporated into the ventral surface. They may still project above the surface, as in most terrestrial forms, but in aquatic ones they have sunk in level with the body armour and form coxal plates or epimera, as they do also in the Nicoletiellidae and Demodicidae. A similar state of affairs arises in the Acaridiae (Plate IX, fig. 2). The side walls of the coxae are retained and project inwards into the body, forming apodemata to which muscles are attached. The arrangement of these apodemata relative to each other, is made use of by systematists. In most oribatids, too, the coxae are completely incorporated into the ventral body surface.

Reductions in the number of segments also occurs in connection with particular habits of life. The immature stages of the Demodicidae do not have the full complement of segments, and in parasitic forms there is often a

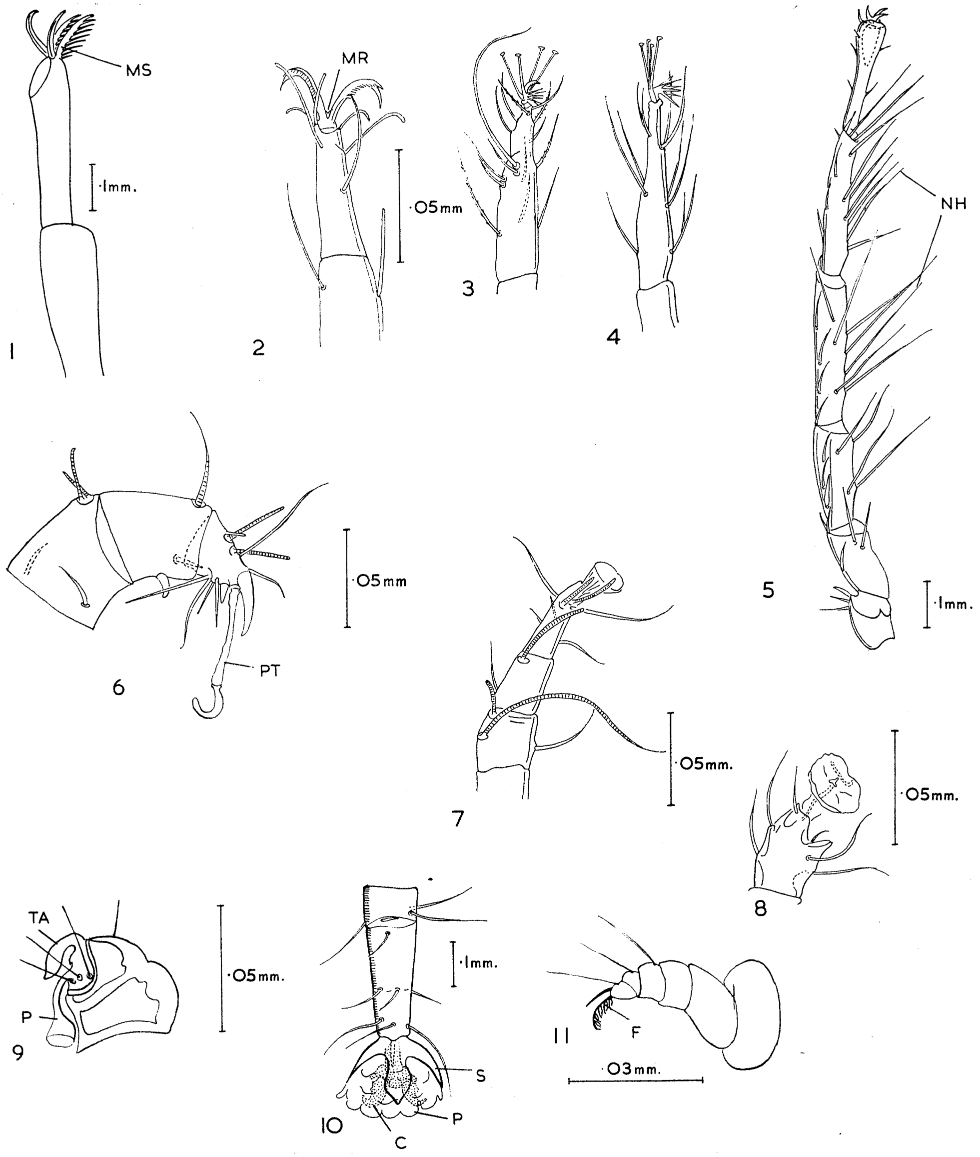

PLATE XLV. **1.** *Allothrombium fuliginosum* (Hermann); lateral view of right leg III. MS modified setae. **2.** *Copidognathus fabricii* (Lohmann) ♀; dorsal view of left leg I. MR reduced median claw. **3.** *Metatetranychus ulmi* (Koch); lateral view of left tarsus I. **4.** *Tetranychus telarius* (Linné) ♀; external view of left leg IV. **5.** *Unionicola crassipes* (Müller) ♀; ventral view of left leg III. NH natatory 'hairs'. **6.** *Hyadesia algivorans* (Michael); external view of right leg I. **7.** *Otodectes cynotis* (Hering) ♀; dorsal view of right leg I. **8.** *Mesalges similis* (Berrese) ♂; dorsal view of right tarsus II. **9.** *Microlichus uncus* (Vitzthum) ♀; lateral view of right tarsus I. P pulvillus, TA tarsal claw **10.** *Spinturnix vespertilionis* (Scopoli) nymph; left atrsus III. **11.** *Eriophyes ribis* (Westwood); external view of left leg II. F feathered claw.

reduction due to fusion of segments. In tarsonemids, the genu and tibia of leg IV may fuse (Plate XLIV, fig. 7). Legs I and II in *Schizocarpus* are only two-jointed and have become single-segmented in *Chirodiscus.*

Apart from modifications of actual legs, the number of legs may be modified as well (Plate XXI, fig. 1). Thus the males of *Eutarsopolipus* and *Podapolipus* and the female of *Tarsopolipus*, have only three pairs of legs and the female of *Podapolipus*, only one pair.

The tarsus of the acarine leg is provided with claws, associated with which there is frequently a pulvillus or some other suctorial device (Plate XLIV, figs. 2 and 8); the claws may be surrounded by a soft fold of integument or be borne on a long stalk. Since these claws in the Sarcoptiformes and Trombidiformes are birefringent in polarized light, as are many of the body setae, F. Grandjean (1925) considers them to be modified setae. This is in agreement with the views of H. A. Pagenstecher (1862), A. S. Packard (1870), E. Dahl (1884) and others who considered the claws of insects and arachnids to be modified setae.

It would seem that the Acari were primitively tridactyl, though this condition is rarely met with, because the varied habits of life within the group have led to profound modifications. The larvae or nymphs of primitive oribatids, such as *Acaronychus*, *Palaeacarus* and *Aphelacarus*, are tridactyl (Plate XLIV, fig. 1) and this condition can be traced in the various suborders, where it has been modified to a mono- or didactyl condition. S. Hirst described a fossil form, *Protacarus crani*, from the Devonian, in 1923, which showed three bent setae at the tarsal tip, with their roots very close together.

There are two ways in which this tridactyl condition becomes modified. Loss of the middle claw leaves a didactyl state, seen in the majority of the Mesostigmata and Trombidiformes (Plate XLV, figs. 1, 2); loss of lateral claws gives the monodactyl arrangement seen in some oribatids (Plate XLIV, fig. 3) and, in a yet more modified form, in Acaridiae (Plate XLIV, figs. 4 and 5). Modifications of the median claw, without its loss, also occur in the Trombidiformes, and some specialized oribatids become secondarily tridactyl by the subdivision of the median claw and loss of lateral claws. The flexible membrane which joins the claws to the tarsus may become elongated to form a pretarsus, traversed by the tendons operating the claws. This is seen well developed in the Mesostigmata (Plate XLIV, fig. 2). The pretarsus is continued as rounded (Gamasides) or pointed (Uropodina) lobes above and below the two claws. The pretarsus is stiffened by two ribs of chitin, which may project beyond it as needle-like processes (Macrochelidae). The tendons end on a disc-shaped structure at the base of the claws and suckers and, by their pull, the claws and sucker lobes are drawn together, and may be retracted partially within the pretarsus. In the ticks, the Argasids and the Ixodides lose the dorsal flaps of the pretarsus. In forms which are found on the surface of Myriapods, the claws are lost and the sucking flaps emphasized (*Julolaelaps*) (Plate XIII, fig. 4), and the same sort of modification occurs in myrmecophilous and termitophilous species. The whole ambulacral apparatus may be lost on leg I, if it assumes a sensory function, as in the Macrochelidae. The Uropodina habitually carry leg I raised up above the body like antennae, and many gamasids tap the substrate with leg I as they walk, the leg taking little, if any, part in the actual walking; this also applies to ticks. The legs of the male may be modified in connection with copulation (Plate XV, fig. 1); thus, leg II of the male Parasitidae is thickened and bears apophyses on the femur (Plate XLIV, fig. 6), the distal joints bend back and grip the legs of the female against these. In the Laelaptidae there are thorn-like spines in place of the apophyses. In the Tarsonemini, the males often have leg IV (Plate XLIV, fig. 7) short and thick and no longer functional in walking; this leg grips the female.

In the Trombidiformes, the Parasitengona (trombids and erythaeids) show modification of the middle claw to some extent; in the larvae and nymphs it is thinner and often differently curved, while the adults are didactyl, the median claw being lost. The pectinate structures of *Allothrombium* and *Corethrothrombium* are, in all probability, pectinate setae (Plate XLV, fig. 1). The Nicoletiellidae also have a weak median claw on legs II, III and IV, leg I being didactyl. The larval hydrachnellids, like the terrestrial Parasitengona, have three claws, the middle one being very small, and the adults are didactyl. The Eleutherengona and the hydrachnids remain tridactyl. The median claw of *Pachygnathus* has small lateral processes at its base. In some of the Rhaphignathidae, Cryptognathidae, Cheyletidae and Tetrapodili, the claw is the axis of a double row of obliquely directed processes (Plate XLV, fig. 11). The lateral claws of the Tetrapodili are very minute. In Rhagidiidae, Tydeidae and Eupodidae, the median claw is flattened and bears little processes at its edges, whilst in the Tetranychidae (Plate XLV, figs. 3, 4), the lateral claws become subdivided into two, each little process ending in a knob. The single median claw is subdivided into two in *Schizotetranychus*, into four in *Tetranychus* (Plate XLV, fig. 4), and is lost in *Anystis*.

In the bdellids, leg I loses its ambulacral apparatus and is only sensory, foreshadowing its great elongation and antenna-like appearance in *Linopodes* and *Cheletomorpha*. The aquatic Trombidiformes have the legs variously fringed with 'hairs' for swimming (Plate XLV, fig. 5) and leg IV of male hydrachnellids is modified to hook on to the trochanter of the female, for example in *Pseudofeltria*.

The Sarcoptiformes have, as a group, lost the lateral claws and the remaining median one becomes very modified. Apart from the primitive oribatids previously mentioned, the larvae and nymphs are monodactyl. The adults may be tridactyl or didactyl. This is presumed to be a secondary condition since it is limited to the adult very often, and then may occur on some legs only (tarsus IV of *Heterobelba*, legs II, III and IV of *Heterozetes*), and variations may occur to produce didactyly in normally monodactyl species.

The Legs

In the Acaridiae, the lateral claws are lost and the pretarsus, often well developed, carries at its end a bell-shaped or lobed sucker (Plate XLV, figs. 6, 8, 9) surrounding a very small claw. The pretarsus is very long in *Ensliniella* and *Hyadesia* (Plate XLV, fig. 6), but almost absent in *Sennertia*. The sucker is collar-like in *Carpoglyphus*, but may be much enlarged in *Heteropsorus*. In forms epizoic on birds or mammals, the claw is frequently lost and is sometimes functionally replaced by a claw formed from the tarsus on certain legs. The tarsus of leg I of the females of *Microlichus* (Plate XLV, fig. 9) and *Myialges* shows this type of modification; there it is used, in the first case, for anchoring to the nervures of the wings of Diptera where the eggs are laid and, in the second case, for attachment to the abdomen of Diptera or Mallophaga. The claw is also lost in *Cytodites*.

Modifications of the legs occur in some of the males of many bird epizoites, and some free-living forms too, giving rise to heteromorphic males. The classification of bird epizoites is largely based on these heteromorphic males. Leg III is often enlarged and its joints variously modified, for example in *Analgopsis*, *Mesalges* and *Megninia*. Leg IV is modified in *Xolalges*, *Pteralloptes* and *Xoloptes*. These modified legs are assumed to be clasping organs; however, homeomorphic males occur which do not possess them. In the Psoroptidae leg IV of the male is shortened, and leg III used to clasp the female.

The typical leg musculature is shown on Plate XXV, fig. 1.

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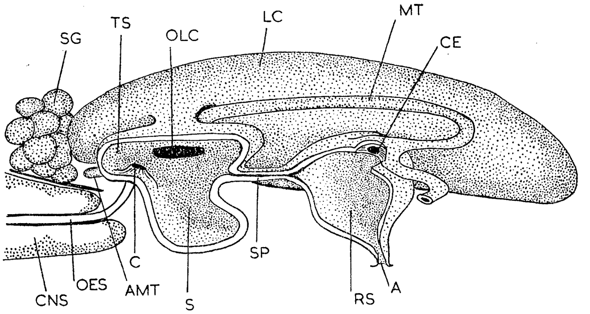
CHAPTER XI

The Alimentary Canal

THERE are four main types of acarine gut, as E. Reuter (1909) has shown. All possess an anterior heavily cuticularized part, the pharynx, which forms the suctorial apparatus. This part is certainly derived from the stomodaeum. A long narrow oesophagus, which penetrates the central nervous system, and which may, in some forms, have a very thin lining, probably of a cuticular nature, is also present. This oesophagus, at any rate in *Acarus siro* (Linnaeus, 1758), is an anterior production of the midgut region, and its sharp differentiation from the pharynx in the vast majority of mites, suggests that it is not of stomodaeal origin. The oesophagus opens into a stomach which, in common with other Arthropoda, carries a number of caeca. Posteriorly the stomach passes via a separate part of the midgut, of different form in the different suborders, into the rectum, which is derived from the proctodaeum and lined with cuticle. Unlike most arthropods, the arachnid proctodaeum is not very deep and the rectum is consequently not very long. At some point between rectum and stomach, the excretory canals join the gut, except in the Trombidiformes where the stomach ends blindly, and the posterior body opening is called a 'uropore', being the opening of a single median excretory canal alone. The main types of acarine gut arise from modifications of the stomach and its caeca, and from modifications of that part of the midgut between stomach and rectum.

In the parasitic forms, the oesophagus leads back into a small stomach, which is really the junction of a number of paired caeca (Plate XLVI, fig. 1). From the stomach an intestinal region leads back to a region, called by many, the hindgut ('Enddarm' of German authors); this is a roomy vesicle which opens by the rectal valves, the anus being near the end of the body on the ventral surface. In the Gamasides the oesophagus is a narrow tube, whose walls show no very clear nuclei and which is not lined with chitin. In *Halarachne* E. Steding (1924) described a wall of cubical epithelium, whilst in *Ornithonyssus* the wall has the appearance of a pavement epithelium. Typically the oesophagus enters the stomach on the antero-ventral surface and projects slightly into its cavity, a device also met with in the other suborders, and presumably preventing regurgitation of the stomach contents. From the stomach, three pairs of caeca arise, two of them dorsal. The dorsal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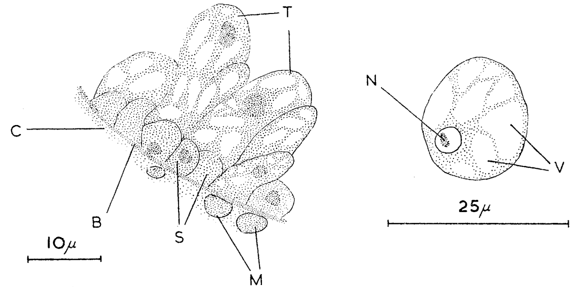
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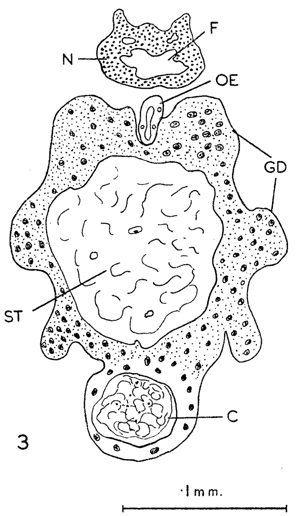
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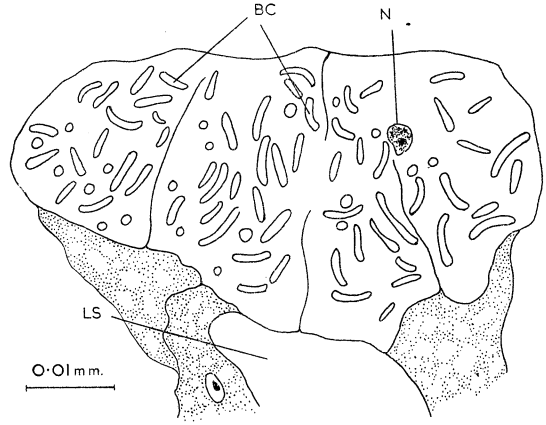
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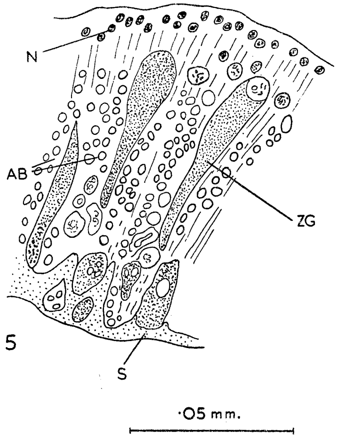
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caeca extend anteriorly and posteriorly, and usually the posterior pair are by far the larger (Plate XLVIII, fig. 1). A smaller pair of caeca arise from the posterior wall of the stomach ventrally, and extend backwards; these are missing, it is said, in the male *Haemogamasus* (see A. D. Michael, 1892), in both sexes of *Halarachne* (see E. Steding, 1924) and are very small in the female of *Ornithonyssus bacoti* (see T. E. Hughes, 1952). The extent of these caeca depends on the state of feeding, being completely collapsed in the starved animal and, after repletion, strongly dilated, so that the whole opithosoma is distended and turgid. The Spinturnicidae have a relatively small body, and the gut caeca push into the rather stout legs.

