

STUDIES ON THE BRITISH DERMANYSIDAE
(ACARI : MESOSTIGMATA)
PART I EXTERNAL MORPHOLOGY



BY

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SYNOPSIS

The external morphology of the British representatives of the acarine family Dermanyssidae is reviewed with particular reference to the modifications in morphology associated with the adoption of a parasitic mode of life.

INTRODUCTION

THE family Dermanyssidae (including Laelapidae, Haemogamasidae and Macronyssidae) comprises free-living species inhabiting soil and humus as well as forms displaying various degrees of association with vertebrate and invertebrate animals. Associations with other animals range from predatory species living in the nests of insects, birds and mammals to facultative and obligatory ectoparasites of the nesting animal. At present the classification of the Dermanyssidae is largely based on the study of the parasitic forms whose economic importance as vectors or potential vectors of disease has overshadowed the taxonomic importance of their free-living relatives. Recent key works on the parasitic Dermanyssidae have been produced by Bregetova (1956), Strandtmann & Wharton (1958) and by Zumpt & Till (1961).

The British representatives of this family number about 75 species and these exhibit a wide range of structural and biological adaptations to the variety of ecological niches they have successfully colonized. This first contribution to a taxonomic revision of the British Dermanyssidae deals with the external morphology of the group.

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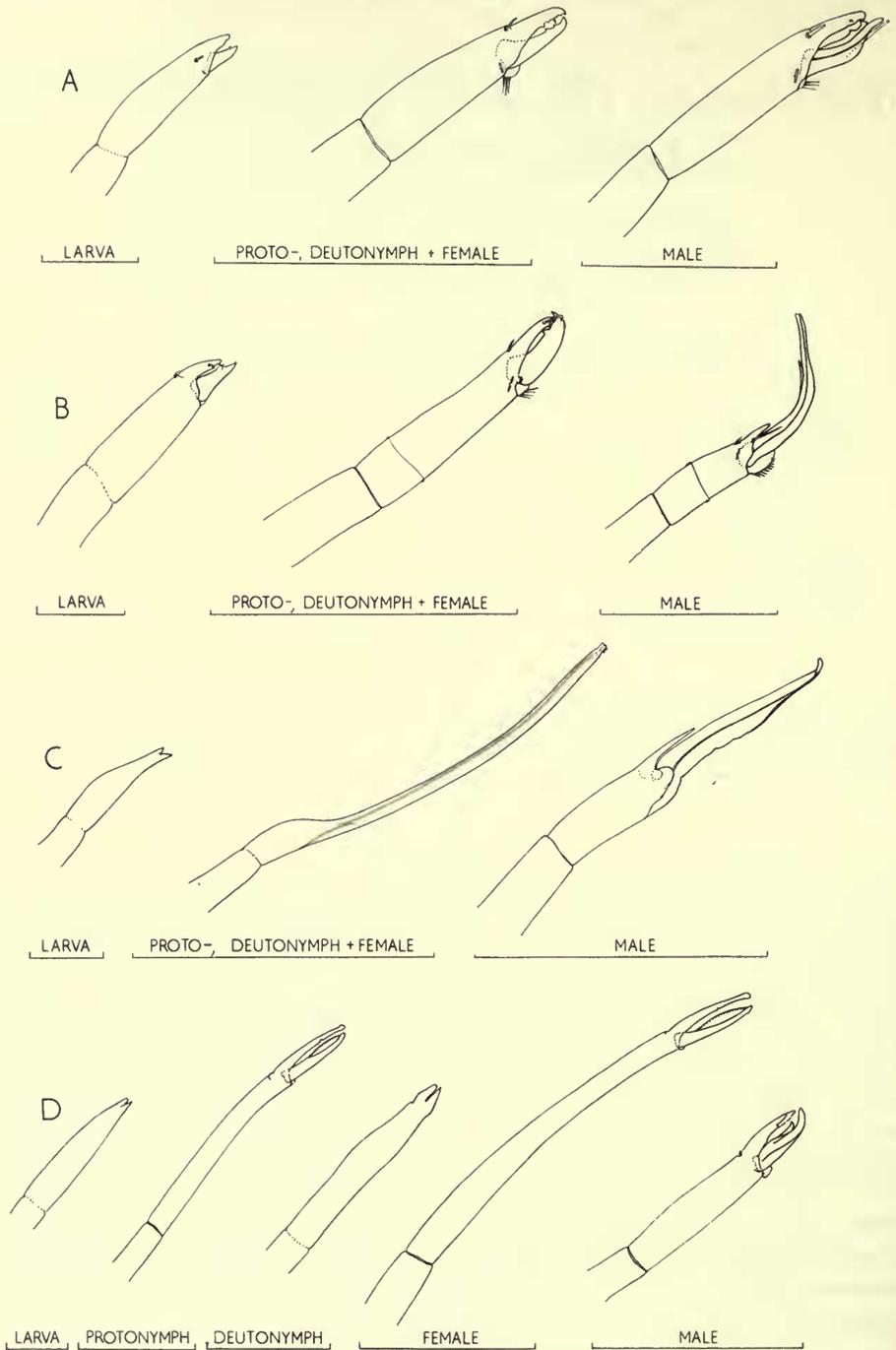


FIG. 1. Chelicerae of the immature and adult stages of : A. *Holostaspis vitzthumi* (Womersley) ; B. *Laelaps echidnina* Berlese ; C. *Dermanyssus gallinae* (Degeer) ; D. *Ornithonyssus bacoti* (Hirst).

EXTERNAL MORPHOLOGY

Gnathosoma

Chelicerae: The chelicerae, paired pre-oral trophic appendages, of the Dermanyssidae are three segmented (Text-fig. 1). The short proximal segment to which the cheliceral retractor muscles are attached is articulated to the longer second segment by a condylar process located on its internal (paraxial) face. Distally the second segment forms the fixed digit (*f. d.*) of the chelicera and the third segment or movable digit (*m. d.*) is articulated ventrally to the fixed digit by arthrodistal membrane and two condyles developed on the limb of the second segment which engage acetabula on the movable digit (Text-fig. 2E). The movable digit is operated by a pair of opposed muscles originating within the proximal segment and connected to the digit by a dorsal levator tendon and a ventral depressor tendon. The arthrodistal membrane at the base of the movable digit is usually produced into setiform processes.

In the free-living and the majority of the nest-inhabiting members of the family, the cheliceral shaft is of approximately equal diameter throughout its length and the ratio of the length of the first to the second segment is in the region of 1 : 1.5-3.5. The external (antiaxial) face of the chelicera bears a dorsal seta (*d. s.*), a lateral fissure (*lat. l. f.*) and a simple *pilus dentilis* (*p. d.*)¹, the latter being situated on the distal half of the fixed digit (Text-fig. 2A-B). A lyriform fissure (*d. l. f.*) associated with the dorsal seta occurs on the dorsal surface of the second segment at the origin of the fixed digit. In some forms this fissure extends to the lateral face of the segment. The fixed digit is provided with a variable number of teeth, but the movable digit in the nymphae and females is normally bidentate. In the male the movable digit, usually unidentate, carries on its external face a grooved spermadactyl (*sp.*). This process shows considerable diversity in form but its distal portion is invariably free (Text-fig. 2F-G). At the larval stage the chelicerae are well-developed and have a full complement of setae and fissures. The digits are weaker and less strongly dentate than in subsequent developmental stages since this stage is non-feeding (Text-fig. 1A). The chelicerae of the nymphae and female are essentially similar in form, the only differences being in their relative sizes and occasionally in the number of teeth on the fixed digit.

This basic type of chelicera, encountered in the polyphagous free-living forms, has become variously adapted for specialized feeding in the facultative and obligatory parasitic species of the family. Modifications are evident in the form of the cheliceral shafts, the digits and associated structures, and in the ontogenetic development of the chelicerae.

The form of the shaft (first and second segments) in the larva, nymphae and female of the facultative parasites, for example *Androlaelaps*, *Laelaps* and *Haemogamasus*, is fundamentally the same as in the free-living forms although in the males there is a tendency for a shortening of the second segment (Text-fig. 1B). In obligatory parasites the relative lengths of the first and second segments of the chelicera in the

¹ Van der Hammen (1964) has suggested replacing the term *pilus dentilis* by "cheliseta" since the former is "too long". To change such a well-established and universally accepted term for such a trivial reason is unwarranted!

non-feeding larva are similar to those in the same developmental stage of the free-living forms and facultative parasites but the distal half of the second segment generally shows some attenuation. The feeding nymphae and female, with few

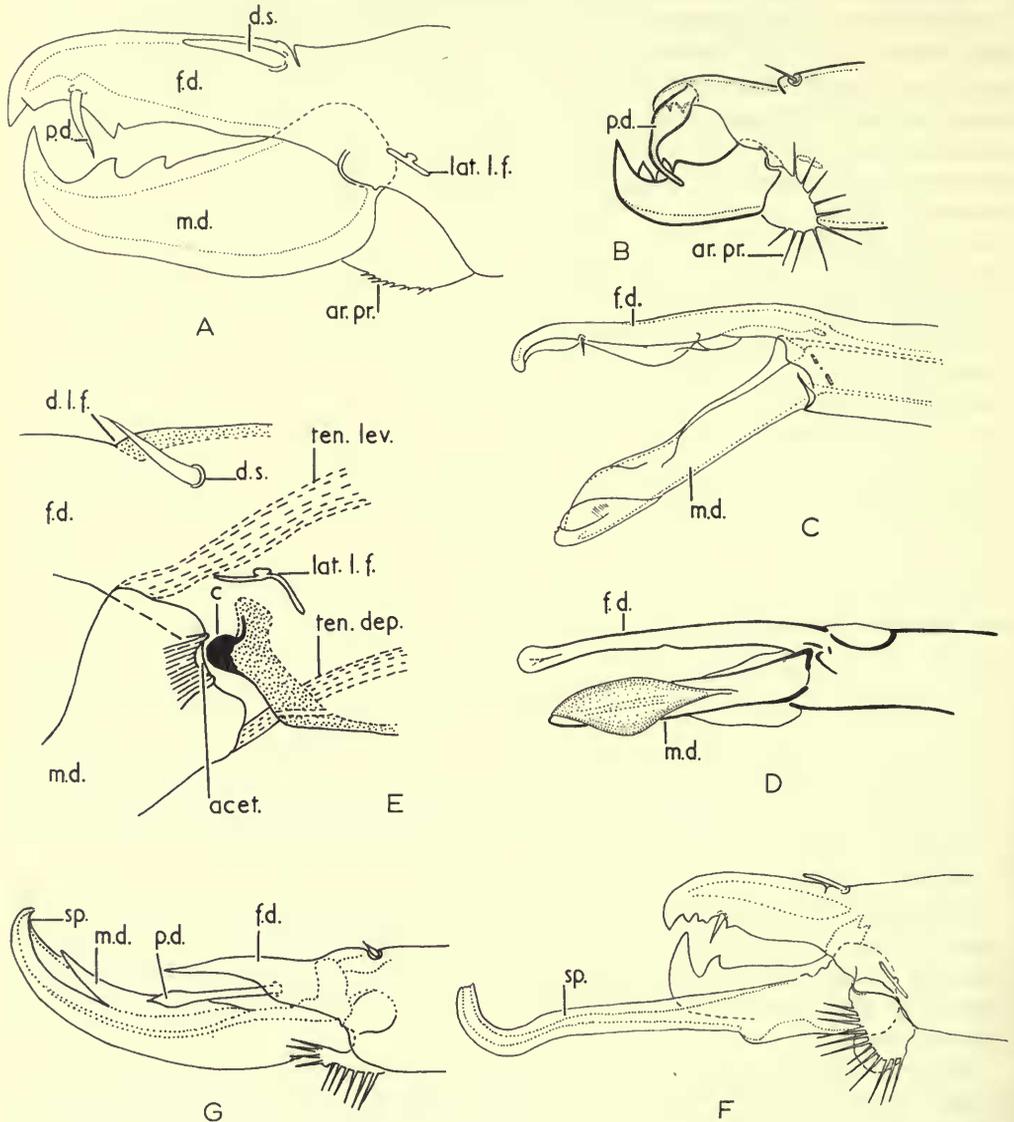


FIG. 2. Cheliceral digits of certain Dermanyssidae. A. *Eulaelaps stabularis* (Koch) female; B. *Androlaelaps fahrenheitzi* (Berlese) female; C. *Haemogamasus hirsutus* Berlese female; D. *Ornithonyssus bacoti* (Hirst) female; E. condylar articulation of the movable digit in a free-living Gamasine mite; F. *Hypoaspis (H.) krameri* (Canestrini) male; G. *Laelaps hilaris* Koch male.

exceptions, show a distinct lengthening of the second segment in relation to the first. Both nymphae and female of *Dermanyssus* have the second segment enormously elongated so that the chelicerae resemble stylets (Text-fig. 1C). A less spectacular elongation of this segment is also evident in the feeding stages of the Macronyssinae (Text-fig. 1D) in which the mesial surface of the segment is distinctly flattened. An interesting phenomenon in this group is the marked difference between the chelicerae of the feeding protonymph and the non-feeding deutonymph, the chelicerae of the latter reverting to the form in the non-feeding larva. Two main types of male chelicerae are present, one (*Dermanyssus*) in which the second segment is not more than twice the length of the first and the other (*Ornithonyssus*) in which the second segment is about three to four times the length of the first. This difference in the length of the second segment appears to be related to the length of the spermadactyl (see below).

The modifications of the digits and their associated structures are diverse and often complex. With few exceptions, the digits of the larva, nymphae and female of the facultative parasites retain their chelate-dentate form, the major specialization in this group being apparent in the degree of development and form of the setae, fissures and arthrodistal processes. The short slender *pilus dentilis* of the free-living forms is often enlarged and inflated as in post-larval stages of certain species of *Androlaelaps* (Text-fig. 2B), *Laelaps* and *Haemogamasus*. The dorsal seta is usually relatively short and simple, but may be lacking in certain *Androlaelaps*. In *Haemogamasus*, on the other hand, this seta is greatly enlarged and may be simple or spatulate. It tends to migrate ventrally onto the external face of the chelicera and in the male of *H. horridus* (Berlese) it has moved anteriorly onto the fixed digit. The arthrodistal processes may be simple and arranged in the form of a "coronet" as in the free-living species, but in certain members of the *Androlaelaps-Laelaps* complex there is a tendency for a reduction in the number of the processes accompanied by their elongation, for example in *Hyperlaelaps amphibia* Zachvatkin. Lyriform fissures are present in the normal position. Exceptions to the chelate-dentate form of the chelicerae occur in the nymphae and females of some species of *Androlaelaps* and *Haemogamasus*. In the ethiopian species *Androlaelaps cryptomia* (Radford), for example, the fixed digit is reduced to a weakly sclerotized, terminally unhooked process bearing a long *pilus dentilis*, whilst the movable digit is bipartite, comprising a strongly sclerotized, edentate, hooked digit with a less strongly sclerotized, dentate, digitiform process arising externally from its basal portion in much the same way as a spermadactyl on a male chelicera. Both digits in *Haemogamasus hirsutus* Berlese, on the other hand, are somewhat elongated and edentate, and the dorsal seta is lacking (Text-fig. 2C).

Two main types of chelicerae are present in the males of the facultative parasites. The least specialized form occurs in *Eulaelaps* and *Haemogamasus* in which the movable digit, usually unidentate, retains its hooked form and the grooved spermadactyl, free distally, rarely extends beyond the tip of the digit by more than one-third the length of the digit. Arthrodistal processes are reduced or lacking on the chelicerae of this sex. Considerably greater specialization is apparent in the second type which occurs in males of the *Androlaelaps-Laelaps* complex. These are characterized by

the reduction of the fixed digit to a relatively slender, distally tapering process bearing the enlarged *pilus dentilis* and by the size of the grooved spermadactyl which forms the greater part of the movable article of the chelicera (Text-fig. 2G). The typical form of the movable digit is lost although, in most species, its distal portion is recognizable as a slender pointed process protruding dorsally from the grooved spermadactyl. As in the *Haemogamasus*-type the arthrodistal processes often show marked reduction in number and, rarely, the dorsal seta is lost.

As one would expect, the obligatory parasites feeding on the tissue fluids of their hosts show the highest degree of specialization of the chelicerae. The digits in the larva are small, subtriangular, edentate and functionless as trophic appendages. They lack setae and, apparently, fissures (Text-figs. 1C and D). With the exception of the Dermanyssinae, in which the digits are minute but dentate (Text-fig. 1C), the digits of the feeding nymphs and females are very weakly dentate or edentate and lose the hooked form typical of the polyphagous species. In the Macronyssinae, the fixed digit is generally slender and often terminates in a rounded hyaline boss whereas the movable article has an elliptical trough formed by cuticular outgrowths of the digit along its dorsal surface, the normal dentate surface of an unmodified chelicera (Text-fig. 2D). Both the digits are dorsoventrally flattened and grooved along their "cutting" faces in *Hirstionyssus*. We have been unable to see a *pilus dentilis* on the fixed digit although, in some species, a small depression occurs on the digit at the normal site of this sensory seta. The dorsal seta is reduced to a microseta or is lacking. There are no distinct arthrodistal processes. The forms of the chelicerae in the males are comparable to the two types described for the facultative parasites. All macronyssines and *Hirstionyssus* have a relatively short spermadactyl showing varying degrees of fusion with the digit. In the dermanyssines, however, the fixed digit is strongly reduced and it is difficult to distinguish the movable digit from the proximal body of the elongated spermadactyl (Text-fig. 1C). Unlike the facultative parasites, the chelicerae of the males of the obligatory parasites lack a *pilus dentilis* and the dorsal seta, as in the female, is present as a microseta or is lost. The shortening of the second cheliceral segment in the forms with an extremely long spermadactyl (see above) has the effect of strengthening the shaft to counteract the increased weight of the movable digit and its appendage.

In those obligatory parasites (Dermanyssinae and *Hirstionyssus*) in which the two nymphal stages and the female are active and feeding the form of the digits is determined at the protonymphal stage and is retained by the deutonymph and female. In the macronyssines in which the deutonymph is relatively inactive and non-feeding, the specialized functional digits of the protonymph are not developed in the deutonymph whose chelicerae revert to the larval form. At the succeeding feeding female stage, however, the chelicerae resemble those of the protonymph.

Tectum capituli: The tectum², which forms the roof of the gnathosoma and

² At present the term *tectum* is also used to describe a shelf-like structure occurring below the vertex and forming the roof of the camerostome in some Uropodina. It is not a gnathosomal structure and appears to provide a supporting (and protective) shelf for the first pair of legs when the animal is at rest. As such, and to avoid confusion, it seems appropriate to re-name this structure *pedotectum-I* in the Uropodina.

overlies the chelicerae (Text-figs. 3, 4B and D), shows considerable variety in its degree of development and in the form of its anterior margin. In the free-living species and facultative parasites, with the exception of the *Eulaelaps-Haemogamasus* group, the anterior margin is smooth (*Melittiphis*), basically trispinate (*Pseudolaelaps*, Text-fig. 3B) or multidenticulate (*Hypoaspis*, Text-fig. 3A), and does not extend anteriorly to completely cover the hypostome and its associated structures (Text-fig. 4B). Members of the *Eulaelaps-Haemogamasus* group, however, have the free margin of the tectum

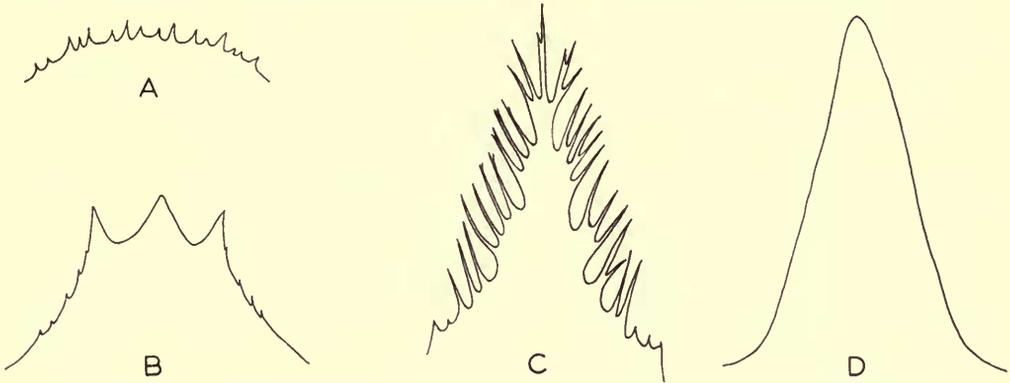


FIG. 3. Tectum capituli of: A. *Hypoaspis (Gaeolaelaps) praesternalis* Willmann; B. *Pseudolaelaps doderoi* (Berlese); C. *Haemogamasus ambulans* (Thorell); D. *Dermanyssus gallinae* (Degeer).

strongly fimbriated and considerably elongated so that it entirely covers the hypostome from above (Text-fig. 3C, 4D). This anterior extension of the tectum is also characteristic of the obligatory parasites (Dermanyssinae, Macronyssinae) and takes the form of a triangular lobe, smooth or denticulate at its tip, whose down-turned lateral margins overlap the lateral walls of a trough formed by the modified internal and external malae of the hypostome (Text-figs. 3D and 5C).

