

THE EXTERNAL MORPHOLOGY OF THE POST-EMBRYONIC
DEVELOPMENTAL STAGES OF *SPINTURNIX MYOTI* KOL.
(ACARI : MESOSTIGMATA)

BY

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Introduction.

Mites of the genus *Spinturnix* Heyden (fam. Spinturnicidae) are exclusively ectoparasites of Chiroptera, especially of the families Natalidae and Vespertilionidae. They occur on the wing membranes, and more rarely on the tail membrane, of the host and exhibit marked morphological and biological adaptations for life in this specialized habitat. RUDNICK (1960) in a major contribution to the taxonomy of the Spinturnicidae has referred to some of these adaptations, for example, the form of the idiosoma and ambulatory appendages, and the intrauterine development of the egg and "larva". No detailed study appears to have been made on the morphology of the immature stages particularly of the ontogenetic development of the idiosomal and leg chaetotaxy which shows such interesting modifications in the parasitic members of related groups in the Dermanyssoidea (EVANS & TILL, 1965).

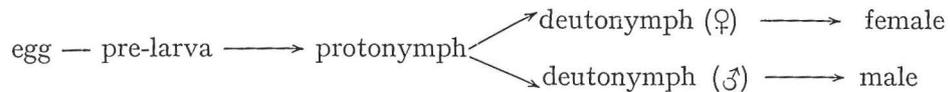
The present account of the morphology of *Spinturnix myoti* Kolenati is based on material collected from *Myotis myotis myotis* at Bergamo, Italy by A. GHIDINI in 1911 (see HIRST, 1927) and preserved in 70 % alcohol.

Life-cycle.

The developmental cycle of the Spinturnicidae has been the subject of considerable discussion in the literature and the opinions of OUDEMANS (1902, 1904 and 1910), VITZTHUM (1932) and BAER (1952), among others, have been reviewed by RUDNICK (loc. cit.). According to this author the life-cycle comprises five distinct

stages : egg, larva, protonymph, deutonymph (male or female) and adult. He considered the "nympha accessoria" of OUDEMANS to be the female deutonymph. I am able to confirm in *S. myoti* the existence of dimorphism at the deutonymphal stage but after numerous dissections of pregnant females I have not succeeded in finding a true larval instar in the life-cycle. The only hexapod stage occurring *in utero* has the characteristics of an embryonic "pre-larva". Thus, the legs, chelicerae and pedipalps are in early stages of development and are closely adpressed to the ventral surface of the idiosoma. Although showing incipient segmentation these appendages, and for that matter also the idiosoma, are devoid of setae. The legs lack ambulacra.

Development appears to proceed directly from the egg to the protonymph by way of the pre-larva ; there is no larval instar comparable to that which normally occurs in the developmental cycle of the Mesostigmata. The life-cycle may be summarized as follows :



External Morphology of S. myoti

Gnathosoma : The gnathosoma is relatively small and lies between the enlarged coxae of the first pair of legs. Certain of its structures show considerable specialization for haematophagy.

The three-segmented chelicerae of the protonymph, deutonymph and female are essentially similar in form. The second segment terminating in a small bidentate fixed digit, is markedly attenuated in its distal half and is about twice the length of the basal (or first) segment (fig. 1 C). A subtriangular movable digit bearing 6-7 sharply pointed teeth along its cutting edge has a condylar-acetabular articulation with the second segment and its movement is controlled by a pair of opposed muscles originating within the basal segment of the chelicera and connected to the digits by tendons -- a dorsal levator (*lev. tend.*) and a ventral depressor (*lev. dep.*). The movable digit overlaps the proximal half of the fixed digit so that its dentate cutting edge is exposed dorsally (fig. 1 C). Lyrifissures, setae and arthrodial processes are absent. In the male the second segment is only moderately attenuated and both digits are relatively long and slender (figs. 1 F & G). Nine or ten retrorse denticles occur on the fixed digit and the movable digit is uni- or bi-dentate. The dorsally directed spermadactyl is free distally and the sperm groove extends along its entire length.

The basis capituli is subrectangular in outline with its length never more than 1.2 times its breadth (fig. 1 A). It bears a pair of conspicuous capitular setae (*c. s.*) but the deutosternal groove and associated denticles are lacking. The absence of the groove and denticles is probably correlated with the reduction of the tritosternum to a small sclerotized platelet. (The main function of the deutosternal denticles in the Gamasina appears to be the retention of the laciniae of the trito-

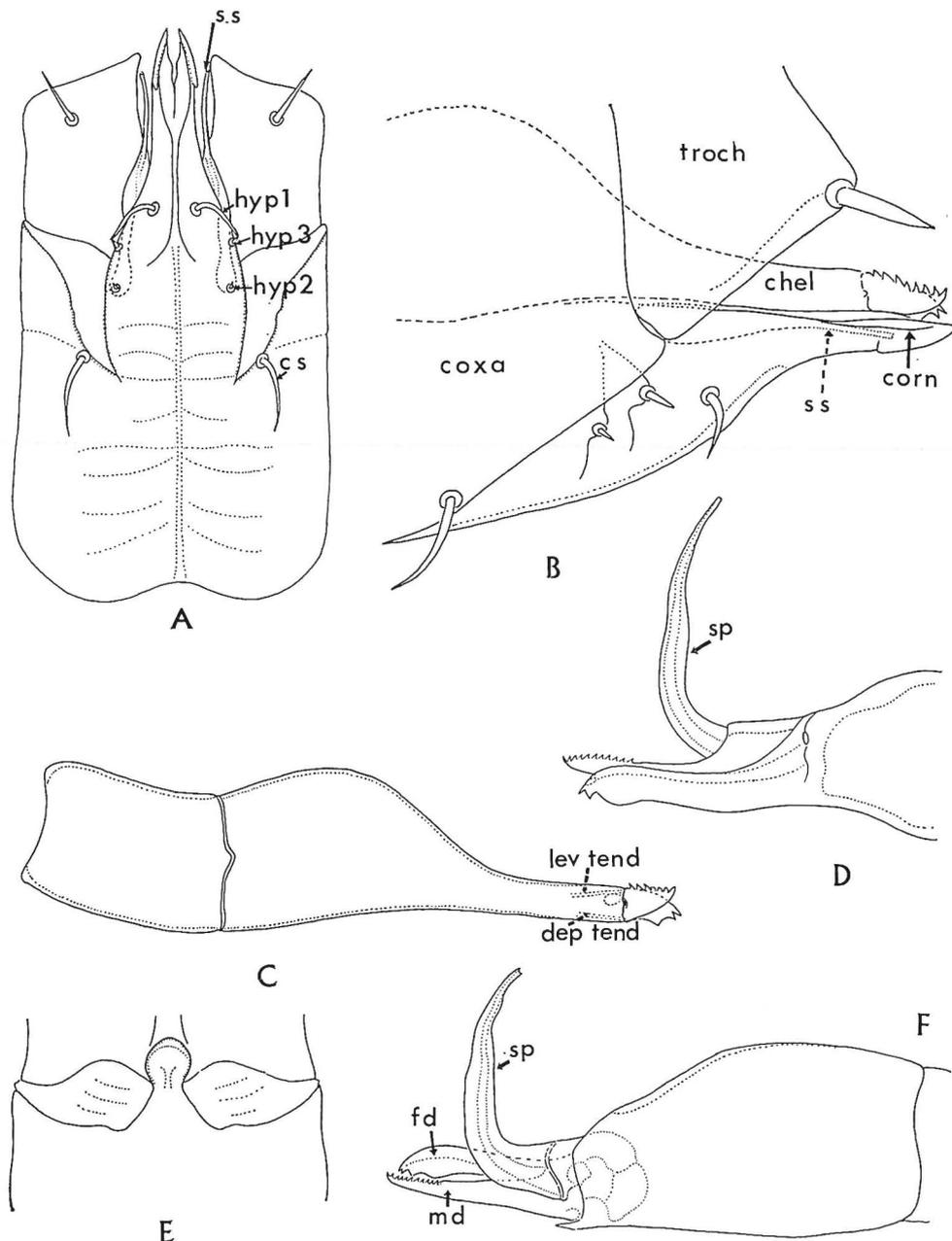


FIG. 1 : *Spinturnix myoti* Kol.