The walls of the stomach and caeca, when empty, consist of a basement membrane, on which stand small cubical cells with basal nuclei, interspersed with which are much larger cells. The larger cells have distal nuclei, are much vacuolated, and, it is suggested, are glandular. With dilation of the gut, the walls become much stretched, the smaller cells form a continuous layer but the glandular ones become nipped off into the lumen, where they lie as spherical bodies (Plate XLVI, fig. 2). In bloodsucking forms, the distention of the stomach and caeca is so great that the walls, in a gorged animal, present the appearance of a pavement epithelium. The cells budded off into the lumen are very weakly basiphil and, in *Ornithonyssus bacoti* (S. Hirst, 1913), they appear to become concerned with the accumulation of faecal material (T. E. Hughes, 1952). This material takes the form of small black spherules (T. E. Hughes, 1954a) within the cells, so that the faeces finally consist of balls of these spherules, mixed with the guanine produced by the excretory tubules.

From the posterior dorsal wall of the stomach a short intestine, which is not glandular, leads into a large vesicular region, frequently termed the rectum ('Rectalblase' of German writers), but better regarded as part of the midgut, since it is not lined with chitin. The intestine meets this region on its ventral side. Laterally and somewhat dorsally, the paired excretory ducts open into it, too, while post-ventrally it communicates, via the short chitinous

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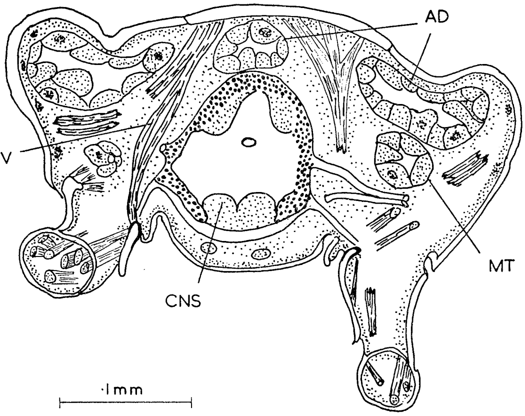
PLATE XLVI. **1.** *Ornithonyssus bacoti* (Hirst) ♀; diagram of reconstruction of alimentary canal. A anus, AMT anterior tip of Malpighian tubule, C opening of oesophagus into stomach, CE common opening of Malpighian tubules, CNS central nervous system, LC lateral caecum, MT Malpighian tubule, OES oesophagus, OLC opening from stomach to lateral caecum, RS rectal sac, S stomach, SG posterior part of salivary gland, SP sphincter between stomach and rectal sac, T.S. anterior tip of stomach. **2.** *Ornithonyssus bacoti* (Hirst); epithelial cells of gut wall. B basement membrane, C connective tissue, M muscle cells, S small cells, T large vacuolated cells; inset—a detached cell from the gut lumen, N nucleolus, V vacuoles. **3.** *Leiodinychus krameri* (Canestrini); horizontal section of gut and central nervous system. C contents of intestine, F fibres, GD glandular diverticula, N nuclei of nerve cells, OE oesophagus, ST stomach. **4.** *Ornithonyssus bacoti* (Hirst) ♀; mycetome. BC bacterial cells, LS lumen of stomach, N nucleus of a cell of the mycetome. **5.** *Holothryus gervaisi* (Thon); epithelium of stomach. AB absorbed granules, N nuclei, S layer of secretion on the free surface of the epithelium, ZG secretion granules in gland cells,

The Alimentary Canal



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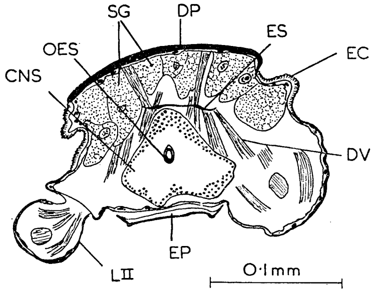

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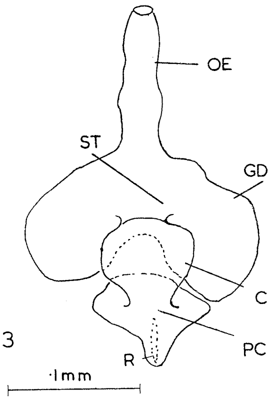

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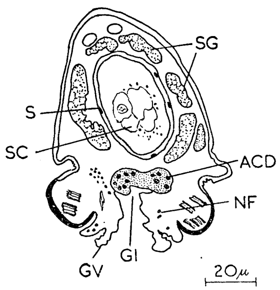

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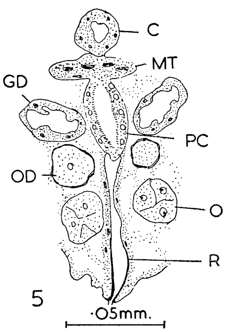

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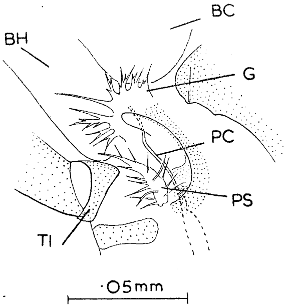

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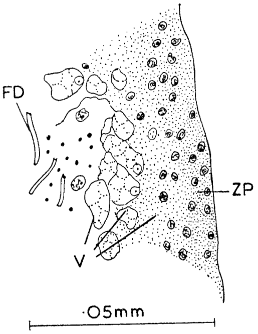

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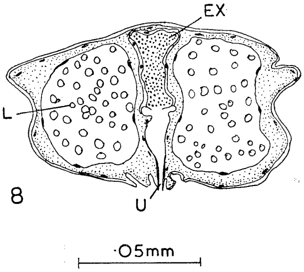

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rectal valves, with the anus. The walls of this region of the gut are composed of a thin epithelium.

The gut wall frequently carries outside the basement membrane, longitudinal or transverse muscle strands. In *Pergamasus*, according to W. Winkler (1888), these form a continuous double coat in the region of the intestine.

In *Ornithonyssus bacoti* the dorsal wall of the stomach consists of very modified cells which contain, what appear to be, micro-organisms (Plate XLVI, fig. 4), similar to those found in the mycetomes of lice. The presence of such organisms would seem to be correlated with the bloodsucking habit, but they do not appear to have been reported in the ticks.

The other principal group of Mesostigmata, the Uropodina, show two main patterns of gut, so far as the stomach and its caeca are concerned. In all the Uropodina investigated, there are two pairs of caeca arising from the stomach (Plate XLVIII, fig. 5), an anterior pair and a posterior pair lying alongside the intestine. The anterior pair of caeca are each subdivided into two. In *Fuscuropoda* and *Urotrachytes* the caeca are tubular; the inner arms of the anterior caeca lie alongside the central nervous system, the outer ones project sideways. In these forms the stomach, as in the Gamasides, is little more than a meeting-point of the caeca. In *Leiodynichus*, however, the stomach is large and the caeca short and broad (Plate XLVI, fig. 3). The intestine and hindgut are both ovoid or spherical, separated from each other and from the stomach by well-marked constrictions. The histology of the gut is said to be similar to that of the Gamasides (Plate XLVII, fig. 7).

In the ticks, the caeca are greatly developed (Plate XLVIII, fig. 4); the stomach, being relatively small, is prolonged anteriorly and posteriorly by paired caeca, of which each of the anterior pair are split into two. The expansion of these caeca on feeding is enormous and leads to a big increase

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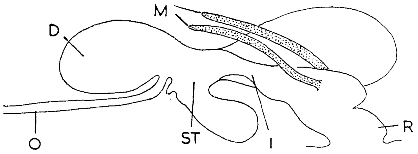
PLATE XLVII. **1.** *Ornithonyssus bacoti* (Hirst) ♀; T.S. body through the central nervous system. AD anterior diverticula of gut, CNS central nervous system, DV dorsoventral muscles, MT Malpighian tubule. **2.** *Ornithonyssus bacoti* (Hirst) ♀; T.S. through the salivary glands. CNS central nervous system, DP dorsal plate, DV dorsoventral muscle, EC extensible cuticle, EP epigynium, ES endosternite, L II leg II, OES oesophagus, SG salivary gland. **3.** *Glycyphagus domesticus* (Degeer); reconstruction of alimentary canal. C colon or intestine, GD gut diverticulum, OE oesophagus, PC postcolon, ST stomach. **4.** *Litrophorus leukarti* (Pagenstecher); T.S. of body through the stomach. ACD anterior extremity of common oviduct, GI genital invagination, GV genital valve, NF nerve of genital valve, S stomach, SC scale cells in stomach, SG salivary gland. **5.** *Acarus siro* (Linné) (= *Tyroglyphus farinae*); T.S. through the postcolon. C colon, GD gut diverticulum, MT Malpighian tubule, O ovary, OD oviduct, PC postcolon, R rectum; inset: cells of postcolon to show the striated border. **6.** *Acarus siro* (Linné); lateral view of anterior part of idiosoma. BC base of chelicera, BH base of hypostome, G Grandjean's organ, PC podocephalic canal, PS pseudostigmatic organ, TI trochanter I. **7.** *Leiodinychus krameri* (Canestrini); T.S. through the stomach wall. FD food consisting of fungal hyphae, V region of progressive vacuolation and disintegration of cells, ZP region of proliferation of cells. **8.** *Cheyletus eruditus* (Schrank) ♀; T.S. of the body in the region of the uropore. L lateral caecum with spherules of ingested food, EX excretory canal, U uropore.



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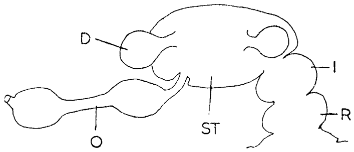

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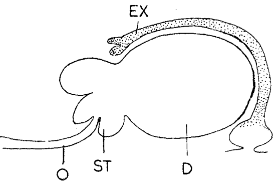

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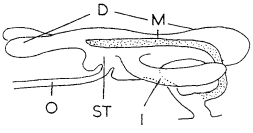

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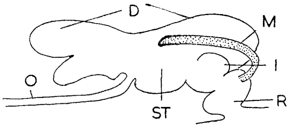

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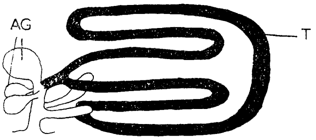

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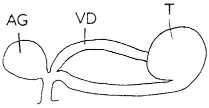

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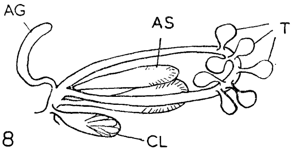

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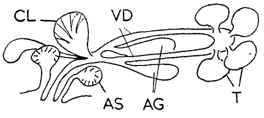

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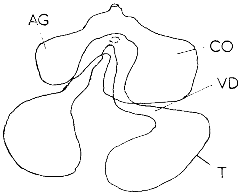

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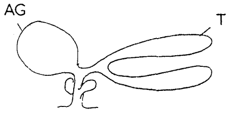

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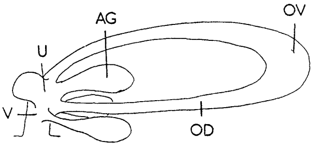

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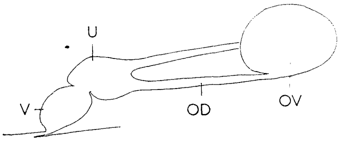

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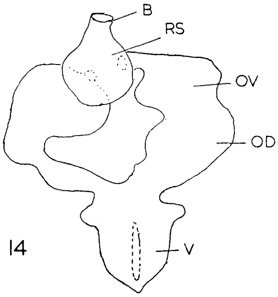

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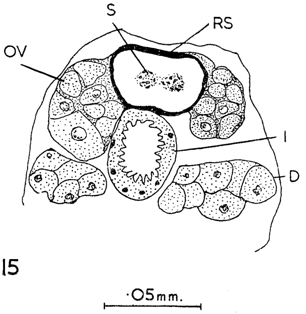

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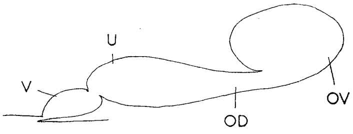

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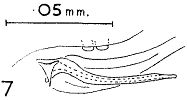

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in size of the animal. This dilation is greater in the Ixodidae than in the Argasidae, on account of the more extensible nature of the ixodid integument. The stomach passes back via a very degenerate intestine to the hindgut. The lumen of the intestine has been shown to be present in *Dermacentor* and *Haemalastor*, but it is often stated that the stomach ends blindly in ticks. In the adults, faecal material passes back from the stomach and the hindgut contains this and the products of the excretory canals.

The histology of the stomach and its caeca is very similar to that of the bloodsucking Gamasides. According to R. Roesler (1934), the wall consists of a layer of cells on a folded basal membrane, including large cells which project into the lumen in the starved female. These cells are, according to him, the degenerating gut epithelium of the preceding nymphal stage, which are later shed into the gut and disintegrate before feeding begins. During feeding, some of the cells throw out pseudopodia-like processes into the lumen. I have failed to find the pavement epithelial-like cells described by R. Roesler (T. E. Hughes, 1954a). In gorged nymphs and adults of *Ixodes* species, I have found cells in the caeca very similar to those found in *Ornithonyssus bacoti* and it would appear that the course of digestion may be similar to that of the bloodsucking Gamasides. The epithelium of the adult tick also contains glandular cells at the beginning of feeding. In the region of the entry of the oesophagus and scattered in the caeca, some cells which appear to be full of a secretion, extend far into the lumen.

The intestine joins the stomach to the hindgut, which lies below the median part of the stomach. As is usual, the wall here is of a pavement epithelium, and the roughly spherical lumen communicates with the anus through the short rectal valves.

In the Notostigmata, the oesophagus is surrounded by constrictor muscles (C. I. With, 1904) and is presumably capable of a peristaltic forcing of solid food (F. Grandjean, 1936), pushed into it by the pharynx, towards the stomach. The stomach is a large sac-like organ with a pair of very shallow anterior caeca. The histology is not well known. Glandular elements appear to be present in the caeca and anterior part of the stomach. An intestine leads

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PLATE XLVIII. **1–5.** Diagrams of alimentary canals: **1.** The parasitiform type. **2.** The oribatid type. **3.** The trombid type. **4.** The ixodid type. **5.** The uropod type. D diverticulum of stomach, EX excretory canal, I intestine, M Malpighian tubule, O oesophagus, R rectum, ST stomach. **6–15.** Diagrams of reproductive systems: **6.** Ixodid ♂. **7.** *Pergamasus* ♂. **8.** Erythraeid ♂. **9.** *Neomolgus* ♂. **10.** Acarid ♂. **11.** Uropod ♂. AG accessory glands, AS apparatus spinulosi, CL camerae lamellosae, CO chambered organ, T testis, VD vas deferens. **12.** Ixodid ♀. **13.** Parasitiform and trombidiform type ♀. **14.** Acarid type ♀. AG accessory glands, OD oviduct, OV ovary, U uterus, V vagina. **15.** *Acarus siro* (Linné); horizontal section of body through the receptaculum seminis. D tip of gut diverticulum, I intestine or colon, OV ovary, RS receptaculum seminis, S male genital products. **16.** Anystid, halacarid and tetrapodiline type ♀. **17.** *Ctenoglyphus plumiger* (Koch); lateral view of penis.

back to the hindgut. The whole gut behind the stomach is apparently very well supplied with muscle strands, which cross it obliquely in all directions. In the Holothyroidea, too, the stomach is very large and the caeca seem to be absent. The epithelium is much more compact than in the other sub-orders (Plate XLVI, fig. 5).

In the Acari, the excretory organs, if present as discrete structures, form part of a functional unit with the gut. Paired excretory tubules (with the exception of the Trombidiformes) open into the region of the hindgut. In the Notostigmata and all the parasitic forms, there is a single pair and in Holothyroidea, two pairs of such tubules. The excretory product of these tubules is guanine, in the form of birefringent spherules which form a paste-like substance, often mixed with faecal material from the gut. The tubules typically open into the hindgut near the point of entry of the intestine. Their contents often show a backwards and forwards movement in the living animal.

In the Mesostigmata, the tubules pass from the junction of intestine and hindgut obliquely up and forwards, running along either side just below the dorsal surface. Between the posterior and anterior caeca they pass downwards and, running beneath the anterior caeca, extend into coxae I in the Gamasides. The walls of these tubules consist of a single layer of large, polygonal cells with central nuclei. These cells stand on a thin basement membrane (Plate XLVII, fig. 1). In a starved animal, the lumen of the tube is small and surrounded by some three or four cells; after feeding and as digestion proceeds, the lumen becomes distended with guanine bodies, but excretory granules are not visible within the cells. It would seem that the nitrogenous waste is, therefore, passed into the lumen of the tubule in some soluble form, and precipitated as guanine bodies subsequently. In the Uropodina, the anterior ends of the tubules do not penetrate into coxae I, but are reflected back alongside the stomach. In the ticks, the excretory tubules are very long, and in ixodids, may exceed twice the body length. They therefore lie in several loops in the starved animal. In a gorged animal, they become irregularly distended with excretory matter, the distribution of which probably depends on the pressure of the gut caeca upon them. In the ticks the hindgut gradually fills up with the product of the tubules. In *Dermacentor* and *Haemalastor*, it is known that faecal material is passed back from the stomach towards the end of each nymphal stage and voided just before ecdysis; faecal material, elaborated in the pseudopodia of the gut cells, passes back in *Ixodes ricinus* (see T. E. Hughes, 1954a).

Apart from the glandular elements of the stomach and caecal epithelium, discrete glands are associated with the acarine gut in the form of salivary glands, which discharge either into the buccal cavity or pre-oral food channel.