Basis capituli and hypostome: The *basis capituli* is formed mainly by the enlarged coxae of the pedipalps which are separated mid-ventrally by a shallow capitular groove whose floor is considered to represent the sternite of the pedipalpal segment (the *deutosternum*). A longitudinal series of antrose *deutosternal denticles* (*d. d.*) occurs on the floor of the capitular groove and the number and form of the denticles show little intraspecific variation (Text-figs. 4-5). Each member of the longitudinal series of denticles may be simple (one denticle) or comprise two to eight denticles arranged in a transverse row (Text-figs. 4-5). In free-living forms the larva appears to have a full longitudinal complement of denticles, but the number of denticles in each transverse row may vary in the succeeding developmental stages. Larvae of obligatory parasites, however, have the deutosternal denticles markedly reduced or absent and it is at the protonymphal stage that the full complement is determined. The number of denticles comprising the longitudinal series appears to be characteristic for certain groups of genera of the Dermanyssidae. Free-living forms and

members of the *Androlaelaps-Laelaps* groups have six, rarely seven, transverse rows of denticles/longitudinal series (Text-fig. 4A) with the number of denticles in the

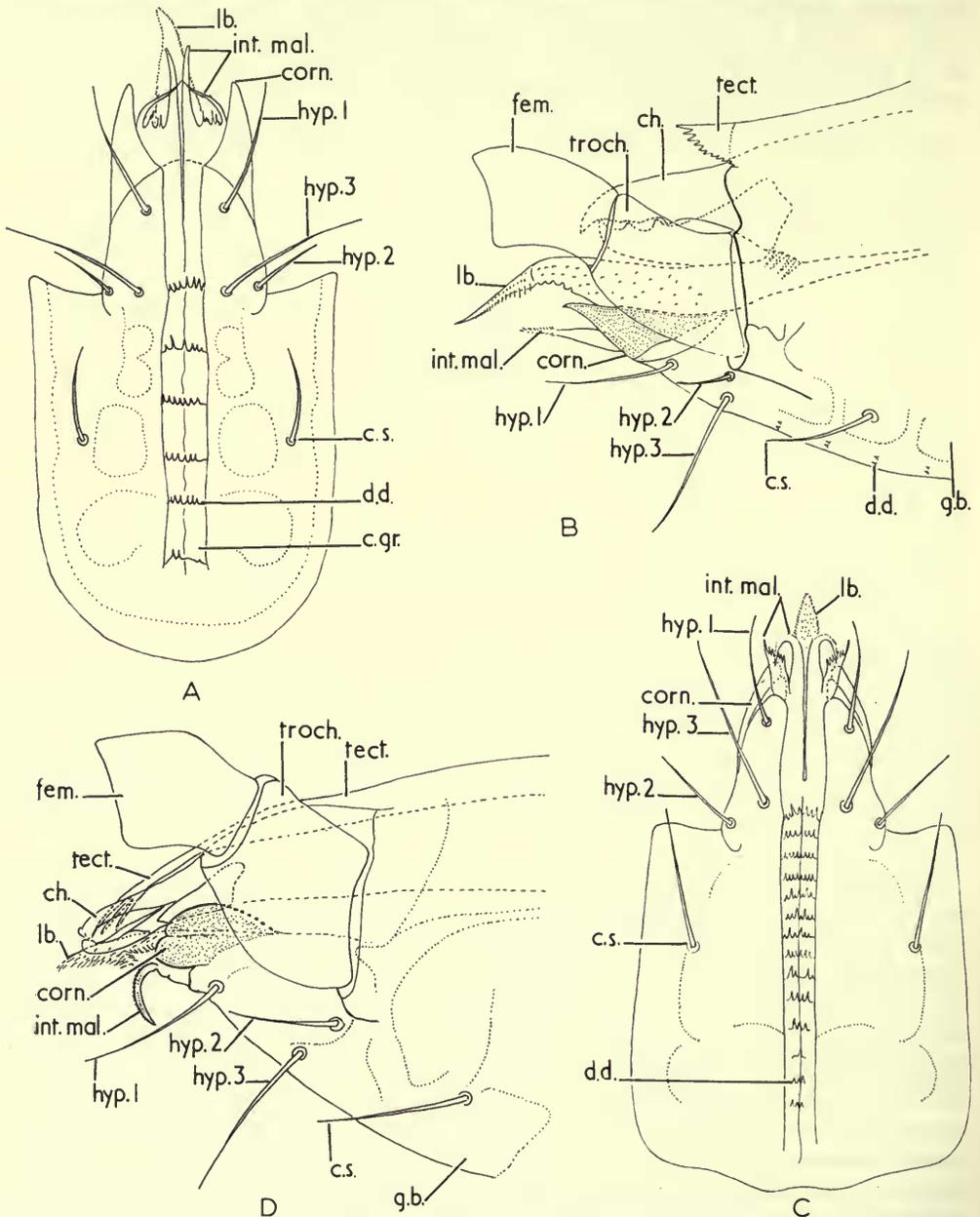


FIG. 4. A-B. Gnathosoma of female of *Cosmolaelaps claviger* (Berlese), A. ventral and B. lateral view. C-D. Gnathosoma of female of *Haemogamasus hirsutus* Berlese, C. ventral and D. lateral view.

transverse rows ranging from two to eight, the lower numbers being present in the facultative parasites of the *Androlaelaps-Laelaps* group. On the other hand, members of the facultatively parasitic *Eulaelaps-Haemogamasus* group always have more than seven transverse rows of denticles/longitudinal series, the usual number ranging between nine and fourteen (Text-fig. 4C). In the obligatory parasites the floor of the capitular groove contains about nine or ten small triangular denticles in a single longitudinal series; rarely, two denticles form a transverse row (Text-fig. 5). A similar longitudinal series of denticles occurs in *Melittiphis* and *Myonyssus* whose feeding habits are uncertain, but in these genera the corniculi (external malae) and the chelicerae do not show the marked modifications of the obligatory parasites (Dermanyssinae and Macronyssinae).

The *basis capituli* bears ventrally a pair of setae, the capitular setae, which first appear at the protonymphal stage (Evans, 1957).

The *hypostome*, divided mid-ventrally by the anterior extension of the capitular groove, bears three pairs of setae (*hyp.* 1, 2, 3) in the nymphae and adults. Setae *hyp.* 2 and 3 form a more or less transverse row of four setae (Text-figs. 4-5). At the larval stage only two pairs of setae are present on the hypostome (*hyp.* 1 and 2); the third pair (*hyp.* 3) first appears at the protonymphal stage. In the free-living forms and in the majority of the facultative parasites the hypostome bears anterolaterally a pair of large, horn-like structures (hypertrophied setae) termed *corniculi* (or *external malae*). The floor of the capitular groove in the region of the hypostome is considered by some acarologists to represent the sternite of the cheliceral segment and is referred to as the *protosternum*. It is divided into two parts by a longitudinal suture and anteriorly each part is produced into variously shaped process (Text-fig. 4) termed *internal malae* (or hypostomal processes).

The main external features of the hypostome in the obligatory parasites are its marked elongation (Text-figs. 5B, C and D) and the modification of the internal malae and corniculi to form a pre-oral trough. The corniculi, analogous structures to the *rutella* of the Cryptostigmata, already show certain deviations from their normal horn-like form in the facultative parasite *Haemogamasus hirsutus* Berlese, where they become modified into flat lobe-like structures (Text-figs. 4C and D). Further specialization of the corniculi results in the complex flange-like structures forming the lateral walls of the hypostomal trough in the obligatory parasites. The ventral floor of this trough in the protonymph and female is formed by the fusion of the internal malae along the longitudinal suture on the floor of the capitular groove (Text-fig. 5B). Owing to the complex nature of the internal malae and corniculi in these specialized parasitic forms, it is difficult to determine their homology with those in the free-living forms. At the non-feeding deutonymphal stage of *Ornithonyssus bacoti* (Hirst) fusion of the internal malae does not occur and although the internal malae and the corniculi are less complex than in the feeding stages it is still difficult to elucidate their homology (Text-fig. 5A). Two interpretations are possible, namely, one in which the short, pointed, internal process is homologous with the internal malae of the free-living forms and the two outer processes with the corniculus, and the second in which only the external article is homologous with the corniculus, the internal pair being

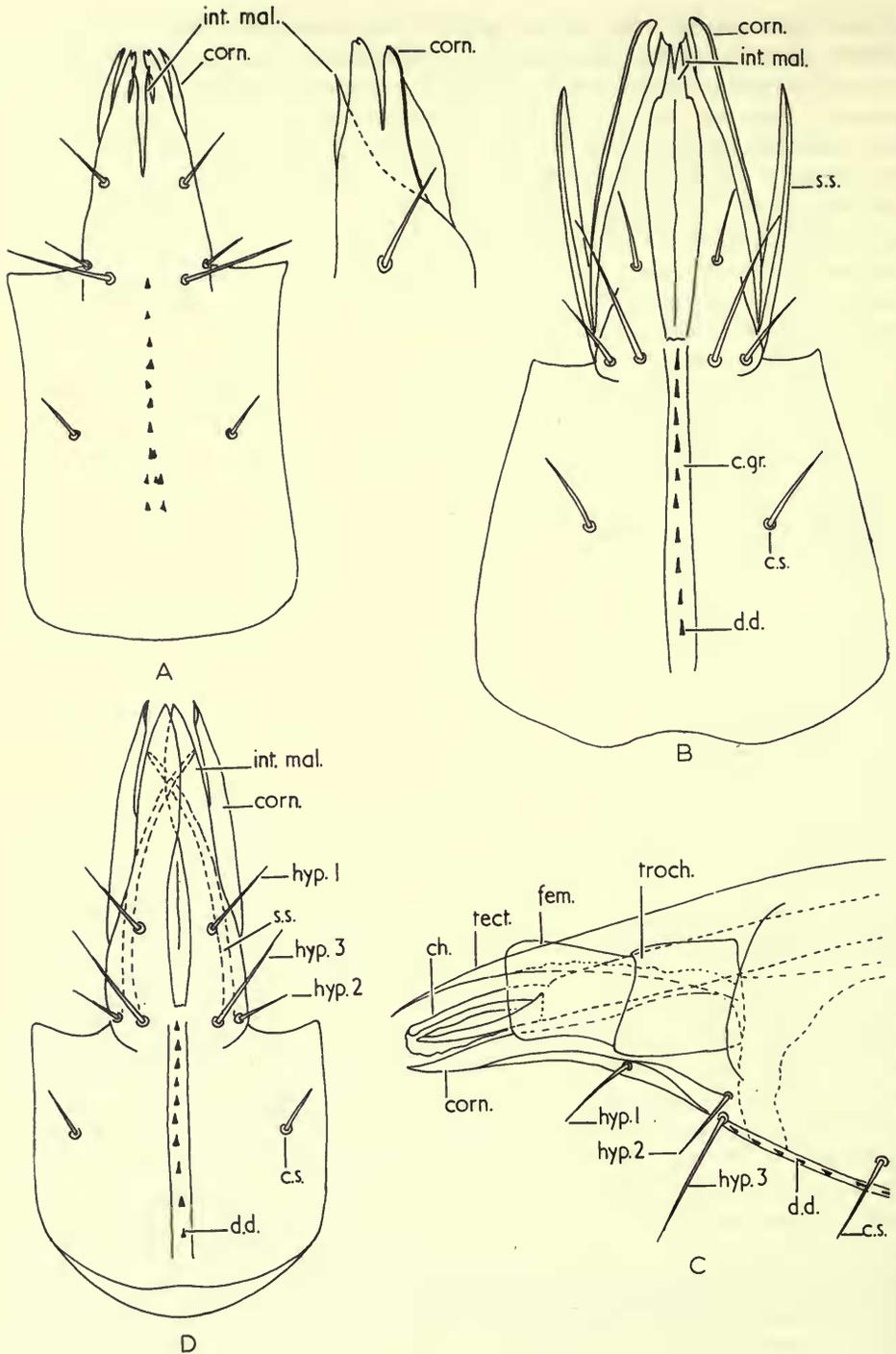


FIG. 5. Gnathosoma of *Ornithonyssus bacoti* (Hirst): A. female deutonymph, ventral and lateral views; B. female, ventral view; C. female, lateral view; D. male, ventral view.

the internal malae. In the male of *O. bacoti* the "internal malae" are in the form of two blades which overlap anteriorly and thus differ quite markedly from the form in the protonymph and female (Text-fig. 5D).

Labrum: The *labrum* (*epipharynx* of some authors), an extension of the dorsal-wall of the pharynx, appears as a long tapering structure between the corniculi and dorsal to the internal malae (Text-fig. 4). In the free-living forms and the facultative parasites the labrum projects beyond the tip of the hypostome but it is usually hidden by the elongated hypostome in the obligatory parasites. Its margin may be fimbriated and in the *Androlaelaps-Laelaps* group it has a distinct median longitudinal groove.

Salivary styli: The paired salivary styli lie laterally, immediately ventral to the chelicerae, and carry the ducts of the salivary glands located in the idiosoma. They are large and particularly well-sclerotized in the obligatory parasites (Text-figs. 5B and D).

In the forms having horn-like corniculi the salivary stylus lies in a lateral or dorsal channel along the length of the corniculus. Thus, the corniculi function as protective guides for the styli.

Pedipalps: The pedipalps have six free segments (trochanter, femur, genu, tibia, tarsus and apotele) of which the terminal segment, the apotele, is represented by a tined seta-like process at the inner basal angle of the tarsus (Text-fig. 6A). Weak condylar processes are present externally on the trochanter and dorsally on the distal margins of the femur and genu. A conspicuous lyrifiform fissure occurs proximally on the dorsal surface of the genu. These appendages have a well-defined chaetotaxy.

The normal ontogenetic sequence of development of the setae of the pedipalp has been defined by Evans (1964) and is characteristic of the free-living forms and of the majority of the facultative parasites of the Dermanyssidae. At the larval instar the trochanter lacks setae; the femur bears four (*al*, *d*₁, *d*₂ and *pl*), the genu five (*al*₁, *d*₁-*d*₃ and *pl*), the tibia 12 and the tarsus 11 setae. One seta (*v*₁) is added to the trochanter, and three setae to the tarsus at the protonymphal stage. A single seta is further added to the trochanter (*v*₂), femur (*d*₃) and genu (*al*₂), and two setae to the tibia at the deutonymphal stage. The deutonymphal chaetotactic pattern is retained by the adults. Thus the segmental formulae for the pedipalp (excluding the apotele which is present in all post-embryonic developmental stages) are: L. (0-4-5-12-11); P. (1-4-5-12-15); D. Ad. (2-5-6-14-15).

Deviations from the normal setal complement occur in both facultative and obligatory parasites as well as in certain myrmecophilous forms and are the result, in many cases, of the retention of the larval complement of setae on a segment in succeeding developmental stages. For example, in the adults of *Laelaspulus* the tibia retains the larval number of setae throughout ontogeny, with the result that the adult formula is (2-5-6-12-15), whilst *Hyperlaelaps amphibia* Zachvatkin retains the larval number on the femur and genu (Text-fig. 6B). In the latter the tibia is also

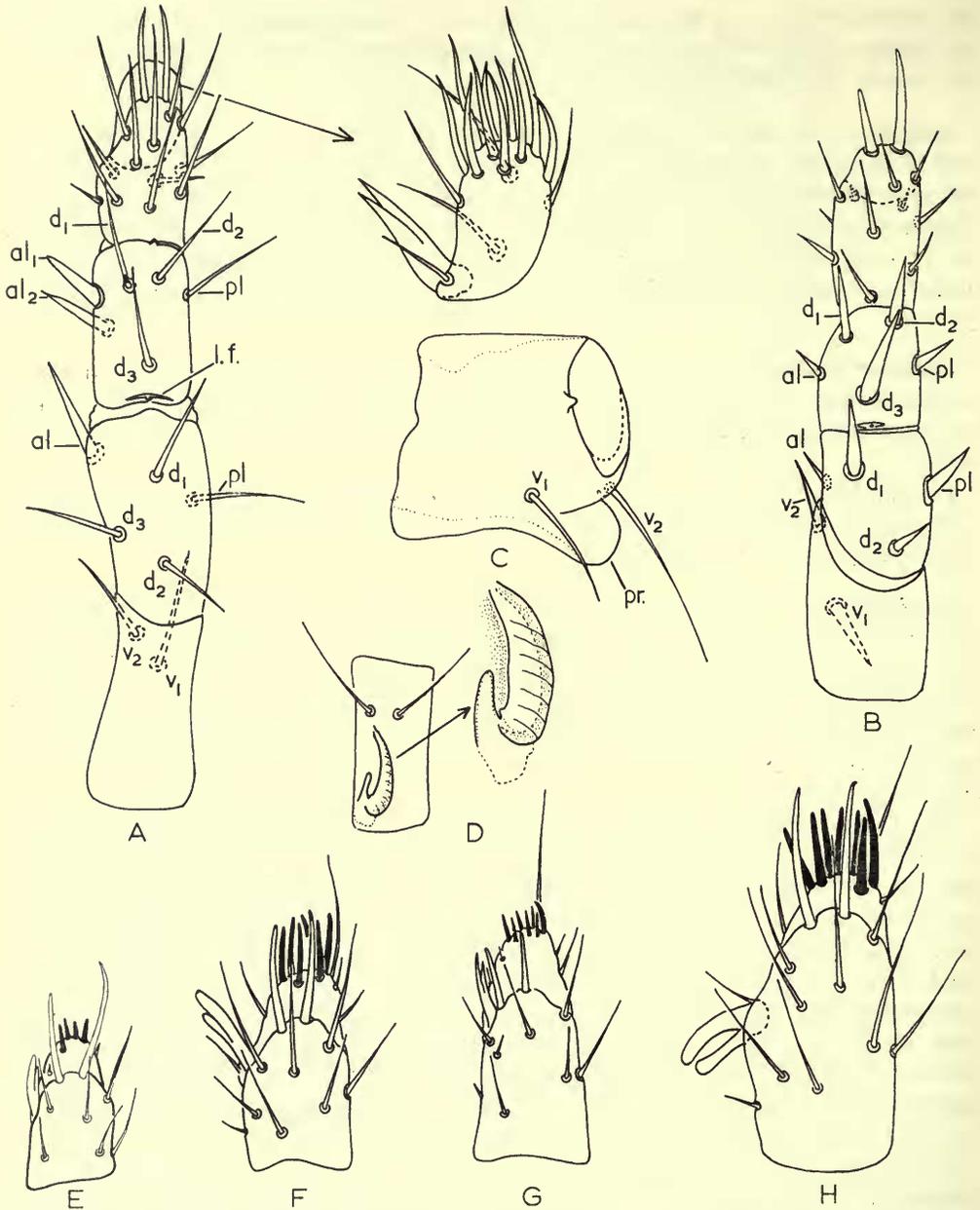


FIG. 6. A. Right pedipalp of *Hypoaspis* (*Gaeolaelaps*) *aculeifer* (Canestrini), dorsal view; B. right pedipalp of *Hyperlaelaps amphibia* Zachvatkin, dorsal view; C. palptrochanter of *Ornithonyssus bacoti* (Hirst) female, external (antiaxial) view; D. palptrochanter of *Eulaelaps stabularis* (Koch) female, ventral view; E-F. right palptibia and tarsus of *Ornithonyssus bacoti* (Hirst), larva (E), protonymph (F), deutonymph (G) and adult (H), in dorsal view.

unideficient in the deutonymph and adult (2-4-5-13-15). Amongst the macronyssines the normal pedipalpal chaetotaxy has been observed only in *Macronyssus*. Members of the other genera of this group show a deficiency in their tibial chaetotaxy. For example, *Sauronyssus*, *Steatonyssus*, *Ophionyssus* and the majority of the species of *Ornithonyssus* have only 13 setae on this segment. Some species of *Pellonyssus*, *Ornithonyssus* (*O. sylviarum*) and *Hirstionyssus* retain the larval complement of 12 in the nymphae and adults.