A. — Venter of gnathosoma of female ; B. — Lateral view of gnathosoma ; C. — Chelicera of female ; D. — Chelicera of male, external view ; E. — Tectum of female ; F. — Chelicera of male, internal view.

c. s., capitular seta ; *chel.*, chelicera ; *corn.*, corniculus ; *dep. tend.*, depressor tendon ; *f. d.*, fixed digit ; *hyp.* 1-3, hypostomal setae ; *lev. tend.*, levator tendon ; *m. d.*, movable digit ; *s. s.*, salivary stylus ; *sp.*, spermadactyl ; *troch.*, trochanter.

sternum along the groove.) Arising anteriorly from the basis capituli is the hypostome which in *S. myoti* is narrow and conspicuously elongated. It is separated from the basis capituli (the coxae of the pedipalps) by incomplete sutures (fig. 1 A). These are particularly clear in a lateral view of the gnathosoma (fig. 1 B).

The venter of the hypostome in the protonymph and succeeding stages bears the normal three pairs of setae. Setae *hyp.* 1 are well-developed and exceed one-half the length of the capitular setae but the posterior hypostomals (*hyp.* 2 & 3) are reduced to microsetae with *hyp.* 3 lying anterior to *hyp.* 2 and slightly exterior to the line connecting *hyp.* 1 and 2. The region anterior to setae *hyp.* 1 is attenuated and comprises the corniculi and internal malae (hypostomal processes). These appear to be fused and form a pre-oral trough (figs. 2 A & B) with the sclero-

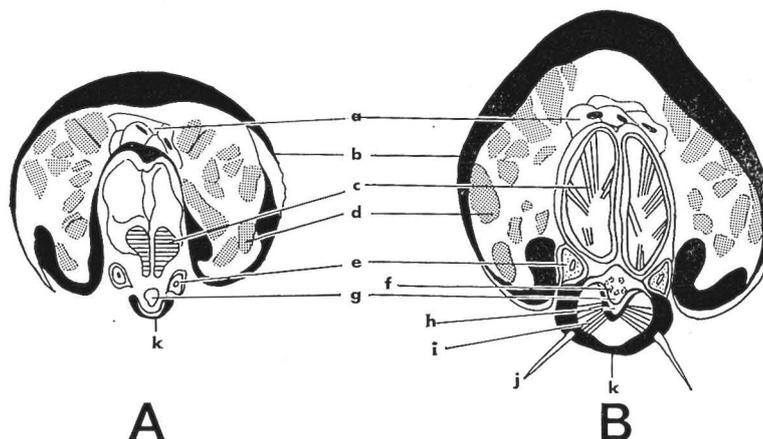


FIG. 2 : *Spinturnix myoti* Kol., female.

A. — Transverse section of the gnathosoma anterior to hypostomal setae 1 ; B. — The same in the region of hypostomal setae 1.

a, salivary glands ; *b*, wall of pedipalpal coxae ; *c*, chelicerae ; *d*, pedipalpal muscles I
e, salivary stylus ; *f*, longitudinal extensor muscles of the labrum ; *g*, labrum ; *h*, pre-oral groove ; *i*, dilator muscles of the pharynx ; *j*, hypostomal seta I ; *k*, hypostome.

tized apical portion of each corniculus developed into a posteriorly directed process reminiscent of the harpoon-like corniculi of certain Ixodorhynchinae. The labrum lies within the pre-oral trough (fig. 2 A) and lateral to it is situated a pair of salivary styli. In *S. myoti* the labrum is relatively short and does not extend beyond the hypostome. The roof of the gnathosoma is formed by the tectum capituli which is produced anteriorly into a strong sclerotized knob (fig. 1 E).

The pedipalp has five free segments and each segment is provided with a stable chaetotaxy (figs. 3 A & B). At the protonymphal instar, the chaetotaxy of the trochanter, femur and genu is normal for the Gamasina (EVANS, 1964) and these segments bear, respectively one (*v*₁), four (*al*₁, *d*₁₋₃ and *pl*) and five (*al*₁, *d*₁₋₃ and *pl*) setae. The tibia carries only eight setae, four fewer than the normal protonymphal

complement while the tarsus is provided with 10 instead of the normal 15 setae. This deficiency in tibial and tarsal chaetotaxy is also apparent in the deutonymph and adult — the protonymphal number of setae being retained by the tarsus and only one seta (n_2) added to the tibia. One seta is added to the femur (d_3) and genu

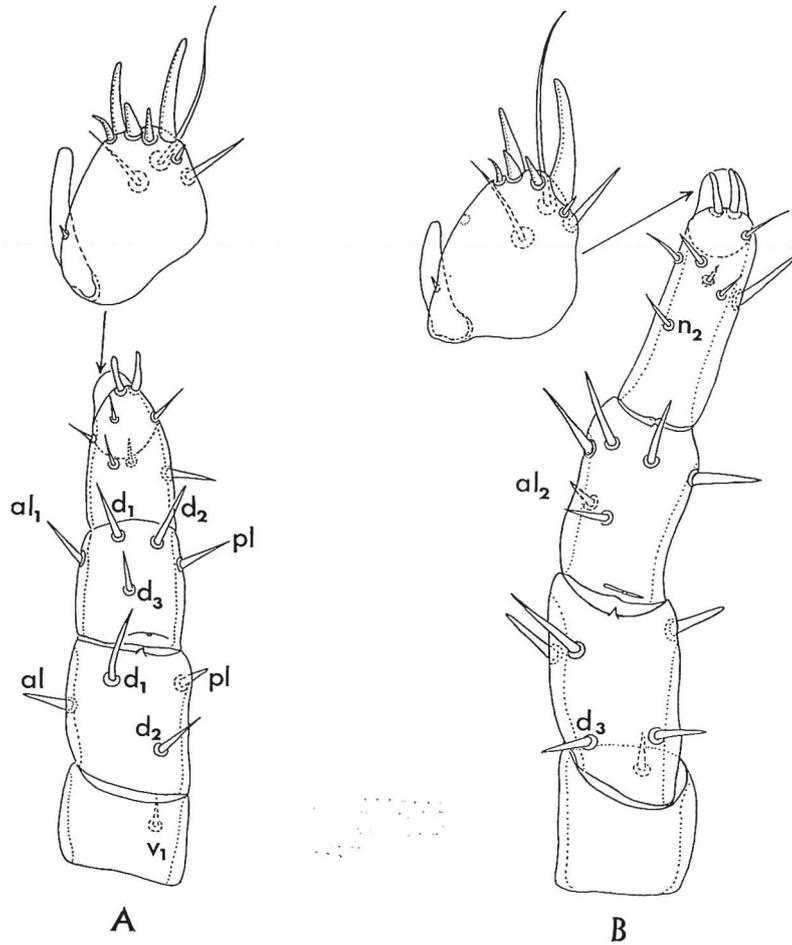


FIG. 3 : *Spinturnix myoti* Kol.

A. — Right pedipalp of the protonymph, dorsal view ; B. — Right pedipalp of female, dorsal view. al_{1-2} , antero-lateral setae ; d_{1-3} , dorsal setae ; n_2 , deutonymphal seta ; pl , postero-lateral seta ; v_1 , ventral seta.

(al_2) at the deutonymphal stage to give the normal complement for these segments. Thus, the pedipalpal chaetotactic formulae are : Pn. (1-4-5-10-10) and Dn., Ad. (1-5-6-11-10). The apotele ($ap.$) is well developed but undivided as in certain members of the Macronyssinae (e.g., *Ichoronyssus*). A conspicuous lyrifissure occurs dorsally near the posterior margin of the palpgenu.

