

THE EXTERNAL ULTRASTRUCTURE AND BIOLOGY OF THE
SPINOSE EAR TICK, OTOBIUS MEGNINI DUGES,
1884 (ACARINA: ARGASIDAE)

By

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CHAPTER I

INTRODUCTION

The Spinose ear tick, Otobius megnini Duges, 1884 is an important but little understood argasid parasite of domestic and wild animals. This tick was originally described by Duges from Guanajuato, Mexico (Duges 1884). Townsend (1893), in one of the earliest records of the presence of this tick in the United States, referred to it as Argas americanum Packard. Later, Marx (1895) published the name Rhynchoprium spinosum and Neumann (1896) renamed it as Ornithodoros megnini (Duges). Banks (1912) erected a new genus for the spinose ear tick and called it Otobius megnini (Duges) which has now been accepted. However, almost simultaneously, this same tick species was described and figured as Otophilus asini from specimens collected from the ears of donkeys and a calf in Bolivia (Keirans 1972). Keirans (1972) concluded that Otophilus asini (Torreggiani 1912) and Otobius megnini were synonyms and placed the generic name Otophilus as a junior synonym of Otobius. This junior synonym is not yet widely used.

As this tick remains attached deep in the folds of the concha and frequently in the external meatus of host animals for periods up to 3 months, it has been widely disseminated through shipment, establishing itself particularly in warmer parts of the world. The tick has been reported from the Southwestern, the Pacific coastal and other warm

regions of the United States (Hooker, et al. 1912, Becklund and Mitchell 1958) and is widely distributed in parts of Mexico, Central and South America (Duges 1884, Cooley and Kohls 1944, Kemper and Peterson 1953). It has also been reported from Hawaii (Harwood and James 1979), South Africa (Theiler and Salisbury 1958), Zambia (MacLeod et al. 1970), British Columbia (Gregson 1953, Rich 1957), India (Sen 1937, Chellappa 1973), Zaire (Schoenaers 1950), Sri Lanka (Ramanujachari and Alwar 1955) Madagascar (Uilenberg et al. 1979) and Argentina (Dios 1930). However, the distribution range of this species is undoubtedly wider than this, considering the wide range of host animals to which it has become adapted. It has been reported on cattle (Becklund and Mitchell 1958), Mountain sheep (Allen 1955), sheep (Chellappa and Alwar 1972), pronghorn antelope (Meleny and Roberts 1970), collared peccary (Meleny 1975), horses (Ramanujachari and Alwar 1955), hares and rabbits (Rodrigues 1977). Under favorable conditions they often attach themselves to other animals such as goats, hogs, dogs and sometimes man (Chellappa 1973, Townsend 1893).

Although economic thresholds of spinose ear tick infestations have not been quantified, this tick is considered a serious pest of livestock and wildlife, and its economic importance is probably much greater than is generally recognized. The tick causes great irritation in the ears of animals, leading to constant head-shaking. The tick injures the tender epidermis of the ears, resulting in ulceration and a condition generally known as 'ear canker'. Heavy infestation may lead to symptoms of 'head heaviness', deafness, lowered vitality, nervousness and unthriftiness followed by loss of muscular coordination, collapse and sometimes death. Old cattle and calves are particularly affected during winter and early

spring when livestock nutritional levels are low (Hooker et al. 1912, Rich 1957, Stiles 1944).

The irritation caused by the tick in dairy cattle reduces milk yield, and in beef cattle, the gain in weight is correspondingly affected. The constant rubbing of ears against fence posts, trees, sides of buildings and other rough objects lacerates the ears, predisposing animals to screw worm infestations and other infections (Rich 1957, Hooker et al. 1912, Stiles 1944).

The isolation of Bacillus anthracis, from the spinose ear ticks, which fed on anthrax infected bovine carcasses indicated that ticks of this species might possibly spread the disease to healthy animals (Stiles 1944). It is not known whether the anthrax organisms can be successfully passed from the nymphal stage through the adult and the eggs to the next generation. Jellison et al. (1948) showed that the this tick was the only species of soft ticks that was capable of harboring Q fever rickettia (Coxiella burnetti). However, Howell, et al. (1943) failed to transmit anaplasmosis through this species both by transstadial and transovarial means. There are several records of the occurrence of the spinose ear tick in the ears of man (Chellappa 1973, Herms 1917, Townsend 1893, Hooker 1908, Hooker et al. 1912). Although such infestations cause great irritation in the ears of infested persons, no fatal case has been attributed to this tick in man.

External Ultrastructural Morphology

Early descriptions of the morphology of this species were reported

by Duges (1884), Townsend (1893), Marx (1895), Neumann (1896), Salmon and Stiles (1901), Banks (1912) and Nuttall et al. (1908). These descriptions, based on light microscopy, provided some useful information on the taxonomic relationships of this species with other ticks within the Argasidae. There is no information on comparative studies of the external ultrastructure of each stage of the spinose ear tick. Such information has enabled researchers to suggest function for specific organ systems in relation to their structures and has contributed to a better understanding of tick phylogenetic relationships (Axtell et al. 1971, Sixl 1971a, Wooley 1972a, Sixl 1972, Feldman-Muhsam 1974, Homsher and Sonenshine 1975, Keirans 1977, Vernick et al. 1978, Axtell and Le Furgey 1979, Keirans et al. 1980, Leonovick 1980, Hume 1981, Conlon 1981).

Despite the obvious advantages of the increased resolution of electron microscopy, only a few studies have used this technique in comparative studies of the ultrastructure of each stage of any one species of ticks (Keirans et al. 1976, Keirans et al. 1980). Chapters II and V of this Thesis report on the ultrastructural morphology of all stages of O. megnini Duges.

Colonization and Biology in the Laboratory

Although this tick has been a subject of interest to many workers interested in pests of livestock, there are no proper accounts of the colonization procedures of this species. Present reports of its life-history lack information on many important parameters.

This species is a one-host tick. Non-feeding adult ticks mate within 1-8 days after molting on the ground. Oliver and Osburn (1977) observed a 2-day old male transferring spermatids to a female and subsequently recovered two endospermatophores full of spermatozoa from that female. Hooker et al. (1912) reported a "tattoo-like" sound made by adults kept in pill boxes and considered it a sexual call. Davis (1934) was able to observe 16 copulations by one male with various females, and two copulations by two different females. Information on other aspects of its life-history were reported by Hooker et al. (1912), Hooker (1908), Herms (1917), Davis (1934), and Koshy et al. (1979).

The purpose of this part of the study was to carry out a detailed investigation of the feeding, development, and survival of this species under laboratory conditions.

Field Biology

Although some studies have been carried out on the biology of this tick under laboratory conditions, there have not been any studies on the biology of this species under field conditions.

The objectives of this part of the study were to elucidate (1) the feeding and drop-off patterns of fed nymphs, including their dispersal, development and nature of resting sites; (2) mating and oviposition parameters in adults; (3) egg development and the behavior pattern of larvae under natural conditions. Such information is essential for formulating sound management practices for the control of this important pest of livestock and wildlife.

CHAPTER II

EXTERNAL ULTRASTRUCTURE

Materials and Methods

Observations were carried out on ticks which were obtained from a laboratory colony maintained in a temperature control chamber (Model No. TA 212 YB, Precision Scientific, Chicago, Ill.) at 26 ± 1 and $65 \pm 5\%$ relative humidity. Ticks were originally collected from cattle (Bos taurus) which were being auctioned at Perkins, Oklahoma. Experimental adults, fed nymphs, unfed larvae and eggs were incubator reared specimens whereas fed larvae and nymphs were collected from host animals by interrupting feeding.

Electron Microscopy

Adults and nymphal ticks were sonicated (Bransonic 220) in 0.3% Triton K-100 to remove debris, followed by rinsing in 90% ethanol. They were air dried and mounted on stubs with silver conducting paint. Ticks were further dried under vacuum (Denton Vacuum Evaporator), gold-palladium coated (Hummer Sputter-Coater) and viewed in a JEOL JSM-35 scanning electron microscope operated at 25kV.

Larval ticks and eggs were mounted on stubs with double-stick tape,

dried under vacuum, gold-palladium coated and viewed. Fed larvae were fixed overnight in 70% ethanol and dehydrated by transfer through a graded series of ethanol with two changes of absolute ethanol. The ticks were critically point dried (Tousimis Sandri PVT-3), mounted on stubs with silver conducting paint, coated and viewed.

Light Microscopy

Additional observations and measurements were made using a Wild Heerbrugg (#376788) microscope fitted with an ocular micrometer. The measurements reported herein were based on tick specimens that were laboratory-reared and that had been allowed to complete engorgement and development on bovine hosts during their parasitic stages.

Results

The descriptions cover the general organization of the external morphology of all stages of Otobius megnini. Specific structures and systems are compared as they occur in each stage. These include the general morphology of the body, integument, orifices, folds, grooves and depressions, paired appendages and capitulum.

General Body Organization

The life stages of this species are dissimilar in appearance. The egg is globular and light brown, while the unfed larva (Fig. 1a) is elongate-oval. The larva is widest just behind the second pair of legs

(or posterior to the second pair of eyes) where it measures 0.325 ± 0.01 mm. Fed larvae are slightly elongate posteriorly and broader in front. The capitulum is also distended anteriorly. The sizes and weights of eggs and larvae are summarized in Table I.

There is only one nymphal stage and this is the most distinct and easily recognized due to its spinose integument (Fig. 1b). The unfed nymph is slightly longer than broad, and is widest between the second and third pair of legs (1.318 ± 0.08 mm). It is slightly constricted at the fourth pair of legs and all legs are purple-white. The organization of the body of fed nymphs is similar to that of unfed nymphs, but the body is highly distended. A feeding nymph is dark blue, but changes to dark brown when fully fed and close to molting. Sizes and weights of fed and unfed nymphs are summarized in Table I.

Adults are shaped like peanut shells, slightly attenuated anteriorly and constricted behind the fourth pair of legs and rounded posteriorly (Fig. 1c). The sexes are similar and are distinguished through the structure of the genital opening. Females are slightly larger than males. The sizes and weights of both males and females are summarized in Table I.

Integument

The granular adult integument has numerous pits and setae (Figs. 1d and 1e) while that of nymphs is very finely striated and spinose and has no pits (Fig. 1b). The larval integument is also very finely striated with symmetrically arranged bristle-like setae (Fig. 1a).

TABLE I
 MEAN MEASUREMENTS OF BODY LENGTH, WIDTH
 AND WEIGHT OF EACH STAGE OF
OTOBIUS MAGNINI DUGES †

Stage	Length†† (mm) (x ± S.D.)	Width (mm) (x ± S.D.)	Weight (mg) (x ± S.D.)
Egg	0.490±0.001	0.390±0.003	0.058± 0.01
Larva			
Unfed	0.620±0.008	0.325±0.01	0.098± 0.01
Fed	3.700±0.24	2.525±0.12	8.330± 2.22
Nymph			
Unfed	2.318±0.12	1.318±0.08	4.06± 0.04
Fed	4.881±1.19	2.712±0.96	78.27±53.04
Adult			
Male	6.458±1.29	4.296±1.05	52.05±13.39
Female	7.767±0.60	5.167±0.49	86.17±32.76

† Based on 33 specimens.

†† From tip of hypostome to posterior end.

The adult integument has numerous pits; each measuring 0.081 ± 0.017 mm in diameter and containing a central tubercle from which a seta arises. The distance between pits is 0.164 ± 0.071 mm. The number of tubercles with setae is much higher on the dorsum, anterior to the point where the body is constricted. Pits are absent on nymphs but in larvae, very small pit-like depressions are symmetrically arranged on both the dorsum and venter. Tubercles from which setae arise are situated in these shallow depressions.

Setae

Various types of setae occur on the body and appendages. In the adults, setae are greatly reduced and are more numerous anterior to the fourth pair of legs. In the camerostome area, there is a high concentration of well developed sensillae.

Nymphs have three types of setae which are numerous and posteriorly directed (Fig. 2). Type A are long and thick, measuring 0.2386 ± 0.013 mm long and 0.0888 ± 0.007 mm thick at the base. This type is distributed from the anterior end of the dorsum to the level of the first pair of legs and can be easily identified only in unfed or partially fed nymphs. Type B setae are short and thick, measuring 0.045 ± 0.001 mm long and 0.0227 ± 0.002 mm thick at the base. Type B spines are continuous with Type A but are restricted to near the margins of the dorsum up to between the third and fourth pair of legs. The two types form a crescentic area with a concavity that is directed posteriorly. Type C spines are bristly setae which cover the remainder of the dorsum. They are 0.0710 ± 0.008 mm long and 0.0068 ± 0.009 mm thick at the base (Fig. 2). On the ventral surface only types A and B spines are present. The setae on the dorsum of larvae number 16 and measure 0.027 ± 0.003 mm long, while 10 setae are symmetrically arranged on the venter.

Dorsal Plate. This structure is absent in both nymphs and adults, but is present in larvae. It is centrally located, elongate and measures 0.220 ± 0.01 mm long and is widest anteriorly (0.115 ± 0.006 mm) just posterior to the level of the second pair of eyes (Fig. 1a).

Eyes. These structures occur only in larvae (Fig. 1a). The anterior pair of eyes lie in a somewhat dorso-lateral position between the first and second pair of legs. The second pair of eyes is located dorsally, behind the second pair of legs. Each eye is 0.008 ± 0.0001 mm in diameter and those on one side are separated from each other by 0.060 ± 0.002 mm.

Orifices

The ventral surface of all stages bears external openings of several body organ systems. Some occur in all stages, whereas others are found only in one or two stages. These natural orifices are the anus, paired spiracles, paired coxal gland openings and the genital aperture (Figs. 4, 5, 6, 7).

Anus. The anal aperture is found in all stages and is situated in the midline of the opisthosomal region of the body. In the larva, it is covered by two semi-circular anal valves which join together to form an apple-like or heart-shaped structure which is slightly enlarged anteriorly (Fig. 4a). Each larval valve is 0.036 ± 0.001 mm long and is widest just below the seta (0.035 ± 0.001 mm). The single seta on each valve is separated from the other by a distance of 0.031 ± 0.008 mm. The anal opening is 0.0411 ± 0.009 mm at its widest and 0.0386 ± 0.007 mm along the midline of the valves.

The plates covering the anal aperture in the nymph (Fig. 4b) are also semi-circular, but the outer margins of individual plates are depressed to form "platforms" from which arise a single pair of setae.

The anal opening in the nymph is ovate, measuring 0.110 ± 0.002 mm at its widest and 0.093 ± 0.006 mm along the midline of the valves and has an "anal notch" at the lower margin.

The anal valves of both males and females are "bean-shaped", each bearing 4 setae (Fig. 4c). The two valves are surrounded by a well developed, slightly ovate annulus measuring 0.131 ± 0.04 mm at its widest axis and 0.095 ± 0.009 mm along the midline of the anal valves. The anal width/body length ratio showed a progressive decrease in the three stages, being highest in larvae (0.062 ± 0.005), 0.040 ± 0.001 in nymphs and lowest in adults (0.0147 ± 0.0052).

Spiracles. In larvae, a pair of "spiracle-like" plates exist ventrally between the 2nd and 3rd pair of legs but have no external openings (Fig. 3d). The spiracles in nymphs are paired structures located dorso-laterally above the fourth pair of legs and project posteriorly. They are conical shaped and are 0.136 ± 0.021 mm long. Within the conical open structure are simple and branched cuticular setae. An "operculum", or lid-like structure with a large central seta, is attached to a cord originating within the atrium and lies on the side of the ostium (Fig. 5a).