In the Mesostigmata, a pair of salivary glands lies in the gnathosoma and extends back into the propodosoma. In *Ornithonyssus bacoti* these glands are racemose glands, whose ducts lead into the bases of the styles of the mouthparts; W. Winkler (1888), too, figures racemose glands in this position in *Poecilochirus*. A. D. Michael's figures give the impression of tubular glands in this position in Macrochelidae. Sig Thor (1903) has also described tubular glands in some unspecified Gamasides and Uropodina, but no such tubular glands were reported in *Halarachne* by E. Steding (1924). In *Ornithonyssus bacoti* the ducts of the salivary glands are chitinous for some distance, and run alongside the cheliceral sheaths, to branch repeatedly into the glandular acini (T. E. Hughes, 1949). The walls of these acini are composed of large rounded cells with a spongy-looking cytoplasm and large nuclei. There does not appear to be more than one type of cell (Plate XLVII, fig. 2).

In the ixodids, there are a pair of racemose glands, the acini of which are composed of two types of cell. The one type of cell lies at the blind ends of the acini, their cytoplasm is very vacuolated and appears to contain a fluid. The other type of cell surrounds the ducts where they leave the acini, and their cytoplasm contains large numbers of granules, before and during the feeding process, which are progressively lost, until the cell shows only a coarsely reticulate cytoplasm. There are also alveoli of cells which have a fibrillar cytoplasm, the processes of which appear to project into the lumen. These were described by A. Bonnet (1906) and K. Samson (1909) as unicellular glands, because no clear cell boundaries are visible. They occur between the other acini and discharge directly into the major branches of the main duct. Their product would seem to be a homogeneous fluid. A. Bonnet called them 'glandes à venin' from their similarity to the poison glands of some snakes.

In argasids, the salivary glands are a single pair, each penetrated by a single long duct, into which alveoli of two types discharge. The greater part of the gland consists of cells which contain granules in the cytoplasm. There is also a collection of alveoli similar to the 'glandes à venin' of Bonnet or 'Pyramidenzellen' of Samson, at the anterior end of the gland on the median side. Cells, corresponding to the fundus cells of ixodids, do not occur in argasids. K. Samson considered such cells to be present in the coxal glands of leg I of *Ornithodorus moubata* (Murray, 1877), but L. E. Robinson and J. Davidson (1913) do not agree that this is so in *Argas persicus* (Oken, 1818). H. Vitzthum (1943) refers to these glands described by Samson as anticoagulant glands. The presence of a gland secreting an anticoagulant in such a position seems unlikely, if the method of feeding of the ticks is taken into consideration. It seems much more probable that the secretion of the salivary glands contains an anticoagulant, and may or may not include also a digestive enzyme.

There only exists C. I. With's (1904) description of the Notostigmata. He gives details of a pair of 'antennary' glands which are tubular structures and lie between the muscles operating the chelicerae; where they discharge is not known. There are also apparently two 'maxillary' glands which lie either side of the pharynx. In the Holothyroidea, K. Thon (1905) described a pair of 'cheliceral' glands, each of which consists of some ten acini. Each acinus consists of a number of large conical cells arranged about a central point to form a globular structure. The ducts of these acini unite into a common duct, which discharges into the space in which the chelicerae slide. There is also a pair of 'maxillary' glands. These are syncitial structures with intracytoplasmic ducts which lead into a main duct, uniting with that of the 'cheliceral' gland of its side. These ducts are lined with chitin and, as in the case of the argasid ticks, the chitin takes the form of a spiral thickening. A pair of 'pedal' glands, similar in structure to the cheliceral glands, opens on coxae I near their bases.

The gut in the Sarcoptiformes is characterized by the development of the mesenteron behind the stomach into a well-defined spherical chamber, the colon of Michael (Plate XLVII, fig. 3), and a post colon which opens ventrally via the anal valves and represents the proctodoeum. In the Acaridiae, the oesophagus is narrow and long and may have a very thin lining of chitin; it opens into the stomach through the antero-ventral wall and projects a little into the lumen.

The stomach is the main part of the gut; and there is a pair of lateral or posterior caeca, which are smaller than the stomach, but variable in the extent of their development; in *Tyrophagus dimidiatus* (C. L. Koch, 1841) they reach the post colon, in *Pseudalloptes aquilinus* (E. L. Trouessart, 1885) they flank the colon, whilst in *Acarus siro* (Linnaeus, 1758) they project obliquely backwards and laterally; in the Psoroptidae they are missing, as they are in the Listrophoridae (T. E. Hughes, 1954b) (Plate XLVII, fig. 4).

In the oribatids, the oesophagus may be a uniformly narrow tube, or it may widen posteriorly into an ingluvies or crop (A. D. Michael, 1883) as in *Phyllotegeus*; in *Belba* this enlargement is a wide cone based on, and nearly as wide as, the stomach. There is a definite muscular cardia at the entrance to the stomach and the whole of this posterior region of the oesophagus has a circular muscle coat. The stomach bears lateral caeca; these may be short as in *Belba*, or almost spherical and joined to the stomach by a hollow stalk in *Lucoppia* (Plate XLVIII, fig. 2).

In the oribatids, there is a pair of proventricular glands (A. D. Michael, 1883) which lie either side of the oesophagus and discharge by short ducts into the stomach. Lönnfors (1930) homologizes these with the anterior caeca of the Parasitidae, and traces a series in Analgesidae, which show a progression from a pair of glandular patches on the anterior stomach wall to a single antero-dorsal patch of big gland cells. He considers that the caeca of the sarcoptiform type are the posterior pair of caeca of Reuter's parasitiform type, the third group.

The junction between the stomach and colon in the Acaridiae lies high on its posterior wall, and is marked by a sphincter. In the oribatids the opening is more ventral, since the whole gut behind the stomach leads almost straight down to the anus. In the Acaridiae the colon (intestine of Vitzthum) is spherical, being separated from the post colon (rectum of Michael, colon of Vitzthum) by another sphincter, and it is at this point that the excretory tubules join the gut (Plate XLVII, fig. 5). The post colon merges ventrally with the rectum which, as usual, is very short, being little more than the rectal valves. The arrangement of the hind part of the gut is essentially similar in oribatids, too. The colon is ovoid, and not so sharply constricted off from the post colon.

Histologically, the gut is similar in both Acaridiae and Oribatei. The stomach and its caeca have no intrinsic musculature; the wall consists of a basement membrane on which stand epithelial cells, many of which project as club-shaped cells into the lumen. In the caeca these cells may practically fill the cavity. They are very vacuolated and, from experiments with stained food, at any rate in *Acarus siro*, take up soluble material, so that the cytoplasm becomes filled with coloured vacuoles (T. E. Hughes, 1950). The stomach and its caeca are the main site of digestion and absorption. Faecal material is passed into the colon, where it forms a compact bolus, which in the Acaridiae, become surrounded by a peritrophic membrane. Within the membrane and mixed with the bolus, guanine granules become apparent. The colon thus appears to be in part excretory. In *Acarus siro* the pH of this region of the gut is raised from between 5·0 and 6·0 to between 7·0 and 8·0 and this may possibly be connected with the deposition of guanine. In the post colon, the faecal pellet becomes more desiccated and denser. The cells of the colon are a low uniform epithelium, while in the post colon there are taller cells with striated borders (Plate XLVII, fig. 5). The paired excretory tubules, if present, join the gut at the junction of colon and post colon. They are relatively short and contain no granules, either in the cells or lumen. Where their histology is known, it appears to resemble that of the post colon. The absence of granules from the sarcoptiform tubules, when seen in section, and the fact that they never appear white in the living animal, although the integument is often thin and transparent, suggest that they have largely lost their excretory function, which has been assumed by the colon.

In Acaridiae which feed on material of a high protein content, like *Histiostoma* on fungal material, the parenchyma of the opisthosoma becomes densely packed with guanine bodies. If *Acarus siro* is fed on a gluten-rich medium, it, too, shows an increase in the number of such guanine bodies, which are normally present in small numbers, especially in old animals (T. E. Hughes, 1950). This suggests that the powers of excretion are not very good since, in Trombidiformes and Parasitiformes, such granules do not appear and their excretory canals have frequently a dense white appearance, due to the presence of guanine spherules.

In the Acaridiae which have been investigated, the salivary glands lie in the podosoma. There are two pairs of glands which, from shape and position, probably coincide with the reniformes and post dorsales of the Trombidiformes. The glands in the Analgasidae and in *Carpoylyphus lactis* (Linnaeus,

1758) have been studied by F. Lönnfors (1930). He considered them to be pseudosalivary glands, opening above coxa I. All other authors agree that the salivary glands open into the buccal cavity. T. E. Hughes (1950) was unable to confirm the openings of any glands into the podocephalic canal of *Acarus siro* (Plate XLVII, fig. 6).

As in many Trombidiformes, the two glands on either side have a common duct and the ducts from the two sides may unite to a common opening into the dorsal side of the buccal cavity. In the oribatids the fusion of glands is considerable, there being a single median mass lying above the supraoesophageal ganglion. The arrangement of the ducts is not clear, but the glands were described in a number of oribatids by A. Berlese (1896).

The Trombidiformes, typically, have a gut which has lost the communication between the stomach and the hindgut (Plate XLVIII, fig. 3). The oesophagus is a narrow tube of circular cross-section which has, according to Sig Thor (1903), a thin chitinous lining. It opens into the anterior part of the stomach on the ventral wall, showing the usual projection in the stomach lumen. There is very frequently a slight depression of the stomach wall, into the bottom of which the oesophagus enters. The stomach is of a very diverse form. The presence of a median dorsal excretory canal, the dorso-ventral musculature and the genital system leads to the development of an irregular system of caeca. A. Croneberg (1879) gives as many as ten in species of *Trombidium*. In *Cheyletus* the stomach is small, and there is a pair of very large posterior caeca (Plate XLVII, fig. 8). The walls of the stomach and caeca contain gland cells, which when exhausted are, according to Sig Thor (1903), cut off into the lumen of the gut and themselves undergo digestion. The cells of the gut wall also contain granules, which in life are in rapid brownian movement within the vacuolated cytoplasm, a condition also met with in the Sarcoptiformes. The gut contents in forms, like *Cheyletus*, which are predaceous, show numbers of spherules, which take up protein stains strongly and are, presumably, the histolysed products of the organs of the prey, which have been pumped into the stomach by the pharynx (Plate XLIII, fig. 1).

In the larger Prostigmata, there may be as many as six pairs and one unpaired glands associated with the mouth. They were classified by Sig Thor (1903) as follows:

1. Glandulae tubulares (canal-like gland of Michael).
2. Gl. reniformes (reniform gland of Michael).
3. Glandulae dorsales anteriores (quadrate salivary gland of Michael).
4. Glandulae dorsales posteriores (pericibal gland of Michael).
5. Glandulae oesophagales anteriores.
6. Glandulae oesophagales posteriores.
7. Gl. trachealis impar (azygous salivary gland of Michael).

The Glandulae tubulares, reniformes and anteriores dorsales open into the podocephalic canal, a tubular structure or a deep groove which, in terrestrial Prostigmata and Endeostigmata, runs from above coxa I round the side of the body to end anteriorly beneath the cheliceral bases. A similar structure occurs in the free-living Acaridiae (Plate XLVII, fig. 6). It was first figured by A. C. Oudemans (1932) who mistook it for a tracheal structure and it has subsequently been investigated in considerable detail by F. Grandjean (1944). The tubular glands, which are long and winding, have a thick epithelial wall with brush border in some, for example *Trombidium* and *Eutrombidium*, but in others, for example *Thyas* and *Lebertia*, the walls are spongy with intracellular canals. The reniform glands lie behind the cheliceral bases, as kidney-shaped structures of big conical cells arranged about a common point, from which the duct arises; while the anterior dorsales are spherical glands of smaller cells above the anterior caeca of the stomach. The posterior dorsales are composed of bigger cells with intracellular canals and lie higher and more lateral than the anterior dorsales. The oesophageal glands, of which the anterior pair are often missing (they are present in the Erythraeidae), lie above the oesophagus, in front of the supraoesophageal ganglion and below the reniform glands; they are made up of paired irregular-shaped masses of small cells. The unpaired gland lies below the crista metopica between the main tracheal trunks; it is a branched tubular gland of large cells with a spongy cytoplasm. Sig Thor (1903) thought it might possibly be a poison gland. Nothing is known of the specific secretions of these glands. In *Cheyletus* only the unpaired gland is present, and there it undoubtedly produces a substance which causes extensive histolysis of the tissues of the prey, which are sucked out, leaving only the empty exoskeleton. The other glands are by no means constant in their presence. The unpaired gland is lacking in *Trombidium* and *Eutrombidium*. In the Halacaridae the post dorsals and reniform glands have a common duct on each side and, together with the unpaired gland, constitute the whole equipment.

The gut of the Tetrapodili is of interest, for here the narrow oesophagus leads into a long tubular stomach without caeca. The stomach wall is an epithelium without clear cell walls, and is devoid of musculature. The stomach narrows somewhat posteriorly and then opens up into a hindgut, which is as wide as the stomach but composed of a pavement epithelium; this communicates with the anus through the chitinous rectal valves.

The Tetrapodili are generally considered to be an offshoot of the tetranychid stem, and it is of interest that recently W. E. Blauvelt (1945) has reported that in *Tetranychus telarius* (Linnaeus, 1758) there is a communication between the single median excretory canal and the anterior dorsal wall of the stomach, which it overlies. This would appear to be the retention of a primitive condition and is probably correlated with the habit in both cases of sap-feeding. The food intake, in the case of sap, contains relatively large proportions of water, which the animal may not need and which the usual trombidiform blind gut would find difficulty in disposing of. In the majority of Trombidiformes, the functioning of the hind part of the gut as an excretory mechanism, already seen in the Sarcoptiformes, has led to a severance of the stomach and its caeca from the colon, and post colon region of the Sarcoptiformes. The hinder part of the gut has thus come to form a median unpaired excretory canal (Plate XLVIII, fig. 3), discharging through the original anus which is often called a uropore in the Trombidiformes, but the arrangement of its valves and muscles clearly shows its anal homology. There is a tendency for the uropore to migrate backwards; thus it is ventral in *Cheyletus*, terminal in the Rhagidiidae, Tetranychidae, and dorsal in *Penthaleus* and *Kongsbergia*. In *Eylais* (A. Croneberg, 1878) the excretory canal is surrounded by a muscle coat, and the spindle-shaped nuclei in the basement membrane mentioned by U. Schmidt (1935) in *Hydrodroma*, suggests the presence of muscles, too, which would help in voiding the contents of the tubule. The actual production of guanine seems to be limited to the anterior parts of the tubule, where the walls consist of tall columnar cells; nearer the uropore the cells become much flatter, this region like the hindgut of Mesostigmata forming a storage space. In the Trombidiformes, instead of being a more or less spherical space, it is bilaterally compressed between the stomach caeca (Plate XLVII, fig. 8). It thus happens that, in animals where the excretory apparatus is well filled, it has the appearance of a median white streak down the dorsal side, its posterior enlargement not being visible. Anteriorly the excretory tubule may be forked in the hydrachnellids and terrestrial Prostigmata, and this fork may represent the remains of paired excretory tubules.

Within the Acari there seems to be a primitive condition, best seen in the Mesostigmata, of paired tubules opening into a hind region of the mesenteron which also receives faecal material from the stomach. This hindgut serves as a storage space, and guanine and faeces are voided through the very short proctodeal rectum, which consists of little more than the rectal valves.

In the Sarcoptiformes and Trombidiformes the excretory tubules have lost their function, which has been taken over by the parts of the mesenteron posterior to the stomach. In the Sarcoptiformes, this has not reached the degree of specialization seen in the Trombidiformes, and there is a marked tendency for the accumulation of guanine granules in the parenchyma of the body. There is also seen in this group, the subdivision of this region of the gut into a colon, where the faecal-cum-excretory bolus is formed, and a post colon, where water is extracted from it. This may very well be correlated with the tendency, in this group, to feed on drier solid food, as is exhibited in the Acaridae particularly. In the majority of the Trombidiformes, the specialization has led to the separation of the hind part of the mesenteron, leaving a blind stomach. Although there may be exceptions to this in the Tetranychidae, there is no continuity of gut generally; in such forms as *Cheyletus*, guanine bodies lie exclusively within the median tubule and there is no junction anteriorly with the stomach.

Functional coxal glands have been described in detail in *Ornithodorus moubata* (Murray, 1877) by Boné (1943) opening between coxae I and II. The female takes in some 6–7 times its weight of blood in 10–30 minutes and excretes from the coxal glands fluid equivalent to about one-third of this weight. Boné showed that the osmotic pressure of the gut contents and of the body fluid is of the same order as that of the blood being ingested. The sodium chloride content of the gut contents is less than that of the body fluid, while the fluid excreted from the coxal glands contains sodium chloride in greater concentration than either. He concluded that fluid is excreted to concentrate the blood, the more mobile ions passing into the body fluid along with water. The excess of ions, mainly sodium chloride, is excreted along with the water by the coxal glands. These ticks then have a discrete osmoregulatory apparatus (A. D. Lees, 1946) in the form of the coxal glands, which histologically resemble those of scorpions and spiders.

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CHAPTER XII

The Reproductive System

THE arachnid reproductive system is primitively paired, since the gonads and their ducts are derived from the symmetrically developed mesoderm. The ducts primitively open in the Acari on the ventral body surface, in the region of the fourth pair of legs, by a single median opening. In the female, particularly, the opening is associated with an inflection of the body wall, which gives rise, in many cases, to a chitin-lined tube, the vagina. The male may be provided with a chitinous penis, but this is by no means always present. The extensive loss of segmentation by the opithsosoma has obliterated all traces of any segmental arrangement which the gonads may once have had. In addition, all degrees of fusion of the paired gonads and their ducts, towards the condition of an unpaired median system, can be traced within the group. Accessory glands are frequently developed in both sexes and are often of considerable complexity, very little is known of their functions.

THE MALE SYSTEM

The testes in the Parasitiformes would appear to have been primitively tubular, being the specialized posterior parts of the paired genital rudiments. They remain as tubular structures in the Uropodina, where there is no sharp differentiation of vasa deferentia (Plate XLVIII, fig. 11). In the ixodid ticks, too, the testes are long tubes winding backwards and forwards in the body, but here their morphologically posterior ends have become united (Plate XLVIII, fig. 6). The restriction of the germinal epithelium to a limited posterior part of the tube, with the consequent sharp differentiation of a testis and vas deferens, is found in *Euryparasitus*; here, too, the testes are joined by a thin posterior connection. Discrete and well-developed paired testes, which remain separate, are characteristic of the Acaridiae, and also occur in *Tetranychus* (Plate XLVIII, fig. 10).