Sclerotization and chaetotaxy of the idiosoma : The dorsum of the idiosoma in the protonymph has two subequal shields, a large anterior podonotal and a considerably smaller pygidial (fig. 4 A). Four pairs of microsetae and two pairs of pores occur on the podonotal shield and two pairs of microsetae and one pair of pores on the pygidial. In addition, the podonotum carries eight pairs of setae on the weakly sclerotized cuticle surrounding the shield, and the opisthonotum two pairs. The chaetotaxy of the podonotum is hypotrichous since typically sixteen pairs of podonotal setae occur in the protonymph of the Gamasina. Following the system of setal nomenclature adopted by LINDQUIST & EVANS (1965), I have attempted to homologise (positionally) the setae represented in *Spinturnix* with those of the holotrichous condition in free-living members of the sub-order. The four pairs on the podonotal shield are considered to represent setae $j4-6$ and $z5$; the two pairs of microsetae lateral to the shield are designated $s4$ and $s5$, and the remaining six pairs of relatively long setae $j1$, $z2$, $z4$, $r2$, $r5$, and $s6$. With the exception of $s5$, these setae normally first appear in the larval instar. Seta $s5$ is protonymphal. The setae on the pygidial shield are designated $J3$ and $Z5$ (both "larval" setae) while I consider the posterior two pairs to be opisthogastric setae which have migrated dorsally as the result of the migration of the anus to a terminal position.

At the deutonymphal stage the podonotal and pygidial shields fuse to form an entire dorsal shield (fig. 5 A). There is no addition of primary setae to the podonotum or to the opisthonotal region of the dorsal shield, thus, the deutonymph retains the primary chaetotactic pattern of the protonymph. Setae $s4$ and $s5$ are located on the lateral integument in the female deutonymph but, owing to the increased sclerotization of the dorsum, are situated on the dorsal shield in the "male". Secondary setae appear on the opisthonotal cuticle in both forms of deutonymph (figs. 5 A & C.). Their number is variable but appears to range from 35-40 setae in the male deutonymph and 25-30 in the female deutonymph.

The chaetotaxy of the adult male is essentially the same as in the male deutonymph, few if any secondary setae being added to the deutonymphal complement. RUDNICK (1960) gives 33-46 secondary setae for this sex. In the adult female, however, the number of secondary setae is more than trebled and ranges from 83-130 (fig. 6 A). Setae $s4$ and $s5$ are situated on the dorsal shield in both sexes.

The most conspicuous feature of the venter of the idiosoma in the protonymph is the extensive area occupied by the enlarged coxae of the legs which extend radially from the weakly defined sternal shield (fig. 4 B). Three pairs of setae are situated on the lateral margins of the sternal shield but sternal lyrifissures appear to be lacking. Owing to the scaly-like ornamentation of the intercoxal region, it is difficult to define the remnant of the tritosternum. The genital setae (*gen.*) which normally first appear in the protonymph occur on unsclerotized integument posterior to the sternal shield. Three pairs of opisthogastric setae usually lie on the cuticle between coxae IV but there is considerable variation in their number and position. One member of the second pair is occasionally absent and the remaining five setae may be arranged asymmetrically. The anal shield is small and surrounds

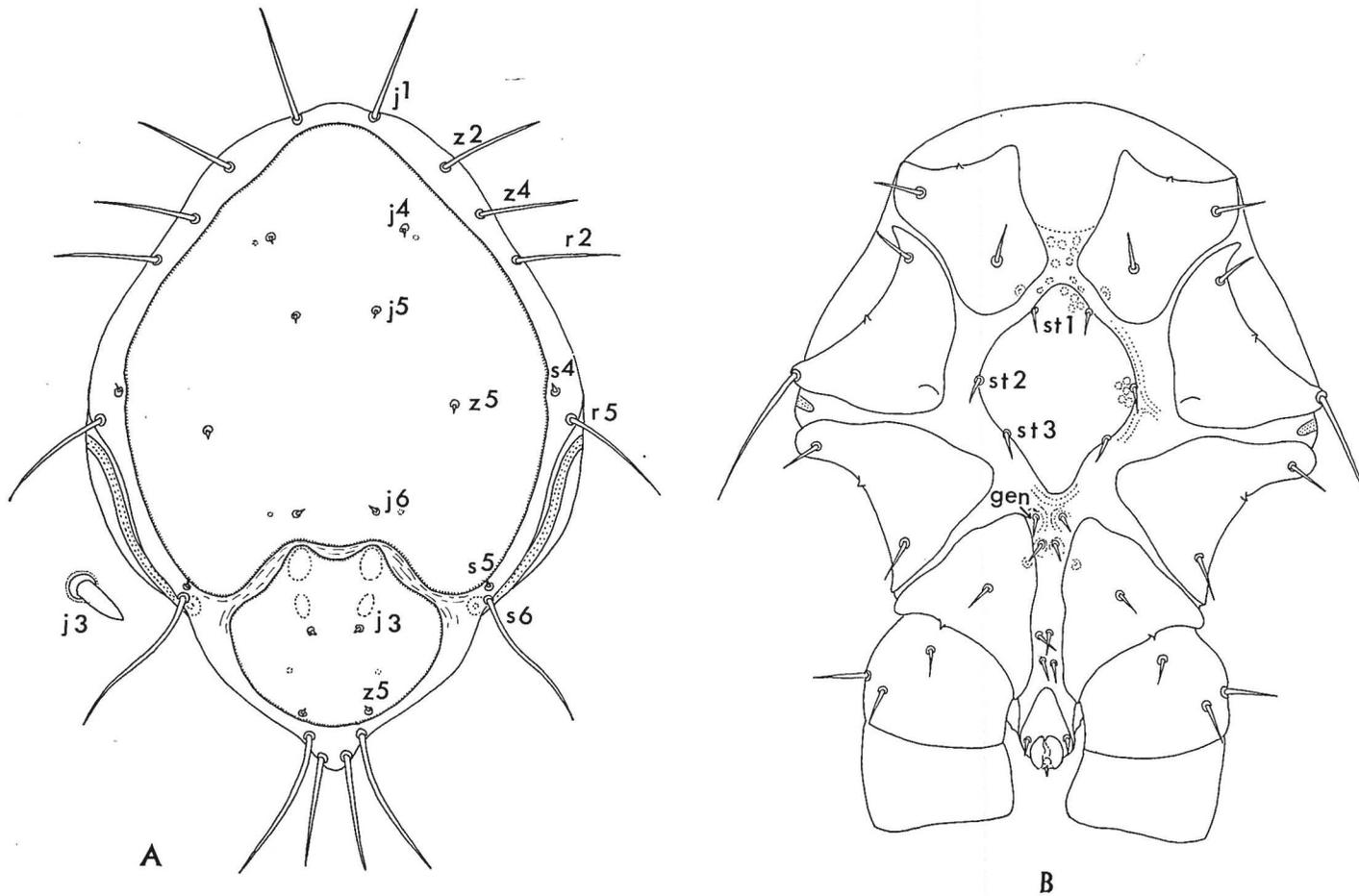


FIG. 4 : *Spinturnix myoti* Kol., protonymph. A. — Dorsum of idiosoma ; B. — Venter of idiosoma.
gen., genital setae ; *j-J*, dorso-central series ; *r*, marginal series ; *s*, lateral series ; *st.* 1-3, sternal setae ; *z-Z*, medio-lateral series.

Erratum : the symbols *j3* and *z5* on the pygidial shield should read *J3* and *Z5*.