The greatest diversity in palpal chaetotaxy occurs in *Dermanyssus*. Only *D. intermedius* Evans & Till appears to have the normal number of setae. Deutonymphs and adults of the other species, except *D. alaudae* (Schrank), have the formula (2-4-6-12-15), indicating that the larval number has been retained on the femur and tibia. In *D. alaudae* the chaetotaxy of the four proximal segments is (2-4-5-7/8); thus, the femur and genu show no increase in setation from the larval condition whereas the tibia displays larval specialization, that is, the segment never bears the complete larval number.

The ontogenetic development of the pedipalpal chaetotaxy in the macronyssines follows the normal pattern on the trochanter, femur and genu only, that is L. (0-4-5), P. (1-4-5) and D. Ad. (2-5-6). At the larval stage of *O. bacoti*, for example, ten setae are present on the tibia and nine setae on the tarsus (Text-fig. 6E). There is an increase to the normal complement of 12 and 15 respectively on these segments in the protonymph whilst in the deutonymph, the protonymphal complement of 12 setae is retained on the tibia and the tarsus shows a regression to about 12 setae. In the adult 13 (unideficient) and 15 (normal) setae are present on the tibia and tarsus respectively. An interesting feature of the chaetotaxy of these distal segments is the reduction in the size and in the number on the tarsus of the hollow eupathidia-like setae in the non-feeding larva and deutonymph (Text-figs. 6E and G).

There is considerable variety in the form of the palpal setae (simple, pilose, leaf-like, spinose etc.) which provides stable taxonomic criteria. Hollow setae superficially resembling eupathidia occur on the tibia and tarsus, and are probably chemo-receptors. A pair is located dorsally on the distal margin of the tibia and a group of nine or ten on the distal half of the tarsus (Text-fig. 6A and H).

A median, longitudinal, keel-like process occurs ventrally on the trochanter of certain macronyssines (Text-fig. 6C). It appears to occur in females only of *Steatonyssus* s. str., some *Pellonyssus* and *Ornithonyssus*, but in both sexes and the protonymphs of *Macronyssus*. Its function is not known.

Both sexes of *Eulaelaps* have a unique organ of probable sensory function on the ventral surface of the trochanter (Text-fig. 6D). It was first observed by Fonseca (1935).

The apotele may be two or three-pronged. A three-pronged apotele occurs in the genera *Ololaelaps*, *Pseudoparasitus*, *Gymnolaelaps* and in some species (*H. hirsutus* and *H. pontiger*) of the genus *Haemogamasus*. The prongs may be slender with the proximal member small and relatively inconspicuous as in *Ololaelaps* and *Pseudoparasitus* or the three prongs may be large and spatulate as in some *Gymnolaelaps*. All the other species we have examined have a two-pronged apotele.

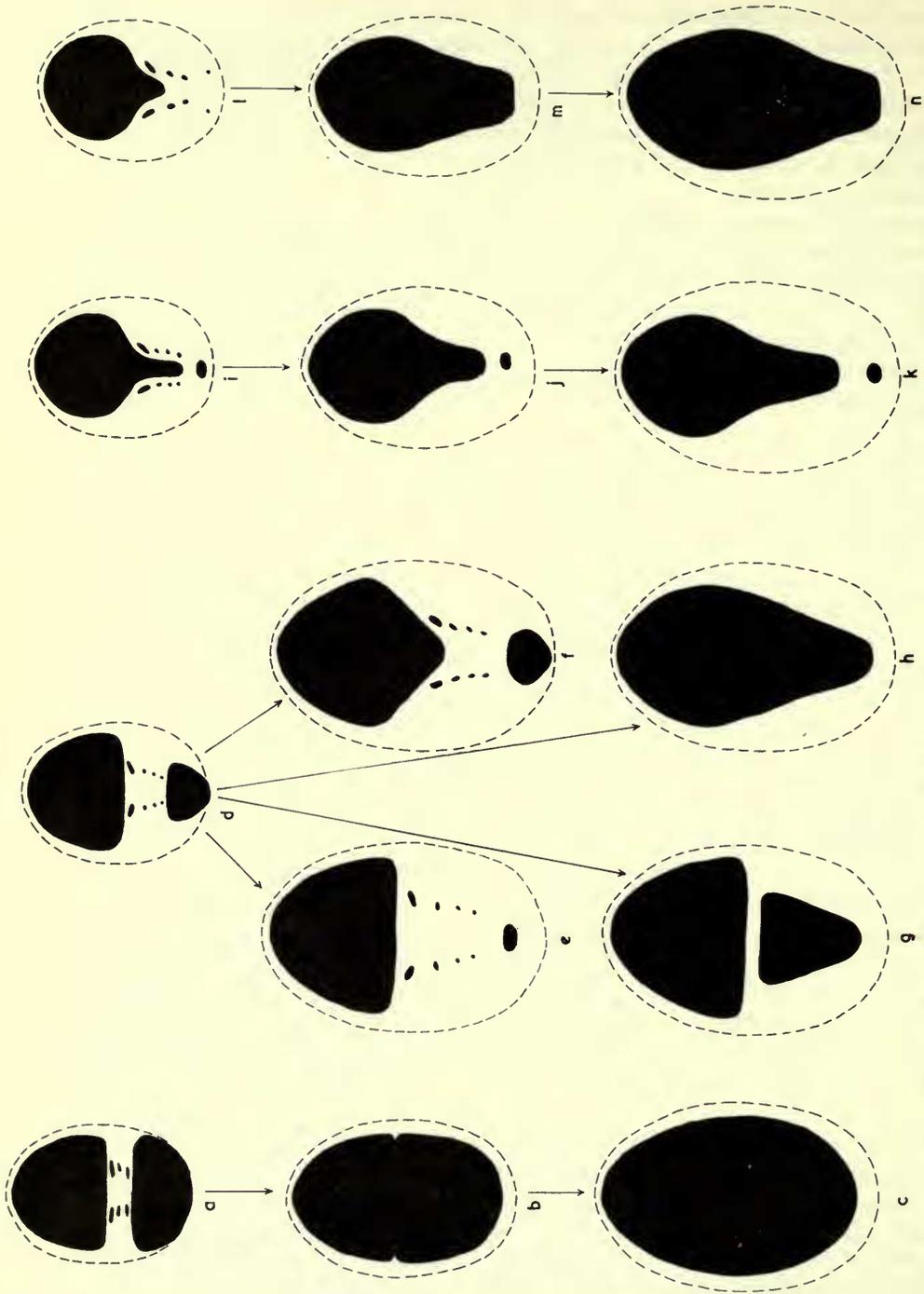


FIG. 7. Semi-diagrammatic representation of the dorsal sclerotization in: the protonymph (a), deutonymph (b) and adult (c) of a free-living or nest-inhabiting dermanyssid; the protonymph of an obligatory parasite of the Macromyssinae (d); females of *Ophionyssus natricis* (Gervais) (e); *Ornithonyssus aridus* Furman and Radovsky (f); *Steatonyssus* (g) and *Macromyssus* (h); the protonymph (i), deutonymph (j) and female (k) of *Liponyssoides sanguineus* (Hirst); the protonymph (l), deutonymph (m) and female (n) of *Dermatomyssus gallinae* (Degeer).

Idiosoma

Dorsal sclerotization: The ontogenetic development of the sclerotization of the dorsum of the idiosoma in the free-living forms and in the facultative ectoparasites follows a definite and constant sequence. In the few larvae we have examined the dorsal sclerotization is relatively indistinct, the *podonotal shield* being the only one discernible (Text-fig. 8A). At the protonymphal stage a large anterior podonotal shield and a smaller posterior *pygidial shield* are always present, and on the striated cuticle between these two scutal elements lie a variable number of *mesonotal scutellae* (Text-fig. 7a). These scutal elements coalesce at the deutonymphal stage; presumably the pygidial shield and the mesonotal scutellae first unite and the resulting opisthonotal shield fuses with the podonotal shield except at its lateral margins to form a single dorsal shield with a pair of lateral incisions (Text-fig. 7b). Further fusion occurs at the adult stage resulting in the disappearance of the lateral incisions (Text-fig. 7c).

In order to allow for the expansion of the idiosoma which is necessary to accommodate the large quantities of tissue fluids taken during feeding, the obligatory parasites show a decrease in idiosomal sclerotization. This is first evident at the protonymphal stage by the reduction in the size of the pygidial shield (Text-fig. 7d). No distinct scutal elements are present in the larva (Text-fig. 8B). In the macro-nyssines the podonotal shield and the mesonotal scutellae of the protonymph resemble

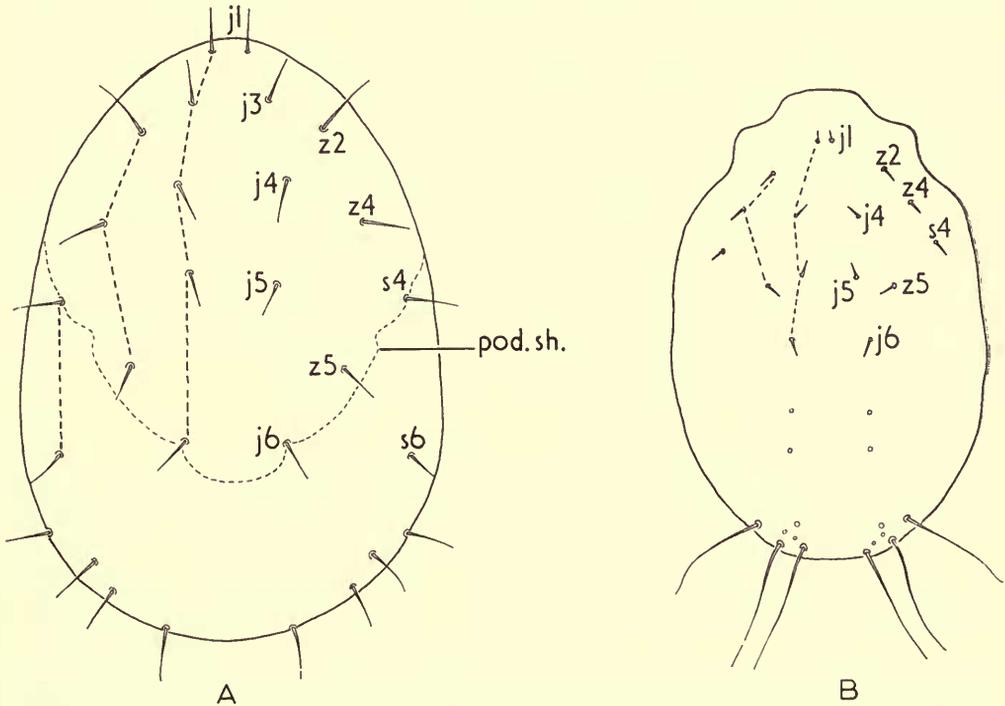


FIG. 8. Dorsal view of the larva of: A. *Holostaspis vitzhumi* (Womersley); B. *Ornithonyssus bursa* (Berlese).

the condition in the same instar of the free-living forms, but the pygidial shield is markedly reduced in size as is evident from its chaetotaxy (Text-figs. 10A and c). The non-feeding deutonymphal stages (male and female) of this group are very weakly sclerotized and it is difficult to differentiate the sclerotized area from the surrounding cuticle. It is probable that the extent of the weakly sclerotized areas is similar to that in their respective adult stages. All males, with the exception of *Steatonyssella*, which has two dorsal shields, have an entire dorsal shield formed as in the free-living species by the fusion of the podonotal, mesonotal and pygidial shields. This is also the condition in the female of *Macronyssus*, *Sauronyssus* and the majority of *Ornithonyssus* (Text-fig. 7h). The females of *Steatonyssus* and *Pellonyssus*, on the other hand, retain a distinct podonotal shield and have a smaller opisthonotal shield consisting of the pygidial and mesonotal elements (Text-fig. 7g). *Ornithonyssus aridus* Furman & Radovsky is exceptional amongst its congeners in retaining more or less the same form of dorsal sclerotization as the protonymph (Text-fig. 7f). The most specialized form occurs in females of *Ophionyssus* where distinct podonotal, mesonotal and pygidial elements are present and the pygidial shield shows a decrease in size in comparison with the protonymph (Text-fig. 7e).

Protonymphs of the Dermanyssinae show a further reduction of the pygidial shield (Text-figs. 7i and l). In the genus *Liponyssoides* the extremely small pygidial shield is either retained by the deutonymph and female as a separate scute (Text-figs. 7j and k) or fused with the remainder of the dorsal shield whilst in *Dermanyssus* the pygidial shield is lacking. The protonymphs of both genera have a strong posterior prolongation of the podonotal shield which extends between the mesonotal scutellae and serves as a more posterior attachment site for the retractor muscles of the greatly elongated cheliceral shafts. At the deutonymphal and adult stages of *Dermanyssus* an entire dorsal shield is usually present and this is probably formed by the posterior extension of the podonotal shield and its fusion with the mesonotal scutellae (Text-figs. 7m and n). Even within this genus there is a considerable variety in the dorsal sclerotization of the deutonymph and female, depending on the degree of development of the posterior prolongation of the podonotal shield. For example, in *D. scutatus* Krantz the posterior extension of the podonotal shield is very weak and bears only the first pair of dorsal opisthonotal setae, and the mesonotal scutellae are retained. The males of the Dermanyssinae have an entire dorsal shield.

Dorsal chaetotaxy: The dorsum of the idiosoma has a well defined chaetotaxy whose ontogenetic development is relatively stable. Deviations from the normal setal complement (the holotrichous condition) are relatively common in the specialized facultative and obligatory parasites and may be the result of hypo- or hypertrichy. The system of nomenclature adopted for the dorsal chaetotaxy in this work is that proposed by Lindquist & Evans (1965) and is a modification of the system used by Hirschmann (1957). In the adult holotrichous condition the dorsum is considered to bear 44 pairs of setae arranged in four longitudinal rows of 11 setae, a dorsal (*j*, *J*), a median (*z*, *Z*), a lateral (*s*, *S*) and a marginal series (*r*, *R*), on each side of the median longitudinal axis of the idiosoma, or alternatively in 11 transverse rows of eight setae.

The setae of the podonotal region are denoted by letters in lower case and those of the opisthonotum by capitals (Text-fig. 9c).

Van der Hammen (1964) has been extremely critical of the "artificial" (we should

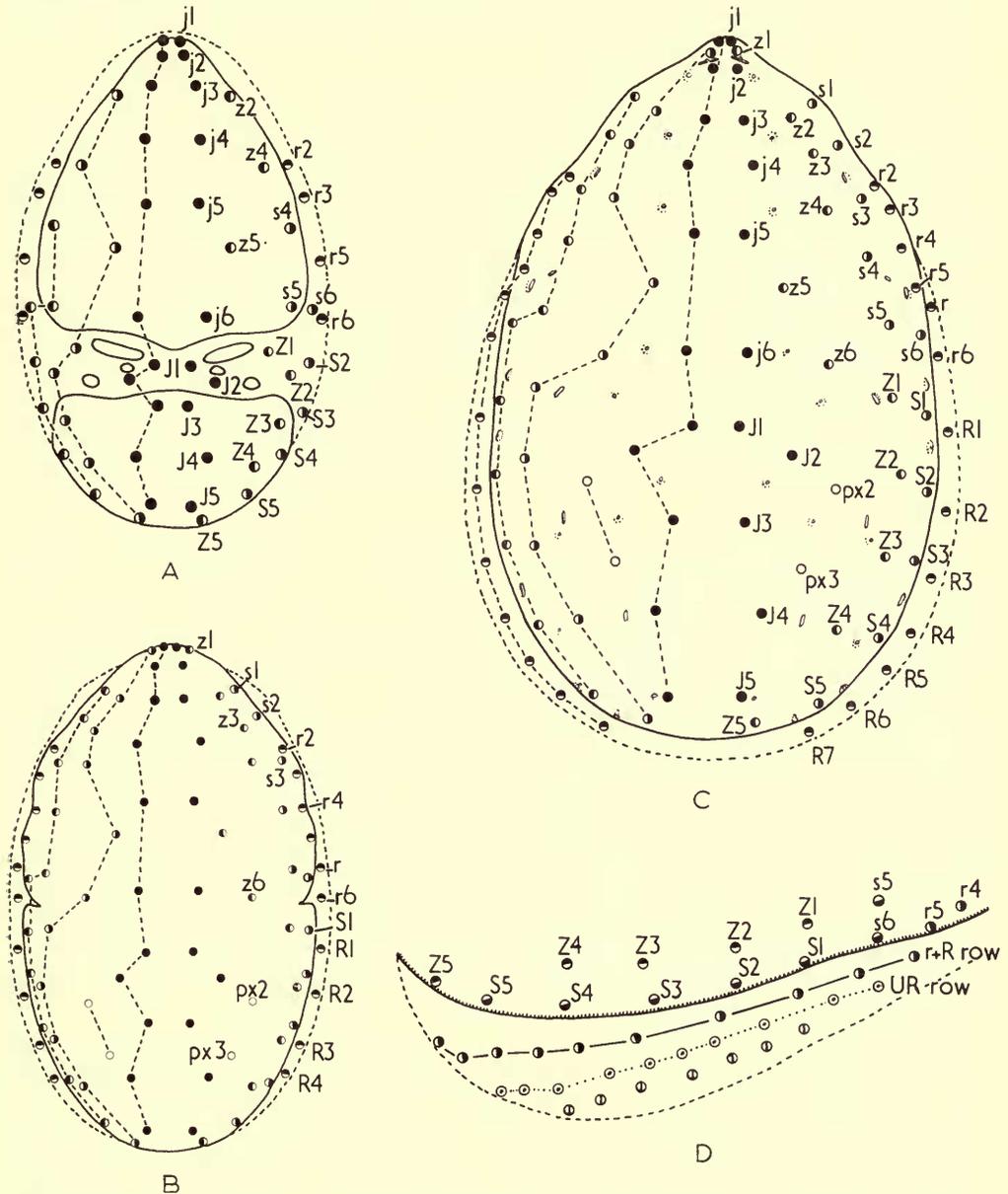


FIG. 9. Semi-diagrammatic representation of the dorsal chaetotaxy in the protonymph (A), deutonymph (B) and adult, dorsal (C) and lateral (D) view, of a free-living or nest-inhabiting dermanyssid (based on *Laelaps*).

prefer to call it "practical") system of setal nomenclature used in the Mesostigmata on the basis that the division of the idiosoma into two regions is probably artificial and useless for notation, since there is no evidence that the posterior margin of the podonotal shield and the anterior margin of the opisthonotal shield represent borders of tagmata. According to this author only a metameric arrangement of setae, that is in transverse rows, has phylogenetic value.