The testes may show further degrees of fusion than a mere posterior junction, so that in *Pergamassus crassipes* (Linnaeus, 1758) the testis is a single median spherical body discharging, however, into paired vasa deferentia (Plate XLVIII, fig. 7). Finally, the fusion may involve the whole of the genital rudiments, so that the testis and its duct are single median structures, as in the tarsonemids and Tetrapodili.

A third type of complication, involving the germinal epithelium, occurs where this becomes subdivided between outgrowths from the original tubular elements, which in this case often become glandular in their hinder regions. In *Haemogamasus*, *Gymnolaelaps* and *Halarachne*, the testis is irregular in outline but the germinal epithelium is entire; complete subdivision of the gonads appears, in the present somewhat restricted state of knowledge, to be confined to the Trombidiformes (Plate XLVIII, fig. 9), and the Oribatei amongst the Sarcoptiformes. In *Lundbladia*, the genital rudiments fuse posteriorly to give a horseshoe-shaped gonadial rudiment, the two arms of which each develop an anterior and posterior outpouching, the germinal epithelium being restricted to the lateral walls of these pouches. The development of such outpouchings has progressed further in *Trombidium*, and in *Allothrombium* they arise, not only from the side arms, but from the posterior cross-connection too. In those instances where the number of testicular vesicles is small, they discharge into paired and symmetrical vasa deferentia, e.g. the Anystidae, but in the hydrachnids, where the number may be upwards of 200, the ducts have become much subdivided and the testicular vesicles dispersed throughout the body.

In the Oribatei, the testes arise as two outgrowths, one posterior and one anterior on the ventro-lateral margin of a large median glandular organ. This median structure, often loosely referred to as the testes, lies below the midgut. It is obviously bilaterally symmetrical, consisting of a median part with a pair of lateral flaps, each of which is indented at its margin to give an anterior and posterior lobe, each of which carries a testis. The most reasonable assumption, in the absence of embryological evidence, is that this glandular structure is derived from the fusion of paired genital ducts, which in their posterior regions have become glandular. The development of a glandular epithelium in those ducts occurs in other groups as well. In the bdellids, known mainly from A. D. Michael's work on *Neomolgus* (1896), the vasa deferentia are glandular from the ductus ejaculatorius. They run forwards, then double back on themselves to connect with a median structure, the testicular bridge, a hollow organ of large cells to which are attached two testes on each side. The germinal epithelium is restricted to the median walls of these testes, their lateral walls being composed of large cells like those of the bridge. The curved vasa deferentia are glandular and, indeed, were called glandulae mucosae by Michael. Here, then, there has been a posterior fusion of glandular ducts and an extension of glandular epithelium into the actual testicular outgrowths themselves.

A similar type of gonad, in part germinal and in part glandular, is found in the Halacaridae where the paired testes have the germinal epithelium restricted to their dorsal walls, while their ventral regions are glandular. Here the vasa deferentia have completely fused to form a thin-walled median sac, into the post-ventral wall of which the two testes discharge, and which probably serves as a vesicula seminalis.

Accessory glands, like the gonads and their ducts, show a wide range of morphological variation (Plate XLVIII, figs. 8 to 11). In *Pergamasus crassipes* amongst the Parasitidae, there is a single pear-shaped accessory gland, attached by its narrow end to the top of the ductus ejaculatorius, just below the point of fusion of the vasa deferentia; it lies just below the suboesophageal ganglion. The Uropodina, too, have a large median gland and, in addition, a pair of small glands which flank the ductus ejaculatorius and discharge near its external end (Plate XLVIII, fig. 11). The Ixodidae have a much more elaborate system; in addition to an unpaired gland, there is a pair of anterior tubular glands ventro-lateral to the median one, and also a posterior pair of tubular glands; all of these discharge into the ductus ejaculatorius. Among the Sarcoptiformes, only the Acaridiae develop accessory glands in the males. In *Tyrolichus* and *Tyrophagus*, there is a single median roomy vesicular gland. In *Carpoglyphus* and *Glycyphagus*, this gland is reduplicated, there being two median glands (Plate XLVIII, fig. 10). One of these is a thin-walled sac whose cells frequently contain a finely granular substance; the other is a thick walled sac-like gland lying below it. The cells of this gland are distally greatly distended by spherules of secretion, and they project so far into the lumen as practically to obliterate it, and to make the organ appear chambered in transverse section. Both glands discharge into the ductus ejaculatorius.

In various members of the Trombidiformes, the accessory glands are numerous and complex. A median unpaired gland, anterior to the ductus ejaculatorius, is found in Anystidae and Leptidae; this gland is duplicated in bdellids and *Erythraeus*, so that there are a ventral and a dorsal anterior gland opening into the ductus ejaculatorius, one above and the other below the chitinous supports of the penis. The Anystidae and *Erythraeus* have, in addition, a pair of posterior glands lying below and to either side of the testes. These glands are peculiar in that they may develop fine setae in their broadened distal ends in the case of *Erythraeus*, and more generally over their inner surface in the case of Anystidae. These setae are called the apparatus spinulosi. The Bdellidae, in the case of *Neomolgus* only, also possess what are probably paired posterior accessory glands, which are said to open, not into the ductus ejaculatorius, but into the vasa deferentia. A peculiarity of the bdellids is the occurrence of a pair of air-filled cavities near the top of the ductus ejaculatorius, opening into the space between the penis and the muscular organ responsible for its protrusion. These sacs are chitinous and provided with internal setae; they would not appear to be homologous with the apparatus spinulosi previously mentioned (Plate XLVIII, fig. 9).

Various of these glands, the dorsal anterior one in *Neomolgus*, the paired posterior glands in *Erythraeus*, are described as having lamellae projecting into the lumen and termed the camerae lamellosae (Plate XLVIII, fig. 8);

these in all probability are the ends of large glandular cells distended by secretion, giving the same effect as in the chambered gland of the Acaridiae.

The ductus ejaculatorius may be derived from the common junction of the two vasa deferentia, or from the median invagination of the body wall, which provides the genital opening. Where the duct is chitinous, as in the Anystidae, where there are setae on its internal surface, it is undoubtedly a derivative of the body wall. In those cases, too, where there is a protrusible end to the duct which may function as a penis, this is most probably the case, but in the majority of mites, the anatomical detail and the embryology are not known in sufficient detail to enable an opinion to be given.

A penis of any sort is entirely lacking in the Parasitiformes as a whole and a spermatophore is placed in the female genital opening by means of the chelicerae, which are often modified for that purpose, as has been previously described. An intromittent organ is, however, widely developed in the Trombidiformes and Sarcoptiformes.

In the bdellids, the distal end of the ductus ejaculatorius projects into the invagination which forms, what may be termed, a phallocrypt; this is surrounded by a mass of muscles and it is to be presumed that the central part can be protruded as an intromittent organ. In the anystids, where setae occur inside the ductus ejaculatorius, there is strong presumptive evidence that this region is eversible. Chitinous struts may develop in the wall of the phallocrypt on which muscles, responsible for the protrusion of the central penis, become inserted. This is found in the halacarids, where a complex skeletal arrangement surrounds the copulatory organ, and in a still more complex pattern in *Trombidium* and *Allothrombium*.

The penis itself may become heavily sclerotized, as in *Cheyletus munroi* (A. M. Hughes, 1947) and the stigmaeids. Here the genital opening has become almost terminal, lying just anterior to the uropore which may be lost. The Acaridiae typically possess a chitinous protrusible organ of this type too (Plate XLVIII, fig. 17), but located in the primitive position between legs IV. The penis is frequently tubular only at its tip, as regards the sclerotized portion: the base being trough-like, with the dorsal wall thin like the ductus ejaculatorius. The Oribatei, however, have a stout tubular protrusible penis.

In those forms where the penis is protrusible, it can be entirely withdrawn and the genital opening closed by valves, which carry on their inner surface sensory organs which are frequently erroneously called genital 'suckers'.

THE FEMALE SYSTEM

The gonads show very much the same types of variation as the testes of the male, if considered throughout the group as a whole. There are, however, often striking differences in the arrangement of the gonads between the males and females of the same species; for example, in those species of

Uropodina where the anatomy is known, the testes are paired but the female has a single unpaired ovary.

The tendency for the genital rudiments to fuse posteriorly is very marked in the female mite. In ixodids, there is a horseshoe-shaped rudiment, the arms of which pass forwards as the anlage of the oviducts (Plate XLVIII, fig. 12). In the young adult, the ovary is still recognizably the posterior region of this rudiment. In the gravid female the long winding oviducts are full of eggs and the ovary is a curved structure like a bunch of grapes. The same type of horseshoe-shaped rudiment is seen in the nymphs of *Erythraeus*, *Leptus*, *Allothrombium* and *Trombidium* and the adult ovary tends to retain this general shape. The two arms of the curved ovary may fuse, too, and thus give a ring-shaped ovary in *Hydryphantes*, *Hydrodroma*, *Hydrachna*, *Lundbladia* and *Piona*. In addition, the ring-shaped ovary may become subdivided by the development of outgrowths in *Hydrachna*, so that the eggs develop in long chains. Similar subdivision of the curved ovary occurs in *Allothrombium* and *Trombidium*.

In the majority of families the ovary is a completely unpaired median structure, produced by a more extensive junction of the posterior parts of the paired rudiment of the genital system. Thus in the Parasitidae, Rhagidiidae, Penthalodidae, Eupodidae, Anystidae, Halacaridae, Bdellidae and Tetrapodili there is a single median ovary (Plate XLVIII, fig. 13).

The oviducts, which are paired in the Uropodina, Ixodidae, Rhagidiidae, Penthalodidae, Eupodidae, Cheyletidae and the Parasitengona among the Trombidiformes, and all the Sarcoptiformes, show various degrees of fusion. The Uropodina show an initial degree of fusion in the form of a short median common duct which connects the paired oviducts to the vagina; this is commonly termed the uterus. Where such a structure is present, the egg acquires its shell, as a rule, while held in the uterus prior to deposition. The Ixodidae also have a short broadened uterus, to the lateral borders of which the long oviducts are attached. The Parasitengona also have long oviducts and a median uterus, in the females of all those species which have been investigated, as do the Rhagidiidae, Penthalodidae and Eupodidae. In Bdellidae, the degree of fusion is greater, though two short oviducts may be retained, according to L. Karpelles (1893).

In the Anystidae, Halacaridae, the Tetrapodili and the Gamasides, there is an unpaired median duct leading to the vaginal invagination of the body wall. This median duct may be differentiated into a narrow oviducal region and a wider thin-walled extensible uterus, in which the eggs complete their differentiation (Plate XLVIII, fig. 16).

H. Vitzthum (1943) makes some distinction between the laelaptid type of animal where, he states, the vagina is lacking, and the parasitid in which there is a vagina as distinct from the uterus, which is separated from the oviduct by a sphincter. It would appear, however, that anatomically the Mesostigmata show two types of vaginal invagination. In the parasitid type, the invagination has become subdivided into an internal thin-walled region, the 'uterus', which receives the egg prior to oviposition, and a more external region, the 'vagina', whose walls become elaborated into a complex system of plates involved in closing the opening. In the laelaptid type, the invagination remains simple and undivided, and constitutes only what Vitzthum terms the uterus; closure of the orifice is brought about by a single posterior plate developed from the body wall.

Accessory organs in the form of glands, receptacula seminis and bursae copulatrices may also be developed. Amongst the Mesostigmata, *Liroaspina* has a muscular sac opening from the genital invagination, which is said to be a receptaculum seminis, and the Ixodidae develop a temporary outpouching of the vagina to serve the same purpose. A. D. Michael (1892a and b) described in *Gymnolaelaps*, *Cosmolaelaps* and the *Macrochelidae* a sac lying dorsal to the ovary, to which it is joined. This 'saccus foeminus' has two anterior horns which are attached to a pair of chitinous annulated tubes closed at both ends, the outer ends of these two tubes being attached to the synarthrodial membrane of leg III. He further said that, if this sac contained anything, it held male genital products. If this is so, they can only have got there by passing through the ovary, a very improbable state of affairs. This description of Michael's probably accounts for the naming of chitinous vesicles, in the neighbourhood of coxa III, receptacula seminis by A. Berlese and others. There is no proof whatever that they are in any way a functional part of the reproductive system.

A well-developed receptaculum seminis is shown by the Acaridiae. A terminal invagination of the body wall forms a small spherical chamber lined with chitin; to the lateral walls of this chamber the two ovaries are joined (Plate XLVIII, figs. 14, 15). In coition, the penis of the male is inserted into this receptaculum. The posterior opening of the receptaculum may be drawn out into a short tubular bursa copulatrix, as in *Glycyphagus*.

In the Tarsonemini, where the second nymph is the copulatory phase, in the female a duct runs back from the single median ovary and swells to form a receptaculum seminis, while its terminal part serves as a bursa copulatrix. The eggs or young, however, appear from the genital opening on the ventral side of the opisthosoma. In vivaparous forms, such as *Pyemotes*, the adult female becomes markedly physogastric and the genital duct enlarges enormously to form a uterus, in which the eggs develop.

Accessory glands as discrete structures occur as paired glands, opening into the vagina in Ixodidae, and unicellular glands discharging into the vagina have been described in Bdellidae; an unpaired accessory gland has been described in *Leptus* as opening into the uterus, and similar glands occur in the terrestrial Parasitengona. The function of such glands appears to be the lubrication of the egg during deposition. It is noticeable that in all cases the accessory glands in the females are relatively less developed than those in the males.

The Female System

The ticks possess a remarkable accessory organ in the form of Gené's organ, a frontal invagination of the gnathosoma above the cheliceral bases. This invagination is glandular and can be everted when the gnathosoma is depressed. During egg-laying the head is bent down to its fullest extent, Gené's organ everted and each egg touches it as it is layed: the secretion of the gland cells is essential to the waterproofing of the egg surface. If eggs are removed from the mite without being allowed to come into contact with the secretion, they speedily become desiccated (A. D. Lees and J. W. L. Beament, 1948).

The vaginal invagination may become variously adapted to form an ovipositor. It may be that it performs this function by simple eversion where the walls are pliant, as in the ticks generally, the Oribatei and the Bdellidae. In the latter group the vaginal wall is armed with setae and a sensory organ, which become external on its eversion. In other cases, the middle of the inversion is protrusible, as distinct from eversible, to give a long ovipositor, as in the Endeostigmata and the Halacaridae, Rhagidiidae, Penthalidae, Eupodidae, Tetranychidae (such as *Petrobia* and *Bryobia*), and the Tetrapodili. The ovipositor is sometimes lobed at its end; that of the Oribatei is trifid at the tip and each lobe carries a bristle, while in the Endeostigmata it is four-lobed. There is not recorded anything in the nature of an ovipositor in the Mesostigmata, the Anystidae or the Parasitengona, in the Trombidiformes or the Acaridiae among the Sarcoptiformes.

From this description of the reproductive system, which is of necessity brief and incomplete as regards several major groups, such as the mites in Rhagidiidae, Penthalidae and Eupodidae, and the Cheyletidae, where only the female internal anatomy is known, some general tendencies can be deduced. The paired genital rudiments, in the majority of cases, show some degree of fusion at their posterior ends which form the gonads. This occurs in both sexes, but not to the same extent in the same family or genus. The invagination of the body wall through which the genital ducts communicate with the exterior, frequently develops a protrusible median region which can become modified as a penis, or as an ovipositor. Finally, the development of accessory glands is much more extensive in the males than in the females. Concerning the functions of such glands, there is almost complete ignorance at the time of writing.

In addition to the papers mentioned in the text, the bibliography at the end of this chapter gives references to others which describe the reproductive systems of the various groups.

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CHAPTER XIII

Development

COMPARATIVELY little is known of the developmental processes of the Acari; the eggs are often difficult to obtain and present many technical problems of orientation and sectioning. In common with other arthropods, the eggs contain considerable quantities of yolk and the amount present influences the type of cleavage.

Total cleavage occurs only in the tarsonemid egg, which contains less yolk than most mite eggs; in the case of the viviparous forms, E. Reuter (1909) described the cleavage of the egg of *Siteroptes graminum* (E. Reuter, 1900) in detail. The first division is equatorial and gives two equal blastomeres, the next results in the formation of four blastomeres, though the cleavage of the first two is not always simultaneous. Finally the egg is divided into sixteen cells, in each of which lies a nucleus surrounded by cytoplasm which extends as a meshwork between the yolk granules. These nuclei, still surrounded by cytoplasm, migrate to the periphery and come to lie in a superficial layer of cytoplasm under the eggshell. Further divisions of the nuclei result in the formation of a blastoderm covering the yolk, which is not further subdivided.

During the later stages of division of these blastodermal cells, some become detached and wander back into the yolk, presumably to function as vitellophage cells. E. A. Brucker (1900) in his paper on *Pyemotes ventricosus* (G. Newport, 1850), indicated that here, too, the egg nucleus lay in the interior of the egg, which underwent total cleavage into eight blastomeres, the nuclei of which then migrated to the surface to initiate a blastoderm.