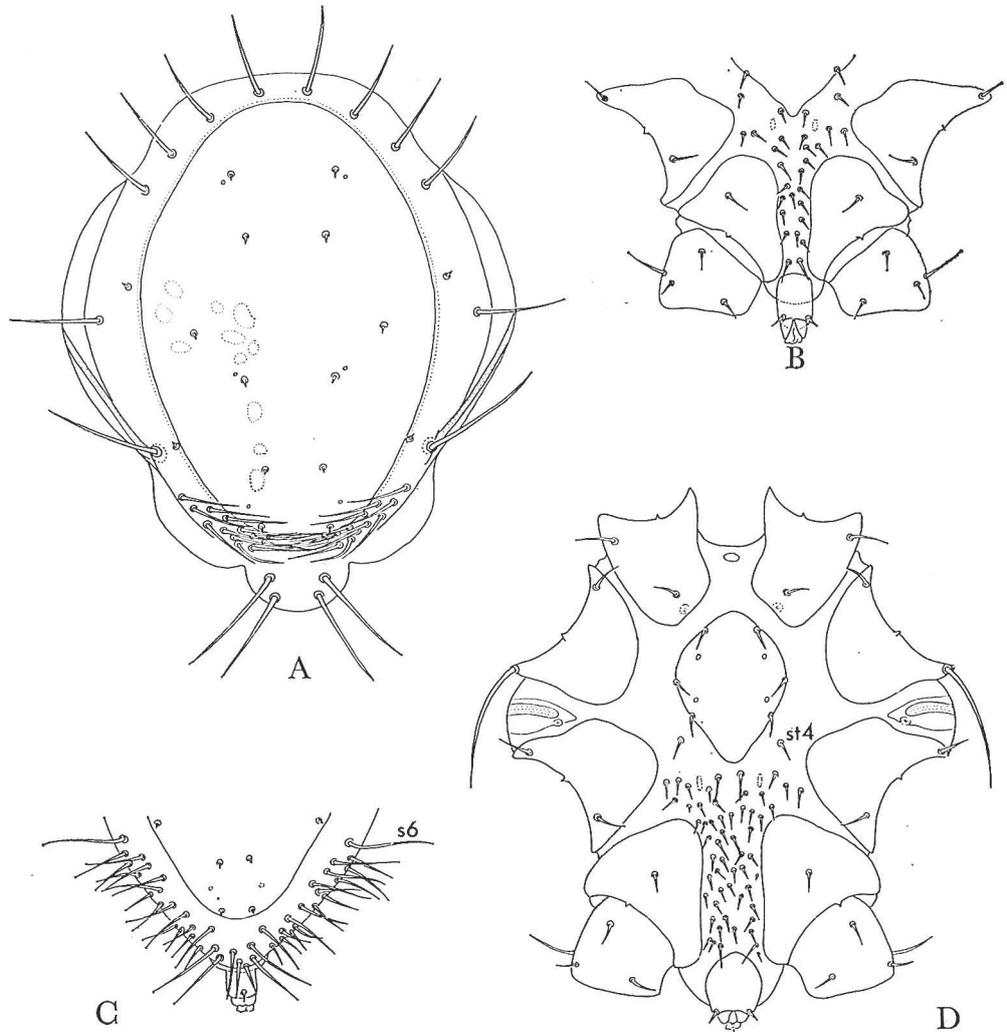


FIG. 5 : *Spinturnix myoti* Kol.

A. — Dorsum of idiosoma of the deutonymph (female) ; B. — Opisthogastric region of the deutonymph (male) ; C. — Opisthotal region of the deutonymph (male) ; venter of idiosoma of the deutonymph (female).

st. 4, metasternal seta.

the terminal anus. Three anal setae are present ; the paranals are located at the level of the anterior margin of the anus while the postanal seta is situated dorsally on the anal tubercle. There are no euanal setae.

In the deutonymph (both male and female) the sternal shield is considerably more heavily sclerotized than in the protonymph. There is marked dimorphism in the outline of the shield between the two "sexes", a feature which is also apparent in the adults. Metasternal setae first appear at this instar and are situated

on the integument lateral to the sternal shield. Two pairs of pores occur on the shield. The remnant of the tritosternum is conspicuous in both forms. "Sexual" dimorphism is also apparent in the opisthogastric chaetotaxy (the male nymph having considerably fewer setae than the female nymph) and in the outline of the anal shield (figs. 5 B & D). The secondary opisthogastric setae developed in the female deutonymph are considerably shorter than the sternal setae and the primary opisthogastric setae. There is some intra-specific variation in the number and length of the setae of the opisthogaster.

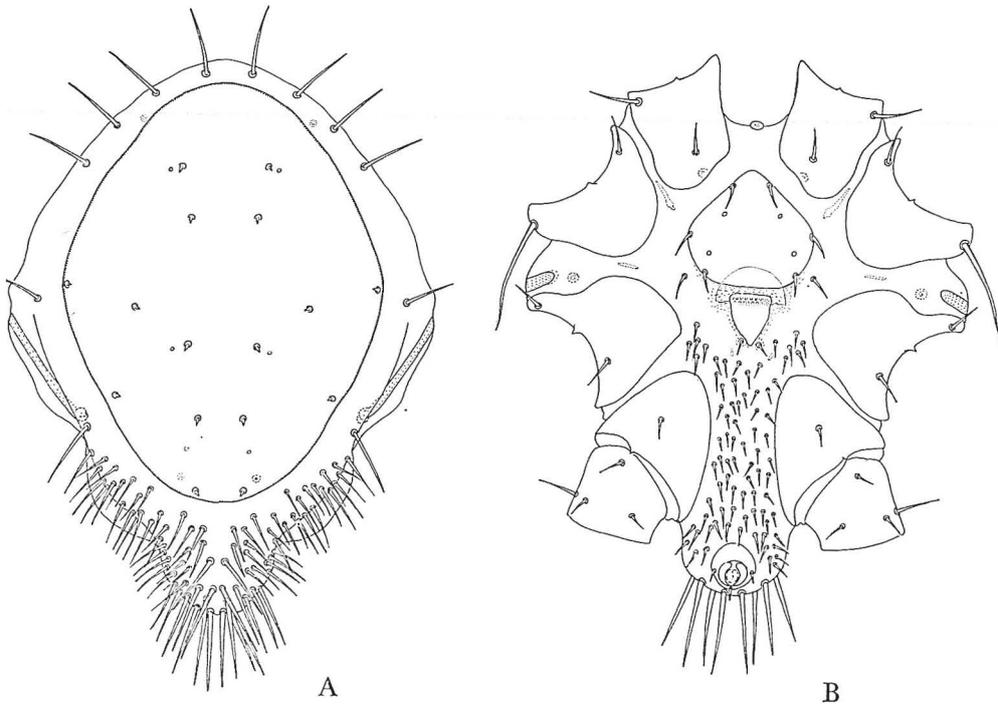


FIG. 6 : *Spinturnix myoti* Kol., female.
A. — Dorsum of idiosoma ; B. — Venter of idiosoma.

All the features showing dimorphism in the deutonymphs are apparent in the adults. The tritosternum in both sexes is represented by a small oval sclerite. In the female the sternal shield bears three pairs of setae and two pairs of pores. Sternal setae 4 (metasternals) are situated on the integument as in the deutonymph (fig. 6 B). The genital shield is small and sub-triangular in outline with the apex directed posteriorly. Its anterior hyaline flap overlaps the posterior margin of the sternal shield and protects the short transverse slit-like genital opening. There are no conspicuously sclerotized genital apodemes. The genital setae lie on the integument near the posterior end of the shield. As in the female deutonymph the opisthogaster is richly provided with secondary setae ranging from 60-100 in number.

The suboval anal shield with its large circular anal opening is provided with the normal three setae.

In the male the sterno-genital shield has four pairs of setae — three pairs of sternals (*st.* 1-3) and one pair of genitals (fig. 7 A). The metasternal setae are situated on the integument as in the female. There are 20-30 opisthogastric setae and the genital orifice is presternal.