Theoretically, a metameric arrangement of setae would be ideal, but how is one to determine metamerism in a group which shows no evidence of idiosomal segmentation during post-embryonic development or for which there is, at present, no embryological evidence upon which to base metamerism? Certainly, the porotaxy of the dorsum shows such variability both in number and form of the "pores" as to be of doubtful value or significance, and we can see no basis for van der Hammen's statement that the "pores" show a metameric arrangement because their position corresponds to the borders of segments. In fact, any attempt to define metameric segmentation in the Mesostigmata on present evidence would be entirely speculative, and a system of setal terminology based upon it could be just as "artificial" as the system in current use. Such terms as "metameric arrangement" and "phylogenetic value" used at present in reference to a system of setal nomenclature in the Mesostigmata can only be classed as "red herrings" whose sole value is to add a pseudo-academic flavour to the text.

The main criterion for a system of setal nomenclature, in the absence of evidence of metamerism or of a primitive setal pattern, should be practicability. By this we mean that reference, for taxonomic purposes, can be made to individual setae and a comparison is possible between the setal patterns of related forms on the basis of "positional homology". The modified Hirschmann system of setal terminology proposed by Lindquist & Evans (1965) enables one to do this except in cases of extreme hypo- or hypertrichy of the dorsal chaetotaxy. This system retains the division of the chaetotaxy into a podonotal and an opisthonotal series since it is of practical value. The podonotal shield is a characteristic feature of the larval and protonymphal stages of the Mesostigmata and is retained as such (except for an increase in sclerotization laterally) in the deutonymphal and adult stages of many species. It can be readily defined by its chaetotaxy. No claim is made that the podonotal and opisthonotal shields define tagmata although it would indeed be surprising if the widespread occurrence of a division of the dorsal sclerotization of the idiosoma in the Mesostigmata at the podonotal-opisthonotal junction was without some functional significance.

Larvae of the Dermanyssidae are weakly sclerotized although it is usually possible in the free-living forms to define a podonotal shield which bears nine pairs of setae (j_1 , j_3 - j_6 , z_2 , z_4 , z_5 and s_4). A tenth pair of podonotal setae (s_6) occurs on the striated cuticle lateral to j_6 (Text-fig. 8A). The chaetotaxy of the opisthonotum is considerably less stable; for example, four pairs of setae are present in this region in some *Holostaspis* and seven pairs in some *Hypoaspis* s. lat. We have not attempted to name these setae. Few larvae of the obligatory parasites have been examined. In *Ornithonyssus bacoti*, for example, the podonotal region shows a deficiency of two

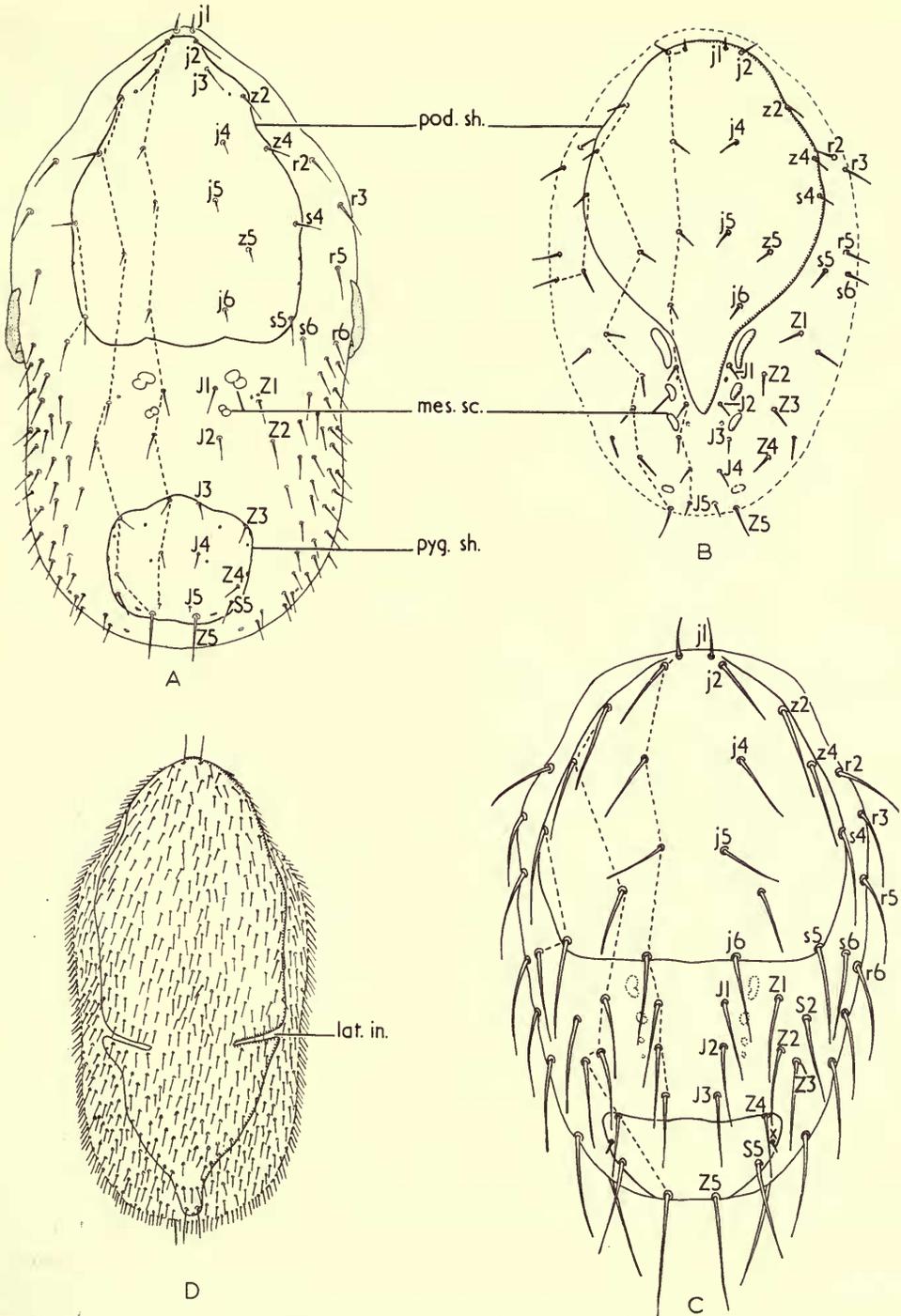


FIG. 10. Dorsum of: A. *Macronyssus flavus* (Kolenati) protonymph; B. *Dermanyssus gallinae* (Degeer) protonymph; C. *Ornithonyssus bacoti* (Hirst) protonymph; D. *Haemogamasus nidi* Michael, deutonymph.

pairs of setae (j_3 and s_6) and the opisthonotum bears only three pairs of long, slender setae. Setae j_3 , however, are present in some larvae of the Macronyssinae but the presence of only six opisthonotal setae appears to be characteristic for the group.

At the protonymphal stage of the free-living forms and the majority of the facultative parasites, the number of podonotal setae is increased to 16 pairs of which eleven pairs (j_2 and s_5 being additional to the nine pairs occurring on the shield in the larva) are situated on the podonotal shield and five pairs (r_2 , r_3 , r_5 , s_6 and r_6) on the cuticle lateral to the shield (Text-fig. 9A). Typically, the pygidial shield bears eight pairs of setae (J_3 - J_5 , Z_3 - Z_5 , S_4 and S_5) and the unsclerotized cuticle of the opisthonotum six pairs (J_1 , J_2 , Z_1 , Z_2 , S_2 and S_3) making a total of 14 pairs of opisthonotal setae and a dorsal complement of 30 pairs. In the facultative parasite *Eulaelaps stabularis* (Koch) the pygidial shield is reduced in size and bears only six pairs of setae (J_3 - J_5 and Z_3 - Z_5), setae S_4 and S_5 lying on striated cuticle. The total number of setae on the opisthonotum is sixteen pairs, an increase of two pairs over the normal. This may be the beginning of the hypertrichy of the dorsum which is so marked in the deutonymph and adult of this species. There is no hypertrichy of the podonotum at this instar. On the other hand, in the protonymphs of *Haemogamasus nidi* Michael there is marked hypertrichy of the lateral and marginal series in both the podonotal and opisthonotal regions.

The podonotal chaetotaxy of the protonymphs of the obligatory parasites is essentially the same as in the free-living forms (Text-fig. 10A). However, there is a tendency for hypotrichy of the j series by the suppression of j_3 , for example in some species of *Dermanyssus*, *Ornithonyssus* and *Pellonyssus*, or of j_3 and j_4 as in *Dermanyssus alaudae* (Schrank). Varying degrees of hypo- and hypertrichy are evident on the opisthonotum. In *Dermanyssus gallinae* (Degeer) the normal complement of J and Z series of setae is present but the S series is deficient, comprising only two pairs of setae (Text-fig. 10B). *O. bacoti* (Text-fig. 10C), on the other hand, shows a deficiency in the number of J setae (J_4 and J_5 being suppressed) whilst *Macronyssus flavus* (Kolenati) has the full complement of J and Z setae, and marked hypertrichy in the region of the S and R series. The widespread occurrence of hypo- and hypertrichy of the opisthonotum in the dermanyssines and macronyssines makes it difficult to use the relative positions of setae as a basis for comparing the chaetotaxy of this region with that of free-living forms, and we have restricted the naming of setae to those regions unaffected by these phenomena.

The full complement of dorsal setae is attained at the deutonymphal stage except possibly in some forms showing extreme hypertrichy (Text-figs. 9B-D). In the majority of the free-living forms and facultative parasites the dorsal, median and lateral series situated on the dorsal shield form six longitudinal rows of eleven setae (or eleven transverse rows of six setae). Setae added to these series at the deutonymphal stage are: z_1 , z_3 , z_6 , s_1 - s_3 and S_1 (Text-fig. 9B). The marginal series on the podonotum is fairly stable and comprises setae r_2 - r_6 (r_4 being added in the deutonymphal instar and r_6 remaining on the lateral integument) although in certain nest inhabiting forms (*Pneumolaelaps*) and facultative parasites (*Laelaps*) hypertrichy of this series is not uncommon. This series (R) and the submarginals (UR) are con-

siderably more variable on the opisthonotum and are commonly affected by hypo- or hypertrichy. *Hypoaspis praesternalis* Willmann, for example, has only one pair of *R* setae whilst in *Pneumolaelaps marginalis* Willmann both series are markedly hypertrichous and each comprises over 25 setae! Differences also occur in the number of opisthonotal marginal series (*R*) between the sexes of a given species and this is first evident at the deutonymphal stage, the male deutonymph and adult male having fewer setae in this series than the female deutonymph and adult female. Two further interesting features of the dorsal chaetotaxy are exhibited by the laelapines. The first is the appearance of a supernumerary row of setae between the *J* and *Z* series of the opisthonotum. This series, which is absent in *Stratiolaelaps*, some *Androlaelaps* and *Hyperlaelaps*, comprises a maximum of three setae/row, referred to as posterior accessories (*px*₁₋₃) by Costa (1961). The maximum complement of *px* setae occurs in some *Androlaelaps*, but the usual number present is two pairs, *px*₂ and *px*₃ (Text-fig. 9c). Only one pair of the series (*px*₂) is present in some *Hyperlaelaps*. The second feature is the tendency for hypertrichy to occur in the region of the *J* series in forms associated with other animals either as nest-inhabitants or facultative parasites. These unpaired setae show considerable intraspecific variability in number and in length. General hypertrichy of the podonotum and opisthonotum occurs at the deutonymphal stage of the *Eulaelaps-Haemogamasus* group and completely obscures the primary chaetotaxy (Text-fig. 10D).

Even within the free-living and facultative forms some hypotrichy of the dorsal and median series of setae is evident. For example, in *Ololaelaps* the deutonymphal setae *z*₁ and *z*₃ are suppressed and in *Ondatralaelaps*³ *j*₃ and *z*₃ are lacking on the podonotum and *J*₃, *J*₄ and *Z*₃ on the opisthonotum. Rarely, in some *Androlaelaps*, a supernumerary seta occurs on the podonotal region of the dorsal shield lateral to *s*₄ and has been referred to as an anterior accessory seta (*ax*) by Costa.

The dorsal chaetotaxy of the deutonymphs of the obligatory parasites is characterized by the tendency for the retardation in the development of the chaetotaxy of the podonotum and the occurrence of hypertrichy in the lateral and marginal series. Further, in the non-feeding deutonymphs of the macronyssines two distinct types of dorsal chaetotaxy are present, corresponding to the form in the adult male and female (Text-figs. 11A and C). Reference has already been made to the hypotrichy of the dorsal series at the larval and protonymphal stages of both dermanyssines and macronyssines, and those setae of the series which are suppressed at the protonymphal stage do not appear in subsequent developmental stages. However, the main feature of retardation in the development of the podonotal chaetotaxy in the deutonymphal stage is most apparent in the suppression of certain setae which normally first appear at this instar, for example, the paravericals (*z*₁), *z*₃, *s*₂ and, particularly in the male, *z*₆ (Text-figs. 11A and C). The chief difference between the chaetotaxy of the male and female non-feeding deutonymphs of the macronyssines is seen in the greater hypertrichy of the idiosoma in the region of the lateral and marginal series of setae in the female.

In all the British members of the Dermanyssidae, the adults appear to retain the

³ *Ondatralaelaps* gen. nov. (type: *Laelaps multispinosa* Banks).

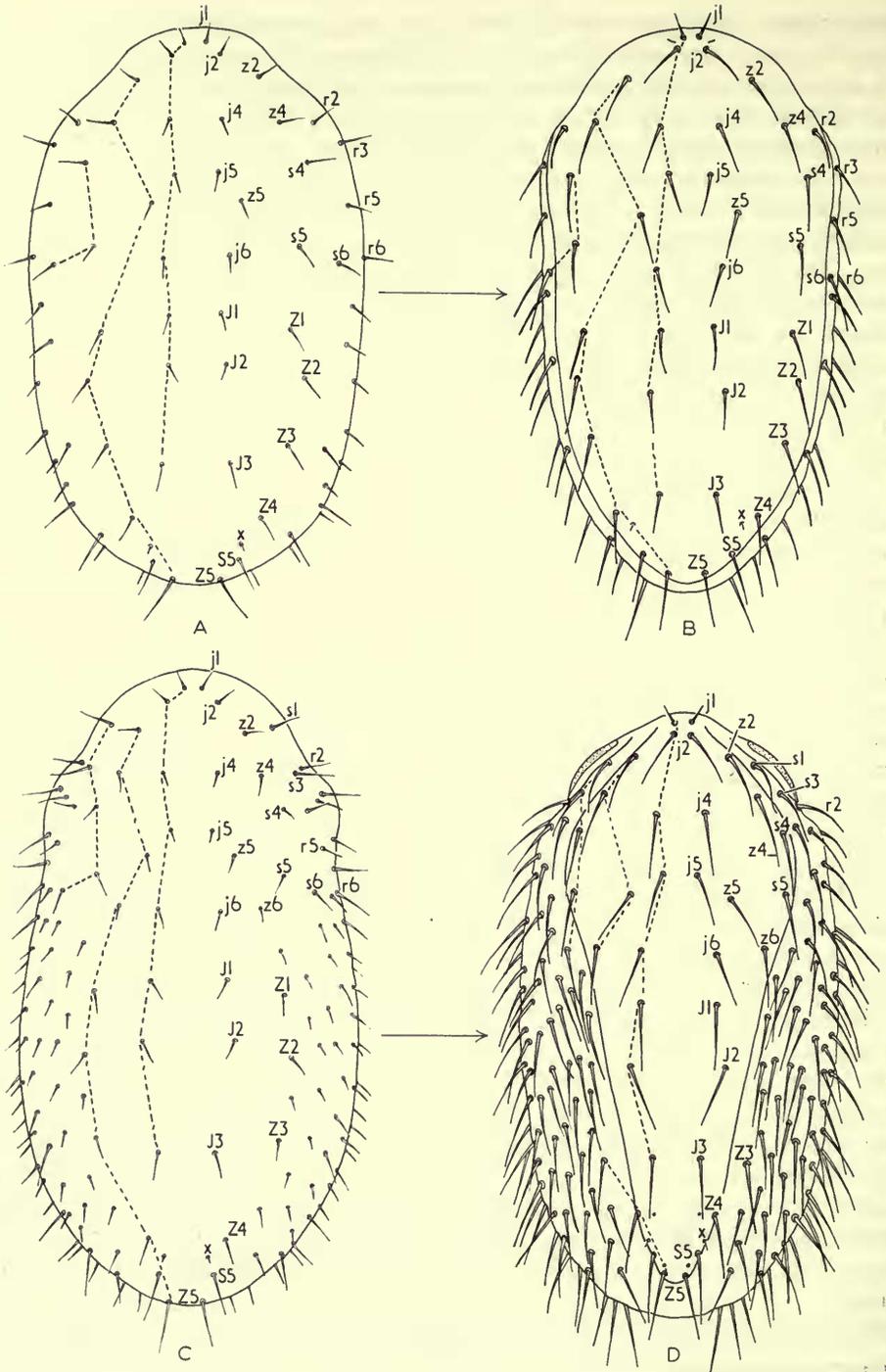


FIG. 11. *Ornithonyssus bacoti* (Hirst). Dorsum of A. male deutonymph ; B. male ; c. female deutonymph ; D. female.

dorsal idiosomal chaetotaxy of the corresponding male or female deutonymph. Males of the obligatory parasites show an increase in the area of dorsal sclerotization compared with the female with the result that certain of the r series and of the z series occurring on unsclerotized cuticle in the female are incorporated on the dorsal shield in the male (Text-figs. 11B and D).

An exception to the basic dorsal chaetotaxy of the Dermanyssidae occurs in the adults (the only known stages) of *Pseudolaelaps doderoi* (Berlese) whose systematic position is problematical. The dorsum is markedly hypotrichous, the podonotum bearing only 15 pairs of setae and the opisthonotum nine pairs.

Some intraspecific variability in the primary chaetotaxy of the opisthonotum is apparent in many obligatory parasites and in some facultative parasites and takes the form of the suppression of one seta of a pair or an asymmetrical arrangement of the setae of a pair. This is particularly evident in members of the genera *Dermanyssus* and *Ondatraelaps*.

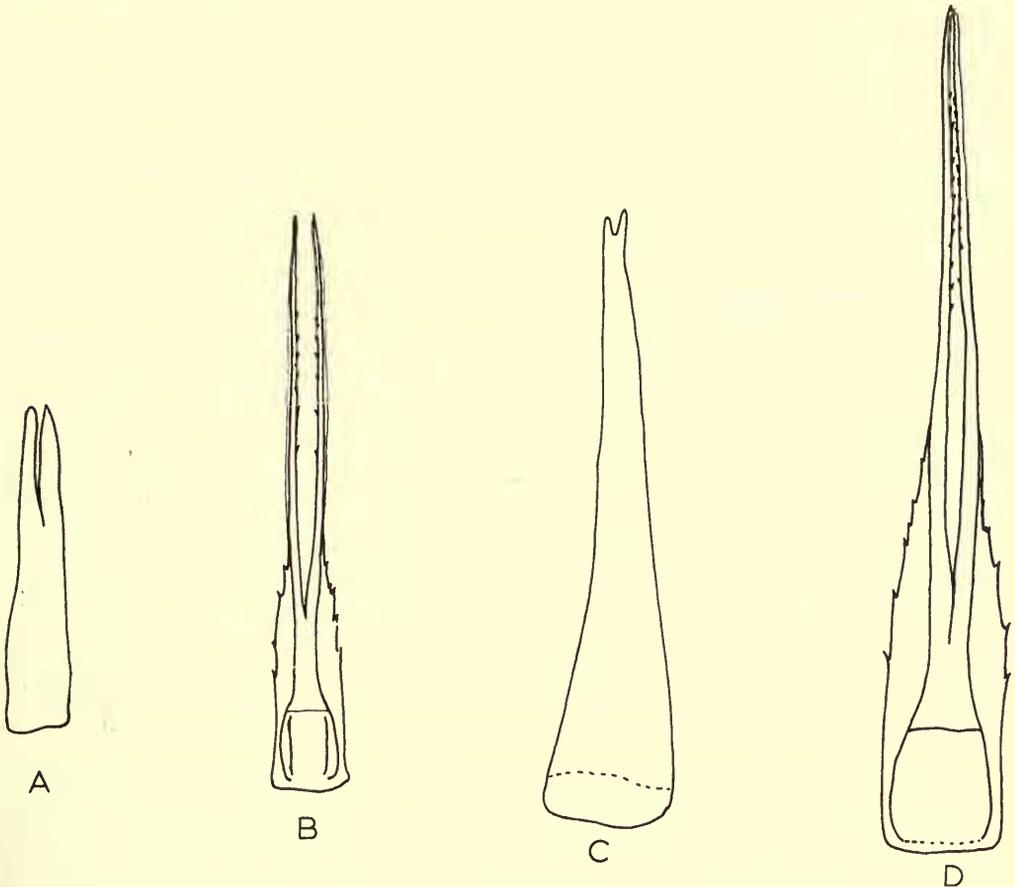


FIG. 12. *Ornithonyssus bacoti* (Hirst). Tritosternum of larva (A), protonymph (B), deutonymph (C) and adult (D).