The spiracles of both females and males are dorso-laterally located above the fourth pair of legs (Fig. 5b). The size and form of the macula and slit-like ostium are similar in both males and females. The spiracular plate of the male may form a small lobe that is dorso-laterally extended. The entire spiracle is 0.290 ± 0.002 mm long in males and 0.254 ± 0.009 mm wide. The surface of the macula is slightly granular and the spiracular plate is very smooth.

Coxal Gland Apertures

These apertures are found in all stages of this species and are located in the space between Coxa I and II. The paired coxal glands of all stages open externally through numerous micropores at the base of Coxa I (Fig. 6).

Genital Anlage

This slit-like opening is found in the nymphal stage and is located along the midline of the ventral surface of the body between Coxa I and II (Fig. 7a).

Genital Aperture

In adults, this occurs in the same relative position as the genital anlage in the nymph. The male genital opening, which is semi-circular, is covered by a flap-like operculum called the apron and is bordered posteriorly by a sub-oval frame that has very few hairs (Fig. 7b). The female genital opening is 1.000 ± 0.17 mm wide. The genital opening of the female is a transverse slit bordered by a frame which is posteriorly sub-oval and forms a narrow ridge anteriorly (Fig. 7c). It is surrounded by the integument which is slightly annular. The narrow frame anterior to the genital aperture bears 26 short, spine-like setae. Although there are a few such setae on the posterior frame, there are numerous short setae (33) at the base of the frame.

Integumentary Folds, Grooves and Depressions

Integumentary folds, grooves and depressions are distinctly present in adults (Fig. 8). In nymphs, grooves are distinct, but folds are faint. Larvae do not possess any integumentary folds, grooves or depressions.

Integumentary Folds

In adult ticks, there are 3 distinct integumentary folds: the camerostome, coxal and supracoxal folds. All three occur on the ventral body surface. The camerostome fold, which is relatively smooth and conspicuous, surrounds the posterior and posterolateral portions of the camerostome within which lies the capitulum. The paired coxal folds are distinctly broad and arise from the posterior ends of Coxae II. "Blunt heels" are formed posterior to the genital opening. They then proceed posteriorly beyond the legs, ending near the posterolateral body margins. The paired supracoxal folds are lateral to the coxae on each side of the body and arise at the anterior end of the body. They proceed posteriorly, lateral to the camerostomal folds and the legs, and terminate slightly posterior to Coxae IV.

The coxal and supracoxal folds are either entirely absent or greatly reduced in the nymph, although there is a smooth "pseudo" fold from which the capitulum arises. There are no obvious integumentary folds in the larvae, apart from the striae which occur extensively.

Integumentary Grooves

There are a number of major grooves which occur in adults of this

species. On the ventral surface, the coxal groove appears to join the left groove at the level of Coxa IV, above the anus. The left coxal groove extends posteriorly to join a broad first post-anal groove which rises at a tangent to the anal frame. The first post-anal groove then disappears on the sides near the posterior angle of the body. A broad median groove arises off the first post-anal groove just below the anal frame and disappears at the second post-anal groove. The pre-anal groove is absent in the adult stage of this tick.

There are a number of grooves on the dorsum of adults which appear as elongated depressions. The individual grooves are very wide and can be seen to be continuous only under very careful examination. Portions of the dorsal grooves are also porous (Fig. 1e).

In the nymphs, the coxal grooves arise between Coxae I and II and narrow into a V-shape at the level of the genital anlage and merge to form a broad median groove that narrows posteriorly. The anal frame lies within the narrow posterior end of the groove which appears to have porous areas. The groove becomes less distinct posterior to the anus but extends to the posterior margin of the nymph. A post-anal groove arises at a tangent to the anal frame and disappears on the posterolateral sides. A pair of small transverse grooves arise in the space between coxae II and III. In fully fed nymphs, grooves are indistinct and only coxal grooves up to the level of the genital anlage are recognizable. A pair of grooves is visible between Coxae II and III in the dorsal-lateral position of unfed nymphs.

Camerostomal Depression

This is the major depression that occurs in the adults (Fig. 9).

It is absent in nymphs and larvae but occurs in both sexes. There is a slight sexual dimorphism in the structure of the depression. In the males it is slightly ovate-shaped, whereas in females, the camerostomal depression is dome-shaped anteriorly and broad posteriorly. In both sexes, the capitulum arises at the posterior margin of the depression. Anteriorly, the depression is beset with numerous setae, which seem to be slightly longer and more confined to the outer anterior margin of the depression in the female as opposed to the males in which the hairs are shorter and more spread within the depression. The camerostome depression in both sexes is bordered anteriorly by the hood and laterally by the camerostome fold.

Paired Appendages

The chelicerae, palps, and legs are paired appendages. In this section, only legs will be considered. There are three pairs of legs in the larva and four pairs in each of the other stages. Each of the legs consists of six segments as follows: The coxa which is sclerotized on the ventral aspect; trochanter; femur, which is sub-divided into a basifemur and telofemur; patella; tibia and the tarsus, which is divided into a basitarsus and a telotarsus (Fig. 10). A two-segmented pretarsus bears a pair of claws. In the larval stage, the second pretarsal segment, bearing a pair of claws, is stalked and has a pad-like pulvulus below the claw. The mean lengths of the segments of leg I and each stage are summarized in Table II.

Setae

All leg segments, except the basifemur, possess setae which are

TABLE II
 AVERAGE LENGTHS OF THE SEGMENTS OF LEG I OF EACH
 STAGE OF OTOBIUS MEGNINI †

Stage	Leg Segment (mm)					
	Coxa	Troncharter	Femur	Patella	Tibia	Tarsus
Larva	0.070 _± 0.004	0.073 _± 0.001	0.132 _± 0.004	0.107 _± 0.003	0.088 _± 0.006	0.177 _± 0.004
Nymph	0.600 _± 0.009	0.300 _± 0.050	0.562 _± 0.069	0.347 _± 0.003	0.344 _± 0.008	0.396 _± 0.021
Adult	0.838 _± 0.170	0.434 _± 0.087	0.612 _± 0.158	0.445 _± 0.027	0.441 _± 0.001	0.507 _± 0.019

† Based on 10 ticks for each stage.

†† Represents \bar{x} and \pm S.D.

arranged in either single or paired longitudinal files. The setae of the tarsus are the most complex (Fig. 11).

Haller's Organ

The capsule and associated sensillae of this paired structure are located on the dorsal aspect of the tarsus of Leg I (Fig. 12). In all three stages, Haller's organ consists of a capsule containing numerous branched sensillae (Fig. 13). In larvae, the capsule is circular (0.002 ± 0.0001 mm in diameter). It occurs as a transverse slit in both nymphs and adults. The length of the slit is 0.059 ± 0.004 mm in nymphs and 0.099 ± 0.005 mm in adults. The tarsal hump, which lies posteriorly to the capsule bears 4 setae. In the larva, 4 cuticular setae overhang the capsule; the 2 middle setae being branched near the base. A large nodiform sensillum occurs in the capsule of Haller's organ in the larva but is absent in nymphs and adults. The overhanging cuticular setae increase in number to about 18 in the nymph and form an arch-like structure over the capsule. The number of cuticular setae in adults increases to 25. The setae are straight and "bridges" appear between individual setae (Fig. 13).

Capitulum

In adults, the capitulum, which bears the mouthparts, is ventrally located in the camerostome depression near the anterior end of the body and is not visible from the dorsal aspect. In the nymphs and larvae, the capitulum is located anteriorly and is visible from the dorsal aspect. The capitulum consists of the basis capituli, the hypostome, the labrum (not visible externally), a pair of chelicerae and a pair of palps (Fig. 14).

Basis Capituli

The basis capituli of adults is small and ventrally is twice as wide as is long (0.891 ± 0.028 mm and 0.314 ± 0.022 mm respectively). From the ventral aspect, the basis of the larvae appears rounded posteriorly and slightly narrowed anteriorly (0.092 ± 0.002 mm wide). The basis capituli in all stages is smooth and microscopic folds typical of the integument of larvae and nymphs are absent.

In the adult, there are six groups of setae found on the venter of the basis capituli (Fig. 14c): one pair of anteromedian post hypostomal setae, two pairs of post-palpal setae, one paired group of anterolateral setae, one pair of anteromedial setae and a paired field of posterior medial setae.

Setal arrangement on the basis capituli of the nymph is similar to that of the adults, except that the anterolateral setae are absent (Fig. 14b) and a single pair of post palpal setae exists. In the larva, there are only two pairs of setae on the basis capituli: one pair of long, post-hypostomal setae (average intersetal distance is 0.015 ± 0.002 mm) and one pair of post-palpal setae (average intersetal distance being 0.083 ± 0.006 mm).

Hypostome

The hypostome is an anterior flattened extension of the ventral part of the basis capituli (Fig. 14). In adults it is greatly reduced, bluntly rounded and teeth and corona are absent. The hypostome of nymphs and larvae bear recurved teeth (denticles) on the ventral surface and terminate in anterior coronas which bear numerous tiny denticles. Both

adult and sub-adult stages possess a median longitudinal groove or preoral canal on the dorsal surface of the hypostome. The mean length of the hypostome (from the tip to post hypostomal setae) in adults is 0.118 ± 0.03 , being longer in the male (0.147 ± 0.013 mm) than in the female (0.088 ± 0.004 mm). In the nymphs the hypostome is 0.294 ± 0.089 mm long. In larvae the hypostome measures 0.178 ± 0.003 mm. The ratio of the hypostome length (in mm) to total body length (from the tip of the hypostome to the posterior end of the idiosoma in mm) is 0.019 ± 0.001 in adults, 0.127 ± 0.008 in nymphs and 0.287 ± 0.01 in larvae.

Posterior to the corona, slightly over three-quarters of the anterior hypostome of nymphs and larvae bears well developed denticles with distinct "overhang". The remaining portion is smooth and without teeth. In larvae, the denticles are arranged 2/2. with each longitudinal file containing about 10 denticles. The arrangement of denticles in nymphs is 3/4. In both larvae and nymphs, the teeth appear to be of uniform size.

Chelicerae

The chelicerae of larvae and nymphs are well developed and lie dorsal to the hypostome (Figs. 15, 16). Each chelicera consists of a cheliceral digit that bears toothed articles, and a single-segmented shaft with sheaths. A bulbous base of the shaft forms, internally, the dorsum of the basis capituli. Each digit bears an external and an internal article and a prominent dorsal process on its internal article. In adults, which do not feed, the cheliceral shaft, digits, articles and teeth are greatly reduced.

Palps

These paired structures are well developed in all stages of this tick. They are leg-like and arise lateral to both the hypostome and chelicerae. Each palp consists of four articles which are freely moveable (Fig. 14). In the larvae, the palp is 0.171 ± 0.002 mm long and the articles are long and slender. In nymphs, the palps are 0.329 ± 0.013 mm long and in adults measure about 0.359 ± 0.06 mm and the segments are nearly as wide as they are long. The numbers of setae on various palpal articles are shown in Table III.

Setae

The total number of setae for each larval and nymphal palpal segment does not exceed a total of 4. Segment I in larvae has no setae, while segment I in nymphs has 1 lateral seta. The distribution of setae on various segments is shown in Table 3. In contrast, palpal segments of adults have numerous setae. Segment I has about 40 setae while segment II has 6 located dorsally, 3 laterally and 4 ventrally. Segment III has 8 and IV has 1 seta (Table III).

Terminal sensillae (Fig. 17) on palpal article IV number 7 in the larva and nymph and increase to 12 in males and 14 in females. In adults these sensillae arise from a pit, except for 1 sensilla which is sub-terminal (Fig. 17).

Discussion

The genus Otobius is distinguished from Argas by the absence of

TABLE III
 NUMBERS OF SETAE ON VARIOUS PALPAL ARTICLES
 OF OTOBIUS MEGNINI

Stage	Palpal Article				Terminal Setae
	I	II	III	IV	
Larva					
Dorsal	0	2	1	1	
Ventral	0	1	1	1	7
Lateral	0	1	1	0	
Nymph					
Dorsal	0	1	2	1	
Ventral	0	1	1	1	7
Lateral	1	1	1	0	
Adult					
Dorsal	25	6	4	1	
Ventral	6	4	1	0	12 [†]
Lateral	9	3	3	0	14 ^{††}

† male

†† female

- Figure 1. Dorsal Surface of Larval, Nymphal and Adult O. megnini.
- O. megnini: (a) O. megnini larval dorsum. Dorsal Plate (dp) and 2 Pairs of Eyes are Apparent (150x)
- (b) Dorsal Surface of Fed Nymph of O. megnini. Spiracles Appear Dorso-laterally (arrows). Setal Types B and C are Visible. Type A is Easily Observed Only in Unfed Nymphs (570x)
- (c) O. megnini Adult Male-dorsal View. (15x)
- (d) Increased Magnification of Adult Integument in Fig. 3 Indicated. Pits (p) Contain a Tubercle (arrow) From Which a Single Seta Arises. (210x)
- (e) Higher Magnification of Adult Integument Indicated in Fig. 1c. Apparent Porose Areas Appear in Grooves on the Dorsal and Ventral Surfaces of Adults (210x)