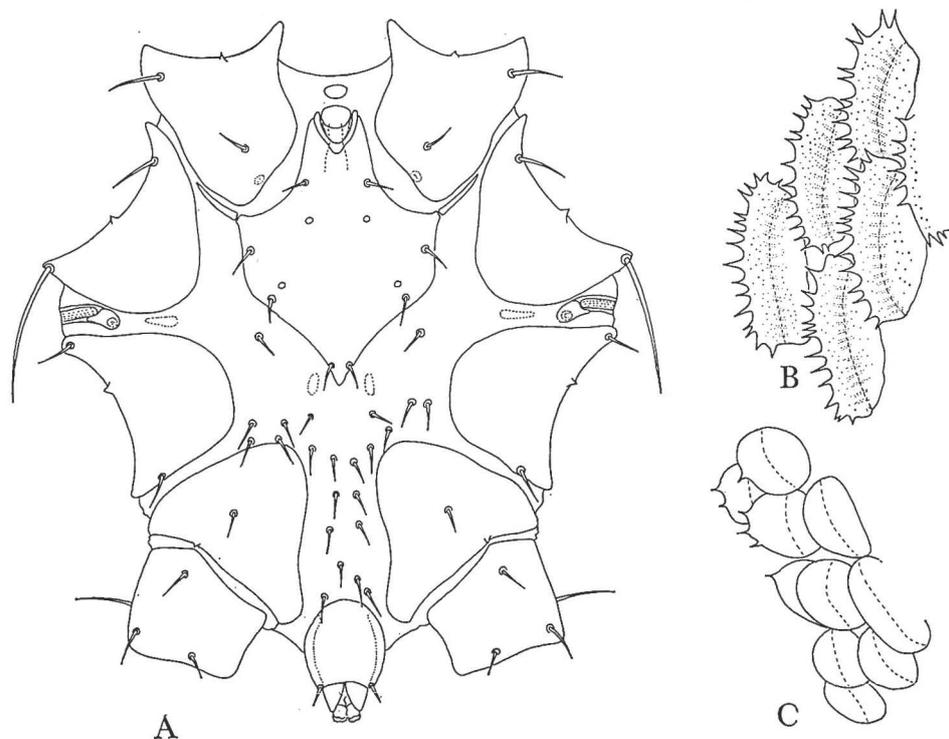


FIG. 7 : *Spinturnix myoti* Kol.

A. — Venter of idiosoma of the male ; B. — Cuticular scales flanking the dorsal shield of the female ; C. — Cuticular scales in posterodorsal region of the female.

Endopodal shields are weakly developed in the adults and appear as sclerotized strips between coxae I & II and II & III. Those between coxae I & II are better developed in the male than in the female and are fused with or abut the anterolateral angles of the sterno-genital shield.

Stigmata and peritremes : The stigmata (one on either side of the idiosoma) are situated laterally immediately dorsal to the third intercoxal space, that is, between coxae III and IV (fig. 6 A). Each opens into a well-defined atrium from which arises four major tracheal trunks, two directed anteriorly, one ventrally and one posteriorly. There is a relatively simple endostigmal skeleton which divides the atrium from the stigmal chamber. The peritremes are of the usual form and are situated dorso-

laterally for the greater part of their length. They bend sharply ventrad in the region of the second intercoxal space so that their distal fifth (or less) is situated ventrally between coxae II and III (fig. 6 B). The peritrematal channel is relatively broad and richly provided with minute acicular processes. At the deutonymphal and adult stages a conspicuous pore occurs near the free end of the peritreme and it is connected to the peritremes by a sclerotized platelet (? peritrematal shield) in the deutonymph and male.

Ornamentation and topography of the cuticle : The dorsal shield(s) in the nymphae and female lacks surface ornamentation except for symmetrically arranged small areas of apparently lighter sclerotized cuticle (fig. 5 A). When examined by a scanning electron microscope, these areas appear as distinct depressions in the shield and possibly indicate the areas of attachment of the main dorsoventral idiosomal muscles (Plate 1 C). Similar depressions are evident on the dorsal shield of the male but in addition its surface is minutely pitted.

The cuticle surrounding the dorsal shield has a distinct scaly appearance (Plate 1 A). In the nymphae the scales have an evenly rounded margin but in the adult female, in addition to their larger and more robust form, the scales have denticulate margins (fig. 7 B). The scales immediately surrounding the dorsal shield are the most conspicuously denticulate and they are directed towards the shield (Plate 1 B). In unfed specimens the scales are closely set and there is considerable overlapping but during feeding the cuticle is stretched and the scales move apart, however, never to the extent that the underlying cuticle is completely exposed. Towards the lateral margins of the idiosoma the scales lose their denticulate margins and resemble the form in the immature stages (fig. 7 C). Two basic types of scales appear on the dorsal integument of the male. These comprise large flat scales with smooth margins, and small triangular, sharply pointed scales. The latter predominate in the region immediately flanking the dorsal shield and in large areas of cuticle in the anterior and posterior regions of the dorsum. The shape of the scales in the female appears to be characteristic of the species and may prove to be useful as a taxonomic criterion.

The entire cuticle of the intercoxal region of the protonymph has a scaly-like form but in the deutonymphs and adults this type of ornamentation is, more or less, restricted to the sclerotized sternal or sterno-genital shield.

In order to accommodate the large quantity of tissue fluids taken during feeding, the cuticle of the idiosoma must possess the facility for stretching while at the same time retaining its overall strength. Preliminary studies of the structure of the cuticle using the techniques of electron microscopy indicate that a network of microfibrils in the deeper regions of the endocuticle probably give the cuticle its elasticity.

Ambulatory appendages and their chaetotaxy : The legs are six segmented excluding the ambulacrum (apotele). Circumsegmental fissures formed by partially or entirely coalesced lyrifissures are present in the basal third of the femora and of tarsi