The dorsal setae in the majority of the Dermanyssidae are slender and smooth or weakly pilose. Exceptions occur in the genera *Stratiolaelaps* and *Cosmolaelaps* where they tend to become leaf-like or spatulate, and in facultative parasites of the *Laelaps*-group in which they may be modified as short robust spines. The vertical setae (jI) sometimes differ in form from the other setae in the region of the vertex.

Dorsal porotaxy: The basic adult and deutonymphal complement of "pores" on the dorsum of the idiosoma appears to be 22 pairs (11 podonotal and 11 opisthonotal) and their distribution in *Laelaps* is shown in Text-fig. 9c. Considerable diversity occurs in the pattern and number of "pores" throughout the family and both hyper- and hypoporosity are not uncommon, particularly in the obligatory parasites.

Tritosternum: The tritosternum⁴ lies between coxae I on the venter of the idiosoma and is present as a biramous structure in all British Dermanyssidae (Text-figs. 12, 15, 16). Its function is unknown. In life, the laciniae lie along the capitular groove and the fine processes (pilae) along their margins possibly engage the denticles of the deutosternum. The basal portion of the tritosternum is longer than wide and the laciniae in the free-living and facultatively parasitic forms are invariably pilose. Many obligatory parasites (Dermanyssinae and Macronyssinae) have a transparent, marginally denticulate border to the tritosternum (Text-fig. 12D). The non-feeding larva and deutonymph of the Macronyssinae have the laciniae of the tritosternum markedly reduced (Text-figs. 12A-D).

Sclerotization and chaetotaxy of the venter: At the larval stage in the free-living forms and in most of the facultative parasites two sclerotized areas are present ventrally; a sternal shield, of varying degrees of sclerotization, inter-coxally and a subtriangular anal shield surrounding the anus which is provided with a pair of valves (Text-fig. 13A). The sternal shield carries three pairs of setae (*st.* 1-3) and the anal shield three setae, comprising a pair of paranals (*pan.*) and an unpaired postanal (*pon.*). There are no *euanal setae*, that is, setae situated on the anal valves. Four pairs of setae occur on the unsclerotized cuticle of the opisthogaster and, according to the system proposed by Lindquist & Evans (1965), these consist of three pairs of internal ventrals (*Jv*1, 2 and 5) and one pair of medio-lateral ventrals (*Zv*2) arranged as in Text-fig. 13A. Stigmata, peritremes and podal sclerites are not present in the larva. In the obligatory parasites there is a marked reduction in sclerotization to the extent that only rarely can one define distinct sternal and anal shields. However, the normal three pairs of sternal setae and the three setae associated with the anal

⁴ Van der Hammen (1964) has rejected the term tritosternum (for *furca*) on the ground that it is "no sternum at all, because a sternum is a distinct plate". However, he considers (without giving any evidence) that the small sclerite occurring in the normal position of a tritosternum in some of the *highly specialized* bat parasites of the family Spinturnicidae represents a "real sternal plate belonging to segment III"! The reason for this must be, by inference, that the structure is a "plate" although, even in this group, the tritosternum is not always a simple plate [cf. *Meristaspis jordani* (Radford)]. Perhaps the tritosternum in some Trachytidae (Uropodina) will also satisfy his "criterion" of a sternum? At present, the origin of the tritosternum is unknown but it seems unnecessary to change such a well-established term, certainly on the "evidence" presented by van der Hammen.

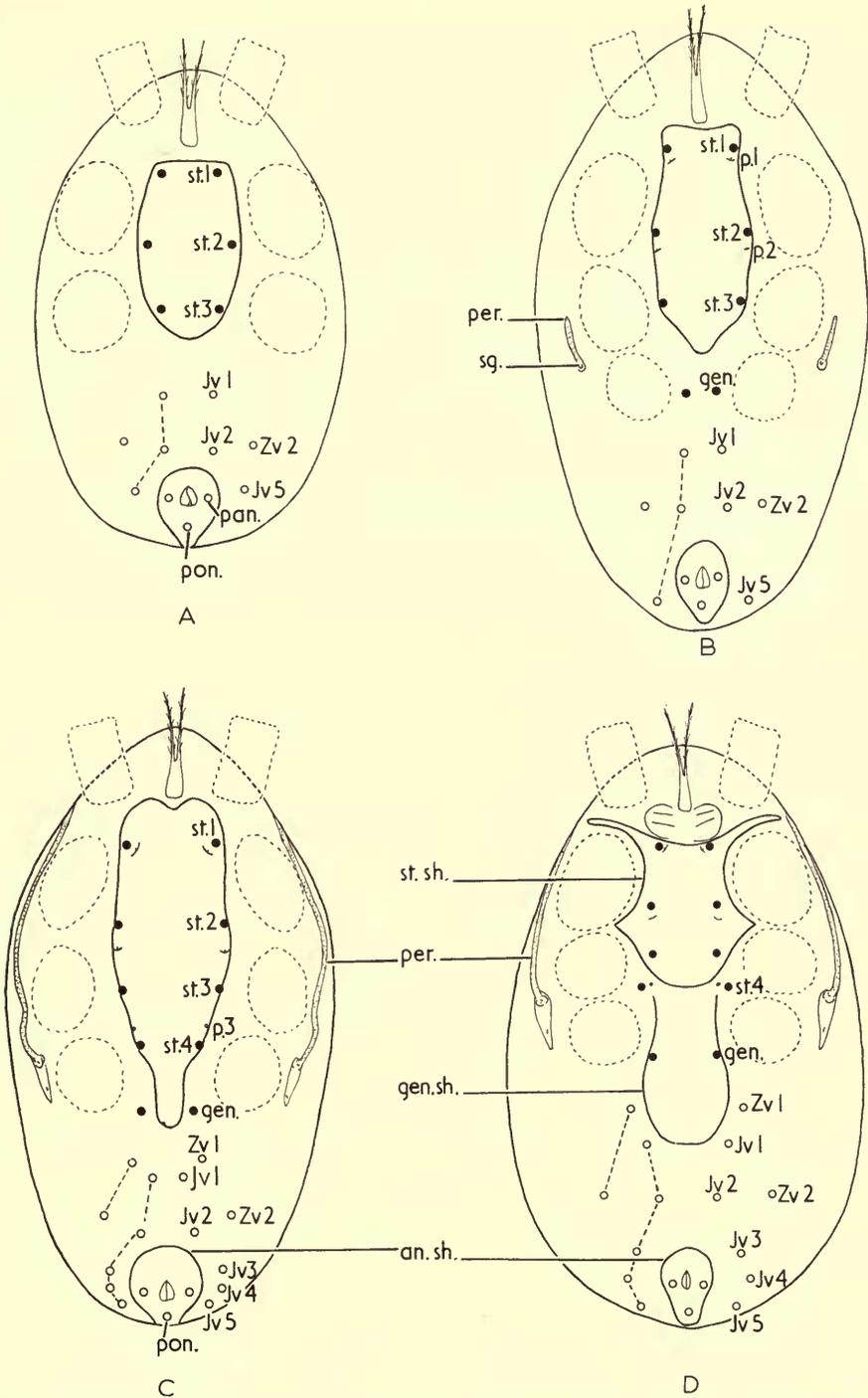


FIG. 13. Semi-diagrammatic representation of the venter of the larva (A), protonymph (B), deutonymph (C) and female (D) of *Hypoaspis (Gaeolaelaps) aculeifer* (Canestrini).

region are present, but there is a retardation in the development of the opisthogastric setae, only one pair (*Jv1*) being developed in some *Dermanyssinae* and two pairs (*Jv1* and 2) in the *Macronyssinae* (Text-fig. 14A).

The sternal and anal shields in the protonymph are generally well-defined and carry the same complement of setae as in the larva (Text-fig. 13B). A pair of genital setae (sometimes present as incipient setae in the larva) and two pairs of lyriform fissures (*p. 1* and *p. 2*) first appear at this instar. In the free-living forms the larval number of setae on the opisthogastric cuticle is retained, but in the obligatory parasites the larval deficiency in opisthogastric setae is rectified and the protonymph now acquires its full complement with the appearance of *Zv2* and *Jv5* (Text-fig. 14B). Hypertrichy of the opisthogastric region may occur at this stage in some *Macronyssinae*, for example, *Macronyssus flavus* (Kolenati). Stigmata with short, anteriorly directed peritremes never extending beyond the anterior margin of coxae III are present lateral to the third coxal interspace. No distinct podal shields occur at the protonymphal stage.

Increased sclerotization and setation of the venter are evident at the deutonymphal stage. The sternal shield, bearing the three pairs of setae and two pairs of fissures present in the protonymph and a fourth pair of setae, the metasternals (*st. 4*) with their associated pores, which first appear at this instar, occupies almost the entire

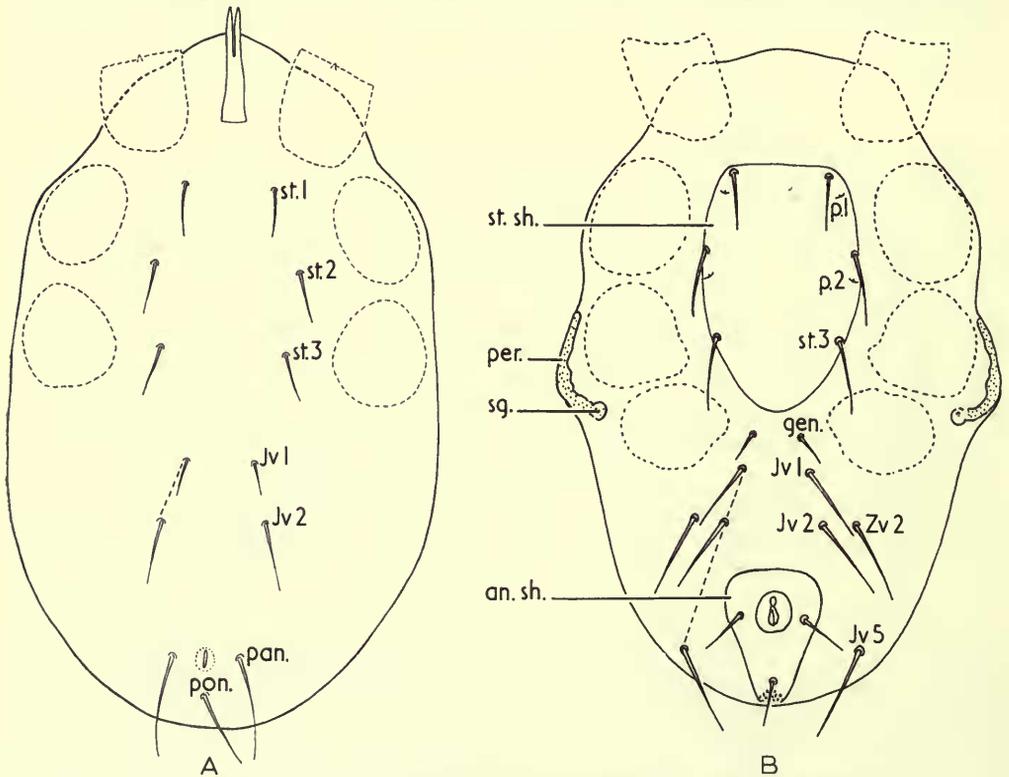


FIG. 14. *Ornithonyssus bacoti* (Hirst). Venter of larva (A) and protonymph (B).

length of the intercoxal region. Its tapered, posterior region extends between the genital setae (Text-fig. 13C). Hypotrachy of the sternal region has been observed in some obligatory parasites, for example, certain species of *Dermanyssus* and *Pellonyssus*, and this is characterized by the absence of the metasternal setae which fail to develop at their normal stage in ontogeny. Certain species of *Haemogamasus*, on the other hand, show a distinct hypertrichy of the sternal chaetotaxy, the secondary setae usually being shorter than the primary. The anal shield more or less retains the form present in the larva and protonymph.

Considerable variation occurs in the chaetotaxy of the opisthogaster in the deutonymph. Normally, the holotrichous condition for this region is seven pairs of setae (*Zv*₁, *Jv*₃ and *Jv*₄ added to the protonymphal complement) and this occurs in certain of the free-living forms, for example, some species of *Hypoaspis* s. lat., *Ololaelaps*, *Pseudoparasitus* and *Stratiolaelaps*. More commonly, however, the region shows some degree of hypertrichy, particularly in the *Eulaelaps*-*Haemogamasus* group and in the obligatory parasites. As in the case of the marginal setae of the dorsum, the male deutonymph often has fewer opisthogastric setae than the female deutonymph. Further, there may be considerable intraspecific variability in the number of opisthogastric setae in deutonymphs of the same "sexual phase". The stigmata are situated in the same position relative to coxae III and IV as in the protonymph, but in all free-living forms and the majority of the facultative parasites the peritreme is considerably longer and usually extends up to or beyond coxa I. Exceptions to this occur in certain of the obligatory parasites (*Dermanyssus*, *Steatonyssus*, *Pellonyssus*, *Ophionyssus*) where the protonymphal form of the peritreme may be retained at the deutonymphal stage. In the free-living forms a weakly developed peritrematal shield is also present and its post-stigmal portion bears a conspicuous pore (Text-fig. 13C). Podal shields are absent except for a weakly sclerotized strip along the posterior border of the coxal cavity of leg IV. Weakly sclerotized metapodalia may be present. An anal shield with the normal three setae is characteristic of the family although in densely hypertrichous forms (*Haemogamasus*) it may carry a number of secondary unpaired setae.

With the exception of the hypertrichous forms showing intraspecific variability of the opisthogastric setae, the adult setal complement of the venter is determined at the deutonymphal stage (male or female). The degree of sclerotization and the size and outline of the shields at the adult stage, however, show great diversity, greater in fact than within any other family of the Mesostigmata. In the female of the free-living forms and the facultative parasites the sternal shield normally bears three pairs of setae (*st.* 1-3) and two pairs of lyriform fissures (*p.* 1 and *p.* 2). It is fused laterally with the endopodal shields of coxae II. More rarely it bears, in addition, the metasternal setae (*st.* 4) and their associated pores (*p.* 3) as in *Ololaelaps* (Text-fig. 15D). The posterior margin of the sternal shield may extend as far as the level of the posterior margin of coxa III, as in *G. aculeifer*. Its anterior margin is often indistinct owing to the sclerotization of the cuticle immediately anterior to the shield. This pre-sternal area of sclerotization may be uniformly sclerotized and reticulated (Text-fig. 15B) or regionally more heavily sclerotized to form pre-endopodal sclerites (Text-

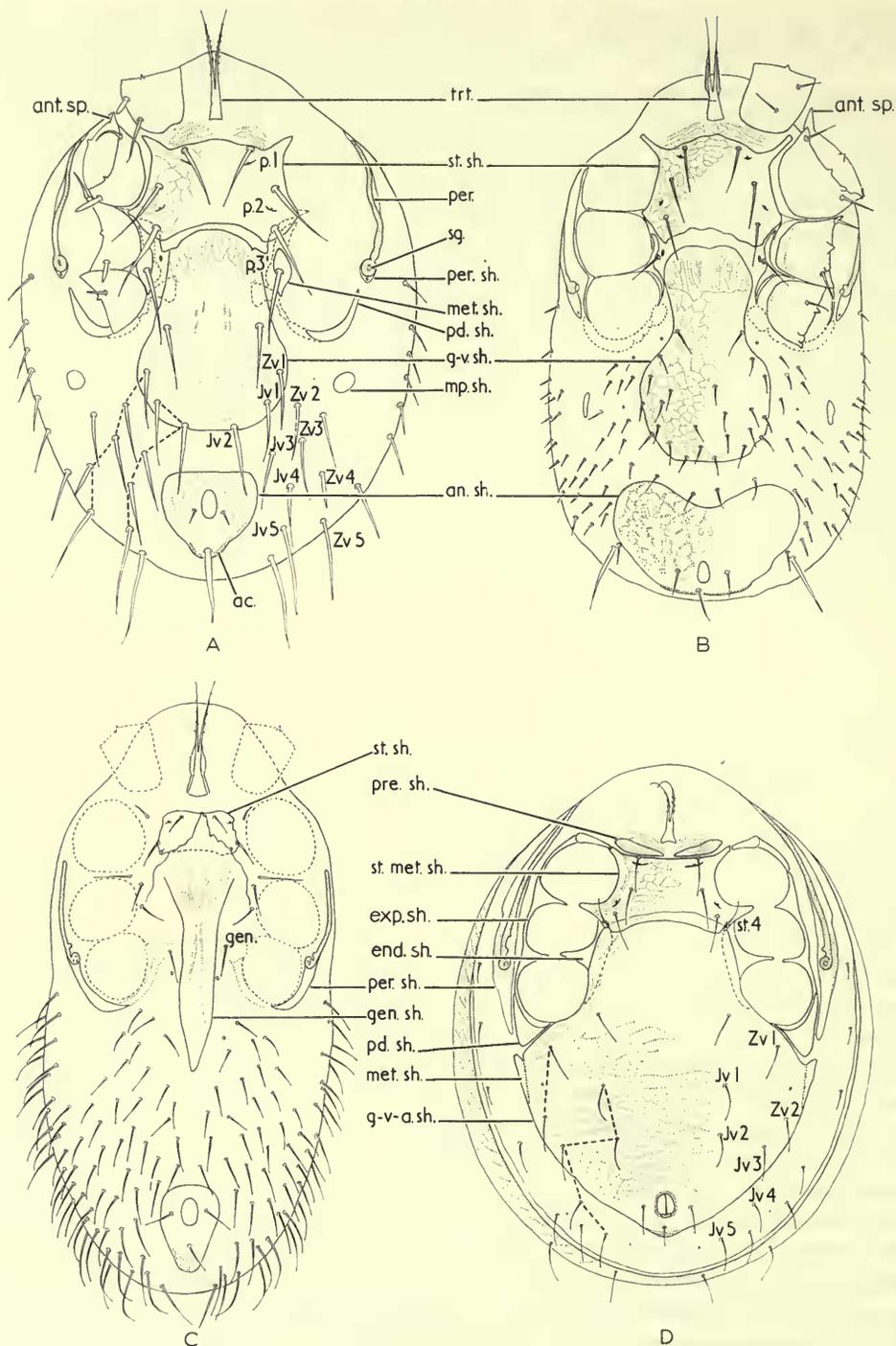


FIG. 15. Venter of female of : A. *Laelaps agilis* Koch ; B. *Myonyssus gigas* (Oudemans) ; C. *Ophionyssus natricis* (Gervais) ; D. *Ololaelaps placentula* (Berlese).

fig. 15D). We have not observed true jugularia in the British members of this family. The surface of the sternal shield is variously ornamented, the ornamentation being in the form of a reticulate pattern of lines, or punctate lines, or scattered punctures. The metasternal setae and pores are normally situated posterior to the sternal shield and lie on striated cuticle or on small metasternal shields which may be free or fused with the endopodal shields of coxae III. In the obligatory parasites the sternal shield is less well developed and rarely fused with the endopodal shields of coxae II. It may bear only two pairs of setae (*st.* 1 and 2) and pores (*p.* 1 and 2) or the normal three pairs of setae and two pairs of pores. In outline it is generally sub-rectangular but in some *Pellonyssus* it is reduced to a narrow, transverse, band-like sclerite. Subcircular "porose" areas occur between sternal setae 1 and 2 in some species of *Macronyssus*. The metasternal setae in this group are usually situated on striated cuticle. They are absent in the adults whose deutonymphs lack these setae.