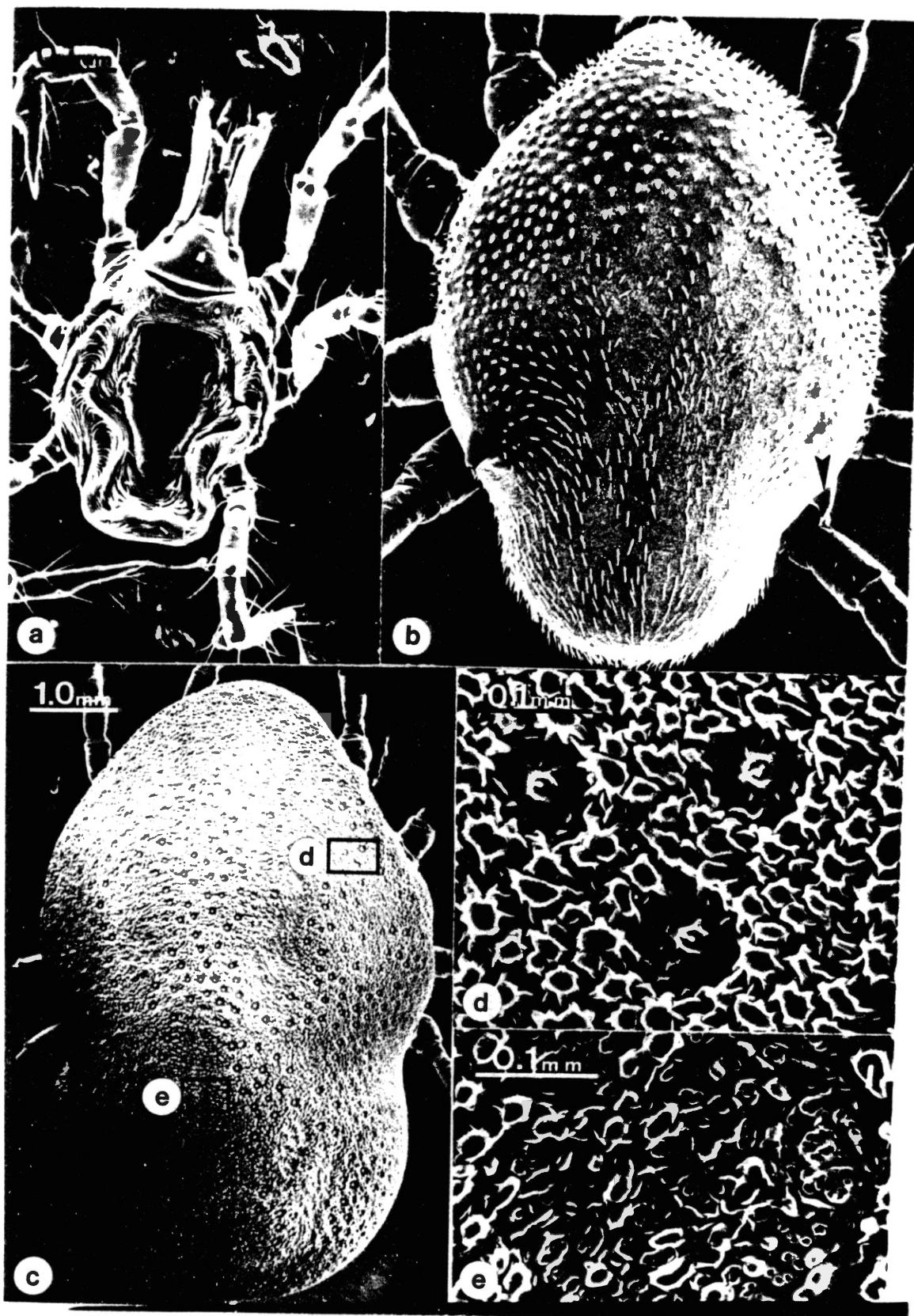
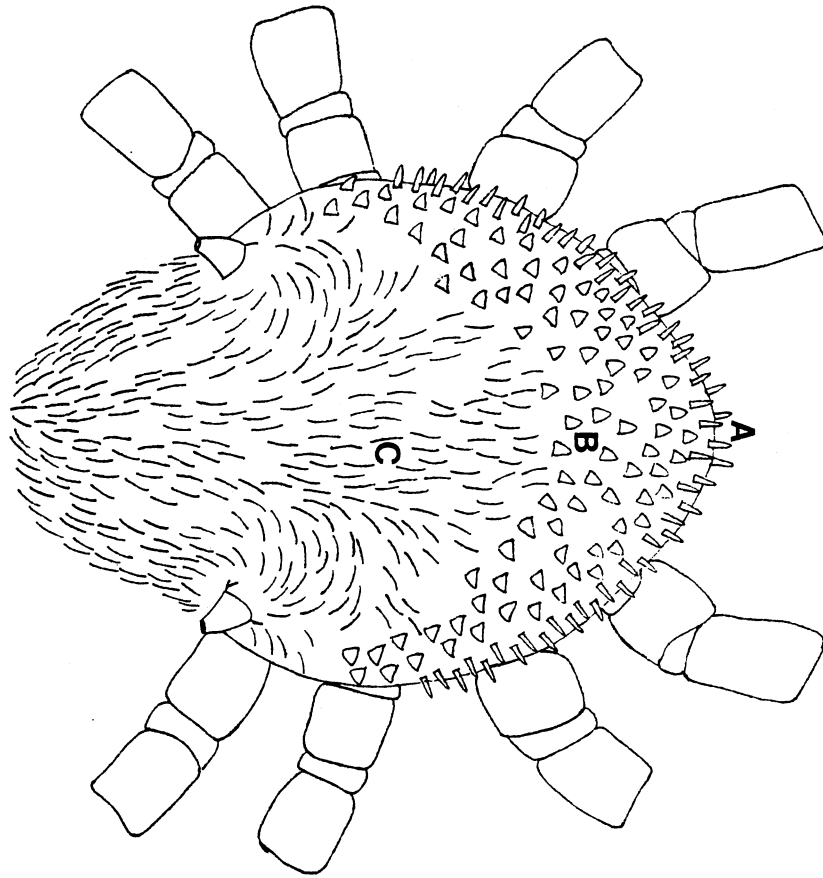


Figure 2. Dorsal Setal Types in O. megnini. Three Distinct
Setal Types Occur On the Dorsum: Types A, B and C.



- Figure 3. Ventral Surface of Larval, Nymphal and Adult O. megnini: (a) O. megnini male. Coxal Pores (Arrows) are Located Between Coxa I and II. Sexes are Differentiated by the Structure of the Genital Apertures (18x)
- (b) O. megnini female. Genital Aperture Occurs Between Paired Coxal Pores (arrows) (18x)
- (c) Genital Anlage (large arrow) Occurs in the Nymph in the Same Relative Position as Genital Opertures in Adults. Paired Coxal Pores Occur at the Base of Coxa I and II (28x)
- (d) Spiracle-like Structures (large arrows) Occur Between Coxa II and III in Larva. Coxal Pores (small arrows) Occur Between Coxae I and II (110x)



Figure 4. Anal Apertures of Larval, Nymphal and Adult *O. megnini*: (a) Larva Anal Aperture is Covered by Two Semi-circular Anal Valves (av) (1683x).

(b) Anal Valves (av) of Nymphal *O. megnini*. A Pair of Setae Arises From Depressed Margins of the Valves (698x).

(c) Anal Valves (av) of Adult *O. megnini*. Valves Bear Four Pairs of Setae (495x)

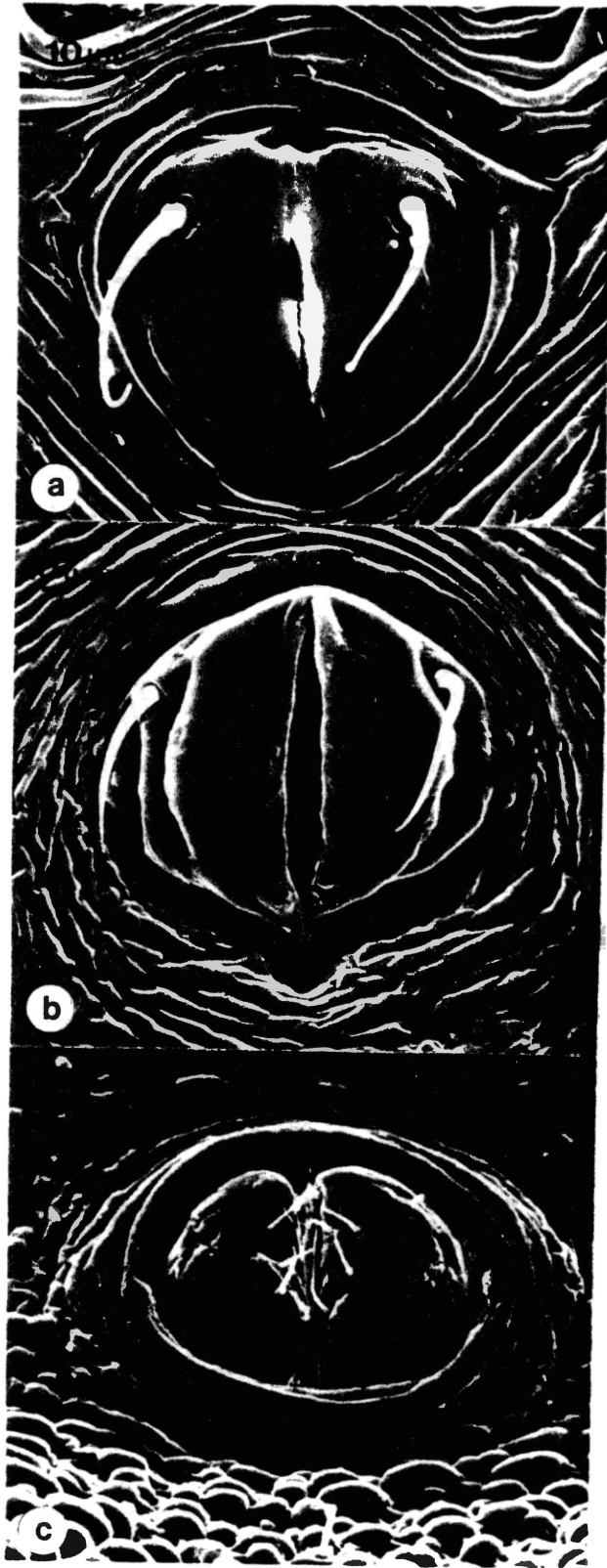


Figure 5. Nymphal and Adult Spiracles of *O. megnini*: (a)
Nymphal Spiracles are Cone-shaped With a Lid-like
Operculum (op) Which Lies to the Side of the
Ostium. Simple and Branched Cuticular Setae (cs)
Occur Around and Inside the Atrium (arrows) (283x)

(b) Adult Spiracles are Covered by a Centrally
Located Macula (m) and Surrounded by a Spiracular
Plate (sp). The Ostium Appears as a Slit Like
Opening (arrows) (224x)

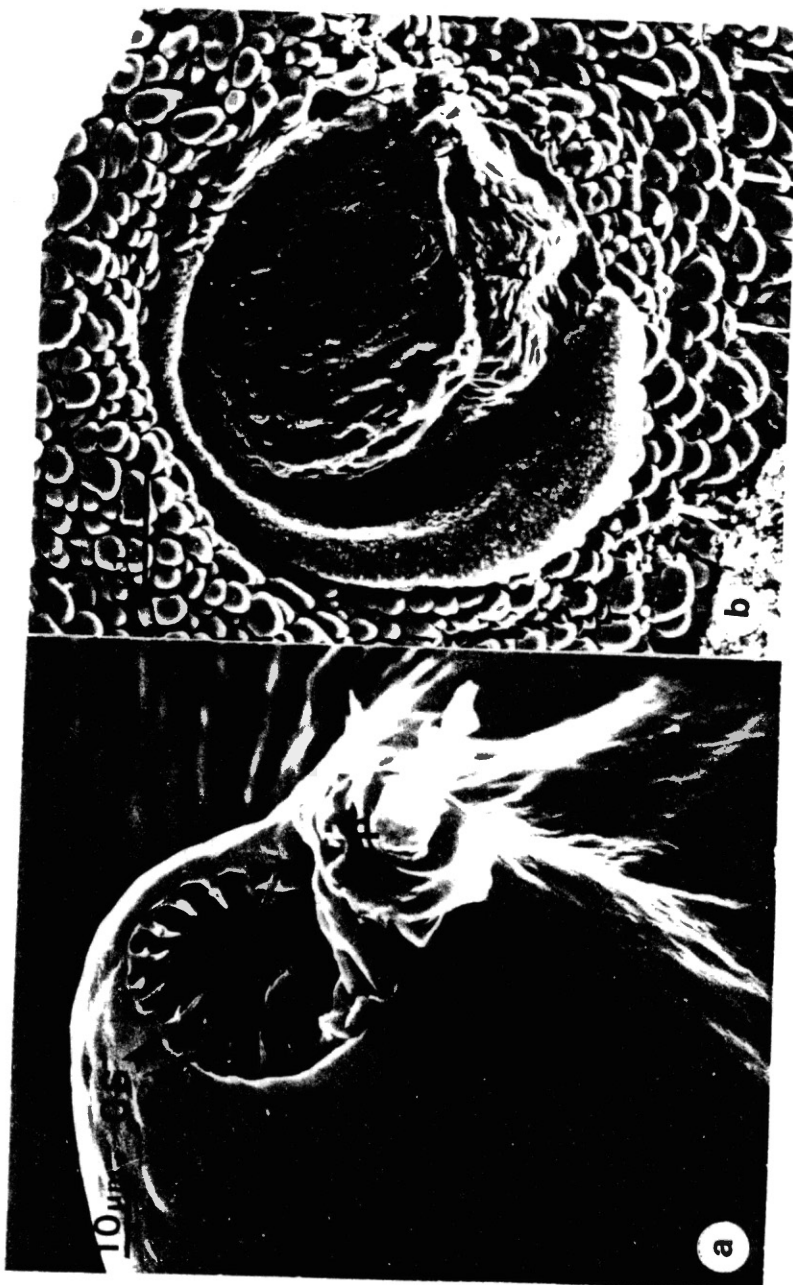


Figure 6. Larval, Nymphal and Adult Coxal Openings in *O. megnini*:

(a) Larval Coxal Pore Opening (1936x)

(b) Nymphal Coxal Pore Opening (313x)

(c) Adult Coxal Pore Opening (382x)

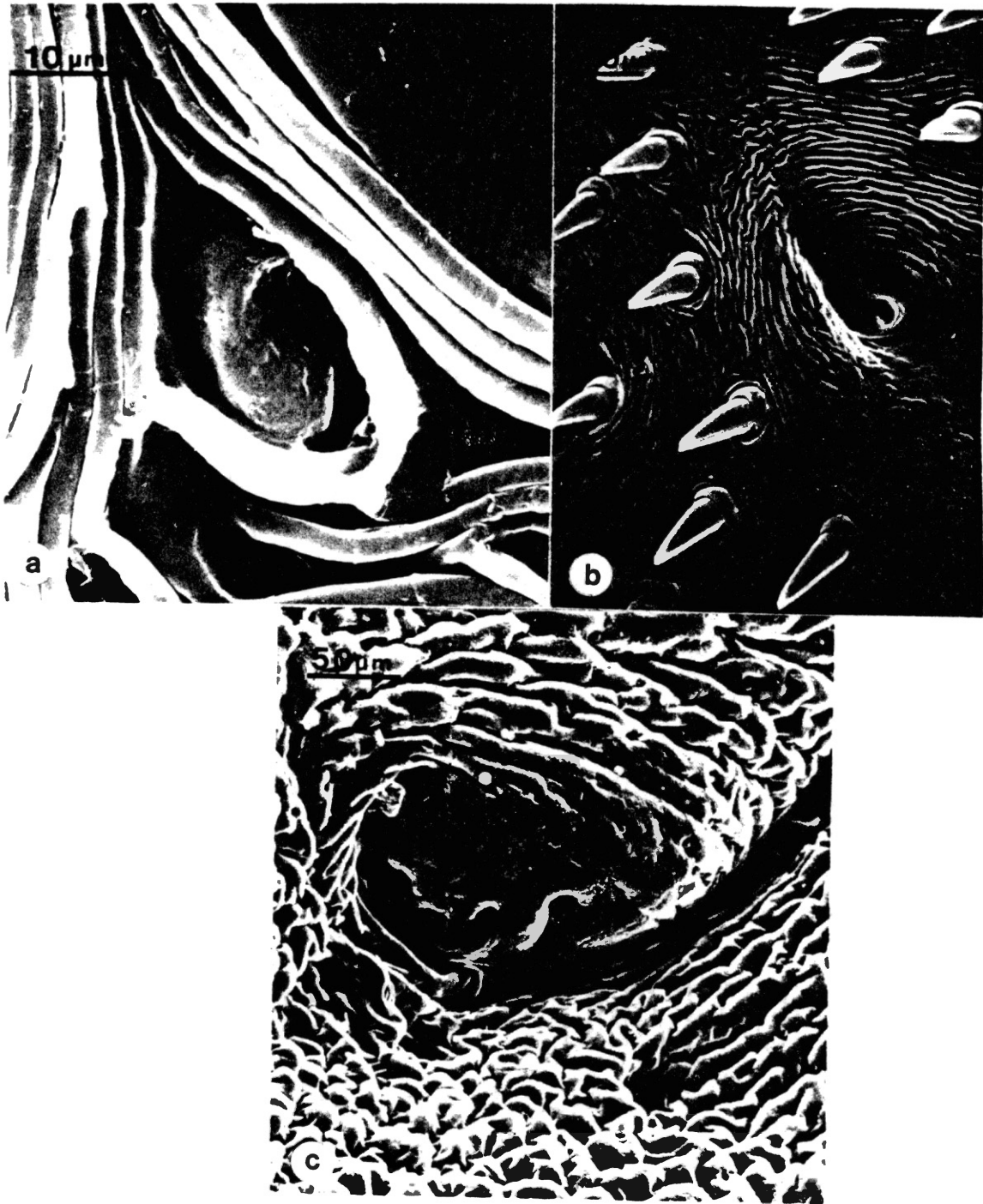


Figure 7. Nymphal Genital Anlage, and Adult Genital Apertures
in O. megnini (726x)