In other Trombidiformes, such as *Cheyletus eruditus* (F. von Paula Schrank, 1781), the nucleus may cleave while still in the depths of the egg, but it may migrate to the surface surrounded by some cytoplasm before cleavage begins; in neither case does the whole egg cleave. The same sort of thing occurs in *Tetranychus* (see E. Claparède, 1868, and H. Vitzthum, 1943). The result in both cases is that the yolk becomes surrounded by a superficial sheet of cytoplasm, in which lie the cleavage nuclei, and from which a meshwork of cytoplasm extends between the yolk granules. In other cases, the nucleus divides while it yet lies in the interior of the egg. For example, J. Wagner (1893) found this to be the case in *Boophilus* and A. Bonnet (1907) described the same type of cleavage in *Hyalomma*, and it also occurs in *Acarus siro*

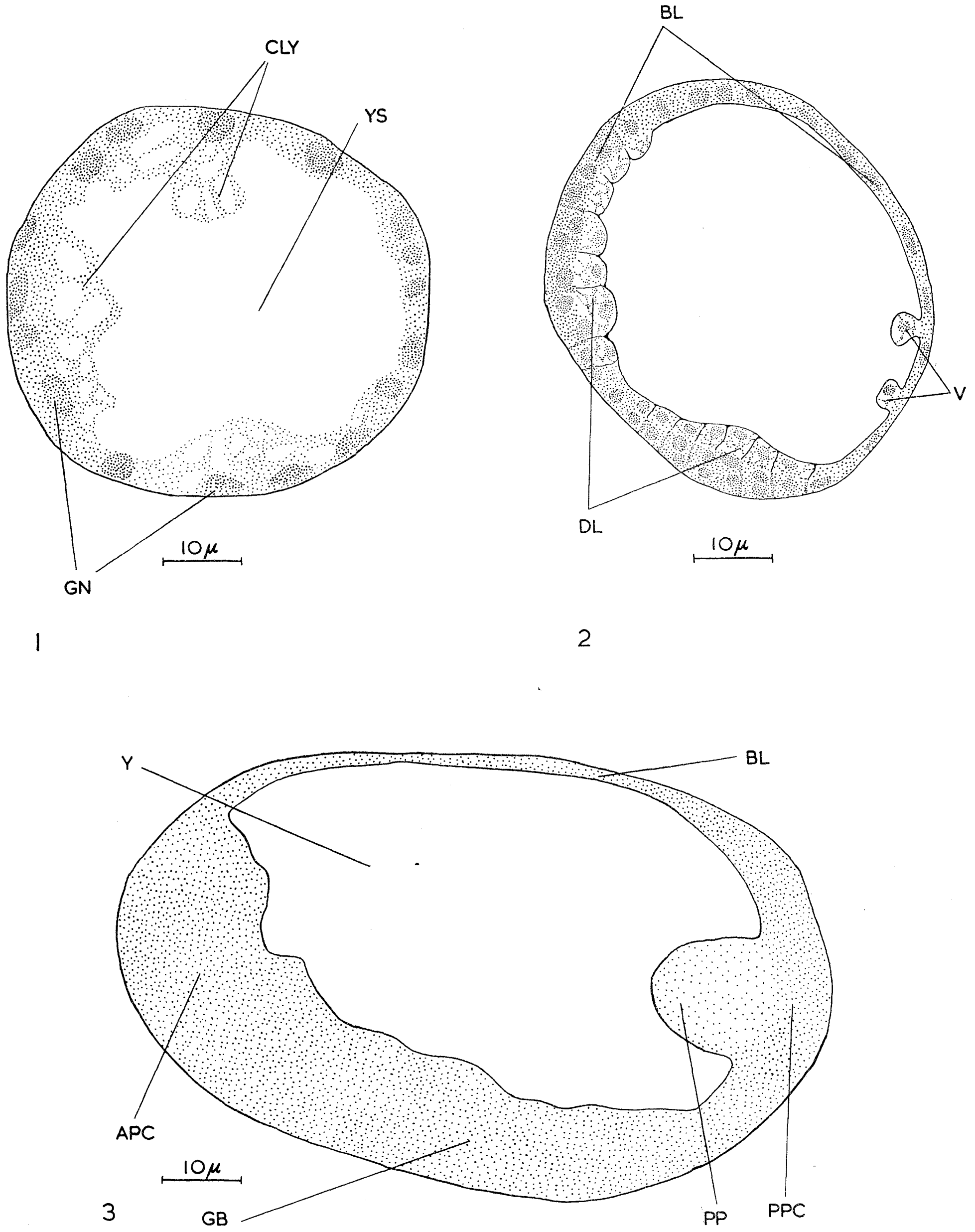


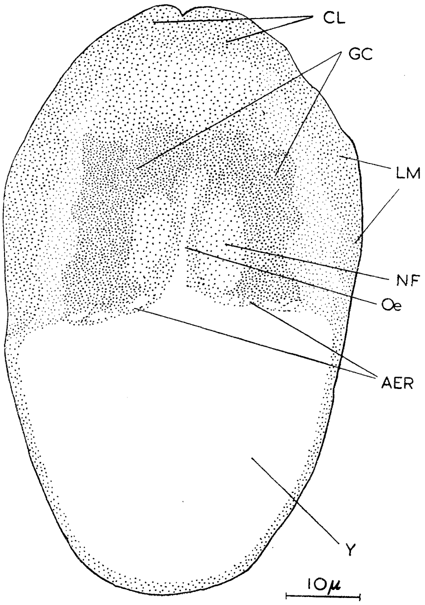
PLATE XLIX. **1.** T.S. Blastoderm of *Acarus siro* (L) (= *Tyroglyphus farinae*) (Linné). CLY cytoplasm in the yolk, GN nuclei of the blastoderm, YS yolk spherules. **2.** T.S. Blastoderm budding off vitellophage cells. BL blastoderm, DL delaminating layer, V vitellophage nuclei. **3.** L.S. to show germ band and polar caps of cells. APC anterior polar cap, BL blastoderm, GB germinal band, PP posterior proliferation, PPC posterior polar cap, Y yolk.

(Linnaeus, 1758) (= *Tyroglyphus farinae*) (T. E. Hughes, 1950). In the three cases described, all the nuclei migrate to the surface, where they continue to divide to form a blastoderm (Plate XLIX, fig. 1) covering the yolk, which is now devoid of any nuclei at all. Later, cells become detached from the blastoderm, migrate back into the yolk and act as vitellophage cells (Plate XLIX, fig. 2). Apparently, in the ticks these cells ultimately disappear; in *Acarus siro* they eventually form part of the midgut wall. V. Salensky (1869) (quoted by H. Vitzthum, 1943) described a similar type of cleavage in *Hydrachna*, and H. Bourguignon (1854) in *Sarcoptes*. It would then appear that this is the usual method of cleavage among the Acari.

The division of nuclei in the blastoderm is not uniform, but proceeds most rapidly along the future ventral surface and at the poles of the egg. There is, thus, established a germinal band with a cephalic and caudal cap of cells which extend on to the dorsal surface (Plate XLIX, fig. 3). The embryo thus exhibits a flexure with the concavity on the dorsal side. The germinal band shows a bilateral symmetry, with a median groove on the surface against the yolk. In the Ixodei and in *Acarus siro*, a proliferation of cells from the posterior end of the germinal band gives rise to the definitive endoderm of the posterior part of the midgut. In the Ixodei, further proliferations of cells lateral to this endodermal mass, are said to give rise to the mesoderm. This is not the case in *Acarus siro*, where the mesoderm arises along the whole length of the germinal band (Plate L, fig. 1).

H. Hafiz (1935) does not mention any such posterior proliferation of endoderm, but in *Cheyletus* the hind end of the alimentary canal is in any case modified. According to him, the germ band becomes divided lengthwise into a median region, the definitive mesoderm, and two lateral plates which grow to meet beneath it and constitute the latero-ventral ectoderm. Here then, as in *Acarus siro*, the mesoderm arises along the length of the germinal band. In the Ixodei, the posterior endodermal mass appears to give rise to the excretory canals and to the rectal sac, which corresponds to the post-colon or non-proctodoeal part of the rectum in the acarid mites. Hafiz described the origin of the single median excretory canal of *Cheyletus*, as arising from a median dorsal furrow of the ectoderm, which closes over and becomes separated off.

In *Acarus siro*, the stomach arises from cells in contact with the yolk on the inner surface of the anterior polar cap of the germinal band, and its lateral caeca arise from the vitellophage cells mentioned earlier. Apparently in *Cheyletus*, these vitellophage cells also give rise to the stomach wall, but the two posterior caeca arise from cells derived in some other way. According to the various accounts of development in ticks, and to W. Winkler's (1888) description of development in *Pergamasus*, and G. Piekarski's (1935) account of development in *Dermanyssus* and *Ophionyssus*, the caeca of the gut are derived from cells which come from the germinal band, but the nature of such cells and their method of origin is by no means clear. It is also a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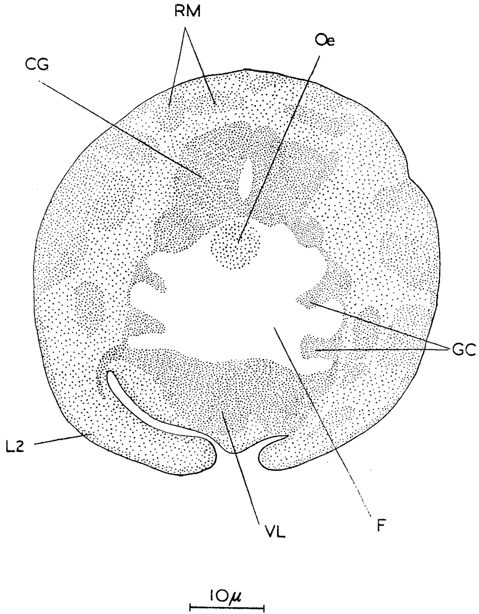
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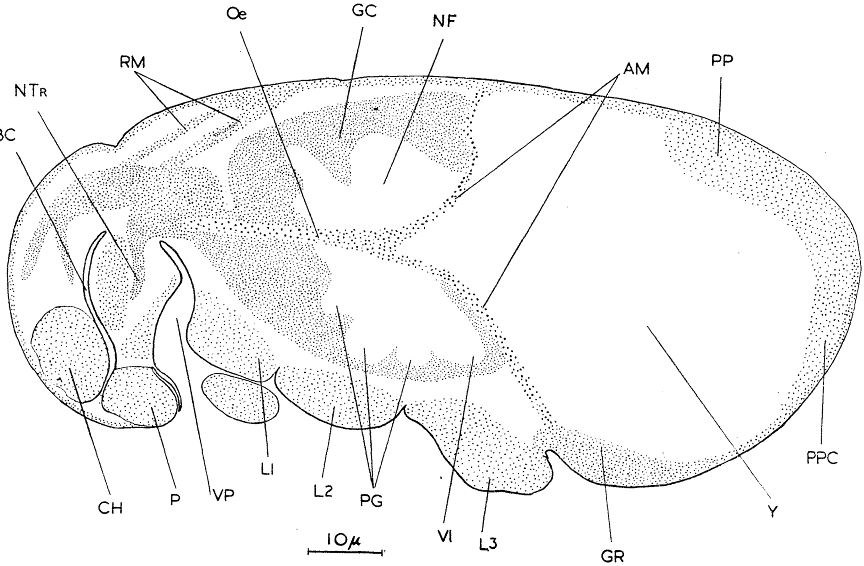
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peculiarity of these mites that at the time of hatching the gut is in any case ill-defined, rendering it still more difficult to interpret the embryological findings.

Anteriorly, an outgrowth of the stomach forms, in *Acarus siro*, an oesophagus which penetrates the ganglionated mass of the central nervous system to join the stomodoeum, which gives rise to the buccal cavity and pharynx. In the ticks paired masses of cells, derived from the cap at the animal pole, constitute the definitive central nervous system and enclose a canal outlined by nuclei; this forms the oesophagus and meets the stomodoeum. In all arachnids, the proctodoeum is relatively short and forms little more than the rectal valves. Except in the prostigmatic Trombidiformes, where the gut is blind posteriorly, the proctodoeum meets the endodermal rectal sac or post-colon of the midgut.

In all cases, the central nervous system arises as a paired mass of cells in its definitive position. There is a very early differentiation of cells into superficial ganglia corresponding to the appendages, and a pair of 'cerebral' ganglia in front of the cheliceral. Posteriorly, the suboesophageal part shows traces of ganglia which corresponded, presumably, to the opisthosomatic segments, but are now largely fused together (Plate L, fig. 2).

The segmentation of the germinal band has been described in a number of forms. In the tarsonemids, two transverse grooves early divide the band into three regions, a short posterior one, the future opisthosoma, a longer anterior region which will become the gnathosoma, and an intermediate region, the future podosoma or leg-bearing region. The podosoma is marked by transverse bands which cut off three segments at first, and later the third divides into two, to give in all four leg-bearing segments, although the larva hatches with only three pairs of legs. Before the podosoma becomes subdivided, the pedipalpal segment is marked off from the anterior region and later the cheliceral segment is defined (Plate L, fig. 3). Finally, from the anterior region, a pre-cheliceral segment is cut off. What is now left of the cephalic lobes is a small mass of cells which ultimately contribute to the central nervous system, and beneath which the stomodoeum sinks in. The chelicerae, thus, arise post-orally and later move forwards and upwards to lie above the mouth.

The opisthosoma shows traces of six segments, but it is said that there is

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PLATE L. **1.** The origin of the mesoderm in *Acarus siro* L. AER anterior endodermal rudiment, CL cephalic lobes, GC ganglion cells, LM limb mesoderm, NF nerve fibres, OE oesophagus, Y yolk. **2.** T.S. through the region of the central nervous system. CG cerebral ganglion, F nerve fibres, GC ganglion cells, L II leg II, OE oesophagus, RM muscles operating gnathosoma, VL ventral lobe. **3.** L.S. showing rudiments of appendages. AM anterior mesenteron, BC buccal cavity, CH chelicera, GC ganglion cells, GR genital rudiment, LI, LII, LIII legs I, II, III, NF nerve fibres, N TR nerve trunks of gnathosoma, OE oseophagus, PP posterior proliferation, PPC posterior polar cap, P pedipalp, PG ganglia of pedal segments, VL ventral lobe of central nervous system, VP ventral pit due to flexure, Y yolk.

no trace of a pregenital segment. These various segments, including the more pronounced ones of the prosoma, are in fact the results of localized cell division and, at any rate in *Acarus siro,* might just as well be called incipient limb buds. In *Cheyletus,* Hafiz described coelomic vesicles arising in these segments. They have not been described in other forms and, from his figures, they appear to be the spaces enclosed by contiguous limb buds and morphologically outside the embryo. The order of segmentation of the germinal band is in agreement with that observed by A. Wallstabe (1908) in spiders and scorpions, where the pedipalpal segment is cut off first and is followed by mesosomatic segments before the establishment of the cheliceral segment.

E. Sicher (1891) suggested that four pairs of limb buds arise in *Tyrophagus longior* (P. Gervais, 1844) corresponding to the four pairs of walking legs of the nymphs and adults, and that the last pair are resorbed before the growth of the pedipalps, which develop later than the limb rudiments and chelicerae. J. Wagner (1893) described the fourth pair of walking legs in *Ixodes*, and F. Supino (1895) described and figured six pairs of appendages as being simultaneously present in the development of *Acarus siro* among other mites. The last pair, he said, were well developed and segmented before resorption. E. Warren (1941) described the fourth pair of legs in the embryo of *Dermanyssus gallinae* as being segmented before resorption. A. Hafiz (1935) only found three pairs of embryonic walking legs in *Cheyletus,* and I found the same condition in *Acarus siro.*

It appears to me that the view expressed by Sicher owes its origin to the alteration of flexure which occurs during development. As the embryo develops, a groove sinks in behind the pedipalpal segment, so that a cephalic flexure bends the gnathosoma forwards and downwards (T. E. Hughes, 1950), thus bringing into ventral view the rapidly differentiating chelicerae. At the same time, the basal parts of the pedipalps are becoming involved in the formation of the gnathosoma, leaving only the palpal part visible, in end view. This might well give the impression of the development of a new pair of small outgrowths behind the chelicerae. The fact that there are still only five pairs of appendages present in all, is accounted for by the suppression of the last pair of walking legs, bringing the arrangement of the limbs into agreement with the hexapodous condition of the larva. Both Sicher and Supino worked with whole mounts and the change in flexure is not so easy to follow as in sagittal sections.

The embryo normally hatches by rupture of the eggshell and emerges as a hexapod larva. In certain cases, however, another membrane is formed inside the shell and is termed a deutovarial membrane; it is a secretion of the blastoderm and the space between it and the eggshell contains a fluid in which are amoebocytes. This membrane often arises during the stage of limb bud formation. The hydrachnellids and some terrestrial trombidiform mites develop such a membrane, but, so far as is known, it does not occur in the Parasitiformes, except among the Ixodei. It has, also, been described among some of the Sarcoptiformes. In the hydrachnellids, the membrane is smooth in *Eylais*, but in most forms it bears various protuberances; *Hydrovolzia*, for example, bears a clump of such protuberances at the cephalic pole. Among the terrestrial forms, *Allothrombium* is almost covered by them, *Cheyletus* has three groups of them and *Myobia* a single spine at the oral end. It has been suggested that these projections serve to rupture the eggshell. However, forms without them, such as *Eylais*, and mites without the membrane at all, rupture their eggshells quite satisfactorily.

While inside the eggshell, the membrane is usually wrinkled; when the shell breaks, the membrane becomes distended and assumes the functions of another shell; this stage is the Deutovum of E. Claparède (1868). The original shape of the egg is lost and the membrane is usually asymmetrically distended over the limb rudiments on the ventral side. The embryo continues its development within this membrane until it is ready to emerge as a larva. In this stage it was termed by C. Walter (1920) 'Schadonophan stadium' and by S. Hirst (1926) the 'pre larva'. There seems no point in giving this particular stage a name, since it is obviously a late embryo, which in some particular cases is freed from the eggshell while still enclosed in a secondary membrane. The rupture of the eggshell does not occur in all forms which develop the membrane. The ticks and such terrestrial forms as *Cheyletus*, and those Sarcoptiformes where the membrane is developed, complete their development to the larval stage within the eggshell.

Among the Trombidiformes, at any rate, analogous structures are found in later developmental stages, between larva and nymph, nymph and adult. The animal passes into a resting state between instars and secretes a new envelope; inside this envelope or apoderma, the reorganization to the next instar takes place. This type of development occurs in the hydrachnellids, Erythraeidae and some other families of Eleutherengona. Described by H. Henking (1882) in *Allothrombium*, the process has been investigated by C. Walter (1920) and A. Meuche (1936) in the hydrachnellids and is apparently the process which was redescribed by B. Jones (1950) as a new method of ecdysis in the mites.

