BULLETIN

of the

FLORIDA MUSEUM OF NATURAL HISTORY

THE REPTILE TICK *APONOMMA GERVAISI* (ACARINA : IXODIDAE) AS A PARASITE OF MONITOR LIZARDS IN PAKISTAN AND INDIA

Walter Auffenberg
Troy Auffenberg

UNIVERSITY OF FLORIDA   GAINESVILLE

This public document was promulgated at an annual cost of $2648.00 OR $2.65 per copy. It makes available to libraries, scholars, and all interested persons the results of researches in the natural sciences, emphasizing the circum-Caribbean region.

Publication date: 3/20/90   Price: $2.65

THE REPTILE TICK *APONOMMA GERVAISI* (ACARINA:IXODIDAE) AS A PARASITE OF MONITOR LIZARDS IN PAKISTAN AND INDIA

Walter Auffenberg and Troy Auffenberg*

ABSTRACT

The common tick of monitor lizards (*Varanus*) in Pakistan, India, and Sri Lanka is *Aponomma gervaisi*. In nature it occurs on only one of three native varanid species (*V. bengalensis*), in spite of the fact that both remaining varanid species in the main area investigated (*V. griseus* and *V. flavescens*) are ecologically and geographically syntopic with *Varanus bengalensis* at the two extreme ecological conditions in which the latter is found. Individuals of *Aponomma gervaisi* do not use their major host (*Varanus bengalensis*) at random. The level of infestation varies between different localities, between different seasons of the year, and between hosts of different sizes.

Attachment sites of adult male and female *Aponomma gervaisi* are very specific. Males occur mainly on the lateral surfaces of the tail and/or in a shallow, medioventral depression immediately behind the cloaca; adult females are usually attached in the axillary or a nearby region. Larval and nymphal site preferences are less distinct than those of the adults, and attachment is probably partly determined by competitive factors. Breeding takes place at the adult female attachment sites.

It is suggested that there is an advantage in adult male ticks aggregating in specific small areas due to the proportionally greater effect of several closely packed individuals on the hosts immune response system, particularly in reference to lymphoid cell density. These cells and body fluids seem to comprise the main food of the males. Male attachment sites are often located in areas of high potential abrasion. Females tend to attach in protected sites. Since females are mainly blood-sucking, there is probably an advantage in dispersed attachment patterns.

Haemaphysalis sindensis Bilques and Masood is placed in the synonymy of *Aponomma gervaisi*.

* Walter Auffenberg is Curator of Herpetology, Florida Museum Natural History, University of Florida, Gainesville FL 32611; his son Troy Auffenberg is a graduate student at the Department of Microbiology and Immunology, College of Medicine, University of Kentucky, Lexington, KY 40536-0084.

RESUMEN

La garrapata común de los lagartos monitores *(Varanus)* en Pakistán, India y Sri Lanka es *Aponomma gervaisi*. En condiciones naturales se le encuentra sólo en una de las tres especies nativas de varanos *(V. bengalensis)*, a pesar de que las otras dos especies que existen en el area estudiada son sintópicas ecológica y geográficamente con *Varanus bengalensis* en los dos extremos de condiciones ecológicas en los que esta última especie habita. Los individuos de *Aponomma gervaisi* no utilizan a su huésped primario *(Varanus bengalensis)* al azar. El nivel de infestación varía entre localidades diferentes, entre estaciones del año, y entre huéspedes de diferentes tamaños.

Los sitios de fijación de las hembras y machos adultos de *Aponomma gervaisi* son muy específicos. Los machos se encuentran principalmente en las superficies laterales de la cola y/o en una depresión medioventral superficial inmediatamente detrás de la cloaca; las hembras adultas usualmente se encuentran fijadas en o cerca de la región axilar. Los sitios preferidos por las larvas y ninfas son menos definidos que los de los adultos, y la fijación está en parte probablemente determinada por factores competitivos. El apareamiento ocurre en los sitios de fijación de las hembras adultas.

Se sugiere que existe una ventaja en que los machos adultos formen agregaciones en areas específicas pequeñas, debido al efecto proporcionalmente mayor de varios individuos agregados cerca unos de otros sobre el sistema de respuesta inmune del huésped, particularmente en referencia a la densidad de células linfoides. Estas células y fluidos corporales parecen representar el principal alimento de los machos. Los sitios de fijación de los machos están frecuentemente localizados en areas de alto potencial de abrasión. Las hembras tienden a fijarse en sitios protegidos. Debido a que las hembras son principalmente chupadoras de sangre, probablemente es ventajoso el fijarse en patrones dispersos.

Se coloca a *Haemaphysalis sindensis* Bilques y Masood en la sinonimia de *Aponomma gervaisi*.

TABLE OF CONTENTS

INTRODUCTION

In spite of the fact that ticks are commonly encountered on reptiles, relatively little work has been conducted on the attachment site preferences of the species that prefer these hosts.   The fairly recent contributions of such workers as C. M. Bull, R. H. Andrews, T. N. Petney, and their associates attest to the fertility and importance of this field of investigation.   However, most of these papers address the question of the role of competition in host attachment sites of parapatric ixodid tick species (i.e. Bull, Sharrad, and Petney 1981; Andrews and Petney 1981; Andrews, Petney, and Bull 1982).   The question of site attachment specificity within members of a single tick species has been addressed less often.   Of particular importance is the recent documentation of sexual separation on reptilian hosts among a very few species of the ixodid genera *Aponomma* and *Hyalomma* (one species each, see Petney and Al-Yaman 1985) and *Amblyomma* (one species, T. Auffenberg 1988).   The conclusion in both these studies was that adult female ticks attach in the anterior part of the body and adult males on the posterior part.

Of particular interest is the work on *Amblyomma helvolum* (T. Auffenberg 1988), for site attachment analyses included two sympatric varanid lizard species (*Varanus olivaceus* [as *V. grayi* in the publication] and *V. salvator*, both in southern Luzon, Philippine Islands).   Several important conclusions were drawn regarding host site attachment preferences of this ectoparasite (an *Aponomma*-like species of eastern India, Southeast Asia and the Indo-Australasian Archipelago); namely, *Amblyomma helvolum* is apparently a varanid lizard specialist, for this parasitic species is common only on species of this lizard family, and only on varanids is a definite site attachment pattern discernible.   The attachment pattern is one in which male *Amblyomma helvolum* are located more posteriorly on the host than female ticks of the same species.   More intriguing is that, while female ticks are most often attached in the axillary region of both host species investigated, the males are mainly attached at the base of the claws on the hind feet of the host *Varanus olivaceus*, and on the median part of the chest and in a medioventral depression at the base of the tail on *V. salvator*.   Thus, the host species seems to determine what particular area of the posterior part of the body will be infested with adult male *Amblyomma helvolum*.

More recently we had an opportunity to study the site attachment patterns of several other species of geographically sympatric varanid lizards in India and Pakistan during the senior author's work on the behavioral ecology of local monitor lizards.   None of these varanids represented the same species as the Philippine ones, nor was the parasite congeneric to that in the earlier study.   Here then was an opportunity to examine spatial distribution of still another reptile tick on the skin surfaces of three congeneric sympatric hosts.

The tick we studied was *Aponomma gervaisi* (Lucas 1847). This ixodid species has a geographic range from Yeman to the southern tropical parts of Nepal and south through all of the Indian Peninsula to Sri Lanka (more eastern localities in the early literature seem to be misidentifications, as are early records from Africa). We found it at elevations from nearly sea level to 700 m; the highest elevational record we have found in the literature is 1000 m (southern India, Siddappaji and Channabasavanna 1981). The distribution (Fig. 1) reflects a common zoogeographic pattern among faunal elements associated with Afro-Indian tropical deciduous forests.

In Pakistan and most of India, *Aponomma gervaisi* is geographically sympatric (Figs. 1, 2) with three species of varanid lizards, i.e. the Bengal monitor *Varanus bengalensis*, desert monitor *V. griseus*, and yellow-headed monitor *V. flavescens*. These three lizard species are sympatric in at least parts of their respective geographic ranges. However, *V. griseus* and *V. flavescens* occur in ecologically divergent habitats. The former lives mainly in arid sandy places (Auffenberg et al. in press a) and the latter in marshes (Auffenberg et al, in press b). *V. bengalensis* is found in both of these habitats, though less in desertic situations. However, if the sandy tracts are within several hundred meters from water, *V. bengalensis* also occurs there. Thus *V. bengalensis* is ecologically sympatric at opposite ends of its environmental spectrum (Auffenberg MS) with each of the remaining species (Fig. 3). It is also sympatric with *Varanus salvator*, which ranges from northeastern India eastward through all of Southeast Asia and most of the Indo-Australian Archipelago.

The few references to *Aponomma gervaisi* on the Indian subcontinent have all been short, stressing geographic range, morphology, or host species. No detailed work has been published on parasite density or seasonal abundance. The only previous mention of any reptile ticks in Pakistan is by Bilques and Masood (1973), who described a new species, *Haemaphysalis sindensis*, from a single individual of *Varanus monitor* (= *V. bengalensis* in current usage) from Sind Province.

The genus *Aponomma* is a member of the family Ixodidae, currently believed to be comprised of about 630 species, and the subfamily Amblyomminae, of 126 species (*Aponomma* and *Amblyomma* only). The subfamily parasitizes mainly reptiles. The genus *Aponomma* is comprised of 24 species. Of these, 22 can be placed in the <strict-total> type of tick-host specificity, as defined by Hoogstraal and Aeschlimann (1982), being found primarily on reptiles; in Asia the hosts are large snakes and varanid lizards.