A Slit-like Genital Anlage Occurs in Nymphal O.
megnini in the Same Relative Position as the
Genital Aperture in Males and Females (b:188x;
c: 58x)

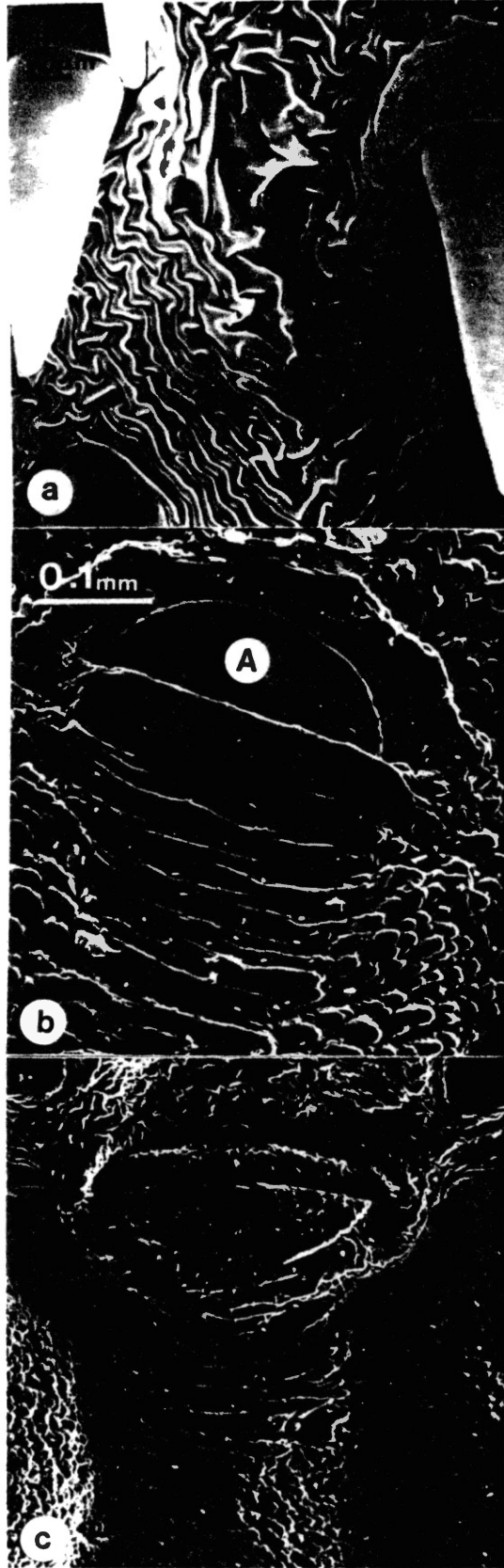


Figure 8. Folds and Grooves of O. megnini
Adults (Ventral Surface)

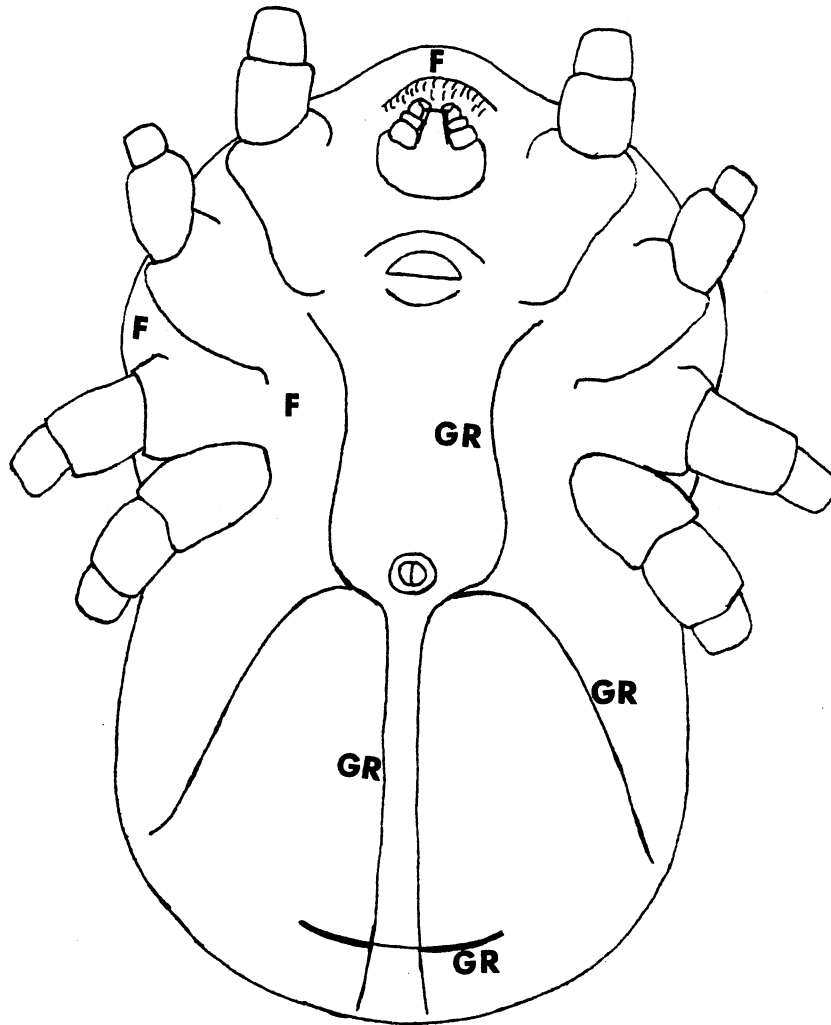


Figure 9. The Camerostomal Depression (c) Occurs Dorsal to the Capitulum (bc) and Contains Numerous Slender Setae (109x)



Figure 10. The Six Segments of Legs of *O. megnini* are: The Tarsus I, Tibia (II), Patella (III), Femur (IV), Trochanter (V) and Coxa (VI).

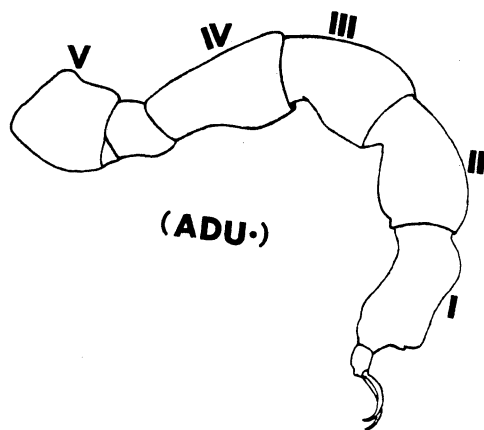
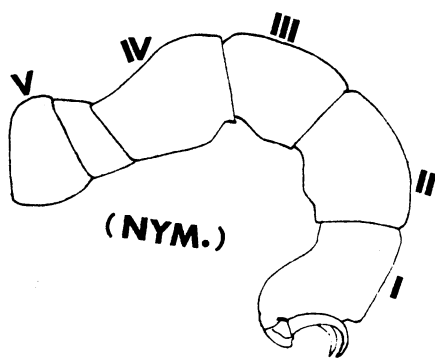
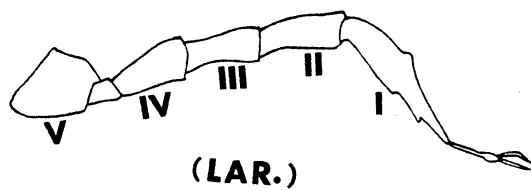


Figure 11. Leg I Setal Arrangement in Larval,
Nymphal and Adult O. megnini

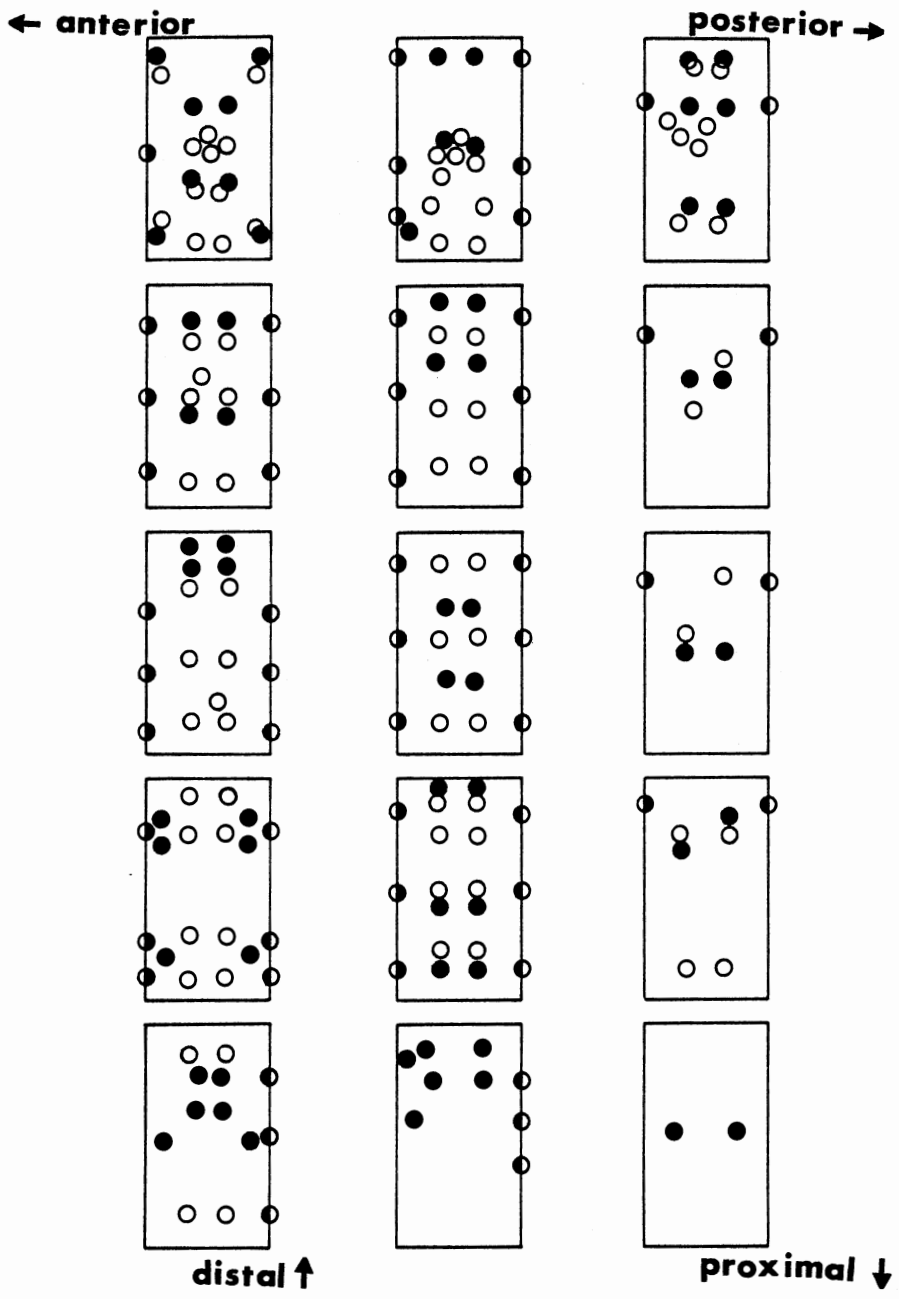


Figure 12. Larval, Nymphal and Adult Haller's Organ of O.
megnini.

(a) Haller's Organ (arrows) on Larval Tarsus I
(573x)

(b) Haller's Organ (arrows) on Nymphal Tarsus I
(179x)

(c) Haller's Organ (arrows) on Adult Tarsus I
(144x)



- Figure 13. Increased Magnification of Haller's Organ in *O. megnini*: (a) The Adult Haller's Organ Consists of a Capsule Containing Branched Sensilla, Overhanging Cuticular Setae (cs) and the Associated Tarsal Hump Setal Group (ths) (766x)
- (b) Increased Magnification of Adult Overhanging Cuticular Setae Showing Bridges (arrows) That Occur Between Individual Seta (4547x)
- (c) Cuticular Setae (cs) Form an Arch-like Structure in the Nymphal Haller's Organ. Associated Tarsal Hump Setae (ths) Occur Distal to the Capsule (1158x)
- (d) Four Branched Cuticular Setae (cs) Overhand the Larval Haller's Organ Proximal to the Tarsal Hump Setae (ths). Simple Setae as Well as a Single Nodiform Sensilla (n) Occur With the Capsule (2526x)



Figure 14. Larval, Nymphal and Adult Capitulum, Respectively.
Various Setal Groups Arise from the Ventral Surface:
Post Palpal Setae, Two Pairs in Adults (pps),
Post Hypostomal Setae (phs), and Anterolateral
Setal Group (als), Anteromedial Setae (ams)
and a Postero-medial Setal Group (pms):
(a) Larva (351x); (b) Nymph (126x); (c) Adult
(130x).