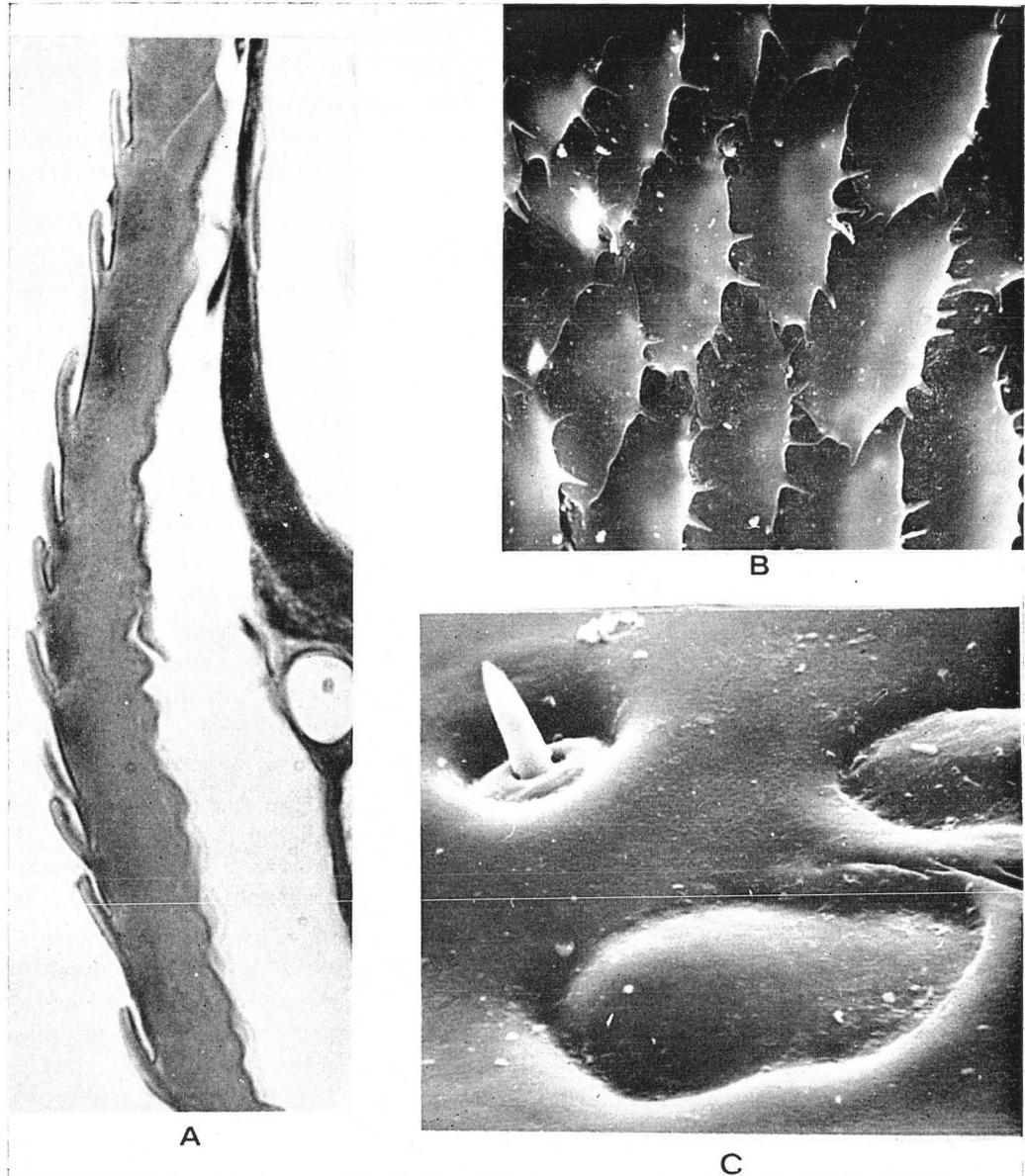


PLATE I : *Spinturinx myoti* Kol., female.

- A. — Transverse section of the cuticle lateral to the dorsal shield at the level of coxa III showing the cuticle developed into a series of folds which constitute the scales. X 765.
- B. — Scanning electron micrograph of the surface of the cuticle flanking the dorsal shield. The denticulate margins of the scales are clearly shown. X 1250
- C. — Similar micrograph of the surface of the dorsal shield showing a micro-seta and « depressions ». X 1400.

II-IV. They are complete on femora I but incomplete ventrally on the other femora. The fissure on tarsus I is restricted to the venter of the segment. Isolated lyrifissures occur dorsally near the proximal margins of tarsi I-IV and in the distal half of tarsi II-IV. All the leg segments are stout, well sclerotized and slightly flattened dorso-ventrally. The terminology for the leg chaetotaxy follows Evans (1963).

All the coxae are large and arranged radially around the sternal or sterno-genital shield in all stages. Coxae I-III each bears two setae and coxae IV only one seta throughout ontogeny. At the protonymphal instar the trochanters each carry four setae with those on the antiaxial faces of trochanter I and II and on the paraxial faces of III and IV longer than the other setae. An antero-lateral seta (*al*) is added to trochanter I, a postero-lateral (*pv*) to trochanters II and III, and an antero-ventral (*av*) to coxa IV at the deutonymphal stage. This setal complement of five setae / trochanter is retained by the adult.

Femora I-IV have 10,8,5, and 4 setae, respectively, in the protonymph and 11,9,6, and 6 in the deutonymph and adult; a ventral seta being added to each of femora I-III and two ventrals to femur IV at the deutonymphal instar. Genu I carries 8 setae, genu II 7 (*av* lacking from genu I pattern) and genua III and IV 6 setae (*av* and *pv* lacking) in the protonymph while in the deutonymph and adult there are 9 setae on genu I and 8 setae on this segment of legs II-IV. Seta *al*₂ (fig. 8 E) is added to the protonymphal complement on genu I in the deutonymph and setae *av* and *pv* to genua II-IV.

Tibiae II-IV in the protonymph have the same chaetotactic pattern (1-1/1, 2/1-1) but tibia I has an additional antero-dorsal setae (fig. 8 D). The chaetotaxy of tibiae II-IV in the deutonymph and adult is identical with that of tibiae II-IV of the protonymph but tibia I has two antero-lateral setae as on genu I of the same developmental stages.

The ontogenetic development of the chaetotaxy of tarsi II-IV is normal for the Gamasina; 17 setae being present in the protonymph and 18 setae in the deutonymph and adult. Unpaired seta *mv* is anterior in position but *md* which first appears in the deutonymph is situated medially and lies in line with *al*₁ and *pl*₁.

Tarsus I in the protonymph bears 26 setae as shown in fig. 9 A. The solenidia-like setae of the sensory field are located dorso-laterally on the antiaxial face of the segment. In addition to the setae on the surface of the segment, there are three minute micro-solenidia situated in a distinct capsule (*cap.*) within the sensory field (figs. 1 A, B & C). At the deutonymphal and adult stages five setae are added to tarsus I, these are indicated by the symbol *n*₂ in fig. 9 B and give a complement of 31 setae, excluding the three capsulated setae, for the segment. The ambulacrum is essentially the same on all legs. It is large with the claws and the pretarsal skeleton strongly developed. The elements of the pretarsal skeleton are typically dermanyssoid (see EVANS & TILL, 1965) and the pulvillus and claws are operated by a pair of antagonistic muscles, the pulvillar retractor and basilar protractor, originating in the tarsus and tibia, respectively.

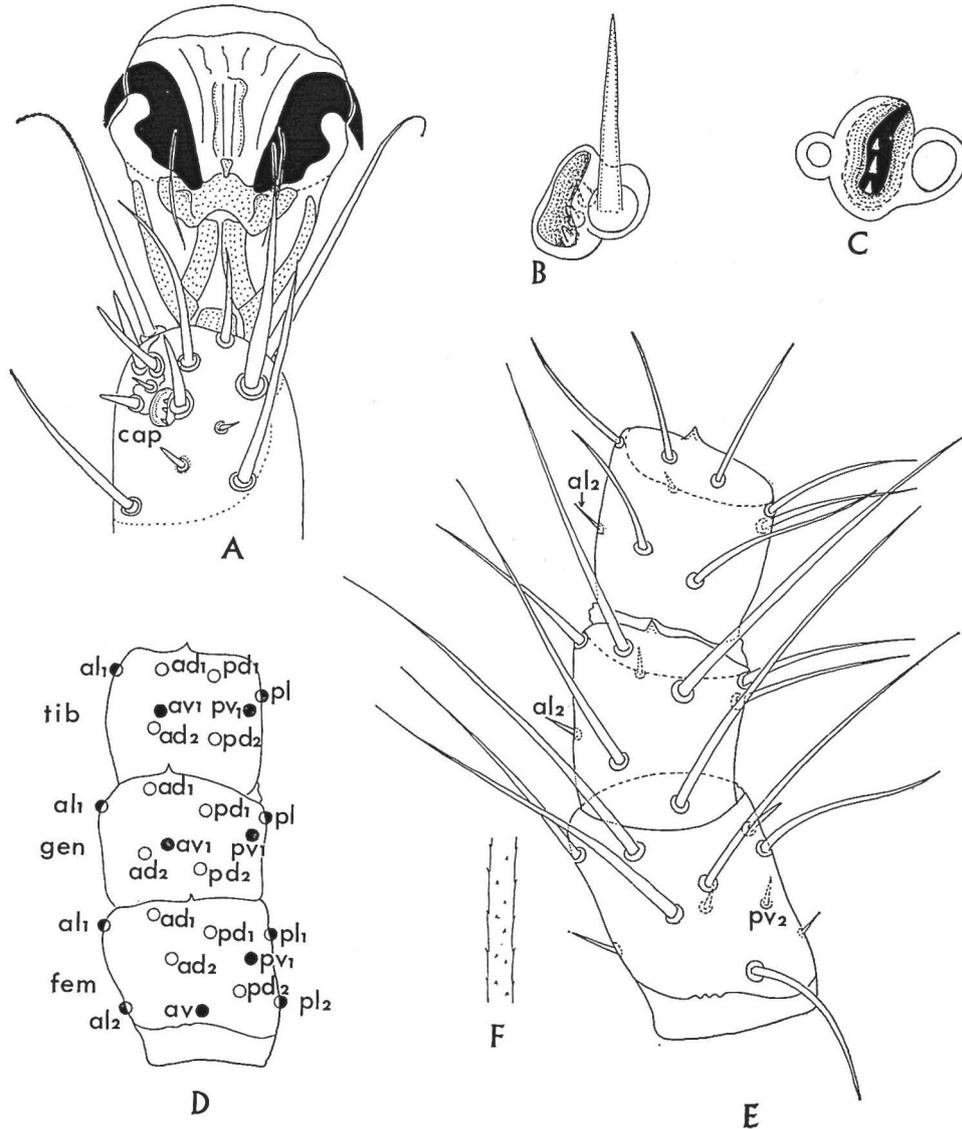


FIG. 8 : *Spinturnix myoti* Kol.