Several *Aponomma* species have been reported to parasitize *Varanus bengalensis* (including the subspecies *V. b. nebulosus*). These are *A. varanensis*, *A. gervaisi*, and *A. laeve*. The latter is a tick of generally mesic forest habitats of the western Ghats of India and Sri Lanka, *Aponomma varanensis* occurs in evergreen to deciduous forests from Sri Lanka and eastern India through
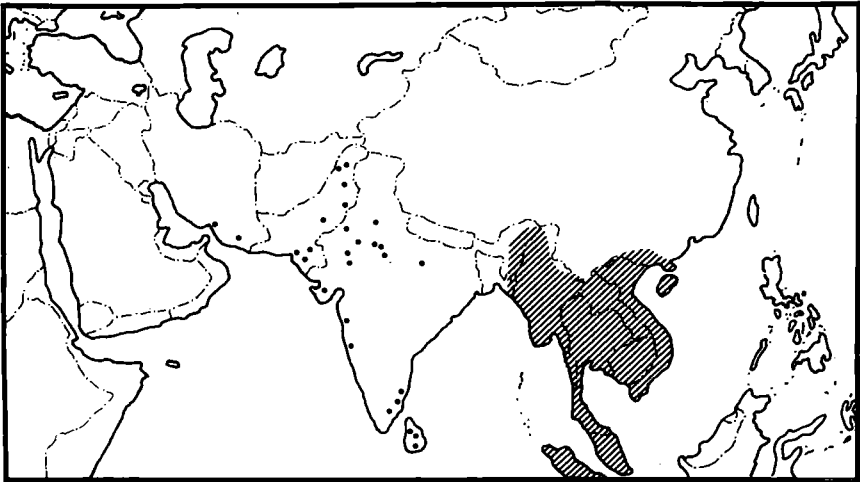
Figure 1. Geographic location of specimens of *Aponomma gervaisi* examined during this study (dots). The general distribution of *Aponomma varanensis* is shown as a cross-hatched area.
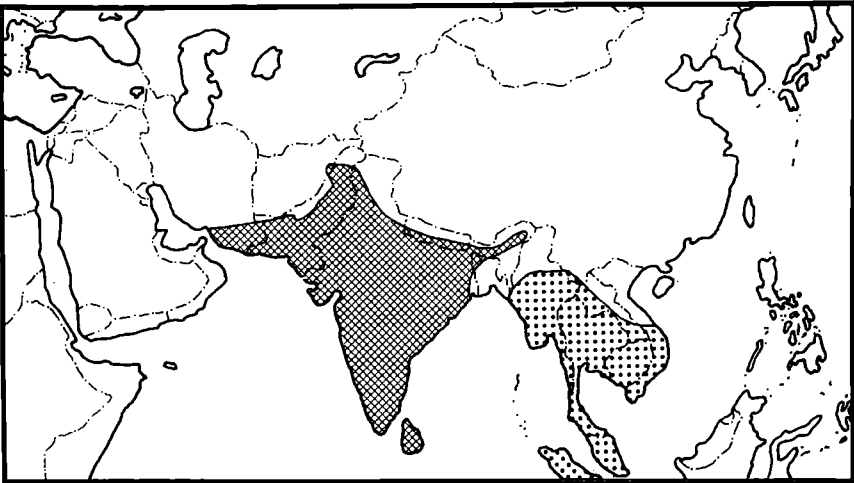

Figure 2. The general geographic ranges of *Varanus bengalensis bengalensis* (cross-hatched) and *V. b. nebulosus* (dots) on the Asian mainland.
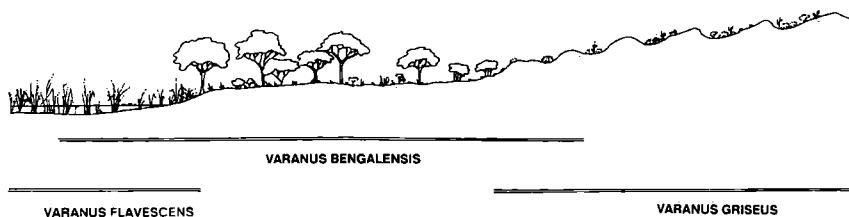
Figure 3. The general habitat relationship of the three varanid lizards within the range of *Aponomma gervaisi*.

Southeast Asia to the Indonesian Archipelago. *A. varanensis* is found primarily on land turtles and varanid lizards. *Aponomma gervaisi* is a reptile tick of generally xeric habitats on the basis of available locality records--usually *Acacia* and other deciduous forests (Yeman to and including southern Nepal, the Indian peninsula, and Sri Lanka). It characteristically parasitizes mainly *Varanus bengalensis*.[1] Both *A. gervaisi* and *A. varanensis* have been most commonly and consistently associated with *Varanus bengalensis bengalensis* and *Varanus bengalensis nebulosus* respectively. The borders of the ranges of both the ticks and the lizards are more or less coincident (compare Figs. 1 and 2).

Previously *Aponomma gervaisi* has been reported from *Varanus bengalensis* by Sharif (1928) from several localities throughout peninsular India and Ceylon, Bhat and Sreenivasan (1981) in western peninsular India, Hoogstraal and Rack (1967) and Nagar et al. (1977), in northern India, Siddappaji and Channabasavanna (1981), Stephan and Rao (1979) in southern India, Warburton (1910) in eastern India. and Deraniyagala (1953) and Seneviratna (1985) in Sri Lanka. *Haemaphysalis sindensis*, described as a new species by Bilques and Masood (1973), was found on an individual of *Varanus bengalensis* from near Karachi, Pakistan. This name should be referred to the synonomy of *Aponomma gervaisi* (see below). Other species reported as (occasional) hosts of *A. gervaisi* are provided in Table 1. These comprise only one species of lizard and several of rather large snakes.

[1] *A. varanensis* has been called *A. quadratum, A. barbouri, A lucasi*, and as a variety of *A. gervaisi* in the older literature. *A. varanensis* and *A. gervaisi* are possibly subspecifically related, though this and other nomenclatorial questions will have to await future study of material from many localities. As Hoogstraal and Rack have stressed (1967), the Asiatic species of *Aponomma* are in need of critical study. The most recent taxonomic review of the entire genus is by Kaufman (1972).

Table 1. Hosts (excluding *Varanus bengalensis* [= *V. cepidianus*]) from which *Aponomma gervaisi* has been reported.

Host	Source
Lizards	
Indian Garden Lizard, *Calotes versicolor*	Warburton 1910
Snakes	
"snake"	Nagar et al. 1977
Rock python (*Python molurus*)	Wall 1921, Seneviratna 1985
Dhaman, *Ptyas mucosus*	Warburton 1910 (as *Zamenis mucosus*)
Common Cobra, *Naja naja*	Sharif 1928; Warburton 1910;
(= *N. tripudians*)	Siddappaji and Channabasavanna 1981
	Seneviratna 1985.
King Cobra, *Ophiophaga hannah*	Bhat and Sreenivasan 1981;
	Stephan and Rao 1979

The present study was undertaken mainly to determine whether in *Aponomma gervaisi* there is (1) a different pattern in site attachment of adult males and females that is consistent with that found with *Amblyomma helvolum* (i.e. females anterior, males posterior) and, (2) whether the preferred attachment sites of this tick also vary with different host varanid species.

ACKNOWLEDGEMENTS

METHODS

A total of 381 monitor lizards were examined during this study, as follows: 73 *Varanus griseus*, 90 *V. flavescens*, and 218 *Varanus bengalensis* (79 Pakistan, 120 India, 19 Sri Lanka). Most host specimens were seen alive and the ticks sexed and counted on different parts of the body;

some preserved museum specimens are included in the analyses for months in which field samples were insufficient in number (the ticks rarely detach themselves from the skin when the lizards are preserved). Selected samples of ticks were preserved and later studied in detail under magnification at the Florida Museum of Natural History.

Designated parts of the body for which total ticks/host were indicated each time in the field are shown in Figure 4. Of special significance is a shallow somewhat longitudinal depression on the ventral side of the tail base, hereafter called the "pit," in which ticks are often attached.

The total area of exposed skin in each of the designated sample areas was calculated by first skinning an adult *V. bengalensis* and then cutting out each of the sample areas. These fresh pieces of skin were then placed on a sheet of 1 X 1 mm graph paper. Each representative skin sample was carefully traced and the surface area calculated by counting the 1 mm^2 squares in each tracing (see Table 2).

Table 2. Skin area and frequency of attachment by adult males and females, and by nymphs of *Aponomma gervaisi*.

	Skin Area (% of total area)	Males (N = 909) (% of total)	Females (N = 420) (% of total)	Nymphs (N = 439) (% of total)
Pit	0.04	41.0	0.4	0.5
Deltoid	0.12	0.1	9.7	0.2
Fingers*	0.13	0.0	0.0	8.0
Toes**	0.16	0.1	0.5	0.9
Posting.	0.20	0.0	0.0	16.9
Cloaca	0.39	0.4	1.5	8.4
Axilla	0.47	0.7	60.4	15.5
Inguinal	0.58	0.3	0.3	8.0
Head	1.67	0.3	2.0	0.0
Chin	1.90	0.0	2.3	0.0
Throat	2.36	0.0	6.6	3.9
Arm	3.54	0.0	8.1	12.3
Leg	5.12	0.0	0.7	8.4
Neck	5.91	0.0	3.2	0.0
Chest	8.70	< 0.1	3.0	0.0
Lateral	14.56	0.7	0.5	13.4
Tail	16.39	50.4	0.0	1.4
Belly	17.30	0.3	1.0	2.1
Dorsal	20.46	0.4	0.0	0.2

* Between fingers
** Between toes
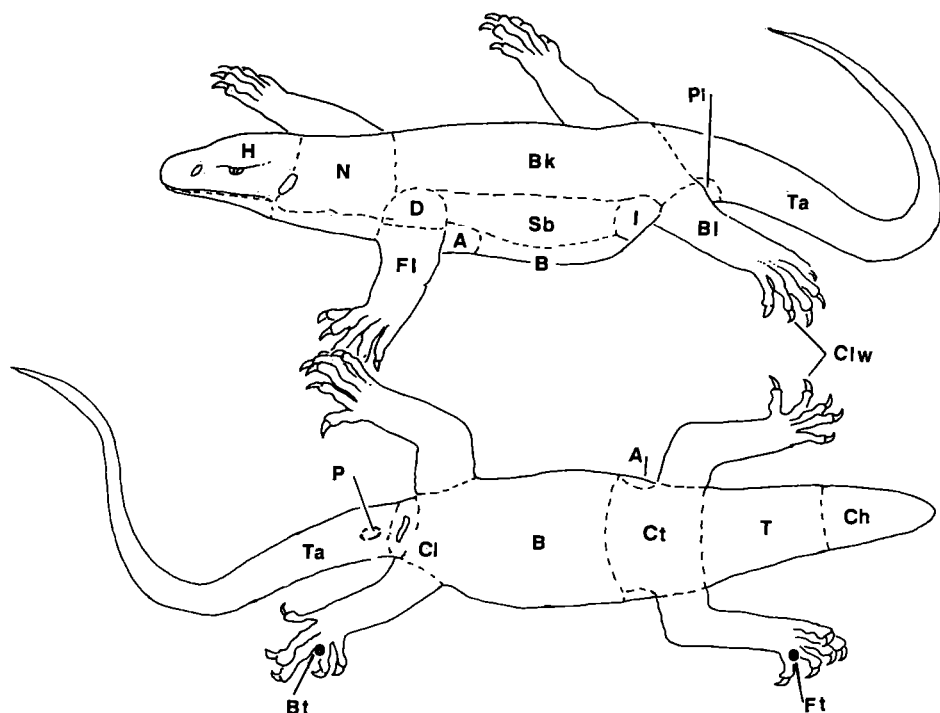
Figure 4. Tick attachment site classification used in this paper. Top, dorsal and lateral surfaces: bottom, ventral surface.   Abbreviations: A=axillary; B=belly; Bk, back; Bl=back leg; Bt=between hind toes; Ch=chin; Cl=cloacal periphery; Clw = base of claws; Ct=chest; D=deltoid; Fl=front leg; Ft between front toes; H=top and sides of head; I=inguinal; N=nape; P=pit; Pi=post-inguinal; Sb=side of body; Ta=sides of tail; Th=throat.