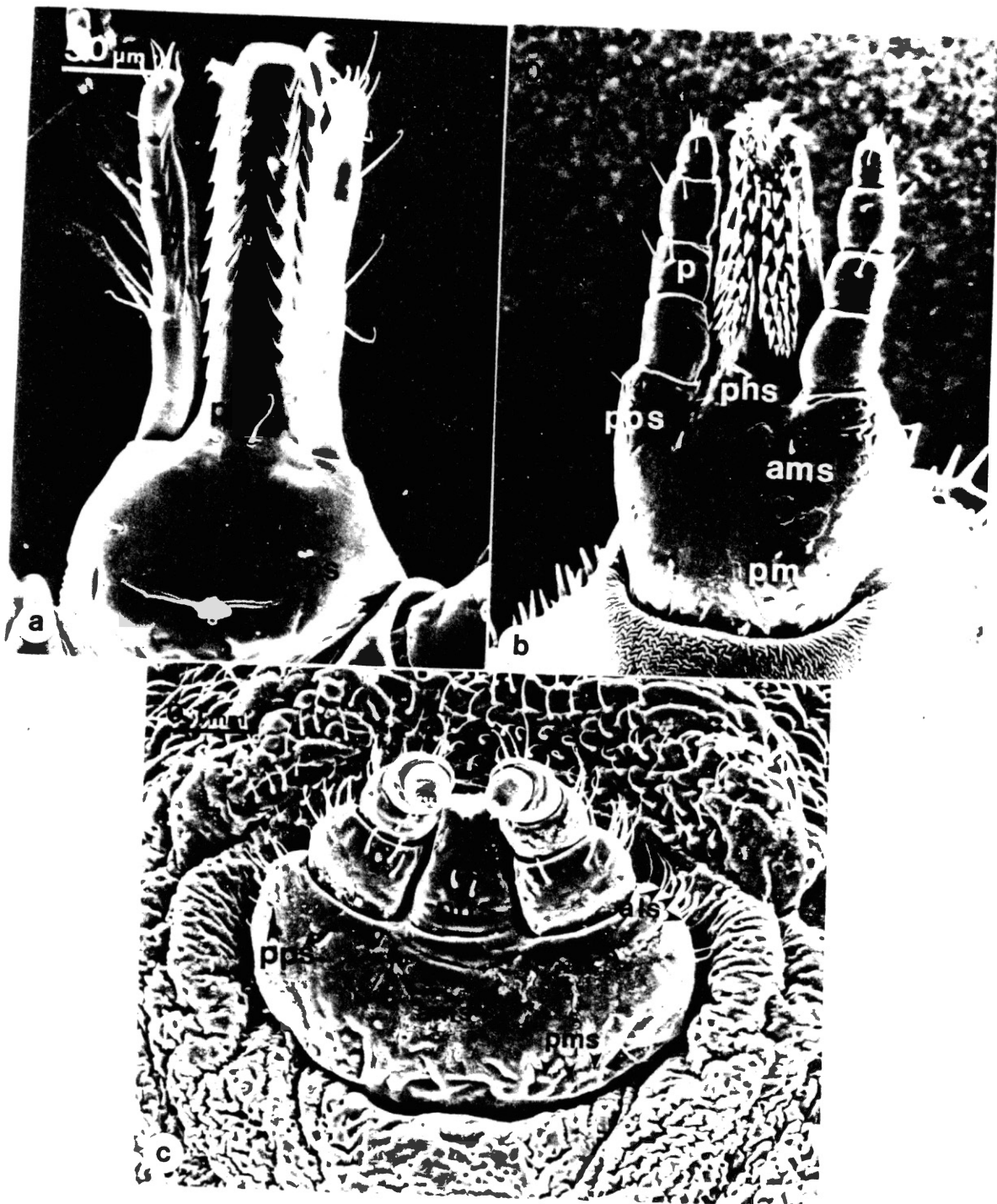


Figure 15. Higher Magnification of a Larval Hypostome Showing
the External (ex) and Internal (in) Articles
Which Make up the Chelicerae, Corona (c) and
Palps (p) (1073x)

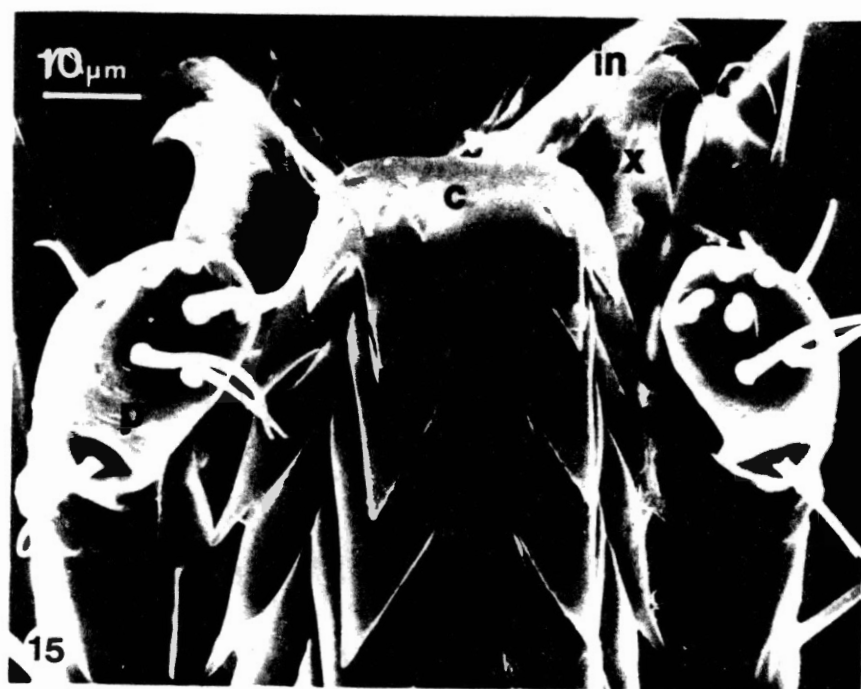


Figure 16. Nymphal Hypostome: Dorsal Aspect Showing External (ex) and Internal (in) Cheliceral Articles, the Dorsal Process (dp) and Palps (p) (196x).

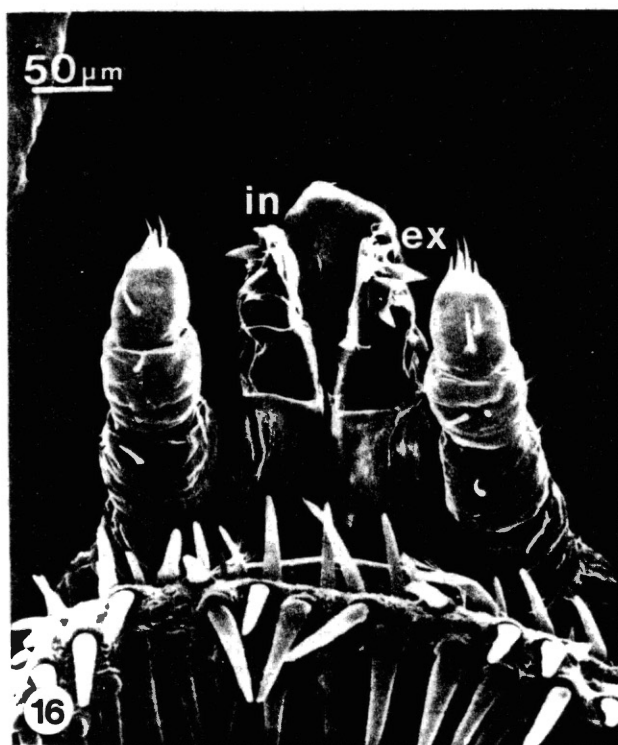
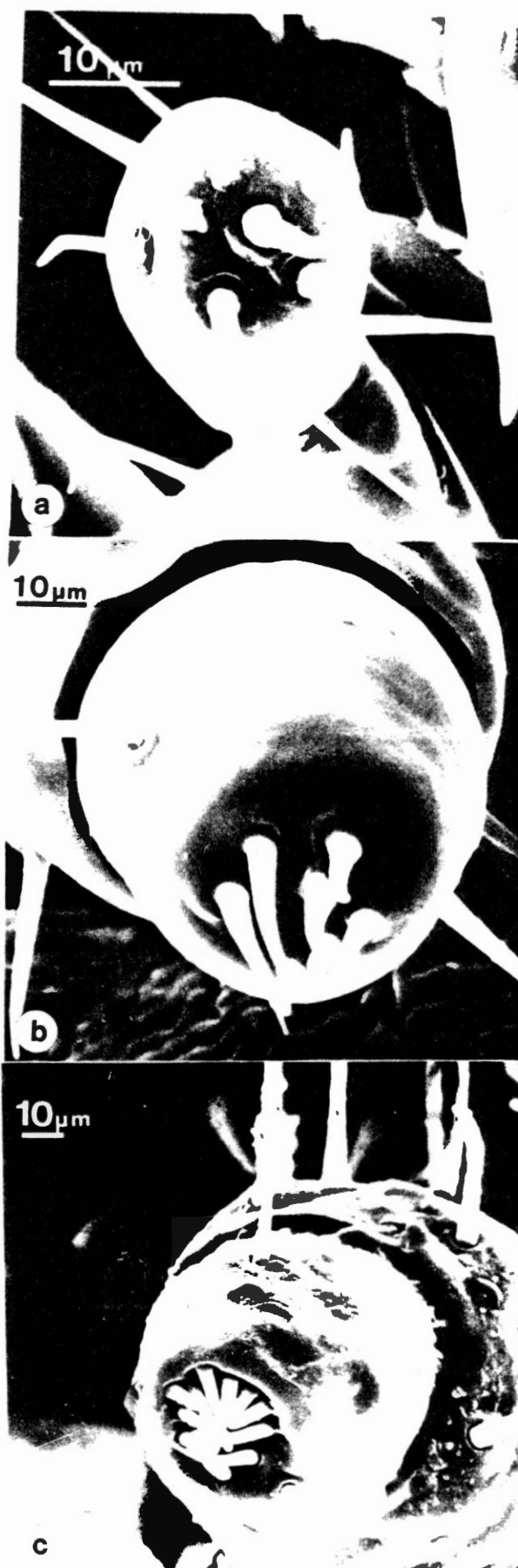


Figure 17. Terminal Palpal Setae in the Larva, Nymph and Adult
O. megnini: (a) Larva (1148x); (b) Nymph (1046x);
(c) Adult (690x).



a sutural line between dorsal and ventral surfaces and from the Antricola by having a hypostome which is neither broad at the base nor scoop-like. They resemble the Ornithodoros from which they are distinguished primarily on the basis of the integument of nymphs which is beset with spines in Otobius (Cooley and Kohls 1944). The general body outline of O. megnini is similar to the other known species in the genus (O. lagophilus) and there is agreement among various workers on its basic body organization (Salmon and Stiles 1901, Nuttall et al. 1908, Davis 1934, Cooley and Kohls 1944). The sizes and weights of all stages of O. megnini are summarized in Table I.

The nymphal stage differs distinctly from all other soft ticks in three main respects; the body is narrowed posteriorly in unfed specimens, the spiracles are conical and the body is beset with large numbers of three types of spines arranged in a regular pattern. The nymphs of Otobius lagophilus resemble those of O. megnini but can be separated from the latter species on the basis of its smaller size, mildly convex spiracles and slender setae (Cooley and Kohls 1944).

Morphological and biological evidence accrued in this study shows that there is only one nymphal stage. This conclusion is supported by observations reported by Hooker (1908) and Koshy et al. (1979) and contradicts the idea of two nymphal stages reported by some workers (Cooley and Kohls 1944).

Integument

The integument of O. megnini resembles that of Ornithodoros

species in bearing setae, pits and sensillae but differs from them in lacking true mammillae and discs. The dorsal pits of adults are an important taxonomic character in distinguishing O. megnini from O. lagophilus. In the latter species, the numerous pits on the dorsum are separated by a distance of the diameter or less (Cooley and Kohls 1944); whereas, in O. megnini the pits on the dorsum are separated by a distance of twice or more the diameter of one pit. The pits, which are more numerous on the anterior part of the body, contain centrally located tubercles from which setae arise. Setae of nymphs do not arise from pits, although in larvae they arise from tubercles situated in very small pit-like depressions.

The setae on the integument of adults are greatly reduced except for those on palps, legs and in the camerostome area.

The dorsal setae of nymphs are important in distinguishing O. lagophilus from O. megnini. In the former species, the setae are all of one size (Cooley and Kohls 1944) whereas in O. megnini three types of setae have been identified on the dorsum of nymphs and have been designated types A, B and C (Fig. 2).

Kohls et al. (1965) described the setal arrangement on the dorsum and venter of larvae of O. megnini and considered it a useful taxonomic character to be used in conjunction with other morphological characters to distinguish this species from other larvae in the subfamily Ornithodorinae.

The dorsal plate occurs in the larvae of both species of Otobius and is common in the subfamily Ornithodorinae. It is 0.220 ± 0.01 mm

long and 0.115 ± 0.006 mm at its widest point (just below the second pair of eyes). Kohls et al. (1965) reported slightly higher values for both length (0.239 - 0.260) and width (0.140 - 0.161 mm). Although the plate in O. lagophilus is also elongate and widest anteriorly, it is not narrowed posteriorly as in O. megnini.

Eyes are absent in nymphs nor adults. However, two pairs of eyes are present on the dorsum of larvae. Each eye is 0.003 ± 0.0001 mm in diameter and those on one side are separated from each other by 0.060 ± 0.002 mm. Kohls et al. (1965) reported that the first pair of eyes, located dorsal-laterally between the first and second pair of legs is larger than the second pair, lying dorsally behind the second pair of legs. However, these workers did not give measurements of these structures. In this study the difference in the sizes of eyes has not been confirmed.

Orifices

The external openings of O. megnini show many interesting features, many of which occur in the Argasidae. The anal aperture of larval O. megnini is similar to that of O. lagophilus and many other argasids in being covered by a pair of semi-circular valves that bear a pair of setae. The nymphal anal valves are also semi-circular and bear a single pair of setae. The "bean-shaped" valves in adults bear 4 pairs of setae.

There is no external morphological evidence to suggest the presence of respiratory structures in larvae, although a pair of "spiracle-like" plates exist ventrally between the second and third pair of legs (Fig.

3d). These structures, however, lack an external opening. Sonenshine (1962) reported that larval O. kelleyi also lack a respiratory system; but Theodor and Costa (1961) reported that an external slit which leads to an atrium exists in larvae of two species of Ornithodoros (O. lahorensis and O. delanoei acinus) between Coxa I and II. Although a respiratory system was found in some larval Argas, it was not observed in several other Argas and Ornithodoros larvae (Theodor and Costa 1951).

True spiracles occur in O. megnini nymphs and adults. The nymphal respiratory structures differ significantly from all other species in the Argasid family. The conical shape and dorso-lateral position has only been observed in O. megnini.

Coxal gland apertures occur as narrow slits in larvae and nymphs and open externally through numerous micropores in adults. In O. kelleyi the coxal gland apertures occur as a pair of small narrow slits between Coxa I and II of both nymphs and adults.

The genital anlage or the pre-genital opening (Fig. 7a) in O. megnini is present throughout the life of the single nymphal stage and occurs as a distinct pore and not as a pore-like depression as reported in O. kelleyi (Sonenshine 1962).

The frame surrounding the female genital opening bears a number of short setae (Fig. 7c). The male genital opening does not have setae. There are no comparable studies on these structures in the other Otobius species (O. lagophilus). However, Sonenshine (1962) also observed that the male genital aperture in O. kelleyi lacked setae, while the frame surrounding the genital opening in the female bore a total of 26 setae.

Integumentary Folds, Grooves and Depressions

In O. megnini the patterns of integumental folds, grooves and the camerostomal depression are characteristic of adults and nymphal argasid ticks. This species differs from O. lagophilus in which the camerostome and a definite hood are not apparent. In both species, the coxal and supracoxal folds are less evident in well fed specimens (Cooley and Kohls 1944). The most distinctive features of grooves in adults are the absence of the pre-anal groove and the reduction of the median and the first and post anal grooves. The grooves on both the dorsum and venter appear to be porous and serve as muscle attachment sites. The apparent porousness of the grooves has not been demonstrated in related argasid ticks.

The structure of the camerostomal depression is reported in O. megnini but there is no comparable information on the other known species (O. lagophilus) of this genus. The depression is absent in larvae and nymphs but is definite and deep in both sexes. The two most prominent features of the depression are the absence of cheeks that surround it anterolaterally in many argasid ticks (Cooley and Kohls 1944) and the large number of long setae within the depression (Fig. 9).

Paired Appendages

There are very few studies which have provided detailed comparative information on all the leg segments of ticks, although the tarsus of leg I has received considerable attention (Sonenshine 1962).

According to Snodgrass (1948) the designation of true leg segments

is based on the presence of movable joints and separate muscles. He recognized six jointed segments in each leg (Fig. 10). The length of each leg segment is shown in Table II.