The fully fed hydrachnellid larva enters into a resting state in which it becomes the 'Nymphochrysalis', with its legs fully extended. The epidermis retracts from the exoskeleton, muscle attachments are lost and extensive dedifferentiation of tissues sets in. The space beneath the old exoskeleton is filled with fluid and amoebocytes, and a new envelope is secreted over the surface of the now rounded-up and partially dedifferentiated animal. Henking thought that the amoebocytes which remain between the new and old cuticles secreted this new structure, within which takes place the redifferentiation of limb buds, now including the fourth pair of walking legs, and a new epidermis and exoskeleton. This pupa-like body within the old larval cuticle was called, by Walter, the 'Nymphanostadium'. The surface of the apoderma may be smooth and the whole thing egg-shaped, as in *Pterygosoma*.

It may, however, bulge out over the limb buds, and in *Pimeliaphilus*, there are individual outpouchings over each leg, and these outpouchings bear traces of segmentation. Finally, by rupture of this envelope and the larval cuticle, the nymph emerges.

In those forms which show this type of development, there is only one nymphal instar, and a similar resting stage occurs between it and the adult. This penultimate stage was termed by Walter the 'Teleiophanostadium' and the resting nymph the 'Teleiochrysalis'. Both the Nymphanostadium and Teleiophanostadium show great reduction of the appendages, especially those of the gnathosoma. There are, on the apodermata, a pair of curved sclerotized thickenings which, possibly, represent the chelicerae, and an invagination, which may represent the pharynx. On the posterior ventral surface, sucker-like organs develop in the same relative position, but fewer in number in the case of the nymphochrysalis, than those on the adult.

The Acaridiae, among the Sarcoptiformes, differ from the Oribatei in having two nymphal stages instead of three in the normal course of events. Certain individuals may, however, pass through an extra instar between the first nymphal and penultimate stages of the life cycle. This extra instar is, presumably, the deutonymph or second nymphal stage and it is always strongly heteromorphic and devoid of mouthparts. The deutonymph may take one of two forms: a largely immobile chrysalis-like body (Plate VIII, fig. 3), the legs being very reduced (Plate X, fig. 3) or absent altogether, or a highly motile dispersive phase provided with suckers in the region of the anus (Plate X, fig. 2) and often well-developed claws, for attachment to other animals, which act as vectors. The forms are often called the hypopus stage.

In *Glycyphagus domesticus* (Degeer, 1771) a large proportion of individuals pass through this deutonymphal stage, which is exactly similar to the Nymphochrysalis or Teleiochrysalis already discussed. The first nymph about to pass into this condition becomes immobile, the epidermis becomes detached from the exoskeleton and a new envelope is secreted, inside which the final nymphal instar differentiates. As in the trombidiform mites, the production of this chrysalis-like body is accompanied by extensive dedifferentiation of the muscles and alimentary canal, no trace of limbs remains visible externally. The tritonymph emerges by rupture of the apoderma and the first nymphal cuticle. There is, thus, no essential difference here from the conditions studied by Walter, Meuche and others in the Trombidiformes, and even closer parallels can be drawn. The apoderma of *Pimeliaphilus* shows outpouchings corresponding to legs with traces of segmentation. The deutonymphs developed by some of the feather mites among the Acaridiae, also show reduced legs; these, however, are presumably functional at some stage, since such forms are found subcutaneously in the connective tissue and there are no exuvia with them, so that they must be slightly motile at some stage of their development. Such deutonymphs are produced by *Falculifer rostratus*

(Buchholz, 1869) (Plate XVI, fig. 1) and *Kramerella*, for example. They are, as it were, intermediate between the glycyphagid type and the fully motile deutonymphs like those of the Anoetidae.

The motile deutonymph is much more heavily sclerotized than any other instar of the life cycle; it may be of infrequent occurrence as in *Acarus siro* (=*T. farinae*), or the majority of individuals may pass through this stage as in the Anoetidae, or all individuals may do so as in *Chaetodactylus*. *Acarus siro* has the peculiar power of being able to produce either type of deutonymph. Thus there can be little doubt that they are homologous stages in the life cycle and represent a nymphal instar suppressed in some individuals of some species or in whole species, genera or families. The non-motile deutonymph of *Acarus siro* (Plate X, fig. 3) possesses very reduced legs, particularly the third and fourth pairs, which is an intermediate stage towards their complete loss, as in *Glycyphagus domesticus*. It also shows the remains of a very reduced sucker plate on the opisthosoma, such sucker plates being typical of the motile type of deutonymph.

In the Trombidiformes, which, on the basis of Grandjean's work on actinochitin, are related to the Acaridiae, the nymphochrysalis and teleiochrysalis occur in the positions which could be occupied by the first and the last nymphal instars of a life cycle which included three nymphal stages.

It is said that the hypopus of the Acaridiae arises as a result of adverse conditions. In the case of *Histiostoma laboratorium* (R. Hughes, 1950), its further development is stimulated by the presence of Vitamin B_2, according to R. Perron (1954).

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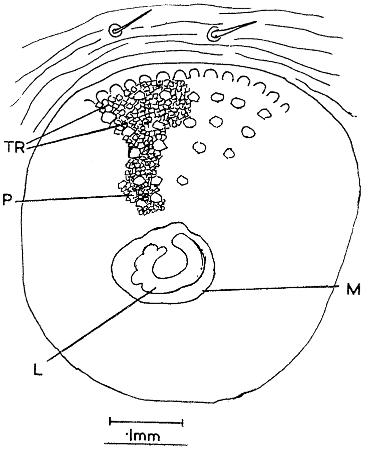
CHAPTER XIV

The Respiratory System

SPECIAL respiratory systems in the form of tracheae are not invariably present. Small lightly chitinized forms, such as the Acaridiae, respire apparently by direct diffusion through the integument. Forms with larger bodies and heavier integuments develop tracheal trunks, from which fine tracheoles arise; these tracheoles do not branch.

A. C. Oudemans (1905) propounded a system of classification based on the position of the spiracles. This was to a great extent artificial and was criticized by K. Thon (1905); for example the Uropodina were grouped with the Holothyroidea as the Parastigmata, because the stigmata lie between coxae II and III. However, parts of the nomenclature have been retained, for example the Prostigmata as part of the Trombidiformes, where the stigmata lie in front of the chelicerae. From the variety of position and nature of the spiracles within the Acari, it would appear that the tracheal system has been of independent origin within various groups. C. I. With (1904) created the suborder Notostigmata for *Opilioacarus* with its eight opisthosomatic stigmata. Here the spiracles lie in the first four opisthosomatic segments (Plate I) and the tracheae lead inwards and soon acquire a spiral thickening. The anterior trachea branches into three, one branch running forwards, one laterally and the third posteriorly; from the second and third stigmata tracheae run forwards into the podosoma and backwards into the opisthosoma, the fourth tracheae are weakly developed.

The Parasitiformes show a diversity of arrangement of the spiracles. In the ixodids they lie behind coxa IV, while in the argasids they are found more laterally and in front of coxa IV. Especially in the ixodids, the openings are covered by a complex 'stigma plate' (K. Samson, 1909) (Plate LI, fig. 1). In the ixodids the stigma plate has a crescentic slit or ostium in it, which leads into a cavity, at the base of which opens the atrium from which the tracheal trunks arise. The ostium is surrounded posteriorly and laterally by a hard sclerotized region, the macula, which anteriorly merges with a swollen lip; by apposition to the macula, this can close the ostium. Completely surrounding these structures lies the peritrematal plate, which appears porous. From the surface of the plate strands of chitin pass down through the peritrematal cavity to the floor of this space. The strands are arranged in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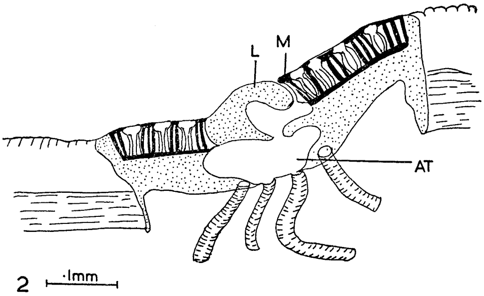
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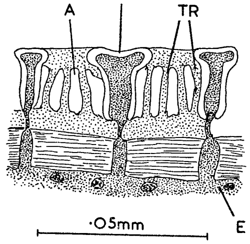
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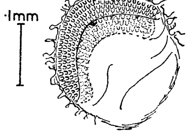
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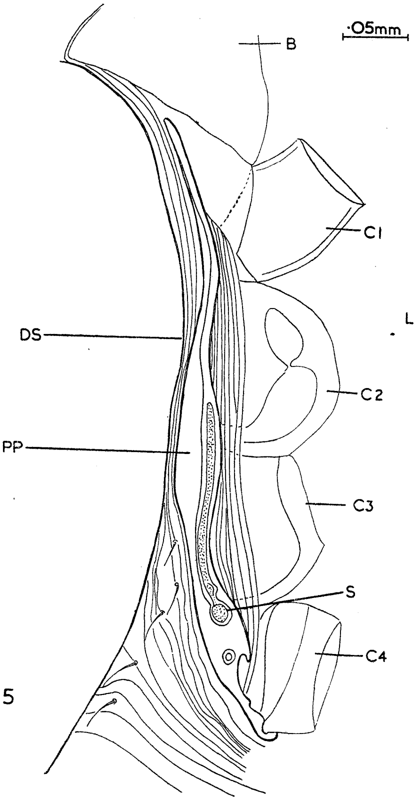
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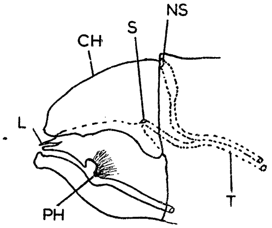
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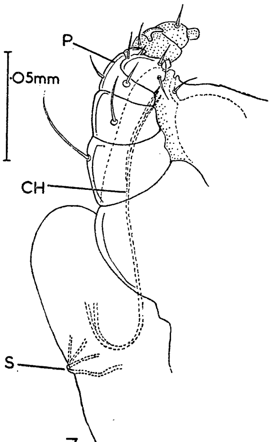
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small groups round rather larger columns, which are hollow. Processes of the epidermal cells below the floor of the peritrematal cavity, pass up into these columns and expand in the thickness of the peritrematal plate (Plate LI, figs. 2, 3). It is this arrangement of strands round the protoplasm-filled columns which gives the porose appearance to the plate in surface view. From the floor of the peritrematal cavity opens an atrium giving off the tracheal trunks. In the argasids, the structures are essentially similar, but Browning (1954) considers the plate to be imperforate. The peritrematal area is restricted to the anterior region of the spiracular plate (Plate L, fig. 4).

The so-called spiracles of larval ticks reported by D. E. Salmon and C. W. Stiles (1902), and described by L. Delpy (1938) in a number of genera are, according to J. Dinnik and F. Zumpt (1949), sense organs which are also glandular. In any case no tracheae have ever been demonstrated as arising from them, and the probability is that they are dermal glands.

In the Mesostigmata, the Gamasides have a single pair of spiracles behind coxa III and very frequently the opening is ringed by chitinous projections, giving it a ridged appearance. In the Uropodina the spiracle lies between coxae II and III; it would appear, however, that in both cases it is associated with the segment of the third leg. The air reaches the spiracle through a peritrematal canal or groove (Plate LI, fig. 5) ('Stigmakanal' of Kramer, 'Stigmarinner' of Winkler). The peritreme runs obliquely forwards and outwards to the side of the body, where there is an opening to the air, according to Vitzthum (1943); it then turns forwards and, in the Gamasides, runs straight forwards to end blindly above leg I as a rule. There may also be a projection of the peritreme behind the spiracle, e.g. *Veigaia* species. In the Uropodina, the development of the leg groove, into which the leg fits, leads to the peritreme taking a much more complex course. In the Gamasides the peritreme lies in a peritrematal plate (see section on exoskeleton, p. 99) which may fuse with the other body plates. These plates usually appear first in the deutonymph; in young stages the peritremata are shorter and more superficial.

In parasitic and myrmecophilous forms the peritremata are often shorter, as in the Spinturnicidae, where they are rotated towards the dorsal surface,

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PLATE LI. **1.** *Ixodes ricinus* (Linné); surface view of stigma plate of ♀. L lip, M macula, P clear plaques (so-called pores), TR ends of trabeculae. **2.** *Ixodes ricinus* (Linné); T.S. stigma of ♀. AT atrium, L lip, M macula **3.** *Ixodes ricinus* (Linné); detailed structure of stigma plate. A air spaces, E epidermis, P clear plaques filled with protoplasmic extension from the epidermis, TR trabeculae. **4.** *Argas persicus* (Oken); spiracular plate. **5.** *Haemogamasus pontiger* (Berlese) ♀; lateral view of peritreme. B base of gnathosoma, C1–4 coxae of legs I–IV, DS edge of dorsal shield, PP peritrematal plate, S stigma. **6.** *Retetydeus*; diagram of spiracular arrangement. CH cheliceral base, L labrum, NS neostigma at end of a neostigmatic process, PH pharynx, S stigma, T tracheal trunks. **7.** *Metatetranychus ulmi* (Koch); lateral view of gnathosoma. CH cheliceral stylet, P palp, S stigma.

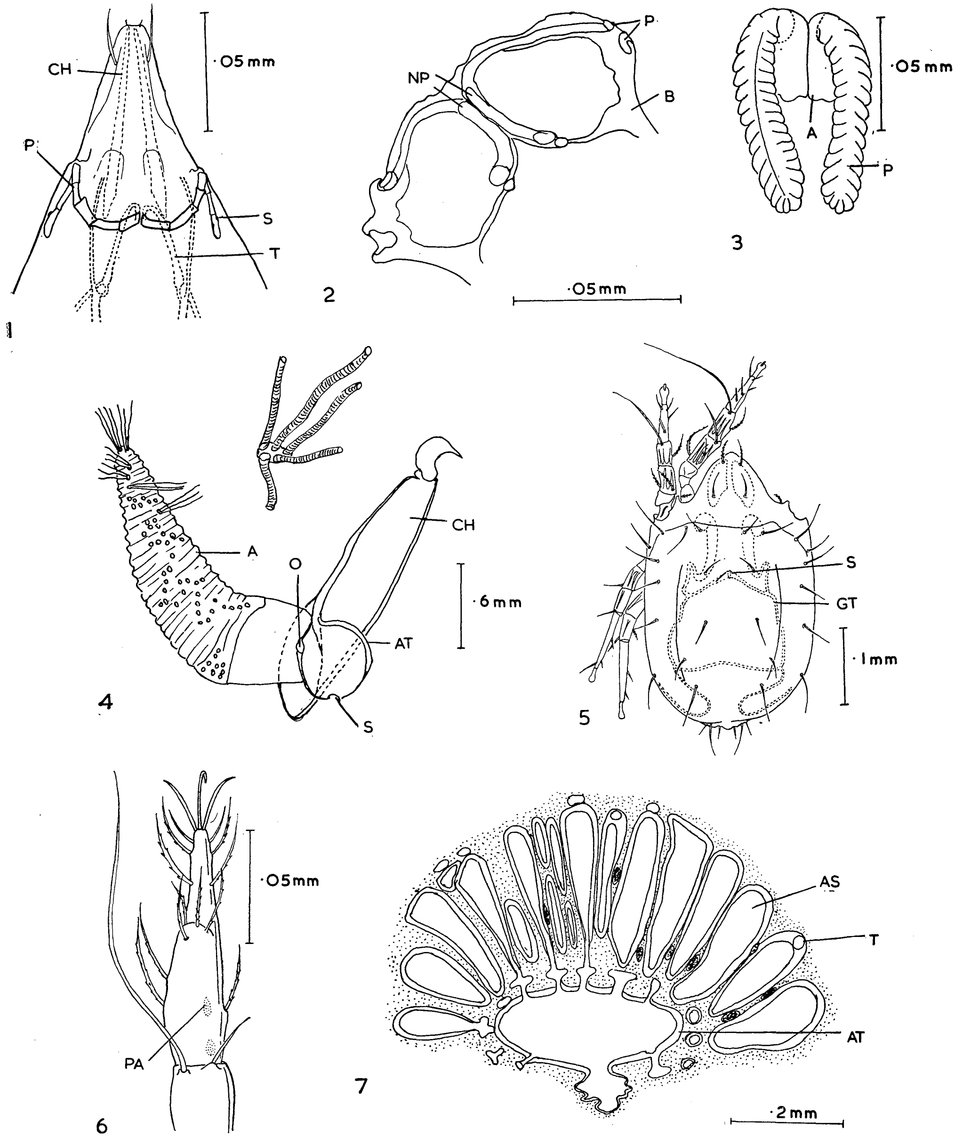

PLATE LII. **1.** *Cheyletus eruditus* (Schrank) ♀; dorsal view of rostrum to show the peritrematal canal. CH chelicerae, P peritrematal canal, S stigma, T tracheal trunk. **2.** *Cheyletus eruditus* (Schrank); T.S. through the gnathosoma. B basis capituli, P peritrematal canal, NP neostigmatal processes leading to the peritreme. **3.** *Allothrombium fuliginosum* (Hermann); the chambered peritreme. A air sacs, P the peritrematal sac. **4.** *Dinothrombium tinctorium* (Berlese); chelicera and air sacs of the left side. A air sac, AT atrium, CH chelicera, O opening from atrium to air sac, S stigma. **5.** *Gohieria fusca* (Oudemans); dorsal view. GT genital tracheae, S stigma. **6.** *Oppia nitens* (Koch); dorsal view of left tarsus I. PA porous areas. **7.** *Holothyrus gervaisi* (Thon); section of the chambered organ. AS air sac, AT atrium, T trachea.

since the mite clings tightly to the bat's wing membrane. The peritremata appear to replace, functionally, the atria of the ticks. They are usually smooth tubes, but in some cases are ridged internally, giving a chambered appearance, as in *Halarachne*. From the spiracle a short tracheal trunk runs backwards and divides into about half a dozen tracheae, and these subdivide into a large number of small tracheae, which supply the various organs. There may be a direct cross-connection between the two main trunks.

The Trombidiformes show a considerable diversity in the arrangement of their spiracles, as they do in most other respects. In the Prostigmata, F. Grandjean (1938), basing his opinion on the conditions found in *Retetydeus*, has postulated a primitive condition in which there were two pairs of spiracles, one pair opening below the cheliceral bases in the groove between the coxae, air reaching them from the upper side of the gnathosoma. A second pair lies higher up between the cheliceral bases, opening into a narrow pit or vestibule which sinks down from below the overhang of the podosoma, where it overlaps the gnathosoma (Plate LI, fig. 6). The opening of this pit, previously figured by S. Hirst and by A. C. Oudemans, was called a neostigma by Grandjean.