All host animals were sexed, weighed (to nearest g), and measured (standard lizard snout-vent length = SVL below, to nearest mm). Field aspects of the study were conducted during all months of the year, from June 1984 through September 1987, in order to obtain information on seasonal aspects of tick infestation.

RESULTS

Identity of Ticks

All ticks examined during this study were identified as *Aponomma gervaisi*.   This includes material from Sind Province, Pakistan, from where *Haemaphysalis sindensis* was described by Bilques and Masood (1973) from a

single adult *Varanus bengalensis*. *Haemaphysalis* is a common mammalian ectoparasite but rarely found on reptiles. No *Haemaphysalis* species have been reported from any Oriental reptiles to date (see Hoogstraal and Rack 1969 for discussion of Asiatic members of this genus). This fact, plus our consistent identification of all Sindhi reptile ticks as *Aponomma gervaisi* during the course of the study, leads us to the conclusion that the holotype of *Haemaphysalis sindensis* should be referred to the genus *Aponomma* (which is normally restricted to reptilian hosts). We base this on a number of salient characters mentioned in the holotype description. These are (1) the distinctive color pattern, (2) the shape of the coxal spurs, and (3) the appearance of the festoons on the idiosoma. Unfortunately the presence of eyes could not be determined in view of the unavailability of the holotype.[2] When placed in the correct genus, it becomes clear that *Haemaphysalis sindensis* Bilques and Masood 1973 is a synonym of *Aponomma gervaisi* Lucas 1847. The latter is the most common ixodid tick parasitizing *Varanus bengalensis* throughout the western half of its range.

In southern India and Sri Lanka, *A. laeve* occasionally infests *Varanus bengalensis*, but it is apparently found mainly on large snakes. In Southeast Asia, *A. varanensis* is the common tick of *Varanus bengalensis*, though in the same area *Amblyomma helvolum* is the the most frequent tick species parasitizing other varanids (i.e. *Varanus salvator*). Indeed, T. Auffenberg (1988) has shown that this tick seems specifically adapted to this varanid host.

Because *Aponomma gervaisi* has not previously been adequately illustrated, we include appropriate drawings in Figures 5 and 6.

Percent Infestation

Nagar et al. (1977) show that in the New Delhi area only 5.2 percent of all snakes they examined were infested by *Aponomma gervaisi*, whereas 21.4 percent of all Bengal monitor lizards in the same area were infested. These data originate from small samples. No other appropriate data occur in the literature. Our work in Pakistan shows that the tick is only a rare snake parasite (< 2.0 %, N= 56), and then only in larger, terrestrial (nonfossorial) species. Furthermore, the extensive present data provide a basis for analyzing the extent of both seasonal and geographic infection levels in Bengal monitors.

In a random sample of 58 adult *Varanus bengalensis* from Sind Province, Pakistan, 92% were infested; 90 % of a sample of 70 adults from the

---

[2] The University of Karachi was closed due to political disturbances during a trip made specifically to examine the type.
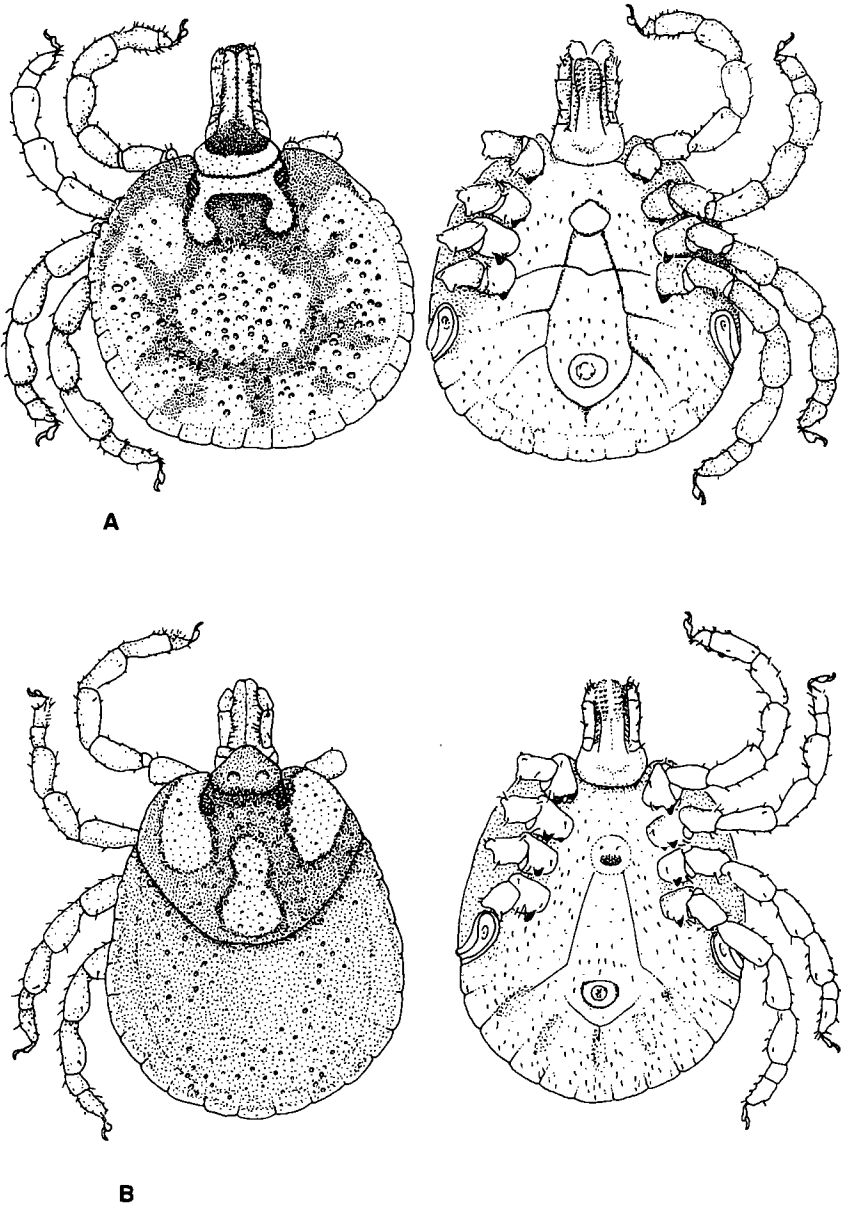
Figure 5. *Aponomma gervaisi* Thatta, Sind Province, Pakistan. A, Adult male, dorsal and ventral views. B, Adult female, dorsal and ventral views.
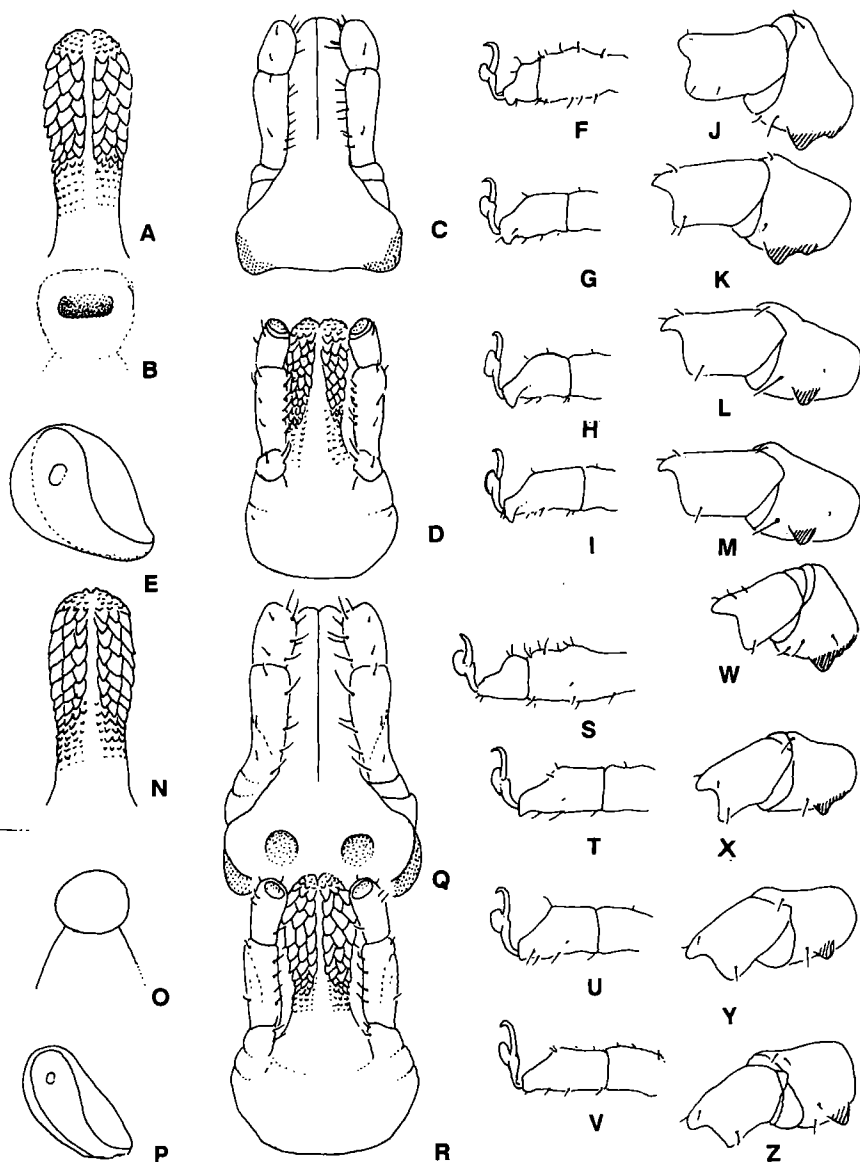
Figure 6. Enlarged views of anatomical parts of *Aponomma gervaisi*, Thatta, Sind Prov., Pakistan. Male A-M; (A) hypostome, ventral view; (B) shape of genital aperture; (C) capitulum, dorsal view; (D) same, ventral view; (E) spiracle; (F-J) terminal part of legs I-IV respectively; (K-M) coxae I-IV respectively, showing shape of the coxal spurs. Female, N-Z; (N) hypostome, ventral view; (O) shape of genital aperture; (p) spiracle; (Q) capitulum, dorsal view; (R) same, ventral view; (S-V) terminal part of legs I-IV respectively; (W-Z) coxae I-IV, showing shape of coxal spurs.