Sonenshine (1962) has pointed out that except for the tarsus of leg I, the arrangement of setae on the legs of the various stages of ticks has not been documented. In the Otobius spp. this information was completely lacking. The setae of tarsus I has been used in the generic recognition of larval ixodid ticks (Clifford and Anastos 1960) and in the identification of larvae of certain Ornithodoros and Argas species (Dumbleton 1958, Sonenshine et al. 1962).

Haller's organ, which occurs on the tarsus of leg I of both ixodid and argasid ticks has been a subject of considerable research and its ultrastructure has been reported in a number of tick species (Homsher and Sonenshine 1975, Conlon et al. 1981, Homsher and Sonenshine 1977, Roshdy 1972, Sixl 1971). However, there are no published comparative ultrastructure studies on Haller's organ in the genus Otobius. It differs markedly from all other ticks by the absence of an anterior pit and in the number and structure of various cuticular setae in and around the capsule (Fig. 13).

Capitulum

There are no detailed studies on the capitulum of ticks of the genus Otobius and no intrageneric comparisons can be made regarding the various structures associated with it. However, detailed light and electron microscopic studies of the capitulum in some argasid ticks have been reported (Robinson and Davison 1913, Sonenshine 1962, Hoogstraal

1976).

In adult O. megnini the sub-rectangular basis capituli is similar to that of other argasid ticks in articulating with the idiosoma and in being partially withdrawn into the camerostomal depression. In contrast, larval and nymphal basis capituli occupy an exposed terminal position. The size and setal pattern of this structure are often of taxonomic value for differentiating the species of the Argasidae (Sonenshine 1962).

The hypostome of both larvae and nymphs have well developed recurved denticles which enable them to remain attached to host animals for 7 months or more. The hypostome of non-feeding adults is greatly reduced, without teeth and is similar to that of non-feeding adults of O. lagophilus.

The chelicerae of larval and nymphal O. megnini are structurally similar to those of other argasid ticks. Each cheliceral digit bears external and internal articles (Figs. 15, 16). The external article consists of 2 teeth, a very large lower one and a small upper one. The internal article bears a single tooth and also has a prominent dorsal process. Although the chelicerae of adults are greatly reduced, they still retain the same structural organization as found in the sub-adult stages. There is no comparable information on the chelicerae of the other species of Otobius. However, electron microscope studies of these structures have been reported on other ticks (Sixl 1972).

The leg-like palps are probably the most elaborate structures of the capitulum in all three stages of O. megnini. The terminal sensillae found on palpal article IV of larvae and nymphs increase from about 7 to a range of 12 to 14 in adults. In adults, the setae on individual

articles are most numerous on palpal article I (40), 13 on segment II, 8 on segment III and 1 on IV (Table III). There is no comparable information on the arrangement of palpal setae in the other species of Otobius and studies on other argasid genera have been limited.

CHAPTER III

COLONIZATION AND BIOLOGY IN THE LABORATORY

Materials and Methods

The colony of Otobius megnini Duges, was established from nymphs collected from animals of unknown origin that were sold at auction at Perkins, about 10 miles south of Stillwater, Oklahoma. Ticks were collected from animals that were secured in a stanchion for pregnancy testing, numbering, and blood collection for Bang's tests. A spatula was used to 'Scoop' out ticks from the ears of animals. Both fed larvae and nymphs were placed in the glass vials containing moistened tissue paper and transported to the laboratory.

In the laboratory, the ear wax covering the ticks was removed by carefully wiping them with tissue paper. These ticks were usually partially and fully fed nymphs with a few fed larvae. They were then weighed using a Mettler H51 balance (Mettler Instr. Corp., Heightstown, N. J.) and those weighing less than 20 mg were placed on rabbits (Oryctolagus cuniculus) and steers, (Bos taurus) so they could feed and complete development. Ticks weighing more than 20 mg were left for molting into adults at $26 \pm 1^{\circ}\text{C}$. and a humidity of $65 \pm 5\%$ R.H.. Fed larvae were allowed to molt at the same temperature but with 85 ± 2 relative humidity. Those that molted into nymphs were placed on either

rabbits or steers to complete development.

Nymphs that completed feeding on experimentally infested host animals and those collected at Perkins that initially weighed more than 20 mg were individually weighed, placed in a glass vial and numbered. The nymphs were then kept in a temperature control chamber Model No. TA 212 YB (Precision Scientific, Chicago, Ill. U.S.A.) maintained at a constant temperature of $26 \pm 1^\circ$ and a humidity of $65 \pm 5\%$ R. H. that was achieved by filling a pan in the temperature control chamber with water and sand.

As nymphs molted into adults, they were sexed using a dissecting microscope (Bausch and Lomb, U.S.A.) and weighed. Paired males and females were placed in a glass vial (about 18 cm^3) and placed in a temperature control chamber. The following parameters were then studied in each pair of adults: pre-mating period, pre-oviposition period, oviposition period, frequency and duration of intermissions during oviposition, incubation period of eggs and longevity.

Newly emerged larvae were left in glass vials in which eggs had been laid and placed in a tightly closed dessicator containing a solution of potassium chloride (KCl) that gave a humidity of $85.0 \pm 2\%$ R.H. (Winston and Bates 1960).

Larvae, which were at least 10 days old were placed in the ears of rabbits and steers using ear bags (Bailey 1960). Rabbits were fitted with a hard plastic collar that prevented them from scratching. Feeding spinose ear ticks stimulated excessive wax production that was injurious to ticks. The presence of ear bags made from nylon stocking (No Nonsense Fashions, Inc. 1980, Burlington, N.C., USA) further stimulated wax secretion. Thus, as soon as infested larvae had fed for at least 3 days,

ear bags were removed. They were again placed on animals for 4 days beginning the 7th day after infestation to prevent newly molted but unattached nymphs from escaping. As soon as newly molted nymphs had reattached, ear bags were then permanently removed from the host to increase air circulation that also appeared to be a factor in wax secretion. Fed nymphs were collected from the ears of host animals using a curved pair of forceps after they had detached on their own or when they appeared fully fed.

Tick feeding and development parameters were observed in larvae and nymphs while on the host. These parameters included larval pre-attachment time, feeding time, engorged weights, molting period, weight of newly molted nymphs, nymphal pre-attachment period, and nymphal feeding period. As fed larvae do not detach from the host prior to molting, engorged weights of this stage were determined by removing several larvae that had fed.

The phenomenon of limb regeneration was studied in 18 freshly molted adult ticks. In each experimental tick, the leg was amputated at a specific segment level, either at base of tronchater, femur, patella, tibia or tarsus. These experiments were conducted over several months to avoid any possible depletion of the colony.

The humidity level in the incubator was constantly monitored using an Airguide hygrometer (Airguide Instr. Co. Chicago, Ill. U.S.A.) while the temperature was monitored using a centigrade thermometer.

Results

Attachment of larvae released on host animals was completed within

hours after release. Unusual attachment patterns were observed in larvae which attached on the outside of the ear, on the host's face and even beneath the eyelids.

The larval feeding period and fed weight are reported in Table IV. Fed larvae remained attached within the ears of host animals. The larval molting period and molting success (percent) are reported in Table IV. However, only about 10% of fed larvae were able to molt into nymphs when fed larvae were removed from ears and placed in glass vials which were kept in the incubator maintained at $26 \pm ^\circ$. ($85 \pm 2\%$ R.H.). The longevity of unfed larvae was 78 ± 28.1 days under the same incubator conditions.

The weight of newly emerged nymphs and the pre-attachment period are reported in Table V. Newly molted active nymphs were not observed leaving the ears of host animals. The minimum nymphal feeding period was 20 days, and the mean was 38.2 days for those that dropped on their own. However, nymphs generally remained attached for long periods (up to 7 months) and in most cases they were only manually removed from host animals when they appeared fully fed, using size and brown coloration as indicators.

Nymphs do not complete feeding at the same time, although they congregate together during feeding. Only about 20% of attached nymphs were observed to be fully fed at any one time. Attached nymphs do not change feeding sites, although a partially fed nymph may reattach and complete feeding if it is dislodged during feeding.

The nymphal fed weight, molting period, and molting success (percent) are summarized in Table V. A fed weight of 26 ± 2.1 mg was found essential before successful molting of nymphs could

TABLE IV
 FEEDING AND DEVELOPMENT PARAMETERS OF
 LARVAL OTOBIUS MEGNINI ON BOVINE
 HOSTS AND IN THE LABORATORY†

PARAMETER	$\bar{x} \pm$ S. D.
Unfed Wt (mg)†	0.1 \pm 0.01
Fed Wt (mg)†	8.3 \pm 2.2
Pre-attachment Period (days)	2.0 \pm 1.1
Feeding Period (days)	4.7 \pm 2.1
Molting Period (days)	4.2 \pm 1.7
Molting Success (%)	92.1 \pm 1.6
Longevity (unfed larvae) (days)	78.0 \pm 28.1

† 26 \pm 1°C; 85 \pm 2% R. H.

TABLE V
 FEEDING AND DEVELOPMENT PARAMETERS OF
 NYMPHAL OTOBIUS MEGNINI IN THE
 LABORATORY+ AND ON
 BOVINE HOSTS++

PARAMETER	$\bar{x} \pm$ S. D.
Unfed Wt. (mg)	4.1 \pm 0.4
Fed Wt. (mg)	78.3 \pm 53.2
Pre-attachment Period (days)++	2.5 \pm 1.2
Feeding Period (days) ++	38.2 \pm 7.4
Minimum/Maximum feeding period (days)	20 - 210
Molting Period (days)	7.5 \pm 1.6
Molting Success (%)	98.1 \pm 1.9

+ 26 \pm 1°C; 65 \pm 2% R.H.

++ Observations made while on bovine hosts

occur. Fully fed nymphs which weighed above the mean fed weight (Table V.) tended to molt into females rather than males.

The weights of newly emerged adults are reported in Table VI. The mean weight of females was 24.68% higher than the mean weight for both sexes. Prior to molting into adults, fed nymphs lost about 16.5% of their weight (13.45 through water elimination and digestion and 3.05% through old skin). The ratio of males to females in the emerging adults was 1:1.3 under laboratory conditions. A "tattoo-like" sound was frequently produced prior to mating. The premating and pre-oviposition periods are reported in Table VI. Upon the start of oviposition eggs were laid continuously for the first two days and thereafter intermittently. There was a mean of 12.3 ± 4.7 intermissions (or periods of non-egg laying) each lasting an average of 4.88 days with a range of 1-47 days. The typical intermittent oviposition by female O. megnini is shown in Figure 18.

The total egg output per female, mean oviposition period, and the critical and reproductive egg indices (CEI, REI) are summarized in Table VI. The weight of a newly laid egg was 0.058 ± 0.003 mg. The incubation period was 12.4 ± 2.5 days. The egg hatching success of O. megnini was high ($92.18 \pm 7.39\%$).

Longevity. Female O. megnini which had mated and oviposited, did not live as long as males. The mean longevity for adults was 170.25 days with females living from 34-367 days and males living from 39-426 days. One female lived for 270 days after completing ovipositing.

Limb Regeneration. The phenomenon of limb regeneration was studied in 18 freshly molted adult ticks each of which had a single leg amputated at a specific leg segment except leg II. Full limb

TABLE VI
DEVELOPMENT AND OVIPOSITION PARAMETERS OF ADULT
OTOBIUS MEGNINI IN THE LABORATORY†

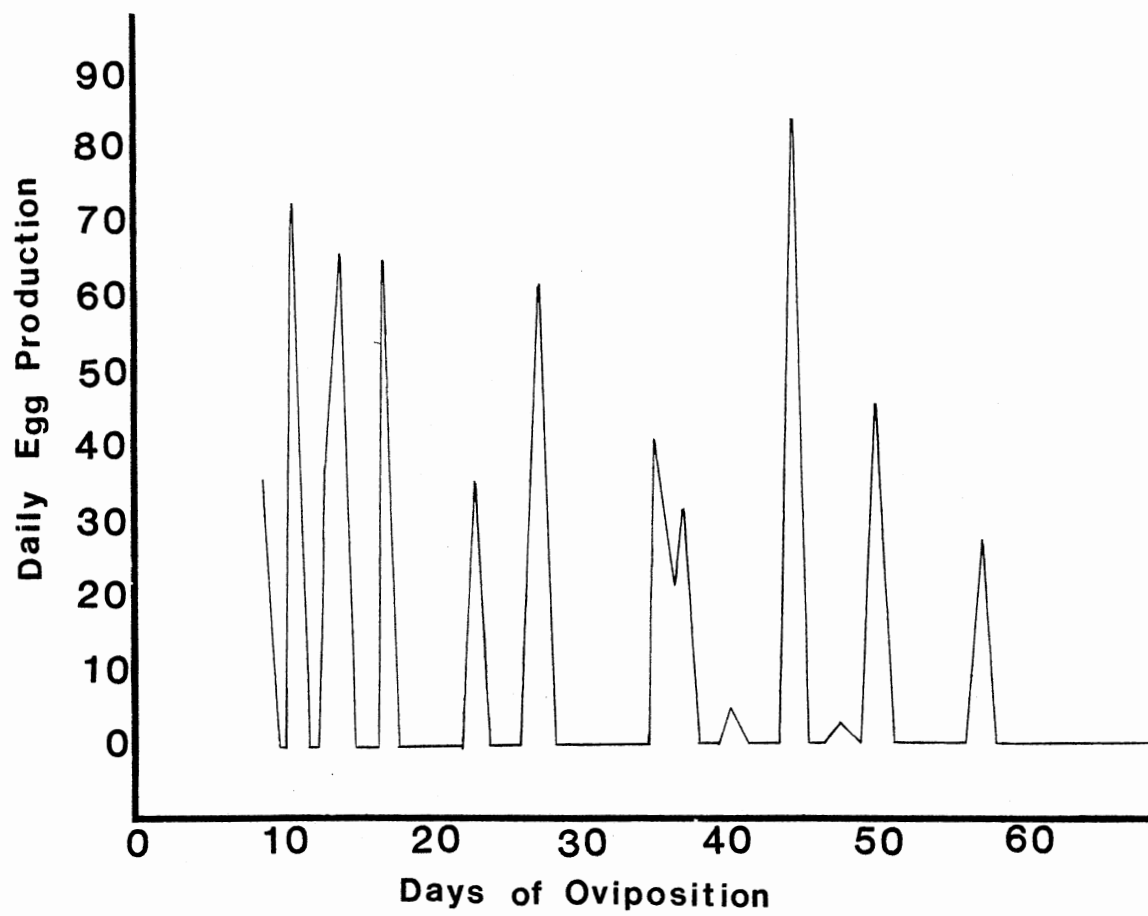
PARAMETER	$\bar{X} \pm$ S. D.
Adult Wt (mg)††	69.1 \pm 43.83
Female	86.17 \pm 32.7
Male	52.0 \pm 13.4
Pre-mating Period (days)	5.4 \pm 2.5
Egg Laying Stoppages (Intermissions) (days)	12.3 \pm 4.7
Duration of Intermission	4.8 \pm 3.76
Total Oviposition Period (days)	52.2 \pm 7.5
Egg Output:	
Total No.	789.9 \pm 199.5
CEI ††	160.9 \pm 40.7
REI †††	9.3 \pm 2.4

† $26 \pm 1^{\circ}\text{C}$; $85 \pm 2\%$ R.H.