The female genital orifice (with its apodemes) appears as a transverse slit at the level of the fourth coxae. Associated with this orifice, and extending posterior to it, is a characteristic genital shield bearing the genital setae. Anteriorly the shield has a hyaline flap of varying degrees of development. In its least specialized form the genital shield is more or less flask-shaped and bears only the genital setae (Text-fig. 13D) but, with the exception of the obligatory parasites, there is a general tendency for an increase in the size of the shield and the incorporation with it of a number of opisthogastric setae. Such a shield is termed *genito-ventral* (Text-figs. 15A-B). Marked hypertrichy of the genital shield occurs in *Eulaelaps*, *Haemogamasus* and *Myonyssus*. The genital shield shows some reduction in size in the obligatory parasites and tapers in its posterior half. In some macronyssines the reduction in size and the posterior tapering of the shield is very marked; the resulting shield is slender and does not carry the genital setae (Text-fig. 15C). The anterior hyaline flap is usually extensive in these obligatory parasites and its tapering anterior region may extend beyond the anterior margin of the sternal shield.

All the British dermanyssids have an anal shield bearing the three setae normally associated with the anus. It is typically sub-triangular or pear-shaped. An exception occurs in the genus *Myonyssus* (Text-fig. 15B) in which it is considerably broader than long. The region posterior and lateral to the postanal seta is invariably provided with aciculae. Secondary unpaired setae occur on the anal shield of some members of the genus *Haemogamasus*.

The ventral sclerotization of the female of *Ololaelaps* is exceptional in that there is a fusion of the genito-ventral, metapodal and anal elements to form a compound shield occupying almost the entire area of the opisthogaster (Text-fig. 15D).

The endo- and exopodal shields form a more or less complete framework enclosing coxal cavities II-IV in many of the free-living forms and facultative parasites. In *Pseudoparasitus*, *Ololaelaps*, *Laelaspulus* and some species of *Holostaspis* and *Gymnolaelaps*, the podal elements behind coxae IV become greatly enlarged (Text-fig. 15D). Varying degrees of reduction of the exopodal shields occur in the genera *Hypoaspis*, *Haemogamasus* and *Laelaps* and in the obligatory parasites only fragments of the podal shields remain, the most conspicuous being the one behind coxa IV.

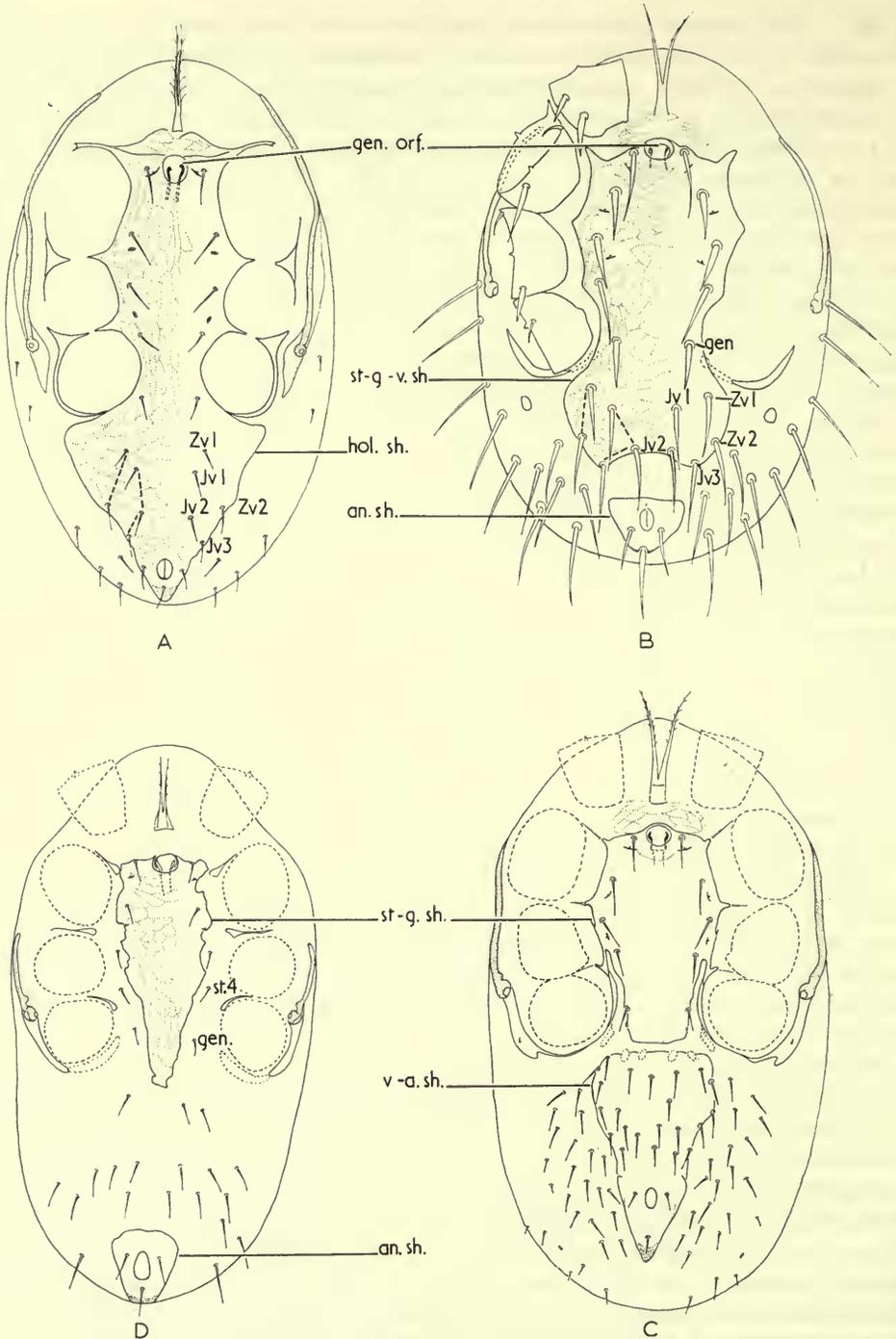


FIG. 16. Venter of male of: A. *Hypoaspis (Gaeolaelaps) aculeifer* (Canestrini); B. *Hyperlaelaps microti* (Ewing); C. *Macronyssus* sp.; D. *Ophionyssus natricis* (Gervais).

Metapodal shields are variable in form and number. In most free-living forms they are small, oval, elliptical or elongate bodies, but in *Eulaelaps* they become large subtriangular structures. Obligatory parasites usually have only one pair which is weakly sclerotized and difficult to discern. The metapodals may fuse with the genito-ventral shield as in *Ololaelaps* (Text-fig. 15D).

Stigmata and peritremes are of basically the same form as in the deutonymph. The peritrematal shield is fused with the dorsal shield anteriorly, except in some obligatory parasites. Posteriorly it may be free or fused with the podal shield in the region of coxa IV (Text-figs. 15A-C).

Typically, the males have a holovertral shield formed by the fusion of the sternal, metasternal, endopodal, genital, ventral and anal shields. It carries the four pairs of sternal setae, the genital setae, the three setae associated with the anus and a variable number of opisthogastric setae (Text-fig. 16A). In the free-living forms and the facultative parasites it is generally expanded posterior to coxae IV, but in some macronyssines it shows little or no expansion in this region. Deviations from the typical holovertral shield are apparent in some facultative and obligatory parasites. *Hyperlaelaps*, for example, has a compound sternito-genito-ventral shield and a separate anal shield (Text-fig. 16B). Further reduction of the ventral sclerotization occurs in *Ophionyssus natricis* (Degeer), the sclerotized areas comprising a sternito-genital and a separate anal shield (Text-fig. 16D). Certain species of *Macronyssus* show another variant in having a sternito-genital and a separate ventro-anal shield (Text-fig. 16C). The genital orifice, closed by a single valve, is always situated near the anterior margin of the "sternal shield" and is flanked by the first pair of sternal setae.

Legs

Segmental chaetotaxy: Without exception the legs are seven-segmented, the terminal segment being represented by the ambulacrum. The segments, from coxa to tarsus, have a well-defined chaetotaxy and the system of nomenclature and formulae for the segmental chaetotaxy follows that proposed by Evans (1963). This system, based on the observed ontogenetic development of the leg chaetotaxy in over 100 species of Gamasina and which has subsequently been found to be applicable to the Uropodina and Antennophorina, has been criticized by van der Hammen (1964) who, with little success, attempted to apply Grandjean's nomenclatural system for the leg chaetotaxy of the Oribatei and allied Actinochaeta to an adult macrochelid mite. His criticisms are: (a) that the existence of a basic whorl of setae on a segment was ignored; (b) that no attention was paid to the presence of the unpaired dorsal seta, *d*, and (c) that the segmental formulae are of little or no comparative value. Are these criticisms of the Evans system valid in the light of the observed segmental chaetotactic patterns on the legs of the Mesostigmata? In our opinion they are not, for the following reasons:

Grandjean (1940) considers the basic element of the segmental chaetotaxy to be a ring or whorl of setae consisting of a maximum of seven (oribatologists refer to this condition as "primitive"), namely, an unpaired dorsal, two pairs of laterals and one

pair of ventrals. The existence of a whorl of setae on the segment was not ignored by Evans and is implicit in his segmental formula

$$\left(al \begin{array}{c} ad \\ av \end{array} , \begin{array}{c} pd \\ pv \end{array} \rightarrow pl \right)$$

which van der Hammen overlooked and instead based his criticism on a simpler formula

$$\left(al \begin{array}{c} \text{dorsals} \\ \text{ventrals} \end{array} \rightarrow pl \right)$$

which was adopted only in those cases where the extreme non-cylindrical form of the segments (the femora and trochanters) made it impossible to distinguish the anterior and posterior members of the dorsal and ventral series. As regards the presence of an unpaired dorsal seta, there is no evidence from observed segmental patterns that such a seta exists on any leg segment (excluding perhaps tarsus I which has not been studied in detail) of the larva or any segments, excluding the tarsi, in subsequent developmental stages of the Gamasina and Uropodina. Van der Hammen's statement that Evans "did not pay attention to the definition of the unpaired dorsal seta *d* . . ." is contrary to the facts and one wonders whether the author has read

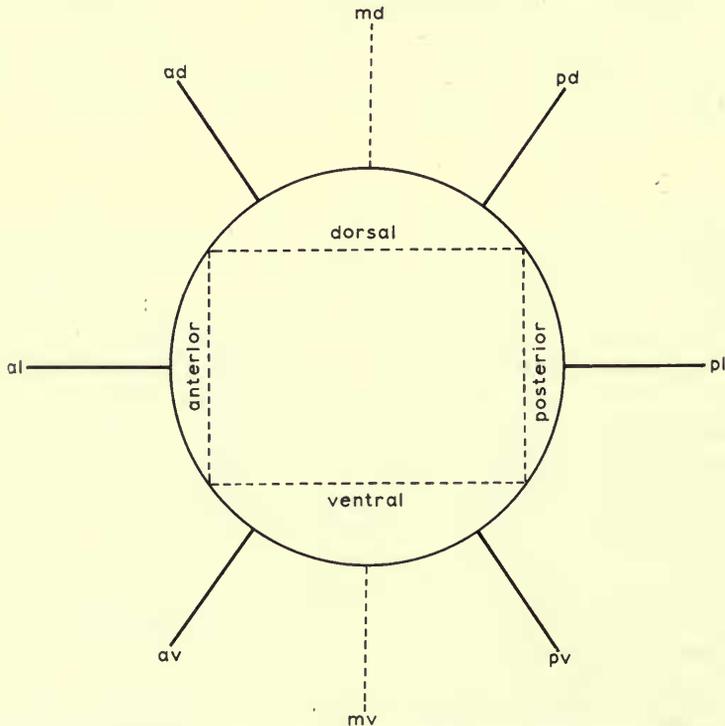


FIG. 17. Diagrammatic representation of the setal positions on a leg segment of a dermanyssid mite.

beyond the "introduction" in Evans' 1963 paper! In this paper attention is drawn to the appearance on tarsi II-IV of an unpaired dorsal and ventral seta at the protonymphal and deutonymphal stages respectively, and these are referred to as medio-dorsal (*md*) and medio-ventral (*mv*). If the observed position of these unpaired setae reflects their primary position on these segments, then the maximum complement of a segmental whorl in the Mesostigmata would be eight setae as shown diagrammatically in Text-fig. 17. Owing to a regression in the dorsal and ventral setae, the maximum complement of a whorl is apparently not present on other segments of the legs.

Van der Hammen's attempt to define the unpaired dorsal seta on the leg segments is characterized by such statements as "impossible to conclude whether the three plumose setae with a dorsal position are really *d*", "possibly dorsal plumose setae" and "probably dorsal setae". This uncertainty is inevitable and arises from an attempt to make the chaetotactic patterns fit a pre-conceived system. It is surprising that van der Hammen has used "probably dorsal setae" only in reference to certain setae on the dorsal surface of femur II, one of the segments showing an extreme non-cylindrical form which affects the primary chaetotactic pattern of the segment. In those forms which have a less specialized femur II, that is, the segment is more or less cylindrical, the longitudinal arrangement of the setae on its dorsal surface resembles that of genu II for which van der Hammen finds it impossible to define unpaired dorsal setae! The "migration" of setae from their normal (primary) position relative to other setae on a segment is common and is not only due to the asymmetrical development of the segment. More often the "migration" occurs as the result of the absence of one member of a "pair" of setae on the segment. The remaining seta often develops in an intermediate position along an imaginary line which would have connected the bases of the "pair". For example, four setae (*av*₁, *av*₂, *pv*₁, *pv*₂) whose bases form the corners of a rectangle often occur on the ventral surface of tibia I in the Gamasina, but in some groups *pv*₂ is lacking and the remaining member of the pair (*av*₂) may migrate to occupy a median position on the segment at the level of the line joining the bases of *av*₂ and *pv*₂ in the forms with four ventral setae. Such deviations from the normal distribution of setae on a segment add to the difficulty of applying any system of setal nomenclature based on "positional homology".

We reject van der Hammen's criticism of the segmental formulae which have proved to be of considerable practical value in referring to the segmental chaetotaxy. This author's alternative formula, which he considers "more logical" (?), depends on the recognition of unpaired dorsal setae and is completely impracticable.

It seems appropriate, in the present context, to refer to another fundamental difference between the system of nomenclature proposed by Evans and that used for the Actinochaeta. Although in both systems the positions of setae are defined in relation to certain faces of the segment, the lateral faces in the Grandjean system are defined according to the natural position of the limb relative to the longitudinal axis of the body, the anteriorly directed first two pairs of legs and the posteriorly directed legs III and IV having paraxial and anti-axial faces. In the system used in the Meso-

stigmata, on the other hand, the definition of the lateral faces (anterior and posterior) is not based on the natural, but on the artificial position of the limb, that is, when it is extended laterally at right angles to the longitudinal axis of the idiosoma. Adopting Grandjean's terminology for the lateral faces of the legs in the Mesostigmata would necessitate referring to the anterior and posterior faces of legs I and II as paraxial and anti-axial respectively, since these legs are directed anteriorly, retaining anterior and posterior for legs III which are directed laterally, and referring to the anterior and posterior faces of legs IV as anti-axial and paraxial respectively, since these limbs are directed posteriorly. In comparison with the existing system of setal terminology in the Mesostigmata, the advantages gained, if any, by basing the system on two (or three) different terminologies for the lateral faces of the limbs, would be at the expense of simplicity and practicability.

The segmental chaetotaxy of the legs in the larval dermanyssids we have examined is constant and normal for the Gamasina, as defined by Evans (1963). At the protonymphal stage one seta is added to the ventral surface of femur II and one medio-dorsal seta to each of tarsi II-IV, giving the following chaetotaxy:—

	I	II	III	IV
coxa . . .	2	2	2	I
trochanter . . .	$I-\frac{0}{2}-I$	$I-\frac{0}{2}-I$	$I-\frac{1}{2}-0$	$I-\frac{1}{2}-0$
femur . . .	$2-\frac{4}{2}-2$	$I-\frac{4}{2}-I$	$I-\frac{3}{1}-0$	$I-\frac{3}{0}-0$
genu . . .	$I-\frac{2}{1}, \frac{2}{1}-I$	$I-\frac{2}{0}, \frac{2}{0}-I$	$I-\frac{2}{0}, \frac{2}{0}-I$	$I-\frac{2}{0}, \frac{2}{0}-0$
tibia . . .	$I-\frac{1}{1}, \frac{2}{1}-I$	$I-\frac{1}{1}, \frac{2}{1}-I$	$I-\frac{1}{1}, \frac{2}{1}-I$	$I-\frac{1}{1}, \frac{2}{1}-I$
tarsus ⁵ . . .	—	$3-\frac{3}{2}, \frac{1}{0}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{0}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{0}, \frac{3}{2}-3$

Genus IV in the protonymphae of *Ophionyssus* and *Sauronyssus*, is exceptional in having six setae ($I-\frac{2}{0}, \frac{2}{0}-I$).

The deutonymphal and adult⁶ segmental complements in the free-living forms, for example, *Ololaelaps*, *Pseudoparasitus*, some *Hypoaspis* s. lat. and *Cosmolaelaps* is extremely constant. The segmental chaetotaxy may be summarized as follows:—

	I	II	III	IV
coxa . . .	2	2	2	I
trochanter . . .	$I-\frac{1}{3}-I$	$I-\frac{0}{3}-I$	$I-\frac{1}{3}-0$	$I-\frac{1}{3}-0$
femur . . .	$2-\frac{5}{4}-2$	$2-\frac{5}{3}-I$	$I-\frac{3}{1}-I$	$I-\frac{3}{1}-I$
genu . . .	$2-\frac{3}{2}, \frac{3}{1}-2$	$2-\frac{3}{1}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-I$	$2-\frac{2}{1}, \frac{3}{0}-I$
tibia . . .	$2-\frac{3}{2}, \frac{3}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-2$	$2-\frac{1}{1}, \frac{2}{1}-I$	$2-\frac{1}{1}, \frac{3}{1}-2$
tarsus ⁵ . . .	—	$3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$

Certain nest-inhabiting forms and facultative and obligatory parasites show considerable diversity in the segmental chaetotaxy of the legs at the deutonymphal and adult stages and these are discussed below. In the semi-diagrammatic representations of the segmental chaetotaxy in Text-fig. 18 the patterns marked (a) are considered to be the normal types for the family.

⁵ The chaetotaxy of tarsus I has not been studied in detail.

⁶ The deutonymphal complement of setae is invariably retained by the adult.