State of Uttar Pradesh, India; and 77% of a sample of 38 adults from Sri Lanka. The desert region of Gujarat and Rajasthan States in India had the lowest infestation percentage we found throughout the range of this tick; only 32 percent of a sample of 38 adults were infested. It is clear that while some geographic variation in infestation percentage does seem to occur, the infestation rate of adult *Varanus bengalensis* is high throughout the entire range of this tick species. There is no other reptile species in Pakistan-India that can be demonstrated to have an infestation rate even one sixth as great (see below for other varanid species in Indo-Pakistan area). We conclude that this species of varanid lizard is a major host of *Aponomma gervaisi*.

Number Ticks/Host

No wild caught *Varanus griseus* or *V. flavescens* had any ticks, regardless of geographic origin of the host, time of year, or host size. However, if adults of either monitor species were placed in confinement where *V. bengalensis* had been kept earlier, *Aponomma gervaisi* nymphs and adults of both sexes attached themselves to a few of these captive lizards. This was noted in three *V. flavescens* (1 nymph in the axilla of one host lizard, 2 nymphs in the axilla of another, and 3 adult females in the axilla and 2 adult males on the belly of the third). Ticks also attached themselves to three captive *V. griseus* (1 male in the medioventral caudal pit of one host, 1 male in the pit and 7 nymphs near the cloaca on another host, and a single male in the pit of the last host). We conclude that (1) *Aponomma gervaisi* is rarely (ever ?) a natural parasite of *Varanus griseus* and *V. flavescens*, and (2), when it does attach to them (in captivity), it does so in a pattern more or less consistent with that demonstrated for its major host, *Varanus bengalensis* (see below).

Only three *Aponomma gervaisi* were found on any of the 382 individuals of 53 other species of terrestrial reptiles collected in Pakistan and northern India (including snakes and lizards of several families, but no land tortoises). However in the same places and during the same times, 1509 individuals of *Aponomma gervaisi* were found on 218 individuals of *Varanus bengalensis*.

Overall, 87 percent of all adult *Varanus bengalensis* examined in the field throughout that part of its range coincident with that of *Aponomma gervaisi* carried at least one adult tick; most had many more. The most we counted in the field/host was 103 (host SVL 372 mm), but in captivity one large male (SVL 536 mm) carried 416 adult ticks (though appeared listless and stopped eating, presumably as a result of the heavy infection). The overall average number of adult ticks per *V. bengalensis* was 10.8 ± 10.5. The large standard deviation reflects the great variation in number of adult ticks per host.

There is no statistically significant difference in the number of ticks found on male and female monitor lizards. However, statistically significant positive correlations (<5%) can be demonstrated between the number of adult ticks/host and host SVL in all the populations studied ($r = 0.63$ for populations from Northern India [$N = 70$], 0.64 for Southern India [$N = 39$], 0.75 for Sri Lanka [$N = 38$], and 0.50 for Pakistan [$N = 58$]). An analysis of R^2 (coefficient of determination) demonstrates that in populations from northern India, 40% of the total variation in number of ticks/host is associated with the regression; 41% in southern India, 56% in Sri Lanka and 25% in Pakistan. Individuals with SVL < 260 mm never had any ticks. Since hosts of this size are known to be in their second year of life (Auffenberg MS), it follows that neither nymphs nor adult ticks attach themselves to *V. bengalensis* during the lizards first year of life. This is probably partly related to the fact that during the first year, juveniles over most of the species' range spend much of their active time in the trees. This does not however, account for the fact that juveniles in relatively treeless parts of Pakistan also lack ticks. The entire matter of the circumstances under which monitor lizards acquire their tick loads needs additional study.

Nymphal ticks were found on 22.9 percent of all *V. bengalensis* examined. The average number of nymphs/host was 14.3; the maximum number recorded is by Nagar et al. (1977), who report 254 from one individual captured near New Delhi.

Larval forms are much less frequently seen. The average was 2.3/host, but we have found as many as 21 on a single host. The relative rarity of larval stages (at least one larva occurs on only 3.3 percent of all adult monitors collected) suggests that this life stage will be found to parasitize other host species as well. Of the total infected hosts, 46 percent possessed only adult ticks, 30 percent had adults and nymphs, and only 2.9 percent carried only nymphal ticks.

Within the range of *Aponomma gervaisi*, the infestation patterns of adult male and female ticks over four geographic samples covering large areas (Pakistan, northern India, southern India, and Sri Lanka) are statistically homogeneous (Kruskal and Wallis ANOVA [one way] test: $X^2_3 = 1.04$, not significantly different). However, some spatial heterogeneity of infestation patterns can be demonstrated over even shorter distances. The best example is drawn from data within the Pakistan sample. Here a series of 61 monitor lizards from a southern Pakistan subset (Sind Province) has a significantly lower mean number of ticks/host than a series of 32 similar sized monitors from the north (Punjab Province); mean south 3.9 male and 2.0 female ticks/host, mean north 13.8 and 6.6/host respectively, students t-test 2.65, *df* 91, with a probability < 0.01. Results are provided in Table 3. Bull (1978) obtained similar results in infestation rates of adult ticks from different localities on Australian lizards.
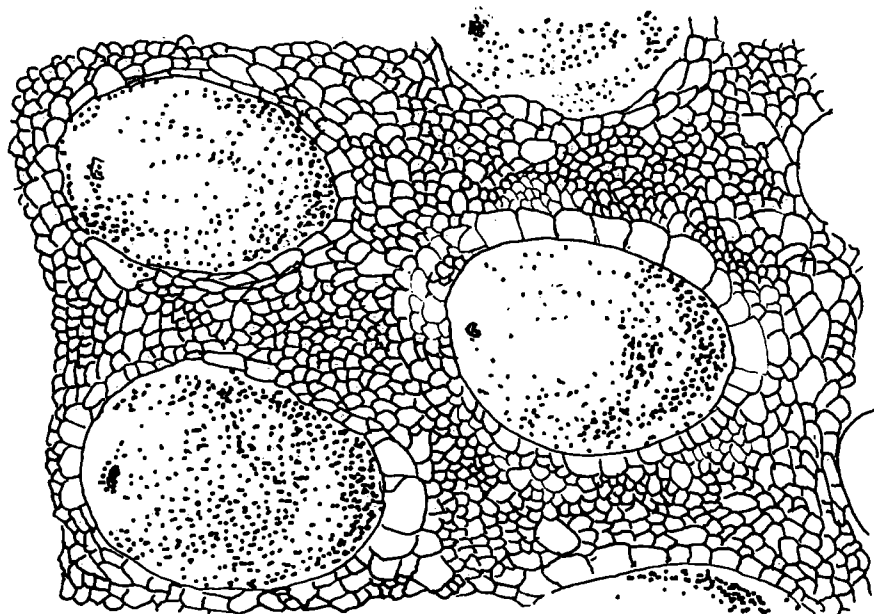
Figure 7. *Varanus b. bengalensis* inguinal skin surface, showing general similarity of large scales and surrounding "scalettes" to the adult tick carapace and its festoons.

In Pakistan, 71.3 percent of all adult ticks on the hosts are males (sex ratio 7.1 males per 2.9 females). In India and Sri Lanka, (no significant differences between them), male ticks comprise 60.0 percent of the adult population on the hosts (6.0 males per 4.0 females). The difference between the Pakistan and India-Sri Lanka sex ratios is not, however, statistically significant at the 5 percent level.

Size and Color

Our results show statistically significant correlation between tick and scale size in geographically disparate populations of both *Aponomma* ticks and *Varanus bengalensis*.

In general, the combination of body shape and color pattern of the scutum, particularly in male ticks of the subfamily Amblyomminae, are remarkably similar to the general scale morphology of varanid lizards (first pointed out by Flower 1896 and Deraniyagala 1953). On close inspection, the skin of varanid lizards is very different from that of any other Asian

Table 3. Mean number of individuals of *Aponomma gervaisi* per *Varanus bengalensis* host in northern (Punjab Province) and southern (Sind Province) Pakistan during the same months of the year. M = males, F = females, N = number host examined.

Month	Sind Province			Punjab Province		
	M	F	N	M	F	N
March	4.2	2.1	23	8.7	15.5	6
July	3.3	3.2	9	10.8	6.4	· 16
August	4.2	0.7	29	20.2	2.3	10
Overall mean	3.9	2.0	61	13.8	6.6	32

reptile group. There is a dominant, large central scale, surrounded, usually at one end only, by much smaller "scalettes" (Fig. 7). The combination of tick color pattern and the presence of festoons combine to make the males inconspicuous when attached between the body scales (scale morphology varies over the surface of the body, legs, and tail). However, this generality becomes more striking when combined with color and size details of those ticks most frequently found on *Varanus bengalensis*.