†† CEI = mg of eggs per mg of female (33 females)

††† REI = No. of eggs per mg of female (33 females)

Figure 18. Typical Intermittent Oviposition by Female *O.*
megnini ($26 \pm 1^{\circ}\text{C}$; $65 \pm 5\%$).



regeneration did not occur. However, incomplete limb regeneration occurred in the hind leg that had been amputated at the distal end of coxal IV. The rate of regeneration was very slow. It started about 10 days after amputation, and it took about two weeks to grow up to the patella level.

Discussion

This study has indicated that the spinose ear tick has a very unusual life-cycle and has brought out many features of interest which were not previously reported or were only poorly documented. Larvae of O. megnini experimentally infested on rabbits attached not only inside the ears of animals, but also were able to attach, feed and molt into nymphs on the outside of the ears, on the face, on eyelids, and even beneath eyelids of host rabbits. It is possible that this anomalous infestation pattern occurs widely in nature, for Bulman and Walker (1979) have also reported an unusual feeding site on cattle for the immature stages of this species. These workers found larvae and nymphs of O. megnini feeding under the tail. Another interesting feature associated with attachment was that even when equal numbers of larvae were released on both ears, ticks tended to congregate mainly in one ear and particularly around one spot, especially the outer part of the concha.

The larval feeding period of 4.7 ± 2.1 days and molting period of 4.2 ± 1.7 days were comparable to those obtained by Koshy et al. (1979) for this species. The larval molting period was considerably shorter than that of hard ticks which take up to 4 times longer to molt

(Wanchinga and Sonenshine 1978). It was shown that although fed larvae remain attached on hosts to molt those forcefully removed from animals were still able to molt under suitable conditions but with much reduced success. These studies showed that fed larvae only detach after molting into nymphs which seek a new feeding site. The newly emerged nymphs are light pink-brown in color but change to gray after a few days of feeding. Legs show heavier pink pigmentation in newly molted nymphs. The general morphology of a fully developed nymph has been discussed in Chapter II. The lengthy feeding period of nymphs reported by other workers (Davis 1934, Herms 1917, Hooker et al. 1912, Hooker 1908) has been confirmed in this study. Spinose ear ticks infested on Hereford steers remained attached in host ears for periods over six months, from November, 1982 to June, 1983.

The molting success of nymphs under suitable conditions (98.1%), weight of molted adults (69.1 mg) and post-engorgement weight changes are reported for the first time. Adults do not feed and do not require a blood meal prior to mating and oviposition. The presence of a mating call reported by Hooker et al. (1912) was confirmed and these studies further indicated that the call, which sounds like the warning signal in termite colonies, is made only in the presence of both sexes and appeared to be produced by females as the 2nd and 3rd legs intertwined slightly and then were pulled apart. Ticks were observed in the mating position 1-7 days after molting with a pre-oviposition period of 5.4 ± 2.5 days.

An interesting feature of oviposition was the presence of intermissions (or periods of non egg-laying). An average of 12.3 ± 4.68 intermissions, each lasting an average of 4.8 days (1-49 days), were observed in the oviposition cycles of 20 paired females closely studies.

Otobius megnini does not lay a large number of eggs, and their development appear to have a narrow range of environmental conditions. An average incubation period of 12.40 days was noted. It is interesting to note that although the host-seeking stage is the larval one, longevity of this stage is only about 78.0 ± 28.1 days under suitable conditions, and yet adults, particularly the males, which do not feed, live longest.

The primitive phenomenon of limb regeneration first reported by Davis (1934) in larvae of O. megnini has been confirmed in a single case of one female. Leg IV (left) which had been cut off at the distal end of the coxa was partially regenerated up to the patella level and was used effectively in walking and turning over.

CHAPTER IV

FIELD BIOLOGY

Materials and Methods

Hosts were infested with larvae (at least a month old), obtained from our colony. Prior to infestation, ticks were stimulated by blowing body carbon dioxide (CO₂) and heat over them for a few seconds. The ticks were then infested on Hereford and Holstein steers (Bos taurus) that were confined to a paddock (695.19 m²) at the Efaw farm located 1 mile west of Oklahoma State University. About 2500 larvae were placed on the animal by emptying them directly in the ears and without using any ear bags. One to three animals were infested at monthly intervals, depending on their availability.

Drop-off Pattern

The ticks were observed frequently for larval attachment rate, feeding and molting times. When the newly molted nymphs had reattached within the ears (larvae molt into nymphs while attached in the ears, but newly molted nymphs detach for a few days before reattaching) they were marked with a specific powdered fluorescent paint which was either yellow, blue, green, or red, to determine their drop off pattern. The

ears of animals were then checked regularly during the day. At night, the paddock where infested steers were kept was thoroughly searched using a black ray lamp (Model UVGL-48, Ultra-Violet Products, Inc. San Gabriel, CA), that emitted long wave ultra violet radiation. All materials that dropped from the fluorescent - paint marked ears fluoresced under the black ray and were therefore picked up and checked. These included ticks, ear wax, and other debris. Ticks were recovered from litter and top soil up to a depth of 5 mm. Through direct observation of animals and searching around the paddock the drop-off pattern of nymphs was studied.

Nymphal drop-off and resting sites (any place where a tick remained settled for at least 72 hours) were monitored by searching with the black ray lamp and noting the various places where the ticks may have dropped. To supplement the study of natural detachment, a total of 100 nymphs were manually removed from ears of experimental steers and marked with yellow fluorescent paint. They were then divided into 5 groups of 20 nymphs. Each group of 20 nymphs was placed at a particular place within and around the paddock. The areas selected were those that resembled the usual drop off sites. The rate of dispersal was determined by measuring the distance traveled in relation to time, using a meter rule.

To study larval migration, two groups of larvae, (1500/group were labelled with yellow fluorescent paint by putting small amounts of paint powder in vials containing larvae and shaking the containers. The vials were then opened and placed at the base of a grass tussock at a pre-selected site. The grass tussocks were inspected regularly during diurnal and nocturnal periods for 7 days. The distance that larvae moved

were measured in the same manner as the nymphs.

To study the movement and development of adult spinose ear ticks, forty ticks were used in two separate trials to determine the rate of migration. Each tick (10 males and 10 females) was marked with powdered red fluorescent paint and released at separate localities in groups of four. The distances traveled were noted in centimeters. Mating behaviour, pre-oviposition, oviposition, and incubation periods of eggs and the longevity of adults were also studied.

Eighteen pairs of adults were placed in a fine mesh wire cage (about 36 mm² bottom area), divided into three groups. Group I ticks were placed at various points in the barn. In Group II, the cages were nailed to tree trunks at open heights in the open paddock. Artificial "cracks" were made in the tree trunk in which the cage containing ticks was placed. The small cage was then protected by a larger wire cage. Group III ticks were placed under rocks, fallen trees, and under soil. Development parameters were then studied in each group.

The egg development rate during the winter was studied by placing groups of eggs in artificially made crevices in dry wood and plugging the holes with cotton wool. The wood was then placed in the field and eggs were checked regularly.

Results

The feeding and molting periods of larvae under natural conditions were the same for all seasons and similar to those obtained in the laboratory (Table VII). The drop-off pattern of fed nymphs was also as

TABLE VII
 FEEDING AND DEVELOPMENT PARAMETERS OF LARVAL
OTOBIUS MEGNINI UNDER FIELD CONDITIONS †

Date Infested	Parameter				
	Larvae/Steer (Approximate)	No. Cattle	Color Code	Feeding Period (Days)	Molting Period (Days)
				$\bar{x} \pm \text{S.D.}$	$\bar{x} \pm \text{S.D.}$
11/21/82	2500	3	Yellow	4.5 \pm 1.1	3.9 \pm 0.9
12/21/82	2500	2	Red	4.1 \pm 0.9	4.0 \pm 1.6
1/29/82	2500	2	Blue	4.3 \pm 2.2	4.2 \pm 2.6
2/09/82	2500	1	Green	4.0 \pm 1.9	4.0 \pm 1.7

† November, 1982 - February, 1983

irregular as for those fed under laboratory conditions. Although nymphs remained attached for periods up to six months only a small number engorged simultaneously from each group.

Data on resting sites and dispersal showed that both fully fed and partially fed nymphs (based on their weight) dropped from the ears of infested animals around feeding areas, around fence posts (against which infested animals rubbed their ears vigorously), and around resting areas for animals (Table VIII). The highest number of nymphs were collected from around the poles and the fence (26), followed by food and water points (14). Considering the large number of larvae initially infested (20,000) on the steers, the total ticks recovered (40) represents a low recovery percentage.

The dispersal of fully fed nymphs was found to be limited, moving about 9.6 ± 2.9 cm from the spots where they were placed. They burrowed into the top 2-5 mm of ground debris or top soil.

Neither naturally deposited eggs nor naturally hatched larvae were recovered in this study. Larvae which had been placed manually at the base of grass tussocks were difficult to see during the daytime. However, fluorescing larvae were easily spotted at night under the black light. The maximum observed dispersal distance for larvae was 52.7 ± 7.8 cm.

To study the dispersal and development of adult spinose ear ticks under field conditions, they were placed on the ground at various sites and observed. Spinose ear ticks did not show any tendency to disperse very far. they moved for only 4-5 cm and then secreted themselves in debris or 2-5 mm of top soil. Although ticks were released in pairs they were not seen to mate and no oviposition occurred in such ticks that had

TABLE VIII
 CUMULATIVE RECOVERY OF NATURALLY DROPPING NYMPHS
 OF OTOBIUS MEGNINI AT VARIOUS SITES
 AT THE EFAW FARM †

	Food and Water Points	Poles and Fence	Resting Sites	Other††
Fed Nymphs	10	17	4	1
Partially Fed	4	9	0	0

† December, 1982 - February, 1983

†† Other areas within the paddock

been in the open field for periods up to three months.

Caged males and females which had been placed on tree trunks, under rocks and logs, and in the soil also did not mate and no eggs were laid.

Both free and caged ticks suffered a high rate of parasitism by acrobat ants, Cremastogaster laeviuscular Mayr (Fig. 19) which killed and cannibalized up to 70% of both nymphs and adults not protected by tangle foot. During the winter the ticks died quickly due to excessive moisture, turning bronze-copper in color.

The failure to oviposit under field conditions occurred in both groups of ticks released during the summer/fall and winter seasons.

However, caged adults which had been placed at various points inside the barn during the summer were able to mate and females laid eggs which hatched (Table XI). However, males and females kept in the barn took longer to mate and lay eggs than did laboratory reared specimens. The incubation period was also longer than those laid in the laboratory.

Groups of eggs which had been placed in artificial crevices of dry wood at the beginning of winter (11/16/82) did not hatch until well after the end of winter (4/27/83), giving an incubation period of about 162 days or more. The hatching success was, however, much lower than that obtained in the laboratory.

Discussion

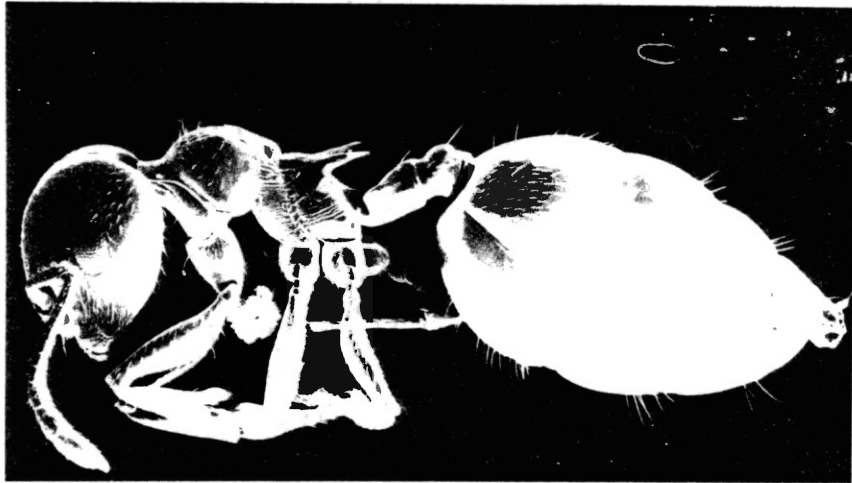
Although the field ecology of ixodid ticks has received much attention (Somenshine and Atwood 1965, Somenshine and Levy 1972, Gray 1959), there is no parallel published information on the field ecology of

TABLE IX
MATING AND OVIPOSITION BY OTOBIUS MEGNINI
HELD IN THE EFAW FARM BARN†

PARAMETER	$\bar{x} \pm$ S. D.
Pre-mating period (days)	6.5 \pm 3.3
Pre-oviposition period (days)	4.6 \pm 2.3
Oviposition period (days)	14.1 \pm 7.2
Egg incubation period (days)	30.5 \pm 5.7

† June, 1982, - October, 1982

Figure 19. Acrobat Ant, Cremastogaster laeviuscular Mayr. (28x)



argasids due to the nidicolous parasitism of most argasids. The tendency to change from temporary parasitism (associated with nest-burrow parasitism) to the more continuous parasitism reaches its greatest development in the species of the genera Otobius and Boophilus. Nymphs of O. megnini could remain attached to host animals for periods up to seven months or more.

The phenomenon of only a small proportion of attached nymphs completing feeding at any particular time may have some adaptive value. For instance, it was observed that nymphs survived the winter on host animals. The possibility of O. megnini overwintering on host animals was supported by the repeated failures to molt by nymphs that naturally dropped to the ground and those that were manually placed at various sites.

The apparent irritation that accompanies infestation of the ears causes host animals to rub vigorously against fence and shelter posts, dislodging the ticks. This accounts for the highest number of both fully fed and partially fed nymphs being recorded around this site (Table VIII). The struggle for food and the frequent visitation of food and water points means that ticks are mechanically dislodged at these places. Very few nymphs (a total of 4) were recovered around animal resting places. The nymphal recovery rate was very low considering the high number of larvae initially infested. The factors which may have contributed to the low recovery rate of fed nymphs included the loss of larvae that occurs during pre-attachment and feeding periods as a result of the host's physiological and behavioral responses. The frequent flooding of study areas with water from either rain or snow caused further losses in nymphs on the ground. The possible loss of fluorescent

paint also meant that a larger number of nymphs may have dropped to the ground than those that were actually picked up.

Larvae of the spinose ear tick are the only host-seeking stage; they showed a stronger tendency for horizontal dispersal (52.7 ± 7.86 cm) than fed nymphs and non-feeding adults. Detached nymphs do not disperse rapidly and far but remain near their drop off sites.

The failure of adults to mate and lay eggs under ambient conditions during both summer and winter seasons suggested that this species required specialized micro-habitats for these functions. The high hatching success of eggs laid by females that mated and oviposited in the barn suggested the reason why animals like horses and cattle, which use such housing structures, are frequently infested by this species.

Egg development studies carried out during the winter showed that apart from the nymphal stage, spinose ear ticks also survive the winter in the egg stage. From these observations it further appears that nymphs are the critical stage in the survival and distribution of this species.

There are no previous reports of the existence of natural enemies and the role they may play in the control of this tick. Acrobat ants, Cremastogaster laeviscular Mayr were observed to be serious predators of caged spinose ear ticks. These ants were able to cannibalize up to 70% of the nymphs and adults if left in the field unprotected by tanglefoot.