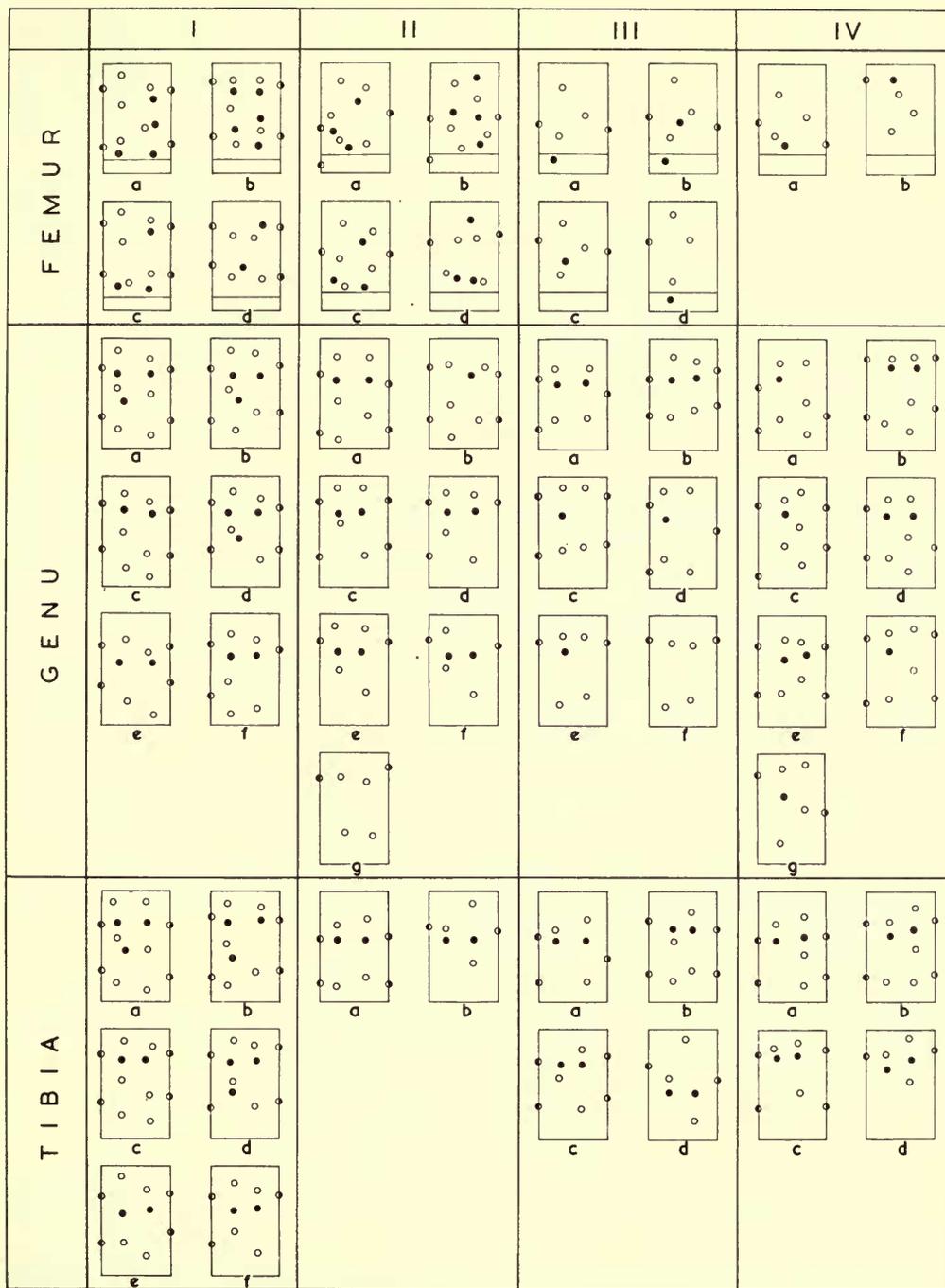


FIG. 18. Semi-diagrammatic representation of the chaetotaxy of selected segments of the legs of the Dermanyssidae.

Coxae I-IV: In the larva coxae I-III each carry two setae and this condition is retained in succeeding developmental stages. Coxa IV bears a single seta in post-larval instars. The coxal setae are normally simple but in many of the facultative parasites (*Laelaps*-group) certain of them, particularly on coxa I, become stout spines or spurs as the result of hypertrophy. Processes of non-setous origin may also occur on certain of the coxae. For example, in many facultative or obligatory parasites a stout, spine-like structure develops on the distal margin of the anterior face of coxa II (Text-figs. 15 A and B) and in *Hirstionyssus* stout spur- or ridge-like processes are present on coxae II and III and sometimes IV. The distal margin of the coxa is produced into a dorsal and a ventral condyle.

Trochanters I-IV: Trochanters I-III at the larval and protonymphal stages and trochanter IV in the protonymph each have four setae. In the deutonymphs and adults trochanter I normally carries six setae and trochanters II-IV five setae. An exception occurs in *Dermanyssus alaudae* (Schrank) which has only five setae ($1-\frac{0}{3}-1$) on trochanter I.

Femora I-IV (Text-fig. 18): Three variants of the normal complement of setae ($2-\frac{3}{1}, \frac{2}{3}-2$) of femur I have been observed. This segment (fig. b) in *Laelaspulus flexuosus* (Michael) shows an addition of one antero-ventral seta to the normal number, giving the formula ($2-\frac{3}{2}, \frac{2}{3}-2$). Many obligatory parasites [*Dermanyssus chelidonis* Oudemans, *D. hirundinis* (Hermann) and *D. quintus* Vitzthum, *Sauronyssus saurarum* (Oudemans) and *Ophionyssus natricis* (Deeger)] show a decrease in the number of ventral setae to three (fig. c) by the suppression of one postero-ventral seta ($2-\frac{3}{1}, \frac{2}{2}-2$). *D. alaudae* is exceptional in retaining the larval complement of setae ($2-\frac{3}{1}, \frac{2}{1}-2$) on this segment throughout ontogeny (fig. d). No setae occur proximal to the circumsegmental fissure.

Exceptions to the normal pattern ($2-\frac{3}{1}, \frac{2}{2}-1$) of femur II have been observed in *Haemogamasus hirsutosimilis* Willmann ($2-\frac{3}{1}, \frac{2}{3}-1$) which has an additional postero-ventral seta (fig. b), in *O. natricis*, *D. quintus* and *S. saurarum* which lack al_2 ($1-\frac{3}{1}, \frac{2}{2}-1$), fig. c, and in *D. alaudae* which differs from the latter group in having only two setae in the antero-dorsal series ($1-\frac{2}{1}, \frac{2}{2}-1$), fig. d. Seta al_2 , when present, is situated proximal to the circumsegmental fissure.

The normal complement of setae on femur III is six ($1-\frac{3}{1}-1$), of which the antero-ventral is situated proximal to the circumsegmental fissure. Although this number of setae also occurs on femur III in *Pellonyssus reedi* (Zumpt and Patterson) the ventral seta is situated distad of the fissure (fig. c). Two other types of chaetotaxy have been observed; in *H. hirsutosimilis* two ventral setae are developed ($1-\frac{3}{2}-1$) fig. b, whilst in *D. alaudae*, *chelidonis* and *hirundinis*, and in *S. saurarum*, the larval complement ($1-\frac{3}{1}-0$) is retained throughout ontogeny (fig. d).

The number of setae on femur IV is remarkably stable and the only exception we have found to the normal pattern ($1-\frac{3}{1}-1$) is in *D. alaudae* which has only five setae ($1-\frac{3}{1}-0$) fig. b.

Genua I-IV (Text-fig. 18): The apparent great diversity in the segmental chaetotaxy of the genua in the Dermanyssidae is somewhat misleading since the majority of the "variants", except on genu IV, occur in a single genus, *Dermanyssus*.

Exceptions to the normal chaetotaxy ($2-\frac{3}{2}, \frac{3}{1}-2$) of genu I are found, with the exception of *Pseudolaelaps doderoi* Berlese, only amongst the obligatory parasites. In *S. saurarum*, *O. natricis* and *D. chelidonis*, the setation is deficient in one postero-dorsal member ($2-\frac{3}{2}, \frac{2}{1}-2$, fig. *b*) whilst in *P. doderoi* and in some populations of *O. sylviarum* an antero-ventral seta is lacking ($2-\frac{3}{1}, \frac{3}{1}-2$, fig. *c*). The remaining three types of chaetotaxy have been observed in *D. hirundinis* ($2-\frac{3}{2}, \frac{2}{1}-2$, fig. *d*), *D. alaudae* ($2-\frac{2}{1}, \frac{2}{1}-2$, fig. *e*) and *D. quintus* ($2-\frac{3}{1}, \frac{2}{1}-1$, fig. *f*).

The normal pattern ($2-\frac{3}{1}, \frac{2}{1}-2$) of genu II occurs in all the British dermanyssids except *P. doderoi* and some species of *Dermanyssus*. In *P. doderoi* the antero-ventral seta is lacking ($2-\frac{3}{0}, \frac{2}{1}-2$ fig. *b*) whilst in *D. chelidonis* the antero-dorsal series is unideficient ($2-\frac{2}{1}, \frac{2}{1}-2$ fig. *c*). Further specializations are seen in *D. quintus* ($2-\frac{2}{1}, \frac{2}{1}-1$, fig. *d*) and in *D. alaudae* which retains the larval complement of setae ($1-\frac{2}{0}, \frac{2}{0}-1$, fig. *g*) throughout ontogeny. The chaetotaxy of this segment shows considerable intraspecific variation in *D. hirundinis* ($2-\frac{2}{1}, \frac{2}{1}-1, 1-\frac{2}{1}, \frac{2}{1}-1$, fig. *e* and $1-\frac{2}{1}, \frac{1}{1}-1$, fig. *f*).

Five different chaetotactic patterns have been observed on genu III, excluding the normal ($2-\frac{2}{1}, \frac{2}{1}-1$). Thus, members of the genera *Ophionyssus* and *Pellonyssus* and *Ornithonyssus bacoti* (Hirst) and *S. saurarum* have ten setae ($2-\frac{2}{1}, \frac{2}{1}-2$, fig. *b*) on this segment; *D. chelidonis* and *O. sylviarum* have nine setae, but differ from the normal form in lacking pv_1 and having two postero-laterals ($2-\frac{2}{1}, \frac{2}{0}-2$, fig. *c*); *Hyperlaelaps amphibia* Zachvatkin and *H. microti* (Ewing), and *P. doderoi* bear 8 setae ($2-\frac{2}{1}, \frac{2}{0}-1$, fig. *d*), *D. hirundinis* has seven setae ($1-\frac{2}{1}, \frac{2}{0}-1$, fig. *e*) and finally, *D. alaudae* retains the larval complement ($1-\frac{2}{0}, \frac{2}{0}-1$, fig. *f*).

Genu IV shows the greatest diversity in chaetotaxy of all leg segments in the British Dermanyssidae. In addition to the normal pattern ($2-\frac{2}{1}, \frac{3}{0}-1$), six other types of chaetotaxy have been observed, namely:—

fig. *b*, ($2-\frac{2}{1}, \frac{3}{1}-2$) in *Pellonyssus*, *Laelaps agilis* Koch, *O. bacoti* and *O. natricis*.

fig. *c*, ($2-\frac{2}{1}, \frac{3}{0}-2$) in *Laelaps echidnina*, *hilaris*, *muris*; *Hyperlaelaps amphibia* and *microti*; *Eulaelaps stabularis* and *nova*; *Androlaelaps casalis* and *fahrenheiti*; *Hypoaspis* (*G.*) *sardoa*; *Ondatraelaps multispinosa* and *Laelaspulus flexuosus*.

fig. *d*, ($2-\frac{2}{1}, \frac{3}{1}-1$) *Pneumolaelaps*, *Hypoaspis* (*G.*) *lubrica*; *Melittiphis alvearius*; *Macronyssus*; *Steatonyssus periblepharus* and *Ornithonyssus sylviarum*.

fig. *e*, ($2-\frac{2}{1}, \frac{2}{1}-2$) in *Sauronyssus saurarum*

fig. *f*, ($2-\frac{2}{1}, \frac{2}{0}-2$) in *Dermanyssus chelidonis*

fig. *g*, ($1-\frac{2}{1}, \frac{2}{0}-1$) in *Dermanyssus alaudae*, *hirundinis* and *quintus*.

Tibiae I-IV (fig. 18): With the exception of *P. doderoi*, deviations from the normal setal pattern of tibia I ($2-\frac{3}{2}, \frac{3}{1}-2$) have been noted only in the obligatory parasites. Three of the "variants" occur in the genus *Dermanyssus*, namely, ($2-\frac{2}{2}, \frac{2}{1}-2$, fig. *d*) in *D. chelidonis* and *hirundinis*; ($2-\frac{2}{1}, \frac{2}{1}-2$, fig. *e*) in *D. alaudae* and ($2-\frac{2}{1}, \frac{2}{1}-1$) fig.

f) in *D. quintus*. The remaining two types ($2-\frac{3}{2}, \frac{2}{1}-2$, fig. b) and ($2-\frac{3}{1}, \frac{3}{1}-2$, fig. c) have been found in *Pellonyssus*, *Sauronyssus saurarum* and *Ophionyssus natricis*, and in *P. doderoi* and some forms of *O. sylviarum*, respectively.

The only exceptions to the normal segmental chaetotaxy of tibia II ($2-\frac{2}{1}, \frac{2}{1}-2$) occur in *Dermanyssus alaudae*, *chelidonis*, *hirundinis* and *quintus* which retain the larval complement of setae throughout ontogeny ($1-\frac{1}{1}, \frac{2}{1}-1$, fig. b).

In addition to the normal form ($2-\frac{1}{1}, \frac{2}{1}-1$), the following three types of chaetotaxy are found on tibia III :

fig. b, ($2-\frac{2}{1}, \frac{2}{1}-2$) in the ethiopian species *Steatonyssus tibialis* Till and Evans.

fig. c, ($2-\frac{1}{1}, \frac{2}{1}-2$) in *Pellonyssus*, *Steatonyssus* (except *tibialis*), *Ornithonyssus bacoti* and *sylviarum*; *S. saurarum*, *O. natricis*, *Melittiphis alvearius*, *Hypoaspis* (G.) *sardoa* and *Laelaspulus flexuosus*.

fig. d, ($1-\frac{1}{1}, \frac{2}{1}-1$) in *Hyperlaelaps amphibia* and *Dermanyssus alaudae*, *chelidonis*, *hirundinis* and *quintus*. This is the larval pattern.

Only in the obligatory parasites have we observed variants of the normal chaetotaxy of tibia IV ($2-\frac{1}{1}, \frac{3}{1}-2$). *S. tibialis* has eleven setae on this segment ($2-\frac{2}{1}, \frac{3}{1}-2$, fig. b), *S. saurarum* nine setae ($2-\frac{1}{1}, \frac{2}{1}-2$, fig. c) and *Dermanyssus alaudae*, *chelidonis*, *hirundinis* and *quintus* have the protonymphal complement of seven setae ($1-\frac{1}{1}, \frac{2}{1}-1$, fig. d).

Tarsi I-IV : The chaetotaxy and the form of the distal sensory region of tarsus I have not been studied in detail in the present work. The ontogenetic development of the chaetotaxy of tarsi II-IV is extremely constant, the basic adult complement of eighteen setae ($3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$) being present in the majority of the species. In the obligatory parasites there is a tendency for the reduction in the size of setae ad_1 and pd_1 which may be represented by microsetae or be lacking.

Ambulacra (Text-figs. 19A-D) : Little attention has been paid previously to the structure of the pretarsus and the ambulacrum in the Mesostigmata. The following account of the structure and mode of functioning of the ambulacral apparatus is based on that of *Haemogamasus hirsutus* Berlese.

The striated, sclerotized components of the pretarsus form a more or less rigid sheath. In the distal half of the pretarsus the sclerotized elements of the floor are thickened medially to form two slender, internal, longitudinal struts, the median *pretarsal apodemes* (*ptr. apod.*). Anterior to the apodemes lies a well-defined, dorsally directed U-shaped *basilar sclerite* (*bas. scl.*). It is pivoted by its base to the anterior processes of the pretarsal apodemes. A tendon (basilar tendon, Text-fig. 19D) is attached to the basal region of the basilar sclerite but its origin is difficult to trace in whole mounts of the tarsus and pretarsus. It appears to run ventrally through the tarsus and to be connected to a muscle originating in the tibia. A second unpaired sclerotized structure, the *pulvitractor sclerite* (*pulv. scl.*) is situated medially within the pulvillar mass immediately anterior and

dorsal to the basilar sclerite. In *H. hirsutus* it forms a dorsally directed hook-like process with a bifid base. Its basal limbs are movably articulated with the dorsally directed arms of the basilar sclerite. The paired lateral claws, each with a deep proximo-internal acetabulum, appear also to be articulated with the limbs of the pulvitractor and/or basilar sclerite. Lying dorsal to the apodemes and sclerites is a strong median tendon (*pulvitractor tendon*) connected distally with the pulvillus and by way of the pulvillus to the dorsal hook of the pulvitractor sclerite. It runs the entire length of the pretarsus and is connected to a strong retractor muscle originating within the basi-tarsus. Near the junction of the pretarsus and tarsus the tendon passes between the limbs of a dorsally directed Y-shaped apodeme (*pulvitractor guide*). The lateral elements of the pretarsal sheath are produced distally into denticulate lobes which Krantz (1962) has referred to in the Macrochelidae as the "laterodistal pretarsal elements". In view of their apparent function we propose renaming these lobes the *pretarsal opercula* (*ptr. op.*). The true form of the pulvillus

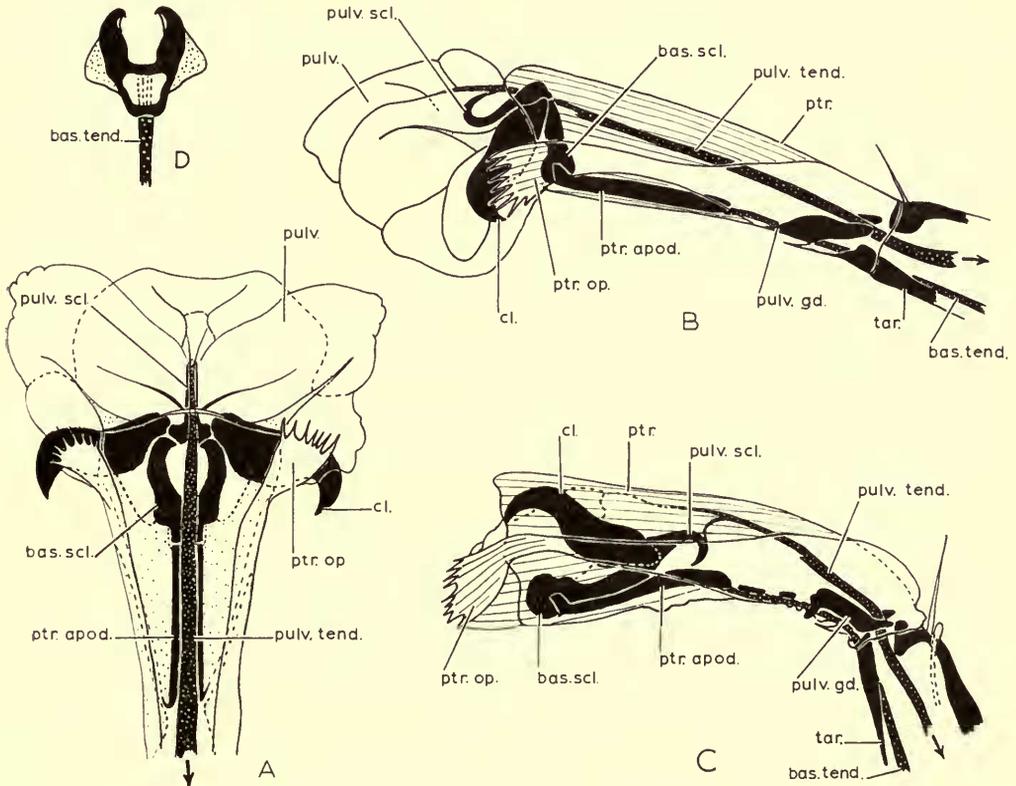


FIG. 19. Ambulacrum and pretarsus of *Haemogamasus hirsutus* Berlese. A. Dorsal view from a compressed preparation; B. partially retracted ambulacrum in lateral view; C. fully retracted ambulacrum in lateral view; D. Basilar sclerite with tendon.

is difficult to ascertain since it is invariably distorted during preparation for study. From compressed mounts it appears to comprise ventral, dorsal and lateral elements. It is provided with weakly sclerotized "veins" (Text-fig. 19A).

The function of the tarsal muscle and its tendon is to withdraw the ambulacrum into the pretarsal sheath and this is made possible by the nature of the articulations between the apodemes of the pretarsus and the basilar sclerite, and between the limbs of the basilar sclerite and the pulvitractor sclerite. As the muscle contracts the backwardly directed pull of the pulvitractor tendon on the pulvillus and on the pulvitractor sclerite causes the pulvillus and the claw-complex (basilar and pulvitractor sclerites and claws) to be retracted into the pretarsal sheath (Text-fig. 19B). At maximum retraction the basilar sclerite and the pulvitractor sclerite lie over the rigid median pretarsal apodemes with the hook of the pulvitractor sclerite directed ventrally and the claws directed anteriorly (Text-fig. 19C). Also at this stage the anterior margins of the pretarsal opercula meet and together form a protective "lid" to the pretarsal sheath.