Varanus bengalensis is currently considered as composed of two geographic races (Mertens 1959). Analysis of considerably larger sample sizes than were available to earlier workers have corroborated this conclusion (W. Auffenberg MS). The eastern subspecies, *V. b. nebulosus*, is distributed from Java to Burma (Fig. 2). There is then a zone of intergradation extending westward through Bangladesh and West Bengal, in which the characters slowly merge with those of the western geographic race, V. b. bengalensis. The latter is found throughout the Gangetic Plain and all of peninsular India, including Sri Lanka, extending into the Indus Valley in Pakistan (Fig. 2). Here it follows the Kabul River to near that city itself; along the southern Mekkran Coast it extends through the basin and range part of southeastern Iran (Seistan). The combined range of these two subspecies is almost exactly coincident with the combined ranges of the tick species *Aponomma gervaisi* and *A. varanensis* (Fig. 1).

The varanid subspecies are distinguished by certain features of their color pattern and scalation. In general, adults of the eastern subspecies *Varanus b. nebulosus* are dark, having much black pigment in the dorsal ground color. This is punctuated with numerous scattered yellow and green spots. This subspecies also has relatively few scale rows encircling the midbody and along the ventral midline (scalation means for various populations vary from 76 to 83

from 76 to 83 and 123 to 133 respectively, based on 384 specimens from scattered localities throughout Southeast Asia; see Mertens 1942 for scale counting method).   On the other hand, the dorsal ground color of adult *Varanus b. bengalensis* is dominated by light brown.   There is little yellow, black, or green in the scheme.   The series of both longitudinal ventral scale rows and those encircling the body have higher mean numbers of scales (84-108 and 135-148 respectively). Because body proportions are identical in both subspecies, this means that the scales are smaller in the western race of *V. bengalensis* and larger in the eastern one. A *t*-test shows the differences to be statistically significant ($t = < 2.58$, $p = < .005$, *df* 386). The reasons for this may be related to problems of water loss in drier, very hot habitats in the western   parts of the geographic range of this lizard, where water can be expected to be in shorter supply. Soule and Kerfoot (1972) have shown that there is a positive correlation between high evaporation rate and scale size in at least some iguanine lizards. If the same explanation pertains to varanid scales, then it follows that those populations of *V. bengalensis* in the driest parts of its range with the smallest scales have the lowest rate of evaporation from the skin surface.

The tick that is most often found on *V. bengalensis* in the deciduous forests of Southeast Asia is *Aponomma varanensis* (W. A. data unpubl.).   The scutum diameter of male *A. varanensis* varies from 2.12 to 3.03 mm, $\overline{X}$ 2.55 ± 0.25 mm. For *Aponomma gervaisi* the scutum diameter of males varies from 1.90 to 2.41 mm, with a $\overline{X}$ 2.15 ± 0.24 mm. The mean difference between them is 0.40 mm ± 0.32. A *t*-test shows that this difference is statistically significant with $p < .01$ ($t = 2.45$, *df* = 31). Thus it is possible that male tick size is related to "grain" size of the substrate. There is no clear relationship between female tick capitulum and monitor scale sizes. In general, females attach in more protected places on the body than males (this study, Table 2, and T. Auffenberg 1988).

Several workers have shown that some predators attack and eat reptile ticks on the ground. Tick predators reported are ants and spiders (Wilkinson 1970), mice (Bull and Sharrad 1981), chickens and the hoopoo bird (Nagar et al. 1977).   Though birds are sometimes known to remove ticks from mammalian hosts, there is no evidence that any predators remove ticks from monitor lizards. Of those predators listed above, all are regularly eaten by *Varanus bengalensis* adults. Tick parasites are also potentially important in depressing reptile tick populations on the host. The chalcid mite *Hunterella hooker* is a common tick parasite in India and is sometimes found on *Aponomma gervaisi* (Soni and Srivastava 1957). However, one cannot imagine that the cryptic morphology and color pattern of *Aponomma gervaisi* is related to such parasitism.

On rare occasions, almost intact, undigested adult ticks have been found in the feces of long-term captive monitor lizards (Lederer 1942), after

they were evidently found and eaten on the floor of the pen. Vogel (1979) believes that some of the scratching he observed in wild *Varanus salvator* was related to removing ticks from themselves. Having removed many ticks from monitors we do not believe this is very likely, as they are decidedly firmly attached. Furthermore, during the dissection of over a thousand monitor lizards from a number of Asiatic species, both in museums and in the wild, we have never found any ticks in the stomachs. Thus, if monitors eat them, it is indeed very rare. We are left with the problem of why particularly the male ticks are so obviously cryptic on monitor lizards. Furthermore, there is no relationship between male tick-size or color-pattern and the places they normally attach (pit and lateral tail surfaces). Thus, if predation is important, it is only so during the time when the male ticks leave these sites to move over the dorsal skin to find receptive females (see below).

Patterns of Site Attachment

Siddappaji and Channabasavanna (1981) suggested (on the basis of only a few observations) that males of *Aponomma gervaisi* tend to be on the "tail region" and females "on the body." Our observations corroborate their conclusions and add important details to this generality.

Table 4 provides data on attachment sites for this species. For adult male ticks, 97.0 percent are found on the tail (posterior to the level of the tail); of these, 46.6 percent are clustered in the pit. In no other part of the body are either males or females so tightly packed (Fig. 8). As stated above, a depressed rather narrow groove on the midventral surface of the tail base is present in almost all monitors (Fig. 4). When ticks attach here they modify the shape of the groove, so that it becomes more depressed, with clear, rather acute borders and a scaleless bottom, comprised of what appears to be scar tissue that extends around the often more or less vertical walls of the pit as well. On the pit walls, the acute upper pit boundary, and the pit bottom, the surfaces are often provided with smaller pit-like depressions. These fit the shape and size of the adult male ticks so that many of the resident males are located in separate small superficial dimples (Fig. 10). The tissue lining the pit is highly modified and lacks the many small blood vessels often associated with new scar tissue. On all parts of the host's body, ticks are always attached in the skin between the scales. However, even here adult males (but not females) modify the immediate area by their presence, eroding or forcing the tissues from around the tick in such a way that a small pit-like depression is formed, even tough caudal scales are minutely, but plainly misshapen at male attachment sites (Fig. 9). This suggests that males either remain in the same site for a long period of time, or that specific sites are repeatedly revisited by

Table 4. Percent of total male (= M) and female (= F) *Apononma gervaisi* attached in different parts of the body.

	Pakistan		India		Sri Lanka		Overall	
	M	F	M	F	M	F	M	F
Axillary	1.9	78.4	<0.1	42.0	<0.1	60.8	0.7	60.4
Shoulder	0.0	5.8	0.2	11.2	<0.1	12.0	0.1	9.7
Throat	0.0	2.6	0.0	9.8	0.0	7.3	0.0	6.6
Arm	0.0	2.6	0.0	11.0	0.0	9.2	0.0	8.1
Chin	0.0	2.6	0.0	2.0	0.0	2.4	0.0	2.3
Belly	0.8	2.1	<0.1	1.0	0.0	0.0	0.3	1.0
Chest	0.0	1.0	0.2	8.0	<0.1	0.0	<0.1	3.0
Neck	0.0	1.6	<0.1	4.6	0.0	3.3	0.0	3.2
Cloaca	1.1	1.6	0.2	2.0	0.0	1.0	0.4	1.5
Head	0.0	0.5	1.0	3.2	<0.1	2.2	0.3	2.0
Lateral	0.03	0.5	<0.1	0.5	2.0	1.0	0.0	0.0
Toes*	0.3	0.0	0.0	1.0	0.0	0.6	0.1	0.54
Dorsal	1.1	0.0	<0.1	0.0	<0.1	0.0	0.4	0.0
Tail	29.1	0.0	51.0	0.0	71.0	0.0	50.4	0.0
Pit	66.0	0.0	43.1	1.2	14.2	0.0	41.0	0.4
Hind leg	0.0	0.0	0.0	1.0	0.0	1.2	0.0	0.7
Inguinal	0.0	0.0	<0.0	0.0	0.0	0.0	0.3	0.3
Posting.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fingers**	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	0.0

* Skin between hind toes.
** Skin between front fingers.

the same, or other males, over a long period of time (clearly years in the case of the pit).