A. — Distal region of tarsus I and ambulacrum of female ; B. & C. — Capsule of the sensory field on tarsus I, D. — Chaetotactic patterns of femur, genu and tibia of leg I of the protonymph ; E. — Chaetotaxy of the femur, genu and tibia of leg I of the female ; F. — Portion of seta ad_2 on femur I.

ad_{1-2} , antero-dorsal setae ; al_{1-2} , antero-lateral setae ; av_1 , antero-ventral seta ; $cap.$, capsule ; $fem.$, femur ; $gen.$, genu ; pd_{1-2} , postero-dorsal setae ; pl_{1-2} , postero-lateral setae ; pv_{1-2} , postero-ventral setae ; $tib.$, tibia.

Setae *pv* are considerably longer and stouter than *av* on the genua and tibiae of legs I and II (fig. 8 E) but *av* are longer and stouter than *pv* on the same segments of legs III and IV. The long setae of the dorsal surface of the leg segments have minute spicules along their length (fig. 8 F).

The leg chaetotaxy of the protonymph is typical for that instar in the Dermanyssoidea except for genu IV which normally lacks a postero-lateral seta : the chaetotaxy of genu IV in *Spinturnix* resembles that of the protonymph of *Ophio-*

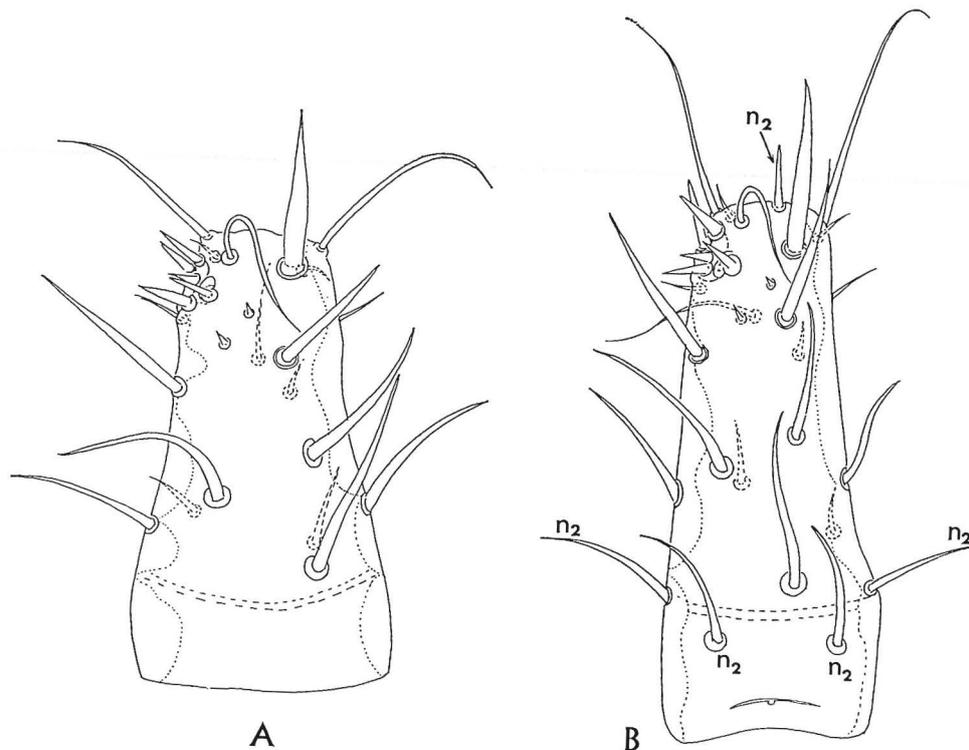


FIG. 9 : *Spinturnix myoti* Kol.

A. — Chaetotaxy of tarsus I (left) of the protonymph, dorsal view ; B. — Same of the deutonymph (female).

*n*₂, deutonymphal setae.

nyssus (Macronyssinae). At the deutonymphal and adult stages, however, the segmental chaetotaxy shows considerable differences from the unspecialized dermanyssoid type as defined by EVANS & TILL (1965). In fact only the coxae, trochanters II-IV, femora III and IV, and tarsi II-IV have the same complement as equivalent post-protonymphal stages of the unspecialized dermanyssoids. The remaining segments display varying degrees of hypotrachy and the protonymphal complement is retained on tibiae II-IV in the deutonymph and adult. Table I summarises the segmental chaetotactic patterns of the legs in *S. myoti*.

TABLE I. Segmental chaetotaxy of the legs of the protonymph (Pn.), deutonymph (Dn.) and adult (Ad.) of *Spinturnix myoti* Kol.

Segment	Leg I		Leg II		Leg III		Leg IV	
	Pn.	Dn. & Ad.						
Coxa	2	2	2	2	2	2	1	1
Trochanter	4	5	4	5	4	5	4	5
Femur	2-4/2-2	2-4/3-2	1-4/2-1	1-4/3-1	1-3/1-0	1-3/2-0	1-3/0-0	1-3/2-0
Genu	1-2/1,2/1-1	2-2/1,2/1-1	1-2/0,2/1-1	1-2/1,2/1-1	1-2/0,2/0-1	1-2/1,2/1-1	1-2/0,2/0-1	1-2/1,2/1-1
Tibia	1-2/1,2/1-1	2-2/1,2/1-1	1-1/1,2/1-1	1-1/1,2/1-1	1-1/1,2/1-1	1-1/1,2/1-1	1-1/1,2/1-1	1-1/1,2/1-1
Tarsus	(see text)		17	18	17	18	17	18

Discussion.

The parasitic members of the Dermanssoidea display a remarkable range of structural and developmental adaptations to the variety of niches which they have invaded and successfully colonised on other arthropods and on reptiles, birds and mammals. Among the most interesting of the structural adaptations are those associated with attachment to the host and with the adoption of haemotophagy while developmental specialization is evident in the occurrence of viviparity, the relegation of a normally active feeding instar to a non-feeding inactive stage and, more rarely, the development of the larva into an active feeding form at the expense of the nymphal stages. Certain of these adaptive features have been alluded to in the above account of the morphology and development of *Spinturnix myoti* and it seems opportune to discuss the extent and significance of the adaptations to parasitism within the Spinturnicidae as a whole.