The mode of extension of the ambulacral apparatus will remain somewhat problematical until the definite origin of the tendon of the basilar sclerite has been elucidated. If, as it appears, it is the tendon of a tibial protractor muscle, then contraction of this muscle would have the effect of pushing forward the basilar sclerite on its pivot when tension through the pulvitractor tendon is released. Thus, the ambulacrum would be operated by a pair of antagonistic muscles, the *pulvillar retractor* and the *basilar protractor*.

The ambulacral apparatus has this basic form throughout the Dermanyssidae although there is considerable diversity in the shape of the sclerotized structures, particularly the basilar and pulvitractor sclerites and the pretarsal opercula, and in the degree of the development of the claws. Normally in the dermanyssines paired claws are present on all legs and those of legs II-IV are usually stronger and larger than those of leg I which is chiefly sensory and not ambulatory in function. Claws are absent or strongly reduced on leg I of *Stratiolaelaps miles* Berlese and *Eulaelaps nova* Vitzthum and on legs I-IV of *Ondatratalaelaps multispinosa* (Banks) and *Laelaps muris* Koch.

Form of the leg setae: The leg setae are generally simple or pilose in form but throughout the family there is a tendency for certain setae, particularly the ventral setae of the femora, genua and tibiae of leg II and the distal setae of tarsi II-IV to enlarge and form stout spine- or spur-like structures (Text-fig. 20C). Hypertrophy of setae on leg II is not restricted to the male as is usual in the Gamasina. Seta av_1 on femur II in both sexes of certain *Androlaelaps* may be affected and, to a lesser extent, seta av_1 on the genu and tibia of this leg. In *Hypoaspis* (*Gaeolaelaps*) *nidicorva*, on the other hand, seta av_2 of femur II hypertrophies (Text-fig. 20A). On the tarsi, setae al_1 , pl_1 , av_1 and pv_1 usually show some enlargement in comparison with other tarsal setae and in *Eulaelaps nova* setae ad_2 , pv_2 and mv on tarsus II are also spur-like (Text-fig. 20B). Some members of *Hirstionyssus* have the tarsal setae av_1 and pv_1 developed into stout hook-like structures.

Certain coxal setae are often enlarged in the *Laelaps*-group and in many of the facultative parasites seta ad_1 and to a lesser extent, seta pd_1 on femur I and II are considerably stronger and longer than other femoral setae. The relative increase in

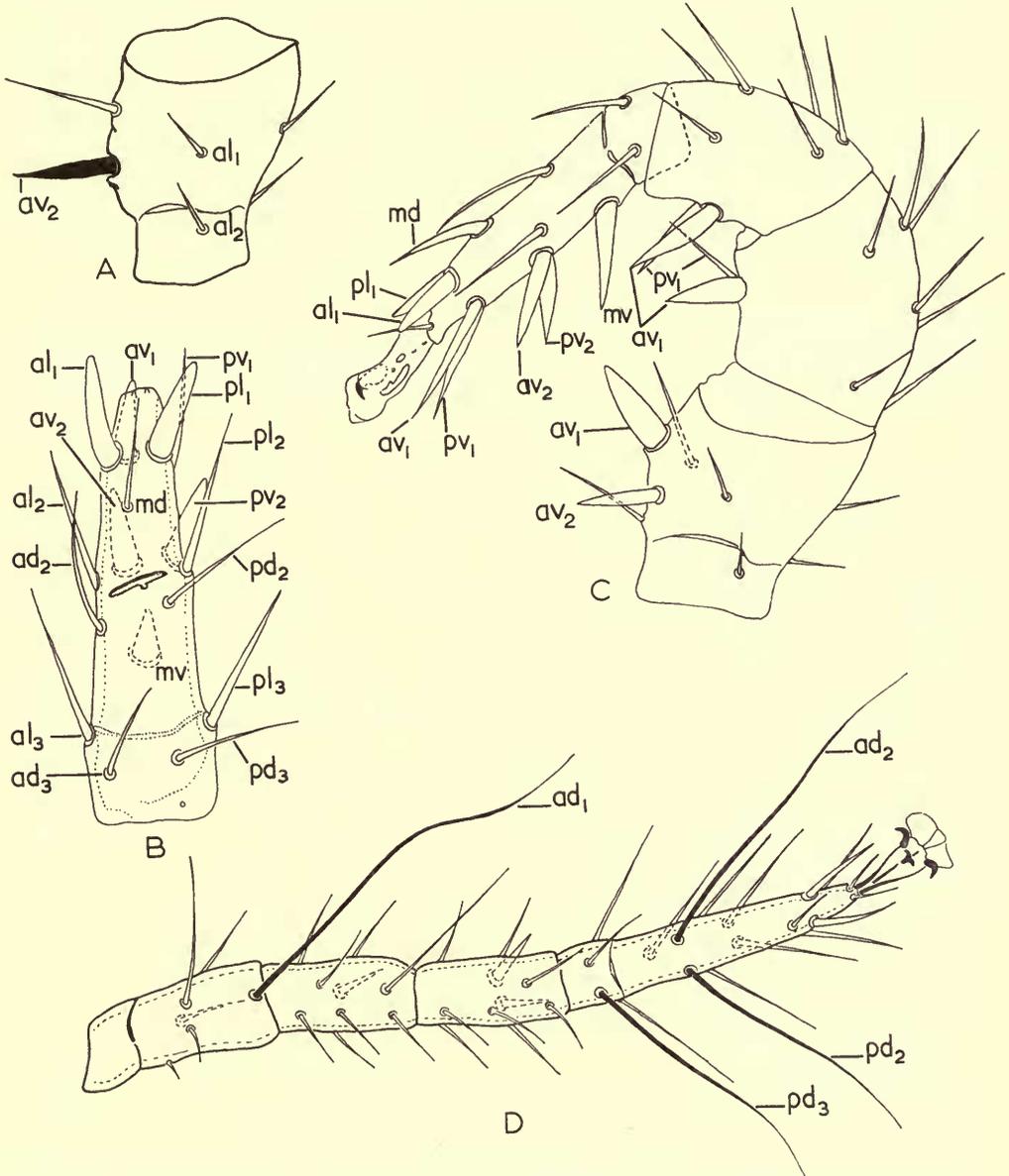


FIG. 20. A. Femur II, anterior view, of *Hypoaspis (Gaeolaelaps) nidicorva* sp. nov. female; B. dorsal view of tarsus II of *Eulaelaps nova* Vitzthum, female; C. anterior view of leg II (femur to tarsus) of *Hypoaspis (H.) krameri* (Canestrini) male; D. dorsal view of leg IV (femur to tarsus) of *Hypoaspis (H.) krameri* (Canestrini).

length of specific leg setae is also apparent in *Hypoaspis (H.) krameri*, for example, on leg IV seta ad_1 on the femur and setae ad_2 , pd_2 and pd_3 on the tarsus are long and whip-like (Text-fig. 20D).

Cuticular processes of non-setous origin: Reference has already been made to the occurrence of setiform or spiniform cuticular processes on the chelicerae at the junction of the second segment and the arthroidal membrane at the base of the movable digit. Such processes are by no means restricted to the trophic appendages but commonly occur at the distal margins of certain pedipalpal and leg segments. Generally, they are better developed on the basal segments of the appendages, particularly the coxae. The processes show considerable diversity in form and number. In their least specialized form (Text-fig. 21A), they appear as a more-or-less

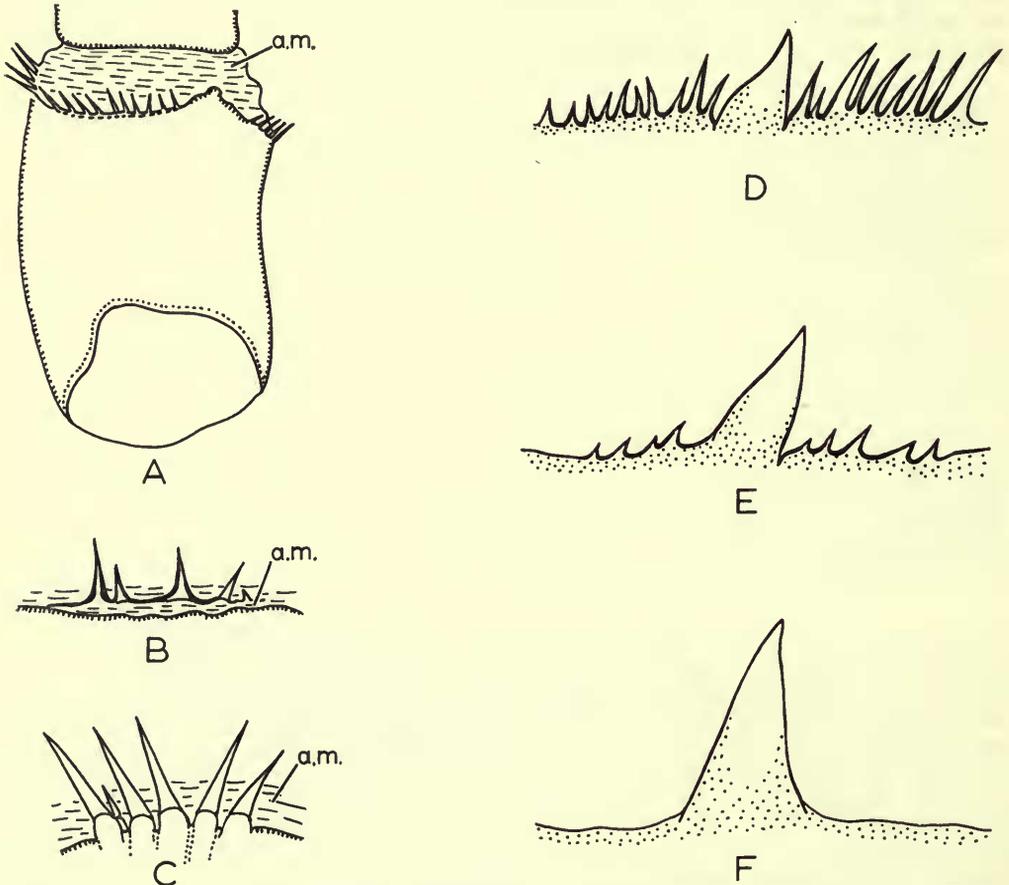


FIG. 21. A. Coxa I of *Haemogamasus hirsutus* Berlese, dorsal view, showing processes on distal margin of segment; B. processes free from distal margin of segment; C. processes fused with distal margin of segment; D-F. processes on distal margin of anterior (paraxial) face of coxa II in D. *Haemogamasus hirsutus* Berlese; E. *Laelaps agilis* Koch; F. *Macroonyssus flavus* (Kolenati).

complete circumsegmental fringe of spines on the distal margin of the segment. The spines appear to have their origin on the arthroal membrane in close proximity to the distal margin of the segment (Text-fig. 21B), but by the sclerotization of the narrow strip of membrane between the segment and the processes, they become incorporated with the segment (Text-fig. 21C). Reduction in the number of processes is common to the extent that only one, two or three spines of the circumsegmental fringe remain and these are usually located on the anterior face of the limb. The remaining process (or processes) is better developed than the individual members of a circumsegmental fringe. It is possible to trace the regression in the number of marginal processes on the anterior face of coxa II in the Dermanyssidae. In free-living species, for example members of the genera *Ololaelaps* and *Pseudoparasitus*, the fringe is composed of spine-like processes of approximately equal size, but in certain of the facultative parasites a medial process of the fringe hypertrophies as in *Haemogamasus hirsutus* (Text-fig. 21D). A similar hypertrophy of a medial process occurs in *Laelaps agilis* but this is also accompanied by a reduction in the number and size of the remaining processes (Text-fig. 21E). Finally, in certain obligatory parasites (*Macronyssus* and *Steatonyssus*) only the hypertrophied medial process remains and this forms the stout anterior coxal spine (Text-figs. 15A and B, 21F).

Van der Hammen (1964) has referred to the cuticular processes on the distal margin of the external face of the *basis capituli* and on the antero-distal margin of coxa I as the latero-coxal setae and has unhesitatingly homologized them with the latero-coxal spines *e* and *e1* in the Actinochaeta. These are not setae and each represents a cuticular process originating from the junction of the segment and the arthroal membrane as described above. In many forms of Mesostigmata a fringe of spines occurs on the distal margins of the lateral face of the *basis capituli* to which the pedipalp trochanter is articulated and throughout the group there is a tendency for a reduction in the number of spines. To designate such a single process, which is rarely present in the group, a latero-coxal seta, seems unwarranted. There is no available evidence upon which to base the homology of the cuticular processes in the Mesostigmata with the latero-coxal spines of the Actinochaeta and we deprecate the application of the symbols *e* and *e1* to any of the cuticular processes associated with the pedipalpal "coxae" or the coxae of leg I, respectively.

Rows of spine-like cuticular processes also occur on the unsclerotized pre-sternal cuticle and regionally on the leg segments and *basis capituli* of many facultative parasites such as *Haemogamasus*. Spur-like structures, not hypertrophied setae, are present on certain of the coxae of *Hirstionyssus*. The functions of these various cuticular processes are not known.

Lyriform fissures: Fissures occur on the femora and tarsi of legs I-IV. Two lyriform fissures in the basal third of each femur are connected and form a complete or interrupted circumsegmental fissure which secondarily divides the segment into proximal and distal sections (Text-figs. 20A and C). The fissures on the basal third of the tarsi similarly divide these segments into two regions, but the circumsegmental fissure on tarsus I is usually less well developed than on the other tarsi. For example, in many obligatory parasites the fissure is interrupted dorsally and the isolated

proximodorsal fissure assumes the characteristic form of a lyriform fissure. A dorsal lyriform fissure, distinct from those forming the circumsegmental fissures, is also present on tarsi II-IV (Text-fig. 20B).

DISCUSSION

Members of the family Dermanyssidae show considerable diversity in morphology and biology largely as the result of the specializations exhibited by the parasitic forms which have become adapted to life in the great variety of niches afforded by their hosts. Within the family the free-living species, on the one hand, and the obligatory parasites, on the other, appear to form the extremes of a morphological continuum, the connecting link between them being provided by the morphological characteristics of nest inhabitants and facultative parasites. Species of these extreme groups have different morphological properties: the free-living forms show little diversity in morphology in comparison with the obligatory parasites which display marked morphological plasticity. This morphological plasticity is evident in the grades of specialization found amongst congeners, for example the degree of specialization of the gnathosoma in *Haemogamasus*, and in the higher incidence of intraspecific variability in morphological "characters".

The most spectacular morphological adaptations are associated with changes in feeding habits, and may be seen in the specialization of the trophic appendages and associated gnathosomal structures and in the reduction of idiosomal sclerotization in the monophagous obligatory parasites. Taxonomic characters based on these adaptive morphological structures have long played a dominant role in the suprageneric classification of the family. Less spectacular, but nevertheless of considerable taxonomic importance, are the differences in chaetotaxy between the free-living and parasitic forms. Deviations from the normal adult chaetotaxy, particularly of the segments of the pedipalps and legs, are due to a retardation in the normal ontogenetic development of the chaetotaxy. The retention of the larval complement of setae on a segment throughout ontogeny (localized neoteny) is not uncommon, although in most cases deficiency in adult chaetotaxy is due to the subnormal number of setae added to the protonymphal complement at the deutonymphal stage. Retardation in normal ontogenetic development also affects the dorsal idiosomal sclerotization in the obligatory parasites which tend to retain, to a greater or lesser degree, the form of the protonymphal scutal elements in succeeding developmental stages. In addition to the structural adaptations, many of the facultative and obligatory parasites show some degree of specialization of the life cycle. There is a general tendency for ovoviviparity and, more rarely, viviparity to occur and in the Macronyssinae the normally active, feeding, deutonymphal stage of the family is replaced by an inactive, non-feeding instar which shows considerable degeneration of the feeding and sensory organs.

The morphological and biological diversity displayed by the Dermanyssidae provides the taxonomist with numerous readily definable characters which are pre-eminently suitable for the practical differentiation of the taxa, that is, for a classification emphasizing differences between species. This is essentially the basis of the present classification of the family where the exaggerated importance given to one or

two morphological characters has resulted in a plethora of supraspecific taxa. Such a classification, which can be readily expressed in key form, serves a very useful purpose as a tool for identification. A more natural classification of the family requires emphasis to be made on resemblances rather than differences between its members, but in the elaboration of such a classification the considerable diversity in the morphology of facultative and obligatory parasites, resulting from variations in the degree of specialization of various parts of the body, not only between groups of species but also amongst closely related (congeneric) species, will inevitably add to the difficulty of defining distinct supraspecific categories.

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ABBREVIATIONS USED IN TEXT-FIGURES

a.m.	arthrodial membrane	bas. scl.	basilar sclerite
ac.	aciculae	bas. tend.	basilar tendon
acet.	acetabulum		
ad ₁₋₃	antero-dorsal setae		
al ₁₋₂	antero-lateral setae	c. gr.	capitular groove
an. sh.	anal shield	c. s.	capitular seta
ant. sp.	anterior spine	ch.	chelicera
ar. pr.	arthrodial processes	cl.	claw
av ₁₋₃	antero-ventral setae	corn.	corniculi

d ₁₋₃	dorsal setae	ptr.	pretarsus
d.d.	deutosternal denticles	ptr. apod.	pretarsal apodeme
d.l.f.	dorsal lyriform fissure	ptr. op.	pretarsal operculum
d.s.	dorsal seta of chelicera	pulv.	pulvillus
		pulv. gd.	pulvitractor guide
end. sh.	endo podal shield	pulv. scl.	pulvitractor sclerite
exp. sh.	expodal shield	pulv. tend.	pulvitractor tendon
		PV ₁₋₂	postero-ventral setae
f.d.	fixed digit	PX ₂₋₃	posterior accessory setae
fem.	femur	pyg. sh.	pygidial shield
g.b.	gnathosomal base	r2-6	marginal series of podonotal setae
g-v. sh.	genito-ventral shield		
g-v-a. sh.	genito-ventro-anal shield	R1-7	marginal series of opisthonotal setae
gen.	genital seta		
gen. orf.	genital orifice		
gen. sh.	genital shield	s1-6	lateral series of podonotal setae
hol. sh.	holoventral shield	S1-5	lateral series of opisthonotal setae
hyp. 1-3	hypostomal setae		
		s.s.	salivary stylus
int. mal.	internal malae	sg.	stigma
		sp.	spermadactyl
j1-6	dorsal series of podonotal setae	st. 1-3	sternal setae
J1-5	dorsal series of opisthonotal setae	st. 4	metasternal seta
		st-g. sh.	sternito-genital shield
Jv1-5	internal ventral setae	st-g-v. sh.	sternito-genito-ventral shield
		st. met. sh.	sterno-metasternal shield
		st. sh.	sternal shield
l. f.	lyriform fissure		
lat. in.	lateral incision	tar.	tarsus
lat. l. f.	lateral lyriform fissure	tect.	tectum capituli
lb.	labrum	ten. dep.	depressor tendon
		ten. lev.	levator tendon
m. d.	movable digit	troch.	trochanter
md.	medio-dorsal seta	trt.	tritosternum
mes. sc.	mesonotal scutellae		
met. sh.	metasternal shield	UR	submarginal series of opisthonotal setae
mp. sh.	metapodal shield		
p. 1-3	pores		
p.d.	pilus dentilis	v ₁₋₂	ventral setae
pan.	paranal seta	v-a. sh.	ventro-anal shield
pd ₁₋₃	postero-dorsal setae		
pd.	podal shield	x	supernumerary seta
per.	peritreme		
per. sh.	peritrematal shield	z1-6	median series of podonotal setae
pl ₁₋₂	postero-lateral setae		
pod. sh.	podonotal shield	Z1-5	median series of opisthonotal setae
pon.	postanal seta		
pr.	process on palp trochanter	Zv1-2	medio-lateral ventral setae