Even those adult males attached in areas other than the pit tend to be found on the posterior part of the body (Table 2, 4). The exception is in the axilla. It is here where most adult females are attached (60.4%). Of 909 males found, 15 were in the axilla, with 4 of these not attached, but walking about the area, and 5 were found on females in a copulatory position, mounted venter to venter; the remainder were attached in the area (temporarily ?). Therefore, it is likely that most or all of .the males in the axilla are there because of the
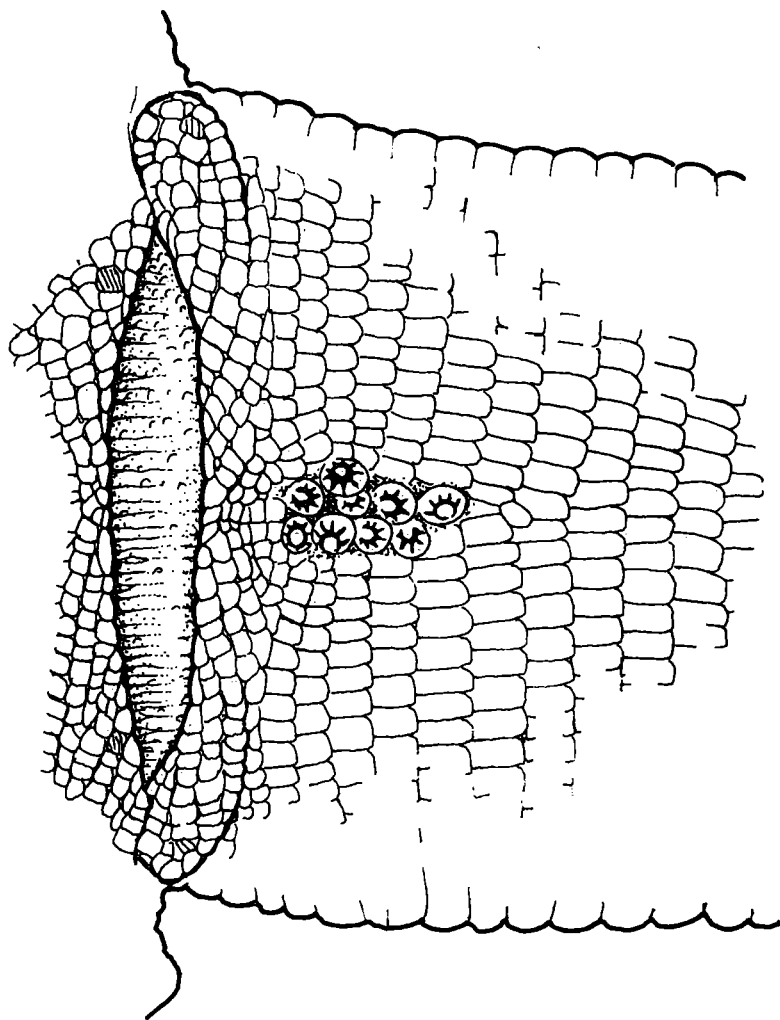
Figure 8.   A pit on the ventral surface of the base of the tail of *Varanus bengalensis* is regularly used by adult males of *Aponomma gervaisi*, where they are often densely aggregated.
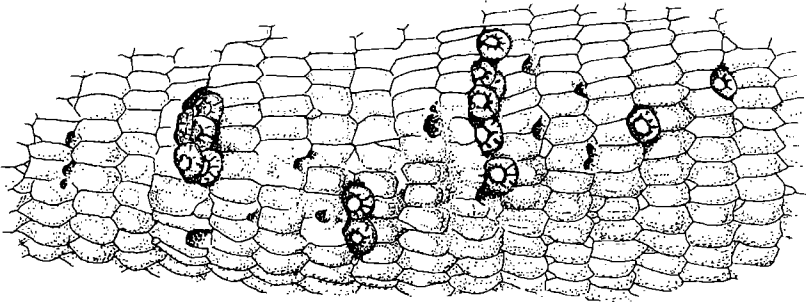
Figure 9. Edges of scales of the lateral surface of the tail of *Varanus b. bengalensis* modified by male ticks after frequent attachment at the same site.
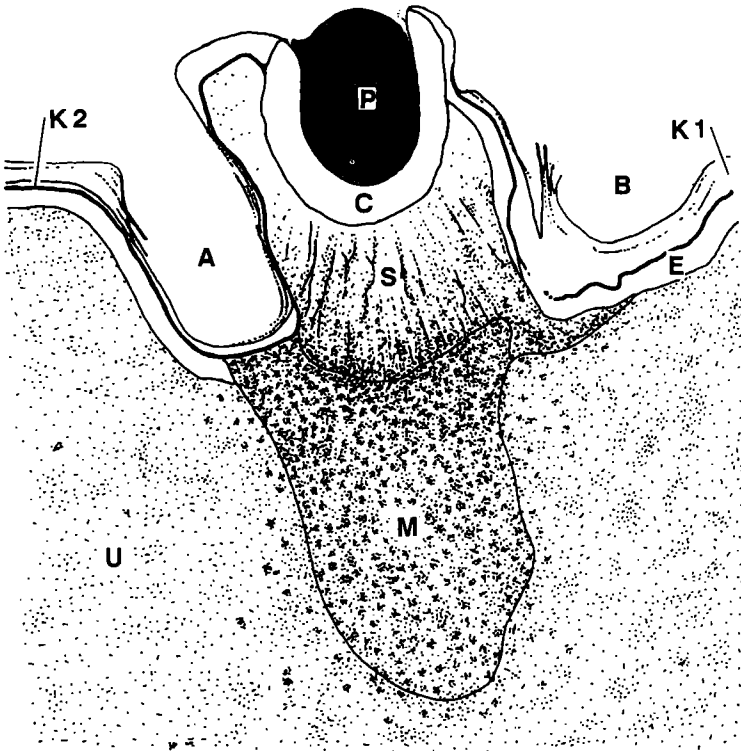
Figure 10. Generalized cross-section of area where mouth parts of adult male tick are inserted into skin of *Varanus b. bengalensis*. (A-B) recently abandoned attachment sites; (C) cementum; (E) epidermis; (K1) keratin alpha layer; (K2) keratin beta layer; (M) zone of macrophage concentration; (P) mouth parts; (S) zone of streaming cellular remains; (U) unaffected dermis.

frequency with which females occur in the same place. Apparently some males leave the posterior part of the body and move anteriorly to mate with sexually active females. The method by which the presence of reproductively receptive females is communicated to males remains unknown (see below).

Females tend to be found in the anterior part of the body; 65.5 percent are associated with the insertion of the front leg (axilla 60.4%, deltoid 8.0% and upper arm 7.1%).

Ticks also occur in large numbers on wounds, sometimes located outside the normal attachment sites, or in numbers considered abnormal for that site. However, in no instance was any female found to be attached to a wound area. The reasons for this may be related to a probable different dietary source of adult males and females (see below).

There is no correlation between the mean size of the sample skin area on adult lizard hosts and the mean number of ticks in each ((Table 2). Certain areas are favored as attachment sites, regardless of their surface extent. Thus the pit, which is extremely small when compared to the remainder of the surface available, is a preferred site of attachment for males, just as the relatively small axillary area is the preferred attachment site of the adult females.

Subsurface Attachment Details

Female *Aponomma gervaisi* attach in highly vascularized areas of relatively thin skin with little cornification. Here they certainly engorge on blood from the numerous capillaries found. The situation in adult males is less clear, as they often attach on the edges of old wounds, or in heavily cornified tissues on the tail, and particularly in the pit at the base of the ventral caudal surface. Because of this, several histological sections were prepared and stained to obtain information on feeding and tissue details. The following is based on slides prepared from male attachment sites on the lateral surfaces of the tail and the pit.

The tissue surrounding these sites under normal conditions is a thick, irregular, moderately dense to loose connective type, with coarse, irregularly oriented collagen bundles. In these areas there are only small amounts of serous exudate (ground substance) between the bundles. It contains freely floating macrophages and small lymphocytes. During inflammatory conditions, the latter become exceptionally numerous and change to macrophages. Eosinophilic leucocytes (uncommon in normal dermal connective tissue of monitors) become very numerous during inflammatory reactions of several types. The large numbers of eosinophils attracted to the affected area

area probably phagotize and destroy immune complexes introduced by the tick mouth parts.

Examination of tissue near the introduced mouth parts of the attached male shows that in the dermis, deeper than the mouth parts, the collagen fiber bundle organization is broken down. In the immediate area there are many larger cells, which become more densely packed the closer one moves to the inflammation center (Fig. 10, M). These appear to be mast and macrophage cells. The closer to the mouth parts one goes, the more abundant a serous, probably mucoid, exudate (ground substance) becomes. In this area, orientation of the cells suggests they are being drawn to the mouth parts, for most of them are aligned longitudinally (parallel) to it, in "flow-lines." There is a fairly sharp differentiation in the highly stained ground material near the mouth parts in the closest, most densely packed zone of the macrophages. Beyond this zone, the ground material is open and clear. Furthermore, the densely packed macrophage zone changes rather quickly to a less dense one. Only the fibroblasts (and leucocytes?) seem to extend beyond this last zone as any indication of tissue inflammation. Immediately surrounding the hypostome is a clear zone of cementum exuded by the tick into the host tissues, apparently to help keep the mouth parts inserted in the skin.

The material in the gut of the tick is also composed of the stained (mucoid?) ground material, as well as what appear to be granules and perhaps even complete nuclei of the cells being drawn into the mouth parts. None of the ingested cells is entire, but such cells are rare near the chelicae in the tissue anyway. The cells seem dissolved, and the contents, as well as the mucoid substance, are being drawn into the mouth parts. Cell wall destruction probably takes place at the macrophage zone, and the difference in ground substance staining is probably due to the cell contents spilling out in that area.

In summary, the feeding male ticks start by lysing the epidermal layer. Feeding occurs by the tick pumping saliva into the tissues through its mouth parts. This causes the cells to break down and the ticks then suck up the resultant broth of lymph and cell debris. However, it is probably the introduction of foreign proteins in the form of the lysing saliva that is most important in this process, for it attracts lymphoid cells towards the hypostome. These lymphoid cells are in turn broken down and ingested. Thus the immune response caused by the saliva produces a steady stream of food material in the form of body fluids and particularly lymphoid cells. There is thus little profitability in changing attachment position, for a flow of nutrients is assured as long as saliva is regularly introduced into the tissues.

This feeding strategy probably explains why male reptile ticks are so often in such dense aggregations. Several males injecting saliva in a small area should produce a proportionately much greater immune response on the part of the host, sending proportionately more lymphoid cells and fluids to the affected area than to an equal number of scattered male parasites. Thus, there

is probably a very distinct advantage for male attachment sites to be clustered. Those sites with the greatest potential for habitat abrasion and injury (ventral body surface, lateral tail surfaces, etc.) may have a higher resident population of lymphoids and may explain why male attachment clusters of the varanid ticks studied so far are often located in those parts of the body where abrasion is expected to be high. It may, as a matter of fact, explain why male *Amblyomma helvolum* prefers the base of the claws as an attachment site in the monitor lizard *Varanus olivaceus*, for this is a species that spends much time in the trees. When climbing, varanids depend entirely on their claws for purchase. Thus the base of the claws is exactly where one would expect much abrasion and stress, and thus probably high densities of resident lymphoid cells. On the other hand, the terrestrial monitor in the same area, *Varanus salvator*, infected by the same tick species would be expected to suffer the greatest abrasion on the median ventral body and tail surface, and this is exactly where the males tend to aggregate. *Varanus bengalensis* is primarily a terrestrial species, and this may explain why one of the major male aggregation sites is also on the ventral surface.

At the same time, this feeding strategy also explains the tendency for male reptile ticks to accumulate on wound edges. Additionally, it explains why they tend to restrict the attachment sites to relatively small parts of the body and why some sites are repeatedly used by a succession of ticks. Such repeated use of the same site produces a pit-like depression with a raised, highly keratinized anterior margin (Fig. 9). The shape of these depressions is such that succeeding resident ticks tend to lie in it in exactly the same way, assuring the new resident that the mouth parts will be inserted in almost the same place as was that of the last resident. Arnold (1986) has postulated that mite pockets in the skin of many lizard species are a way of ameliorating the effects of mite infestations, since he believed they tend to concentrate such infestations to certain parts of the body where they will not disrupt normal cutaneous function. There is no evidence suggesting that this is the case in varanid lizards and their tick parasites. Research is needed to prove whether the lymphoid cells are concentrated in the specific attachment sites even without the parasitizing ticks, or whether they become concentrated only after injection of saliva from the mouth parts.