CHAPTER V

ADAPTIVE AND ONTOGENIC TRENDS

This chapter discusses adaptive and ontogenic trends in the spinose ear tick. Observations related to these trends were made in the course of the major studies on its ultrastructure (Chapter II), laboratory colonization and biology (Chapter III) and its field biology (Chapter IV).

The materials and methods for observing adaptive and ontogenic trends were, therefore, the same as those that were used in Chapter II. Portions of the results and discussion were also part of those obtained in studies of the ultrastructure, laboratory colonization and biology, and field biology of the spinose ear tick.

An appreciation of the adaptive and ontogenic trends in this species is essential to the understanding of its parasitism and to the proper assessment of its potential as a vector of disease. This emphasis has been lacking in many morphological and biological descriptions of this and many other tick species. In addition to adaptive patterns the specific systems and structures discussed in ontogenic trends are the hypostome, spiracles, Haller's organ, palps, eyes and anus.

Adaptive Behaviour

Unlike most argasids which have a characteristic multi-host

life-cycle, Otobius megnini is a one-host tick. Larvae, which are the only host-seeking stage, have retained features essential for successful parasitism. They have two pairs of eyes which are used for vertical orientation during questing and resting activities. These structures are absent in both nymphs and adults (Fig. 1). Larvae feed and molt into nymphs on the host animal. Nymphs re-attach without dropping to the ground. Consequently, the mouth parts of larvae and nymphs are well developed in contrast to non-feeding adults in which the hypostome is vestigial and the chelicerae are greatly reduced (Fig. 14).

Among the ticks, there is a tendency to change from temporary parasitism (associated with nidicolous parasitism of most argasids) to the more continuous parasitism which reaches its greatest development in the species of the genera Otobius and Boophilus. It was observed in this study that O. megnini could remain attached to host animals for up to six months or more. The denticles of the hypostome of larvae and nymphs of O. megnini are strong, recurved and posteriorly directed structures useful in anchoring to host animals for long periods (Fig. 14).

The feeding pattern of the spinose ear tick, unlike most other argasids, is not associated with nidicolous parasitism and like Ornithodoros lahorensis lacks a permanent shelter (Balashov, 1972).

A common feature associated with continuous parasitism is the tendency for particular species of ticks to attach and feed in specific areas on the host (predilection sites). Otobius megnini is the only soft tick and one of the three species of ticks known to have a strong tendency to attach and feed in the ears of host animals. The other two species, Amblyomma maculatum and Rhipicephalus appendiculatus,

are hard ticks and infest the distal portion of the ears. Otobius megnini, however, attaches deep in the folds of the concha which are often filled with wax and other debris. This may have been a major factor in the evolution of the stigmata of nymphs which feed for long periods in such an environment. Nymphal stigmata appeared to have evolved from a lateral position to a dorso-lateral position and to have assumed a conical shape. Stigmata found in nymphs differ very significantly from those found in adults (Fig. 5). In larvae, a pair of "spiracle-like" plates exist ventrally between the 2nd and 3rd pair of legs but have no external openings. The spiracles in nymphs are paired structures located dorso-laterally above the fourth pair of legs and project posteriorly. They are conical shaped and are 0.136 ± 0.021 mm long (Fig. 1). Within the conical open structure are simple and branched cuticular setae (Fig. 5). An "operculum", or lid-like structure with a large central seta, is attached to a cord originating within the atrium and lies on the side of the ostium (Fig. 5).

The spiracles of both females and males are dorso-laterally located above the fourth pair of legs. The size and form of the macula and slit-like ostium are similar in both sexes. The spiracular plate of the male may form a small lobe that is dorso-laterally extended. The entire spiracle is 0.290 ± 0.002 mm long in males and 0.254 ± 0.009 mm wide. The surface of the macula is slightly granular and the spiracular plate is very smooth.

The tendency to attach in the ears may have evolved as a protection against grooming by the host since the tick requires long periods of attachment. Despite this predilection for host ears, Bulman and Walker (1979) have reported an unusual feeding site on cattle for the immature

stages of O. megnini. They found larvae and nymphs of this species feeding under the tail. In this study larvae of this species were observed to attach, feed and molt into nymphs on eye lids and the face of experimentally infested white New Zealand rabbits.

The tendency of O. megnini to attach deep in the ears of host animals and to remain attached for long periods has resulted in its dissemination through trade enabling it to become established in the drier parts of the world.

Ontogenic Trends

Otobius megnini has exhibited many variations between its various life stages in a number of systems and structures. These include the Haller's organ, palps setae, eyes and anus.

Haller's Organ

The capsule and associated sensillae of this paired structure are located on the dorsal aspect of the tarsus of leg I (Fig. 12). In all three life stages Haller's organ consists of a capsule containing numerous branched sensillae. In larvae, the capsule is circular (0.002 ± 0.0001 mm in diameter) (Fig. 13d). It occurs as a transverse slit in both nymphs and adults. The length of the slit is 0.059 ± 0.004 mm in nymphs and 0.099 ± 0.005 mm in adults. The tarsal hump, which lies posteriorly to the capsule bears 4 setae (Fig. 13a). In the larva, 4 cuticular setae overhang the capsule; the 2 middle setae being branched near the base. A large nodiform sensillum occurs in the capsule of Haller's organ in the larva but is absent in nymphs and adults. The "overhanging" cuticular setae increase in number to about 18 in the nymph and form an "arch" over

the capsule (Fig. 13c). The number of cuticular setae in adults increases to 25. The setae are straight and "bridges" appear between individual setae (Fig. 13b).

Haller's organ, has been a subject of considerable research and its ultrastructure has been reported in a number of tick species (Homsher and Sonenshine 1975, Conlon et al. 1981, Homsher and Sonenshine 1977, Roshdy 1972, Sixl 1971). However, there are no published comparative ultrastructure studies on Haller's organ in the genus Otobius. It differs markedly from all other ticks by the absence of an anterior pit and in the number and structure of various cuticular setae in and around the capsule.

Palps

These paired structures are well developed in each life stage. They are leg-like and arise lateral to both the hypostome and chelicerae. Each palp consists of four articles which are freely moveable (Fig. 14). In the larvae, the palp is 0.071 ± 0.002 mm long and the articles are long and slender. In nymphs, the palps are 0.329 ± 0.013 mm long and in adults measure about 0.359 ± 0.06 mm and the segments are nearly as wide as they are long.

The total number of setae for each larval and nymphal palpal segment does not exceed a total of 4. Segment I in larvae has no setae, while segment I in nymphs has 1 lateral seta. The distribution of setae on various segments is shown in Table 3. In contrast, palpal segments of adults have numerous setae. Segment I has about 40 setae while segment II has 6 located dorsally, 3 laterally and 4 ventrally. Segment III has 8 and IV has 1 seta (Table III).

Terminal sensillae (Fig. 17) at the tip of palpal article IV number 7 in the larva and nymph and increase to 12 in males and 14 in females. In adults these sensillae arise from a pit, except for 1 sensilla which is sub-terminal (Fig. 17c).

The leg-like palps are probably the most elaborate structures of the capitulum in all three life stages. The terminal sensillae found on palpal article IV of larvae and nymphs increase from about 7 to a range of 12 to 14 in adults. In adults, the setae on individual articles are most numerous on palpal article I (40), 13 on segment II, 8 on segment III and 1 on IV (Table III). There is no comparable information on the arrangement of palpal setae in the other species of Otobius and studies on other argasid genera have been limited.

Eyes

These structures occur only in larvae (Fig. 1). The anterior pair of eyes lies in a somewhat dorso-lateral position between the first and second pair of legs. The second pair of eyes is located dorsally, behind the second pair of legs. Each eye is 0.003 ± 0.0001 mm in diameter and those on one side are separated from each other by 0.060 ± 0.002 mm. Eyes are absent in nymphs and adults.

Kohls et al. (1965) reported that the anterior pair of eyes was larger than the second pair. However, these workers did not give measurements of these structures. In this study the difference in the sizes of eyes has not been confirmed.

Anus

The anal aperture is found in all life stages and is situated in the

midline of the opisthosomal region of the body (Figs. 3, 4). In the larva, it is covered by two semi-circular anal valves which join together to form an apple-like or heart-shaped structure which is slightly enlarged anteriorly. Each valve is 0.036 ± 0.001 mm long and is widest just below the seta (0.035) mm). The single seta on each valve is separated from the other by a distance of 0.031 ± 0.008 mm. The anal opening is 0.0411 ± 0.009 mm at its widest and 0.0386 ± 0.007 mm along the midline of the valves.

The plates covering the anal aperture in the nymph are also semi-circular, but the outer margins of individual plates are depressed to form "platforms" from which arise a single pair of setae. The anal opening in the nymph is ovate, measuring 0.110 ± 0.002 mm at its widest and 0.093 ± 0.006 mm along the midline of the valves and has an "anal notch" at the lower margin.

The anal valves of both males and females are "bean-shaped", each bearing 4 setae. The two valves are surrounded by a well developed, slightly ovate annulus measuring 0.131 ± 0.04 mm at its widest axis and 0.095 ± 0.009 mm along the midline of the anal valves. The anal width/body length ratio showed a progressive decrease in the three stages (Table II), being highest in larvae (0.062 ± 0.005), 0.040 ± 0.001 in nymphs and lowest in adults (0.0147 ± 0.0052).

The anal aperture of larval O. megnini is similar to that of O. lagophilus and many other argasids in being covered by a pair of semi-circular valves that bear a pair of setae. The nymphal anal valves are also semi-circular and bear a single pair of setae. The "bean-shaped" valves in adults bear 4 pairs of setae.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The external ultrastructure, laboratory and field biology of Otobius megnini Duges, are described for all stages.

The main structures or systems for which the ultrastructure is reported are the general body organization, integument, orifices, folds, grooves and depressions, appendages, and the capitulum.

The egg is globular and is 0.406 ± 0.01 mm in diameter. The unfed larva measures 0.620 ± 0.01 mm from the tip of the hypostome to the posterior end and is widest behind the second pair of legs. The nymph measures 2.318 ± 0.12 mm long and is also widest between the second and third pair of legs, but is constricted behind the fourth pair of legs. Adults resemble peanut shells, and are also constricted behind the fourth pair of legs. Females are generally larger than males. The integument of adults is granular, with numerous pits and setae, while that of nymphs is spinose and bears no pits. The larval integument is finely striated and has fine bristle-like setae. The setae and sensillae of the integument have a consistent pattern of distribution especially in the larval stage which also bears a 0.220 ± 0.01 mm long dorsal plate and two pairs of dorsally located eyes.

The natural orifices include the anus, spiracles, coxal gland apertures, genital anlage and the genital apertures nearly all of which are located on the ventral side of the stages in which they occur. The

anal apertures of larvae and nymphs are covered by two semi-circular anal valves which bear a single pair of setae, whereas the two anal valves of both males and females are "bean-shaped", each bearing 4 setae, and are surrounded by an annulus. Larvae have no external spiracular openings, whereas in nymphs the spiracles are well developed, conical structures which are dorso-laterally located. In adults, spiracles have a flat macula over the ostium and are also dorsal-lateral. The coxal gland apertures, which open between coxa I and II are described. The presence of the genital anlage (pre-genital opening) is reported for the first time in nymphs of O. megnini and genital apertures of adults are also described. The integumentary folds, grooves and depressions are described in detail. The paired appendages which include the chelicerae, palps, and legs are described and compared in the different stages. The unique nature of the structures of Haller's organ in the three stages of this species is fully documented, and ontogenic trends in palpal setae are also described.

The capitulum, which consists of the basis capituli, the hypostome, the labrum (not visible externally), a pair of chelicerae, and a pair of palps, is described in detail except for the labrum. The shape and sizes of these structures including the setal patterns and dentition of the hypostome in all stages are reported. Morphological evidence obtained from the structures of Haller's organ in its three life-stages suggest that this species differs markedly from other argasid ticks.

Laboratory observations on its biology showed a larval fed weight of 8.3 ± 2.2 mg, a pre-attachment period of 2.0 ± 1.1 days, a feeding period of 4.7 ± 2.1 days, a molting period of $4.2 \pm$ days and larval molting success of $92.1 \pm 1.6\%$. It was observed that the mean

anal apertures of larvae and nymphs are covered by two semi-circular anal valves which bear a single pair of setae, whereas the two anal valves of both males and females are "bean-shaped", each bearing 4 setae, and are surrounded by an annulus. Larvae have no external spiracular openings, whereas in nymphs the spiracles are well developed, conical structures which are dorso-laterally located. In adults, spiracles have a flat macula over the ostium and are also dorsal-lateral. The coxal gland apertures, which open between coxa I and II are described. The presence of the genital anlage (pre-genital opening) is reported for the first time in nymphs of O. megnini and genital apertures of adults are also described. The integumentary folds, grooves and depressions are described in detail. The paired appendages which include the chelicerae, palps, and legs are described and compared in the different stages. The unique nature of the structures of Haller's organ in the three stages of this species is fully documented, and ontogenic trends in palpal setae are also described.

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longevity for unfed larvae was 78.0 ± 28.1 days. Unfed larval weight is 4.1 ± 0.4 mg while the fed weight was 78.3 ± 53.2 mg. The significance of the nymphal pre-attachment period (2.5 ± 1.2 days), the long feeding period (38.2 ± 7.4 days) (range: 20 days - 7 months) and molting period (7.5 ± 1.6 days) is discussed. The molting success of nymphs ($98.1 \pm 1.9\%$) was high under laboratory conditions ($26 \pm 1^\circ$; $85 \pm 2\%$ R.H.). Newly molted adults have a mean weight of 69.1 ± 43.83 mg, and a pre-mating period of 3.6 ± 3.5 days. The existence of a mating-oriented sound production has been confirmed in this species. The pre-oviposition period was found to be 5.4 ± 2.5 days whereas the total oviposition period was 52.2 ± 7.5 days.

An interesting feature associated with oviposition is the intermittent nature of this act. The mean egg output was 789 ± 199.5 eggs. The incubation period for eggs was 12.4 ± 2.5 days with a hatching success of $92.18 \pm 7.3\%$. Partial limb regeneration was observed in a single case of one female whose leg had been amputated at the distal end of coxal IV. Data on many other aspects of its life-cycle is reported for the first time.

Observations on its biology under field conditions are reported. The development under natural conditions of attached larvae was similar to that observed on animals kept under animal house conditions. The dropping of fed nymphs from host animals was found to occur more frequently around poles and fences, food and water points, and resting places in that order. Nymphs had a unique drop-off rhythm, with only a few of them from a cluster completing feeding at a time. Both larvae and nymphs tend to aggregate on particular spots while feeding. Fed nymphs and adults were found to have very limited dispersal, but larvae, which

are the host seeking stage, were able to move a distance of 52.7 ± 7.8 cm. Nymphs and adults failed to undergo further development when placed at various places outdoors. Adults kept at various points in the barn were able to mate and lay eggs which hatched after an incubation period of 30.5 ± 5.7 days. It appeared from these winter and Summer/Fall observations that the spinose ear tick survived the winter as attached nymphs and as eggs when deposited in suitable microhabitats, and that nymphs were the critical stage in the survival and distribution of this tick. Acrobat ants, Cremastogaster laeviuscular Mayr were found to be serious predators of O. megnini under field conditions.

Adaptive and ontogenic trends of this tick are also reported. Significant adaptive patterns are discussed in relation to its parasitism. The specific systems and structures discussed in ontogenic trends include the hypostome, spiracles, Haller's organ, palps, eyes and anus.

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