In *Retetydeus* from each spiracle a tracheal trunk runs backwards and soon acquires a spiral thickening. The two tracheal trunks of each side fuse above the level of leg I or leg II; from these two trunks numerous fine tracheae arise at the level of the genital opening, and supply the various organs.

In the Nicoletiellidae and Rhagidiidae, there is a single pair of spiracles opening between the cheliceral bases and having no vestibule ('Stomatostigmata' of Oudemans). In *Bdella* paired tubes lead from the spiracles' original position, as processus neostigmatici, to open at the outside of the cheliceral bases. The openings of these tubes are called neostigmata by Grandjean. In the great majority of Prostigmata, the two processus neostigmatici rise upwards close together between the cheliceral bases. They may then expand and extend on to the gnathosoma to form peritremata (Plate LII, fig. 1) which are often chambered, by the development of internal ridges as in *Cheyletus*. The peritremata may project from the body surface to form the stigma träger of Trägårdh, found in *Bryobia*, other Tetranychids and Pterygosomidae (Plate XX, fig. 1; Plate LI, fig. 7).

In the Cheyletids there has been speculation as to where the actual openings of the peritremata lie. A. Berlese originally thought that they lay middorsally on the gnathosoma; A. C. Oudemans considered they lay at the point where the peritremata bend backwards to run along the sides of the body, this being the position of the openings in forms of Prostigmata lacking the posterior extensions of the peritremata. R. Newstead and N. M. Duvall (1918) postulated, in addition to the openings at these angles, smaller openings at the posterior ends (Plate LII, fig. 1).

In discussing this point, H. Vitzthum (1943) accepts the idea of the neostigmata being at the point where the peritreme bends backwards. There are, however, within the Cheyletidae, genera and species which have peritremata curving back gently, for example in *Cheyletia*, *Cheletomorpha* (Plate IX) and *Cheyletus rabiosus* (Rodendorf, 1940); this opening is then not visible and, in my opinion, it is an optical effect due to the sharp angle formed by the peritremata in those forms which show it. There is, however, an opening near the posterior end which is small and difficult to see (Plate LII, fig. 1) (T. E. Hughes, 1958); sections of *Cheyletus munroi* (Hughes, 1947) and *Cheyletus eruditus* (Schrank, 1781) show no neostigma at the supposed position, nor do they show them in the mid-line (Plate LII, fig. 2).

The Tarsommini carry a pair of spiracles between the gnathosoma and podosoma ('Tracherstigmata' of Oudemans, 1905; 'Heterostigmata' of Berlese, 1899). E. Reuter's work (1909) on *Pediculopsis* forms a basis for the study of this group; the male is a reduced form with a non-functional gnathosoma and would seem to have lost its respiratory system, which is present in the adult female and female nymphs. The females of *Pyemotes ventricosus* (Newport, 1850) have an essentially similar system. The laterally placed spiracles lie just in front of leg I, and from them sinks inwards an atrium, which narrows down and then expands into an ovoid chamber (air sac of Reuter) and then ends in a short tubular region. From the blind end of this tubular part, fine tracheae run into the body. The number of these tracheae is variable between individuals of the same species, and between the left and right sides of an individual.

R. Newstead and H. M. Duvall (1918), in describing *Acarophenax*, refer to a second pair of spiracles lying dorsally between legs I and II, but opening into the tracheal trunks. H. Vitzthum (1943) considered the second pair to be an optical effect, due to the tracheal trunk taking an upward course at this point, and coming to lie below the dorsal integument. The tracheal trunk of each side breaks up into numerous tracheae, which form two bundles on each side. The median bundle of each side approaches its fellow and together they form an unpaired group of tracheae, distributed to the legs.

Another type of arrangement is seen in *Allothrombium*, *Trombicula* and the Erythraeidae, where the tracheal trunks come into more intimate relationships with the chelicerae. In *Allothrombium*, the chelicerae, lying side by side, have between their bases a cavity, whose upper surface is covered by a thin sheet of integument (soi-disant epistome of André, 1934), which is bounded laterally by the peritremata, and posteriorly merges with the general surface. Anteriorly the chambered peritremata (Plate LII, fig. 3) open ventrally, each into a vesicle lying in the cavity between the chelicerae (H. Vitzthum, 1930). From each vesicle a short tube joins a roomy air sac, which is proximally attached to the hollowed-out base of the chelicera and distally lies in the gnathosoma. It is continued by a tube, which ends blindly in front of the central nervous system (Plate LII, fig. 4) and whose walls are stiffened by chitinous ridges. From the posterior end of this tube, numerous perforations lead into tracheae of very small diameter and lacking spiral thickening. In *Trombicula* the peritremata have gone, the spiracle leads directly into a tracheal trunk, without the intervention of any atrial cavities or sacs. The tracheal trunk is short and divides repeatedly into two, to give rise to a moderate number of tracheae. In *Microtrombidium,* the spiracles project slightly above the dorsal surface of the cheliceral bases. From each spiracle, a conical sac narrows downwards in the space between the chelicerae, to become attached to the hollowed-out inner wall of the cheliceral base (H. Vitzthum, 1933). From this point, a tube leads back which breaks up rapidly into innumerable fine tracheae. This tube is partially surrounded by a thick chitinous sheath on its outer side, this sheath being joined to the chelicera at the point of junction with the air sac. This type seems in many ways intermediate between *Trombicula* and *Allothrombium.*

Where the chelicerae are very long and can be withdrawn deep into the body, the prostigmatic arrangements become necessarily modified. In the Erythraeidae, the tracheal trunks are attached at their anterior ends to the hollowed-out inner sides of the chelicerae, by muscles. They are spirally thickened and must be capable of considerable movement. From their points of attachment to the chelicerae, each is continued forwards by, what is presumably homologous to, a processus neostigmaticus (peritremata of Vitzthum), which in its posterior half is stiffened by rings of chitin, but in its anterior half is chambered like the prostigmatic peritreme. These tubes run forwards above the chelicerae, parallel to each other and end anteriorly, where the gnathosoma joins the propodosoma, i.e. well back between the chelicerae. The relationship of these tubes with the cheliceral sheaths is not clear, neither is the position of the spiracular openings, which are presumably the 'neostigma' of Grandjean's nomenclature. They are not conspicuous at all and are probably terminal, though A. C. Oudemans and Sig Thor (1903) consider both *Erythraeus* and *Leptus* to be without spiracles. The tracheal trunks divide into two posteriorly, but the branches are not always equal; from the hind end of each branch, a large number of smooth tracheoles arise, and they become dispersed throughout the body, but are especially numerous round the central nervous system.

In the Cunaxidae, the peritremata sink downwards between the cheliceral bases and join two short tracheal trunks, which break up into small tracheae within the gnathosoma. The halacarids carry the reduction of the tracheal system further. The peritremata are reduced to the vertical part, which lies between the cheliceral bases (tracheal ridge of Hydrachnologists); there are no tracheae joined to these remnants of the peritremata, although they are hollow. K. Viets (1936) was of the opinion that freshwater halacarids have a tracheal system in contrast to marine forms. I have been unable to find any account of their internal anatomy which would support this view.

In such hydrachnellids as retain a respiratory system, there are no peritremata and the spiracular openings (or neostigmata) project slightly above the surface of the gnathosoma, dorsal to the cheliceral bases. They lead down into a pair of elongated air sacs ('Trachealleisten' of Croneberg). These sacs have stout walls and are called air capsules. According to K. Thon (1906), in *Limnochares* two tracheal trunks leave these capsules and broaden out into two air sacs, from whose walls originate numerous fine tracheae. On the other hand, in *Hydrodroma* and *Eylais* the tracheae arise directly from the hind end of the capsules. In *Hydryphantes* the tracheal trunk leaves the mid-ventral side of the air capsule and, in addition, fine tracheae arise from the capsule itself, according to R. von Schaub (1888). H. Vitzthum considers the spiracles to be covered by a gas-permeable but waterproof membrane. *Unionicola*, *Hexatax* and *Pentatax* have no respiratory system posterior to the air capsules. There does not seem to be any obvious correlation between habitat or type of life cycle, and the presence or absence of tracheae.

The Holothyroidea are remarkable in having, what is usually regarded as, two distinct respiratory systems. Above coxa III there lies on each side of the body a slit-like spiracle (Plate II), which leads, via a short tube, into an atrium from which branch a number of short tracheal trunks; these break up terminally into tufts of tracheae. Behind leg IV is a small round pit of lighter colour than the rest of the integument, and at its bottom is a spiracle leading into a tube curved upwards in the thickness of the integument; this widens out into an atrium, the wall of which is perforated, except for a small area dorsally. This atrium is a blind sac curved slightly upwards and each perforation leads into a membranous saclet. These saclets are arranged radially round the atrium and pressed against each other, so that their walls fuse. The whole forms a ball-shaped chambered mass, which K. Thon (1905) said could be dissected out, and which extends forwards as far as the tracheal region, and backwards to the rectum. Thon described a muscular closure mechanism at the entrance of each saclet. I have sectioned these organs but can find no indication of the muscular device which Thon considered controlled the openings of the individual chambers. The whole of the region stains quite uniformly and shows no cellular structure and, in fact, appears to be chitinous (Plate LII, fig. 7). Most of the cavities are empty of anything except air, but in some there is a fine conglomeration of granular matter, and some contain homogeneous heavily staining material which is thrown out into the atrium. This chambered organ is considered to be an accessory respiratory organ. It is of interest that it is in the same position as the so-called oil vesicles of many Acaridiae. These vesicles certainly contain a substance that reduces osmic acid, but there is no evidence that they actually have anything to do with the waterproofing of the cuticle. Moreover, colour changes occur in their contents, in *Acarus siro* placed in 70 per cent alcohol, the whole vesicle becoming darker in colour. During life it is frequently pigmented brown, and it does not take up Sudan III or IV, so that it is at least conceivable that these vesicles are in some way connected with the respiration of this group, which lack tracheae. They are, moreover, somewhat larger in forms, such as *Caloglyphus* and *Rhizoglyphus*, which commonly live in habitats of low oxygen concentration. In *Glycyphagus geniculatus* (H. Vitzthum) they are bright red.

Knowledge of the respiratory system of the oribatids rests very largely on the work of A. D. Michael and F. Grandjean. The tracheal system differs from that of the other groups in lacking any spiral thickening and in being excluded from the legs.

The primitive oribatids, like Hypochthonids and Lohmanniids, do not have tracheal systems. The surface of *Hypochthonius* is covered by minute pores, which F. Grandjean (1933 and 1934a) calls micropores, and he considers that they serve a cutaneous respiratory function. Larger pores, which open individually or in small groups into pits in the integument, he calls macropores; these occur on the hysterosoma, for example in *Hermanniella*, and their function is also considered to be respiratory. Patches of such macropores occur on the legs too (Plate LII, fig. 6), and a series showing their elaboration into respiratory structures can be traced. They normally occur on the median surfaces of trochanters III and IV, and on all the femora. They can, however, occur on other leg joints as well. The area can sink in to form an air pocket ('poche tracheene' of Grandjean) or a distinct air sac, and finally, a diverticulum of the sac, forms a short trachea ('brachytrachea' of Grandjean). Such respiratory structures never extend beyond the joint of their origin.

According to A. D. Michael (1883 and 1887) the body tracheae arise from stigmata lying in the acetabula or depressions, which allow movements of the trochanters, since, with the exception of the acaronychids and palaeacarids, the coxae are fused to the ventral armour. From acetabulum I, a long trachea arises, which in *Galumna* and other higher oribatids divides into two. In the younger stages the trachea is less well developed as a rule; for example, in the larva of *Neoliodes*, there is only an air sac and brachytrachea present. The next acetabulum usually lacks a trachea and spiracle, but the third has a fairly well-developed trachea; acetabulum IV usually lacks a trachea but may have an air sac, for example, in *Hermanniella*. The sinking of the coxae into the ventral surface, results in their porous areas being incorporated too. Thus the apodeme between coxae II and III includes an air cavity, from which arises a trachea, which normally bifurcates. A. D. Michael's findings were based on the results of many dissections, rather than the appearance of the external surface and its openings, and it is my opinion that his views are possibly the more correct. In the absence of the evidence of sectioned material, it is not possible to be certain that the micro- or macropores are, in point of fact, anything other than the ducts of dermal glands, though the pits into which the macropores open, may well allow of a certain amount of cutaneous respiration.

Tracheae associated with the genital system occur in a number of groups. In the oribatids, the genus *Cosmochthonius* has two pairs of such tracheae, whose spiracles lie below the genital valves. A pair of tracheae arises from the anterior end of the genital slit, and passes laterally and then forwards to end about the level of leg II. From the middle of the genital slit, a second pair of tracheae passes backwards into the region of the rectum, curves dorsally and then returns to approximately the level of their origin. This second pair is first developed by the tritonymph; *Haplochthonius* shows a similar condition in the adult.

Among the Acaridiae, genital tracheae are developed by *Goheria*, as a pair of tracheae which I have frequently observed to contain air, although F. Grandjean (1934b) is of the opinion that they are not respiratory organs (Plate LII, fig. 5). Genital tracheae are present, too, in the bdellids among the Trombidiformes; in *Cyta*, they first appear in the protonymph, in *Trachymolgus* in the deutonymph. Typically, in the adult bdellid, each trachea arises from a spiracle in front of the anterior genital sensory organ, for example, in Spinibdellinae, and from there follows a winding course to the gnathosoma. In *Cyta* each trachea branches into two near its origin, while in *Trachymolgus* the single trachea of each side reaches only to leg II, and is broadened distally, so that it is much more like a large spatulate air sac. In the Bdellinae they are present only as short air sacs.

From this brief account of the respiratory system within the Acari it will be seen that, within the various suborders, there is a certain amount of consistency of plan as to the position of spiracles, their association with a peritrematal system and even in the course of the main tracheae. There is, however, no overall agreement and it seems certain that the respiratory system, where present, has been of independent origin within each suborder.

The physiology of respiration within the group is scarcely known. Mites occur in places where the oxygen content may be low, as in bulk stored food material in the case of many acarids. *Acarus siro* is capable of surviving very low oxygen tensions and is not adversely affected by carbon dioxide concentrations much higher than would be expected. The only available experimental data (T. E. Hughes, 1943) indicate that the respiration is a cytochrome oxidase system, in part at any rate, and that some mites can survive up to 30 per cent carbon dioxide concentrations, at normal conditions of humidity and temperature.

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CHAPTER XV

Classification

VARIOUS systems of classification have been advanced in attempts to deal systematically with the forms known at the time, e.g. J. C. Fabricius (1775), Degeer (1778); P. A. Latreille (1795) made the first attempt at what might be called a modern classification, but included pycnogonids and chelifers in the group. W. E. Leach in 1815 set up the order within its recognized limits, and P. Kramer (1877) first emphasized the systematic importance of the spiracles or stigmata in the subdivisions of the order; the system at present adopted is largely based on this. A. Berlese and A. C. Oudemans (1902 and 1906) are largely responsible for the present system, which, however, probably does not at all represent an accurate picture of phylogenetic relationships. The grouping of the Oribatei with the Acaridiae in the suborder Sarcoptiformes, for example, is probably artificial. F. Grandjean (1935) has produced evidence which indicates a closer relationship with the prostigmatic trombids, and his division of the whole order into two groups Actinochitinosi and Anactinochitinosi, on the presence or absence of birefringent cuticle in setae and cheliceral digits, seems a fundamentally sound one.

The system of classification given here is that which has emerged from the works of Berlese, Reuter, Oudemans, Thor, Willmann and others, and is the usually accepted one.

ORDER ACARI

1. S.O. Notostigmata With 1903.

The adults have 4 pairs of stigmata on the dorsal side of the opisthosoma. The coxae of the legs are freely movable; the hysterosoma is dorsally subdivided, not very clearly, into 12 'segments' of which 10 belong to the opisthosoma; the gut is simple without well-marked caeca. All these are primitive characters. The suborder contains a single family, the Opilioacaridae With 1902.

2. S.O. Holothyroidea Reuter 1909.

Unsegmented mites, often very large (*H. braueri* Thor 1906, 7 mm. long) and always heavily cuticularized, having a large dorsal shield which extends over the sides of the body and a flat ventral shield to which the coxae are movably jointed. Two pairs of stigmata are present, the first above coxa III in the membrane between the dorsal and ventral shields, and the second above and behind leg IV, in the edge of the dorsal shield. This second pair of stigmata does not communicate with tracheae, but with a system of air sacs ('chambered organ' of Thon). There are 4 malpighian tubules, whereas in other suborders, only 2 are present, if at all. Palp tarsus carries 2 claws.

3. S.O. Parasitiformes Reuter 1909.

There is a single pair of stigmata present, lying behind leg II, III or IV. The pedipalpal tarsus is usually five-jointed and without a claw. The stomach develops large caeca and there are two long malpighian tubules. This suborder embraces two very distinct groups:

DIVISION I. *Mesostigmata* Canestrini 1891.

Stigmata have peritrematal canals leading to them. The chelicerae of the male may be modified for the transmission of spermatophores, typically 2 claws on the pretarsi of legs II, III and IV. Tarsus I does not carry Haller's organ in its typical form, as seen in the ticks.

The Mesostigmata include:

1. Group Gamasides Leach 1815.

The stigmata lie behind coxae III, seldom IV and the peritremata usually reach to above coxa II, but can be very much shorter. The tritosternum has 2 blades and jugularia are usually present.

The Group Gamasides Leach 1815 includes the following families:

1. Parasitidae Oudemans 1901.
2. Veigaiaidae Oudemans 1939.
3. Neoparasitidae Oudemans 1939.
4. Digamasellidae Evans 1956.
5. Aceosejidae Baker and Wharton 1952.
6. Phytoseiidae Berlese 1916.
7. Macrochelidae Vitzthum 1930.
8. Poecilochiridae Willmann 1940.
9. Pachylaelaptidae Vitzthum 1931.
10. Laelaptidae Berlese 1892.
11. Spinturnicidae Oudemans 1901 (included by Evans 1957 in the Laelaptidae).
12. Rhodacaridae Oudemans 1902.
13. Ixodorhynchidae Ewing 1923.
14. Spelaeorhynchidae Oudemans 1902.
15. Zerconidae Berlese 1892.