The situation in female reptile ticks is entirely different from that of the males. Females apparently feed entirely on blood, drawing their high nutrient food from a capillary bed. Blood supply to any specific dermal area is largely dependent on the capillary density of the immediate area. This being the case, there is probably a distinct advantage in the females dispersing themselves over an appropriate protected site, rather than forming the dense concentrations of lymphoid-feeding males.

Seasonal Patterns of Infestation

The most complete records of seasonal abundance of ticks on *Varanus bengalensis* exist for Pakistan, and this area is used as a guide to what is presumed to be happening seasonally throughout the range of *Aponomma gervaisi*. These data are presented in Figure 11, which shows a strong pattern of seasonal differences in tick frequency on the host animals. The annual pattern is slightly different for male and female ticks. Males clearly show two peaks, one during the winter (December through February) and the other during the monsoon withdrawal phase (September and October). That the frequency of ticks is not entirely related to seasonal difference in monitor activity is demonstrated by the fact that during the winter peak the monitors are inactive--usually brumating in burrows in which they spend the coolest months of the year (Auffenberg, MS). The second male peak (September-October) is during a period of increased monitor foraging activity, when food abundance (primarily insects) is high and lizard fat bodies are enlarging in response to reproductive and reduced food resources during the cool winter and the hot dry spring months of the following year. Though less defined, this is also the time of year when monitors have the most female ticks/host. This correlates with the onset of the cloudy weather and cooler temperatures during the premonsoon of Pakistan's Indus Valley (where most of the specimens of lizards in this study originated).

The lowest monthly mean number of male ticks/host occurs during May, which is also the hottest part of the year in Pakistan and the peak of the dry season. This more or less corresponds with the period of fewest female ticks on *V. bengalensis* (April-June). Our studies on monitor lizards at Bharatpur, India, make it clear that this dry season reduction in number of ticks per lizard is correlated with the appearance of many individuals of *Aponomma gervaisi* in crevices in the parched earth and in and on walls and ceilings of burrows regularly inhabited by large reptiles (i.e. pythons and monitor lizards). Thus the dry season seems to be a period of quiescence for ticks of both sexes.

We know that breeding between male and female *Aponomma gervaisi* takes place on the host. Because of both the number of males and females on the host at this time of year, and the dates of breeding observed on them, we conclude that all breeding takes place during the summer monsoon. The reduction of females on the hosts immediately after July suggests that it is at this time when eggs are laid (generally true of many insect groups in eastern Pakistan and western India, W. Auffenberg MS). The females apparently lay their eggs in the soil (of mainly reptile burrows?). All female hard ticks die after the eggs are laid, and it is presumed that those of *Aponomma gervaisi* do so as well. Thus, it is the male ticks that provide the genetic continuity from
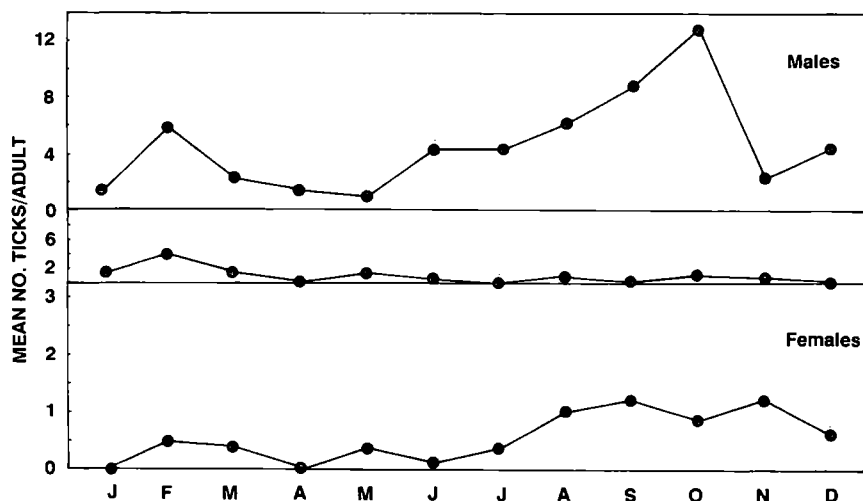
Figure 11. Mean monthly frequency of adult male and female *Aponomma gervaisi* ticks attached to all *Varanus b. bengalensis* collected during the study; the middle graph is the same for nymphs and larvae.

one breeding population to the next. We assume the winter increase in numbers of both male and female ticks is associated with the fact that the lizards are spending much more time in burrows (W. Auffenberg MS), where the ticks are also known to congregate (see above). Table 1 suggests there may also be some geographic variation in seasonal abundance patterns, though the data are too scattered to be completely reliable.

During a year-long study of movement and growth patterns in *Varanus bengalensis* at Haliji Lake, Pakistan, the senior author and the Zoological Survey Department staff captured and marked 61 adults. As part of the study the tick loads of each were tabulated. Of these, 12 individuals were subsequently recaptured (some several times), with the days between varying from 14 to 282. Upon recapture the tick loads were again counted. As a result, data are available on the change in number of ticks/host/season for a series of adult animals in one small area.

These data corroborate what is surmised from Figure 11, namely that it is during the dry season when most ticks leave their hosts. Additionally, the data also show that significant changes in tick number/host may take place over periods as short as 2 weeks. They also indicate that males, females, and nymphs are all affected the same way during the same time of year, either leaving or assembling on individual host lizards at the same time. This is even more interesting when one realizes that on some hosts the ticks of both sexes

and both nymphal and adult life stages may be in a leaving phase and that on other hosts captured and recaptured during the same time, the ticks are in an aggregation phase. The proportions of males, females, and nymphs involved in these movements reflect the ratios in which these categories are expected to occur. We have no idea what triggers these movement patterns, but the fact that they sometimes produce opposite results on different hosts at the same time suggests that it may be related to the host as much as to general climatic conditions. However the results may also reflect a statistical artifact depending on the dispersion of ticks on the ground.

Life History

   Larvae of *Aponomma gervaisi* moult on the host *Varanus bengalensis*. It is here that the nymphs also remain, attached in the same general area as the larvae. Active periods of the larval and nymphal stages in three northern Indian and Pakistan sites probably occur only during the warmer months, as other *Aponomma* species living in seasonally cool areas are inactive during winter (i.e. *A. hydrosauri*, Australia, Bull and Sharrad 1980). Thus we presume that in northern Pakistan and India both larvae and nymphs are active on the host for about eight months and inactive about four months. In seasonally less variable parts of the range (central India to Sri Lanka) we expect they would remain active throughout the year. Adult *Varanus bengalensis* taken from their burrows at this time of year have both nymphs and adult ticks attached to them, suggesting that neither leave their hosts during the cool, quiescent period.
   Molting of the nymphs undoubtedly takes place in the burrows of *Varanus bengalensis*, mainly during the May-June dry season. This is based on the fact that by July thousands of adults may be found in some burrows in Pakistan and northwestern India habitually used by monitors (and an adult, brooding *Python molurus* in one instance). These are positioned in small crevices and holes in the walls and ceiling of the primary burrow, where they hang upside down. Any slight physical disturbance arouses the apparently quiescent adults, and the walls and ceilings of the burrow become completely covered with moving ticks, which rapidly transfer themselves onto any object moving within the burrow. Downes (1984) has demonstrated the same behavior for quiescent nymphs of *Aponomma hydrosauri* (not in host burrows) and the behavior is probably characteristic of quiescent nymphs of *A. gervaisi* in reptile burrows as well. Active nymphs may be attracted to the host by its odor, as Downes has shown for *A. hydrosauri*. Active adults probably depend on actual contact with the host for transfer within the host burrows.

Adult *Aponomma gervaisi* apparently attach themselves to their hosts mainly during the monsoon season (July and August). We base this on the significant increase in number of adult ticks during this time of the year (Fig. 11). The increase is correlated with an increase in the activity level of the monitor lizards. During this time of year they are active for a longer part of the day and move over greater distances than during any other season (W. Auffenberg, MS). There is thus a greater chance of ticks coming into contact with monitor lizards during this time of year than any other.

Breeding takes place on the host (suggested earlier by Siddappaji and Channabasavanna 1981 on basis of a single observation), when one or more males leave their more posterior attachment positions and move anteriorly. Not all males do so, suggesting that either some males have not received whatever information is transmitted from the ovulating female, have ignored the signal, or are not sexually ready to breed at that time. During breeding a single male is mounted venter to venter on the still attached female. Females drop off their host in significantly large numbers during the cool months (December-January, Fig. 11), presumably to lay their eggs in the soil of the monitor lizard burrows.

CONCLUSIONS AND DISCUSSION

During the course of study regarding the behavioral ecology of *Varanus bengalensis*, 381 individuals of this species of varanid lizard were examined for ticks in Pakistan, India, and Sri Lanka. None of the ticks could be assigned to any species other than *Aponomma gervaisi*. Thus, the Indo-Gangetic Plain probably has only one species of reptile tick.

We have shown that 91.4 percent of all adult males of *Aponomma gervaisi* are found on only 16.3 percent of the body surface, whereas 93.3 percent of the adult females are found on 23 percent of the host's body surface. The males are found in more posterior and more extensively keratinized sites than those in which the females occur. These male attachment sites are regularly used by a series of transient adult male ticks. Such regular, sustained attack, produces a depressed, scar-like, inflammatory area from which the males derive their nutrients, which appears to be mainly digested cellular matter, rather than blood. Males are also commonly found in scar tissue in other areas of the body, and it is on such sites where they are sometimes found on other reptilian hosts. On the other hand, adult females are located in highly vascularized sites that have thin, easily penetrated skin (such as the axillary area). Here the females are apparently able to ingest the large supply of highly nutritious blood that is needed for egg production. After mating, females may increase to as much as five times their unmated size, and are thus more susceptible than the

much smaller males to disturbance by host movement through the environment (Smyth 1973; Andrews and Bull 1980, Andrews and Petney 1981). Of the sites on which the females are generally found, the most protected is the inguinal area, being located on the posterior part of the insertion of the upper arm and protected from being brushed off by the limb itself.