All spinturnicids live on the bare regions of the skin of their chiropteran hosts such as the wing and tail membranes, eyelids and eye canthi : there do not appear to be any authenticated records of their occurrence in the fur of the hosts. The marked dorso-ventral compression of the idiosoma and the stout radially arranged legs terminating in large claws are features of all members of the family, with the exception of *Paraspinturnix* which inhabits the anal orifice of *Myotis* spp. and has a distinctly globose idiosoma, and are obvious adaptations for clinging closely to the surface of the skin. Their " life-form " is reminiscent of that of certain Rhinonyssidae which live in the respiratory tract of birds and as in that group the stigmata and peritremes have a tendency to be displaced on to the dorsal surface of the idiosoma. Some authors consider that the dorsal position of the stigmata in the Rhinonyssidae is an adaptation to prevent their obstruction by the nasal mucous in which they live but this reasoning is not appropriate to the Spinturnicidae and it is likely that in the latter the position of the stigmata and peritremes is the direct

result of the dorso-ventral flattening of the idiosoma and the movement of the enlarged coxae to a more marginal position on the idiosoma. The main attachment organs are undoubtedly the strong claws of the legs. In *Ancystropus* and *Meristaspis* which are chiefly found on the eyelids and eye canthi of their hosts, legs I and their ambulacra appear to be specially modified for attachment being considerably enlarged with the segments approximately twice the width of the equivalent segments of legs II to IV. This also appears to be the case in *Oncoscelus* in which the tarsi of enlarged legs I each bears a stout, sharply pointed, retrorse spur.

The major structural adaptations of the gnathosoma accompanying the adoption of haematophagy in the dermanyssoid mites are to be seen in the tendency for the lengthening of the second cheliceral segments, often with a reduction in the size of the digits, and in the elongation of the hypostome together with the fusion of its elements, particularly the hypostomal processes (internal malae) and corniculi, to form a pre-oral trough. These adaptive features are evident in the structure of the gnathosoma of the spinturnicids although in detail both the chelicerae and hypostome exhibit certain unique features which represent a different grade of specialization from that encountered in the Macronyssinae and Dermanyssidae. For example, the form of the cheliceral shafts in the nymphae and female bears a greater resemblance to the condition in certain Ptilonyssinae than to that in the Macronyssinae and Dermanyssidae while the hypostomal elements are relatively simple. The mesial walls of the chelicerae are somewhat convex in outline as opposed to the mesially grooved cheliceral shafts of certain Macronyssinae and Dermanyssidae which when approximate form a distinct channel. This suggests that the spinturnicids are pool rather than vessel feeders.

The evolution of haematophagy in the parasitic dermanyssoids has also been accompanied by the modification of the mid-gut and its diverticula to cope with the increased volume of ingested food and its digestion, and by a decrease in the sclerotization of the idiosomal cuticle to allow for expansion of the body at engorgement. The volume/digestion problem has been solved by increasing the size of the mid-gut and particularly the diverticula. In *S. myoti* the large anterior and posterior diverticula, respectively, extend into the cavities of legs I and IV. Examination of serial sections of partially and fully fed females of *S. myoti* indicates that digestion is essentially intracellular. Large vacuolated digestive cells lining the diverticula ingest the blood meal by phagocytosis and gradually accumulate the waste products of digestion, mainly haematin. The cells which are filled with the waste products are liberated into the lumen of the diverticula and are eventually excreted through the anus. The diverticula lie in direct contact with the muscles, tracheae and other organs and it is probable that the products of digestion pass directly through the walls of the diverticula to these organs. The suggestion that the diverticula of the Gamasina have a gastro-vascular function was made by MÉGNIN as long ago as 1876.

Structural adaptations associated with the necessity for the expansion of the

idiosoma to accommodate the large quantities of tissue fluids ingested by the haematophagous ectoparasitic dermanyssoids have been discussed by EVANS & TILL (1965) and comprise a reduction in the area of sclerotization, both dorsally and ventrally, and the corrugation of the cuticle. In the Spinturnicidae the decrease in dorsal sclerotization is apparent even at the protonymphal stage by the small size of the podonotal and pygidial shields relative to the area of unsclerotized cuticle. Members of the genera *Periglischrus*, and *Paraperiglischrus* retain these two shields in successive developmental stages with little or no increase in the relative area of dorsal sclerotization. Fusion of the protonymphal shields occurs in the deutonymph and adults of the genera *Ancystropus*, *Meristaspis* and *Spinturnix* but the resulting single dorsal shield covers only part of the idiosoma. The main region of expansion is the posterior part of the opisthosoma which becomes markedly distended in fully fed nymphae and females. This is particularly apparent in species of the genus *Periglischrus* which have a large fan-shaped opisthosoma showing regional sclerotization ventrally. These sclerotized areas probably function as sites for muscle attachment as well as a supporting skeleton for the voluminous opisthosoma. The degree of expansion of the opisthosoma is accentuated in gravid females, especially in those containing a fully developed protonymph. Males generally show little enlargement of the posterior region of the opisthosoma. Decrease in ventral sclerotization is evident in the relatively small areas covered by the sternal, genital and anal shields in the female and by sternito-genital shield in the male.

The cuticle surrounding the sclerotized areas of the idiosoma in the majority of the blood-feeding dermanyssoids is strongly corrugated in the unfed stage and allows for the expansion of the idiosoma during feeding. In the Spinturnicidae, particularly the genus *Spinturnix*, the structure of the cuticle is unique among the Dermanyssoidea in that its surface is produced into conspicuous overlapping scales. Limited expansion of the cuticle is possible through the area of folded cuticle at the base of the internal face of each scale. Although the scales move apart during engorgement, the underlying cuticle is never fully exposed. It is probable that the scales have at least two functions, namely, that of protecting the cuticle from the abrasive action of the folding and unfolding of the wing and tail membranes of the host, and that of decreasing water loss through the cuticle since the mites live in comparatively exposed situations on the host.

Obligatory parasitic dermanyssoids invariably show some modification of the chaetotaxy of the idiosoma and appendages when compared with the condition that obtains in the free-living members of the superfamily (EVANS & TILL, 1965). The segmental chaetotaxy of the appendages of the deutonymph and adult often exhibits localized neoteny, that is, the retention of the larval or protonymphal chaetotactic patterns by succeeding developmental stages, and, more rarely, one or more of the pedipalpal segments may show larval specialization of the chaetotaxy in that the segment never attains the normal larval complement of setae throughout ontogeny. Specialization of the idiosomal chaetotaxy is evident, in the hypotrichy

of the primary chaetotaxy and in the development of secondary setae, chiefly on the opisthosoma. Further, parasitic forms tend to show greater intraspecific variability of the chaetotaxy than do the freeliving and facultatively parasitic forms and this is probably the result of decreased selection pressures within the specialized habitats occupied by the parasites. All these phenomena are displayed by the spinturnicids and have been dealt with in the appropriate sections of the description of the external morphology of *S. myoti*. One particularly interesting feature of the leg chaetotaxy of *Spinturnix* is to be seen in the specialization of the sensory field on the tarsus of leg I. The isolation of three micro-solenidia within a cavity is reminiscent of the capsule of Haller's organ of the Metastigmata. Is it possible that the sensilli of the capsule are olfactory as in the ticks ?

The most interesting features of developmental specialization in the Spinturnicidae are the intrauterine development of the protonymph and the suppression of the larval instar in the life-cycle. The larva in both free-living and parasitic Gamasina, with the notable exception of the *Halarachne*-group, is a relatively inactive, non-feeding instar of short duration and is probably the most susceptible of the postembryonic stages to predation and desiccation. As such its free-living existence in the precarious niches occupied by the spinturnicids would be detrimental to the survival rate of the species. It is possible, although I consider unlikely, that the so-called pre-larva of *Spinturnix* represents a degenerate larva rather than an embryonic stage. However, I have been unable to observe any break in the developmental sequence from pre-larva to protonymph. Further study is required to establish the status of the pre-larva.

Summary.

An account is given of the external morphology of the post-embryonic developmental stages of *Spinturnix myoti* Kol. (family Spinturnicidae) with particular reference to the ontogenetic development of the idiosomal, gnathosomal and leg chaetotaxy. Development from the egg through a prelarval stage to the protonymph proceeds *in utero* and the protonymph is born in a fully developed form. The deutonymphal stage shows distinct "sexual" dimorphism. There is no larval form comparable to that normally present in the life-cycle of the Gamasina although the larval stage may be represented by the so-called prelarva.

The extent and significance of the adaptations to ectoparasitism within the Spinturnicidae are discussed.

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