2. The group Liroaspina Trägårdh 1946 included the families Liroaspidae Trägårdh 1946 and Epicriidae Berlese 1885. It was extended by Camin and Gorirossi 1955 to include the Microgyniina of Trägårdh 1942, which comprised the two families Microgyniidae Trägårdh 1942 and Microsejidae Trägårdh 1942, the major groups of Trägårdh now being regarded as super families. The common features of these families are that

the two to five sternal plates are relatively independent, and there is never a fusion between the second and third. The epigynial plate, if fully developed, bears many setae; if reduced, one pair of genital setae.

3. The Group Uropodina Kramer 1881 consists of heavily sclerotized mites with a broad short body, the stigmata being usually near leg II. The chelicerae are usually very long and extremely protrusible, but armed with a weak shear. There are no jugularia and the tritosternum has one or three blades. The epistome always extends forwards as a sharp point. The group includes the following families:

1. Prodinychidae Vitzthum 1916.
2. Phaulodinychidae Berlese 1917.
3. Trachyuropodidae Berlese 1917.
4. Urodinychidae Berlese 1917.
5. Trematuridae Berlese 1917.
6. Uropodidae Berlese 1917.

All these families, except the first, Evans 1957 grouped together as the Uropodidae.

7. Planodiscidae Sellnick 1926.
8. Coxequesomidae Sellnick 1926.
9. Circocyllibanidae Sellnick 1926.

Camin and Gorirossi include here Trägårdh's 1938 Trachytina: the Trachytidae Trägårdh 1938, Polyaspinidae Trägårdh 1941 and the Polyaspidae Berlese 1917, as well as the Diarthrophallina of Trägårdh 1946 created for the family Diarthrophallidae Trägårdh 1946.

The three groups referred to above, Gamasides, Liroaspina and Uropodina, constitute Camin and Gorirossi's Monogynaspida. The following groups they place in an assemblage they term Trigynaspida, with three primary genital plates in the female.

The group Antennophorina Camin and Gorirossi 1955, includes all the trigynaspids, except the Cercomegistidae. Thus the group covers:

(*a*) the Celaenopsina of Trägårdh 1937 with the families
    Celaenopsidae Berlese 1892,
    Diplogyniidae Trägårdh 1941,
    Euzerconidae Trägårdh 1938,
    Schizogyniidae Trägårdh 1950,
(*b*) the Fedrizziina Trägårdh 1937 with the families
    Parantennulidae Willmann 1940,
    Syngynaspidae Trägårdh 1946,
    Antennophoridae Berlese 1886,
    Paramegistidae Trägårdh 1946,
    Fedrizziidae Trägårdh 1937,

the Cercomegistidae being omitted, and (*c*) the Megisthanina Trägårdh 1946, with the single family Megisthanidae Berlese 1914. Camin and Gorirossi created a separate Group Cercomegistina for the single family

Cercomegistidae Trägårdh 1937. I. Trägårdh (1946) had grouped his 'cohorts' into two major divisions: the Agynaspida comprising the Megisthanina, the Liroaspina and Microgyniina, characterized by, what he considered to be, a primitive absence of a female genital shield; the Eugynaspida included all other 'cohorts' and was characterized by the presence of a female genital shield primarily, which if absent, had been secondarily reduced. Camin and Gorirossi's (1955) views on the two types of female genital armature seem prefereable.

DIVISION II. *Ixodides* Leach 1815, or *Metastigmata*.

Ectoparasites of vertebrates, 1 pair of stigmata without tubular peritremata. Tarsus I carries a typical Haller's organ. The chelicerae have a laterally operating shear, and the hypostome forms an elongated structure set with backwardly directed hooks, used to anchor the tick in the host's skin.

Group 1. Ixodei Dugès 1834.

The gnathosoma is visible from above. On either side behind coxa IV, there is a clearly marked perforated stigma plate. The tarsus of the pedipalpal palp is small and sunk into the ventral side of the penultimate segment. In the female, the prosoma has a sclerotized tergum, the scutum and the body behind this being soft. The whole of the dorsal surface of the male is covered by a sclerotized alloscutum. The Family Ixodidae Murray 1877 is the only family in the group.

Group 2. Nuttalliellei Vitzthum 1940.

The palpal tarsi are terminal. The scutum of the female is soft, the position of the stigmata is not known. This group is separated from the Argasides by the fact that the gnathosoma is visible from above. There is a single family: family Nuttalliellidae P. Schulze 1935.

Group 3. Argasides C. L. Koch 1844.

The gnathosoma cannot be seen from above, the stigmata near coxa III have no stigma plates covering them. The palp tarsus is terminal. The integument is leathery, there being no sclerotized plates. There is only one family: family Argasidae G. Canestrini 1890.

4. S.O. Trombidiformes Reuter 1909 or Prostigmata.

The preceding suborders constitute the Anactinochitinosi of Grandjean; the Trombidiformes and the remaining suborder the Sarcoptiformes, constitute his Actinochitinosi. This grouping of the two suborders together on the basis of their possessing birefringent elements in the exoskeleton, especially in some setae and the cheliceral tips, seems taxonomically a sound step. The possession of actinochitin would seem to be strong evidence of a closer genetic relationship between the two suborders possessing it, than exists between them and any of the suborders hitherto considered. In the Trombidiformes, the stigmata are in the region of the gnathosoma, there are 2 or 4 pseudostigmatic setae on the propodosoma dorsally. There is a single median excretory organ derived from the hind part of the gut, the stomach being blind.

The coxae are sunk into the ventral surface of the body and are therefore immovable. The chelicerae are either chelate and freely exposed dorsally, or hook-like and sliding in a trough formed of the hypostome and pedipalpal coxa, or stylet-like and sliding in a tube built up of the epistome, hypostome and pedipalpal coxae combined.

Group 1. Tarsonemini G. Canestrini and Fanzago 1877.
(=Heterostigmata Berlese 1897=Tracheostigmata Oudemans 1906)

The females alone have a tracheal system and stigma behind the pedipalps, from the protonymphal stage onwards. The club-shaped pseudostigmatic organs of the adult female probably correspond to the Trichobothria of other Trombidiformes.

1. Scutacaridae Oudemans 1916.
2. Pyemotidae Oudemans 1937.
3. Tarsonemidae Kramer 1877.
4. Podapolipodidae Oudemans 1931.

Group 2. Endeostigmata Grandjean 1937.

Mites with a soft integument often showing traces of metamerism. There are free endites to the pedipalpal appendages as in the Oribatei, this is in contrast to all other Trombidiformes. There are no visible stigmata.

1. Alycidae G. Canestrini 1891.
2. Nanorchestidae Grandjean 1937.

Group 3. Prostigmata (s. str) Kramer 1877.

The stigmata lie on or above the base of the chelicerae. The Demodicidae and Tetrapodili lack a trachael system and in many cases, the number and position of the stigmata are unknown.

GRADE I. Eleutherengona Oudemans 1909.

These mites are either parasitic throughout the life cycle or not at all. The larva is never parasitic, in contrast to other instars.

1. Nicoletiellidae G. Canestrini 1891.
2. Rhagidiidae Oudemans 1922.
3. Tydeidae Kramer 1877.
4. Ereynetidae Oudemans 1931.
5. Eupodidae C. L. Koch 1842.
6. Penthaleidae Oudemans 1931.
7. Stigmaeidae Oudemans 1931.
8. Anystidae Oudemans 1902.
9. Pterygosomidae Oudemans 1910.
10. Pseudocheylidae Oudemans 1909.
11. Teneriffiidae Sig Thor 1911.
12. Tetranychidae Donnadieu 1875.
13. Phytoptipalpidae Ewing 1922.
14. Raphignathidae Kramer 1877.
15. Cryptognathidae Oudemans 1902.
16. Spelaeognathidae Womersley 1936.
17. Cheyletidae Leach 1814.
18. Demodicidae Nicolet 1855.
19. Bdellidae Dugès 1834.
20. Cunaxidae Sig Thor 1902.
21. Caeculidae Berlese 1883.
22. Halacaridae Murray 1877.
23. Penthalodidae Sig Thor 1933.
24. Porohalacaridae Viets 1933.
25. Myobiidae Mégnin 1877.

GRADE II. Parasitengona Oudemans 1909.

The larvae of all the terrestrial forms and the majority of the aquatic forms are parasitic, the adults free-living. The exceptional family is the Calyptostomidae.

1. Trombidiidae Leach 1814.
2. Hydrovolziidae Sig Thor 1905.
3. Hydrachnidae Leach 1815.
4. Limnocharidae Kramer 1877.
5. Eylaidae Leach 1815.
6. Protziidae Viets 1926.
7. Thyasidae Sig Thor 1929.
8. Ctenothyasidae Lundblad 1936.
9. Hydryphantidae Sig Thor 1900.
10. Eupatrellidae Viets 1935.
11. Thermacaridae Sokolow 1927.
12. Hydrodromidae Viets 1936.
13. Pseudohydryphantidae Viets 1926.
14. Rutripalpidae Sokolow 1934.
15. Teutoniidae Lundblad 1927.
16. Sperchonidae Sig Thor 1900.
17. Clathrosperchonidae Lundblad 1936.
18. Plaumanniidae Lundblad 1936.
19. Anisitsiellidae Viets 1929.
20. Lebertiidae Sig Thor 1900.
21. Atractideidae Sig Thor 1902.
22. Rhynchohydracaridae Lundblad 1936.
23. Mamersopsidae Lundblad 1930.
24. Pontarachnidae Sig Thor 1929.
25. Limnesiidae Sig Thor 1900.
26. Neotorrenticolidae Lundblad 1936.
27. Tyrrelliidae Viets 1935.
28. Hygrobatidae C. L. Koch 1842.
29. Unionicolidae Oudemans 1909.
30. Feltriidae Sig Thor 1929.
31. Nautarachnidae Viets 1935.
32. Pionidae Sig Thor 1909.
33. Atractidellidae Lundblad 1936.
34. Astacocrotonidae Sig Thor 1927.
35. Axonopsidae Viets 1929.
36. Mideidae Viets 1929.
37. Mideopsidae Sig Thor 1928.
38. Mideopsellidae Lundblad 1937.
39. Acalyptonotidae Walter 1911.
40. Athienemanniidae Lundblad 1930.
41. Arrenuridae Sig Thor 1900.
42. Erythraeidae Oudemans 1902.
43. Smarididae Kramer 1878.
44. Calyptostomidae Oudemans 1923.

5. S.O. Sarcoptiformes Reuter 1909.

This group is probably not a natural one; it includes two Divisions: the Acaridiae (Acaridei would be a less confusing term) and the Oribatei. They are placed together because of similarities in appearance of the young forms of the Oribatei and the Acaridiae, although the adults differ very considerably. Moreover, the peculiarities of the female genital system of the Acaridiae would seem to separate them off, while the free endites of the Oribatid pedipalps perhaps affords a link between them and the prostigmatic Trombidiformes. The suborder is characterized by the possession of chelate chelicerae, and an absence of obvious stigmata. Usually there are a pair of vesicles opening laterally on the opisthosoma, the so-called 'oil' glands, and generally speaking, there is a groove marking off the propodosoma. This paucity of characters, especially when it is remembered that the Oribatei have 4 pairs of stigmata concealed at the leg bases, indicates the artificial nature of the group.

DIVISION I. *Acaridiae* Latreille 1802, or *Astigmata.*

No tracheae or stigmata, the gnathosoma usually visible from above. There are typically no well-marked plates developed in the exoskeleton; a weak propodosomatal plate and hysterosomatal plate can be developed, the latter being more typical in epizoic forms, such as Psoroptidae and the feather mites; there are no pseudostigmatic organs. The female genital system has a bursa copulatrix, opening at the hind end of the body. The coxae are fused to the ventral surface and form apodemata. The tarsus carries one claw or none, a pulvillus may also be present.

1. Acaridae Ewing and Nesbitt 1942 = Tyroglyphidae Donnadieu 1868.
2. Canestriniidae Berlese 1884.
3. Linobiidae Oudemans 1908.
4. Hemisarcoptidae Oudemans 1908.
5. Hyadesidae Halbert 1915.
6. Ewingidae Pearse 1929.
7. Myalgesidae Trouessart 1907.
8. Sarcoptidae Trouessart 1892 = Acaridae Oudemans 1904.
9. Psoralgidae Oudemans 1908.
10. Psoroptidae G. Canestrini 1892.
11. Pterolichidae Trouessart 1915.
12. Analgesidae Trouessart 1915.
13. Falculiferidae Oudemans 1908.
14. Dermoglyphidae Mégnin et Trouessart 1883.
15. Proctophyllodidae Mégnin et Trouessart 1883.
16. Epidermoptidae Trouessart 1892.
17. Heteropsoridae Oudemans 1908.
18. Laminosoptidae Vitzthum 1931.
19. Cytoditidae Oudemans 1908.
20. Listrophoridae G. Canestrini 1892.

[Yunker, C. E. (1955) groups the families into superfamilies and cohorts.]

DIVISION II. *Oribatei* Dugès 1833, or *Cryptostigmata*.

Heavily plated mites as adults, the young stages superficially resemble Acaridiae. The gnathosoma in the adult is usually, but not always, sunk into a camerostome. There is usually a pair of pseudostigmatic organs on the propodosoma. The tracheae open at spiracles not easily visible, being sunk into the leg acetabula. The tarsi carry one, two or three claws, which are not accompanied by a pulvillus and are set directly on to the tarsus. The pedipalpal palp has five free joints in the vast majority of forms. The endites of the pedipalps do not normally form a lower lip or labrum as in the Acaridiae. This group differs sufficiently from the Acaridiae to be separated entirely from them and treated as a separate entity. The term Cryptostigmata Berlese 1896 might well be used as a name for them.

Group 1. Aptyctima.

The propodosoma and hysterosoma are fused together or have very limited flexibility on one another.

1. Eulohmanniidae Grandjean 1931.
2. Nanhermannidae Sellnick 1924.
3. Epilohmanniidae Oudemans 1923.
4. Lohmanniidae Grandjean 1931.
5. Acaronychidae Grandjean 1932.
6. Palaeacaridae Grandjean 1932.
7. Parhypochthoniidae Grandjean 1932.
8. Hypochthoniidae Berlese 1910.
9. Trhypochthoniidae Willmann 1931.
10. Malaconothridae Berlese 1916.
11. Camisiidae Sellnick 1928.
12. Hermanniidae Sellnick 1928.
13. Neoliodidae Willmann 1931.
14. Cymbaeremaeidae Willmann 1931.
15. Belbidae Willmann 1931.
16. Eremaeidae Willmann 1931.
17. Carabodidae Willmann 1931.
18. Ameronothridae Willmann 1931.
19. Hermanniellidae Grandjean 1934.
20. Plateremaeidae Trägårdh 1931.
21. Zetorchestidae Michael 1898.
22. Liacaridae Willmann 1931.
23. Gustaviidae Willmann 1931.
24. Tenuialidae Jacot 1929.
25. Oribatulidae Jacot 1929.
26. Oripodidae Jacot 1925.
27. Oribatellidae Jacot 1925.
28. Ceratozetidae Jacot 1925.

. Scheloribatidae Grandjean 1933.
. Microzetidae Grandjean 1936.
. Haplozetidae Grandjean 1936.
. Notaspididae Oudemans 1900.
33. Pelopidae Ewing 1917.
34. Galumnidae Grandjean 1936.
35. Parakalummidae Grandjean 1936.
36. Epactozetidae Grandjean 1936.

roup 2. Ptyctima Oudemans 1906.

The propodosoma is covered by a separate shield and can be bent downards against the hysterosoma. The body surface behind leg IV is heavily ated.

1. Protoplophoridae Jacot 1923.
2. Mesoplophoridae Berlese 1916.
3. Phthiracaridae Perty 1841.

F. Grandjean 1954 gives the following provisional classification of the ribatei, based partly on nymphal, as well as adult characters.

. Palaeacaroidea
    Archeonothridae
    Palaeacaridae
    Ctenacaridae
2. Enarthronota
    Hypochthoniidae
    Eniochthoniidae
    Brachychthoniidae
    Cosmochthoniidae
    Heterochthoniidae
    Sphaerochthoniidae
    Protoplophoridae
    Atopochthoniidae
    Pterochthoniidae
3. Lohmanniidae
4. Eulohmanniidae
5. Parahypochthoniidae
6. Mesoplophoridae
7. Phthiracaroidea
    Oribotritiidae
    Pseudotritiidae
    Phthiracaridae
8. Epilohmanniidae
9. Perlohmanniidae
0. Nothroidea
    Hermanniidae
    Nothridae
    Camisiidae
    Nanhermanniidae
    Trhypochthoniidae
    Malaconothridae
1. Circumdehiscentiae (higher Oribatei)
    Hermanniellidae
    Liodidae
    Gymnodamaeidae
    Belbiae
    Cepheidae
    Microzetidae
    Gustaviidae
    Zetochrestidae
    Ceratoppiidae
    Liacaridae
    Carabodidae
    Oppiidae
    Suctobelbidae
    Thryisomidae
    Hydrozetidae
    Limnozetidae
    Tectocepheidae
    Ameronothridae
    Cymbaeremaeidae
    Micreremidae
    Licneremaeidae
    Scutovertexidae
    Passalozetidae
    Archipteriidae
    Tegoribatidae
    Euzetidae
    Pelopsidae
    Oribatellidae
    Ceratozetidae
    Mycobatidae
    Chamobatidae
    Galumnidae
    Parakalumnidae
    Haplozetidae
    Scheloribatidae
    Oribatulidae
    Zetomotrichidae

6. S.O. Tetrapodili Bremi 1872

(these are best considered as a group of the Trombidiformes).

These mites are all small and parasitic on plants, often causing gall formation. The exoskeleton is ringed with grooves, which gives a false appearance of segmentation to the body. There are never more than two pairs of legs. The gut is simple without stomach caeca.

1. Eriophyidae Nalepa 1898.
2. Phyllocoptidae Nalepa 1898 (now included in the Eriophyidae as a subfamily by H. H. Keifer (1942)).

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