Only 0.4 percent of all females observed were found in any of the "preferred male sites," and 0.8 percent of the males were found in "preferred female sites." The higher percentage for the males is the result of their moving to presumably sexually mature females, where breeding takes place. Not all males move forward at the same time, suggesting that not all receive the message, and/or that not all males are ready to mate at the same time.

Communication from the female to the male is undoubtedly chemical in nature, and in other ticks it has been suggested to be a pheromone moving posteriorly across the host surface (Andrews and Bull 1981). If this were the case, it would seem advantageous for the males to be located closer to the females. But in each species of *Varanus* we have studied so far, we have found that the adult males are always located some distance from the females. Males of the tick *Amblyomma helvolum* attach mainly on the median ventral surface of both the chest and the base of the tail (= the pit in this report) on *Varanus salvator*, while in *Varanus olivaceus* they attach mainly to the base of the claws. In *Varanus bengalensis* the adult males are located both in the pit and on the lateral surface of the basal half of the tail. Thus, at least among varanid lizards, a surface-moving pheromone seems a remote possibility (T. Auffenberg 1988), though an airborne one is likely. Such a pheromone has been shown to be operative in *A. hydrosauri*, Andrews 1982, Andrews and Bull, 1982a, b, and Andrews et al. 1982a. Only an airborne pheromone would be able to be perceived and interpreted over the large area represented in order to attract respondent males to receptive females in the anterior part of the body.

In any event, what is significant in the current tick species is that males are always located posteriorly, and secondly, that they are located in such distinctly different parts of the hosts posterior anatomy. *Aponomma gervaisi* males are never found on the chest, and rarely on the hind feet. On the other hand, the tick *Amblyomma helvolum* is characteristically found on the chest and the base of the claws on *Varanus salvator* and *V. olivaceus* respectively. This attachment site specificity is apparently based on differences in the epidermal/dermal microhabitat.   These differences are most likely of a chemical nature and ultimately related to tissue-mediated immune responses. Male ticks of both *Amblyomma helvolum* and *Aponomma gervaisi* are probably reacting to chemical differences and not to feeding ease or the degree of protection offered by the sites selected on different hosts.

While the pit is clearly an area protected from abrasion (depressed), it is on the ventral surface, where most abrasion probably occurs. The lateral tail

surfaces are also areas where abrasion is very high, for during locomotion, the tail of varanid lizards is constantly undulated from side to side. In fact, that part of the tail which tends to be most abraded from this movement is just where male ticks are most commonly attached. Even on *Varanus olivaceus*, where male ticks are most often found at the base of the hind claws, the preferred site is one of high abrasion. In *Varanus salvator*, the preferred median chest area is another zone of high abrasion. Presented with these distributional facts, we conclude that adult males of these tick species deliberately seek sites regularly and generously abraded. On the other hand, females are obviously responding to an entirely different cue common to all host monitor species and resulting in the same distribution of attachment sites in all host species. While the reasons for this are rather clear in the females, with their relatively larger size resulting from engorgement and their need for a ready supply of blood, it is not at all clear for males of both tick genera. Site selection among males may be the most critical factor from the standpoint of male-female competition and may be related to the ability of members of this sex to remain with the host in the face of particularly difficult environmental pressures to sweep them off (T. Auffenberg 1988).

It is clear that what is needed is a series of carefully controlled experiments under laboratory conditions in which the biochemical and histological aspects of the microenvironment are carefully investigated during initial attachment and later movements on the host, as well as when leaving it. This work serves to again focus attention on that need, as was demonstrated in the earlier work of the junior author on other species of varanid hosts and a different genus of reptile tick.

It has been shown that the life history of this tick is intimately associated with major climatic cycles. This is particularly true in the more xeric parts of the range. Here the immature and mature ticks tend to leave their hosts during the driest parts of the year. Such hot, dry conditions have been shown to lead to rapid water loss and death in other tick species (Bull and Smyth 1973) and is expected to be similarly important in *Aponomma gervaisi*. During this time it enters crevices and burrows in the earth, particularly those regularly used as refuges by its major host *Varanus bengalensis*. Though this monitor species uses these burrows throughout the year (W. Auffenberg 1983), it is during the dry season when the ticks move into the same burrows. Data available for other tick species (Wilkinson 1961, Owen 1975) suggest that they do not disperse when in a refuge. This is suggested for *Aponomma gervaisi* as well, for during this time of year hundreds may be found infecting a single burrow. Presumably, engorged and detached adult females also lay their eggs in the refuges, so that large numbers of larvae may often be found in some burrows during this time of year. When the monitors become particularly active during and immediately following the wet season, the ticks have moulted and reinfested the lizards. On the basis of similar data, Bull (1978) suggested

that this refuging behavior of ticks during the dry season best explains their distribution on the Australian scincid lizard *Trachydosaurus rugosus*. The concentrations of moulting and waiting ticks in some burrows explains why certain monitor lizards are so heavily parasitized and others are not. It also explains why juvenile monitors have fewer, or no ticks (depending on size), for it is known that Bengal monitor lizards in the first year of life spend much time in the trees (W. Auffenberg MS).

The closely related *Aponomma varanensis* parasitizes the same species of lizard in less seasonally affected forests of Southeast Asia, suggesting that this tick species may have a somewhat different seasonal life history pattern than *Aponomma gervaisi*. This is further complicated by the fact that the more eastern populations of *Varanus bengalensis* are much more arboreal than their western conspecifics (W. Auffenberg MS). One would thus expect adults of the eastern monitor populations to have fewer ticks. This is substantiated by our data on regional infestation levels between populations of *Varanus bengalensis*. However, our samples from the eastern extremes of the geographic range are considerably smaller than those from the western sections used in the current study, and we are less confident of our analysis of tick data originating in Southeast Asia. Additionally, it is important to point out that monitor burrows may not be necessary in the life history of monitor lizard ticks. For example, in T. Auffenberg's study of infestation of the Philippine *Varanus olivaceus*, he found approximately the same level of infestation in this non-burrowing species as in the burrow-utilizing *V. bengalensis bengalensis*.

Based on what we now know of the life history of *Aponomma gervaisi*, one would conclude that it is an endophilic species, i.e. all the developmental stages periodically inhabit the same shelter type (*Varanus* burrows). This is reflected in the fact that the hosts of both the immature and mature ticks of this species have the same narrow host specificity (*Varanus bengalensis*). From an evolutionary standpoint, single-host tick species are generally believed to be advanced (Hoogstraal 1978).

Hoogstraal and Aeschlimann (1982) have challenged what they describe as "a common assertion that ticks lack host-specificity", pointing out that a number of tick species are reptile-specialists. We suggest that some of these reptile specialists prefer either turtle, snake, or lizard hosts; those falling into the latter category are frequently specialists on the lizard family Varanidae (*Aponomma gervaisi* and *Amblyomma helvolum*). Not only are these tick species host-specific, but site-specific as well, more so for the adult males.

Varanid lizards have a long fossil history, extending back to the Lower Cretaceous. Because the Superfamily Ixodoidea is believed to have arisen as an obligate parasite of Reptilia during the late Paleozoic or early Mesozoic (Hoogstraal and Aeschlimann 1982), one supposes a long association between ticks and varanid lizards. This may explain the high degree of site attachment

preferences among the varanid tick specialists. It remains to be seen if the high degree of host-site specificity demonstrated on the Asian mainland is also true of reptile ticks in Australia, where varanid lizard diversification (presumably during the mid-Tertiary, W. Auffenberg 1980) is particularly marked.

As is typical for ixodoidid ticks, all female *Aponomma gervaisi* both oviposit and die on the ground, rather than on the host. Bull and Sharrad (1980) have shown that unfed adult *A. hydrosauri* can live for as long as two years without food, and there is no reason to believe that *A. gervaisi* cannot do the same.

The food sources of adult male and female *Aponomma gervaisi* are apparently different. Egg production in females demands an abundant, highly nutritious source, which is satisfied by blood. Adult males digest cellular material associated with immune responses of the host in areas of inflammation. This, as well as the distribution patterns of both males and females on the hosts, suggests there is no site competition between the sexes. On the other hand, there must be intrasexual competition among both males and females for sites appropriate to their particular feeding type. Some of these sites are obviously better than others. For females this means a protected site in the anterior part of the body provided with thin, highly vascularized skin. The ideal location is apparently in and near the axillary region. For males, the lateral surfaces of the tail and the pit seem ideal. The latter is apparently somewhat more preferred, for the ticks are more regularly found there and are frequently also packed remarkably tight. It is obvious that first-comers achieve an attachment site in the pit, those arriving later will not be able to find a place. In time this crowding tends to enlarge and deepen the pit, so that it holds proportionately more male ticks as the monitor lizards become larger (older). The lateral surface of the tail is a large area, and space is always available for many more males than are attached there.

It is not clear why *Aponomma gervaisi* never occur on the two other syntopic monitor species in Pakistan and northern India (*V. griseus* and *V. flavescens*). Parallel situations can be demonstrated in the mesic forests of Southeast Asia, where *Amblyomma helvolum* is regularly found on the semi-aquatic *V. salvator*, yet absent on the similarly semi-aquatic *V. dumerili* living in the same area (T. Auffenberg notes). Of those varanid species that are regularly infested, the pattern of female attachment sites remains the same, centered on the axillary area. This is true even across tick genera (*Amblyomma* and *Aponomma*). For the adult male ticks, the site attachment pattern is distinctly different for each host, even within the same tick species. This has now been demonstrated for *Amblyomma helvolum* and *Aponomma gervaisi*. Thus the males are host-species site-specific.

LITERATURE CITED

Andrews, R. H. 1982. Mating behaviour and reproductive isolation of three species of reptile tick. Anim. Behav. 30:514-20.
____, and C. M. Bull. 1980. Mating behavior in the Australian reptile tick *Aponomma hydrosauri*. Anim. Behav. 28:1280-86.
____, and ____. 1982a.. An attractant pheromone with some common properties in three reptile ticks. Experientia (Basel). 38:99-100.
____, and ____. 1982b. A comparison of mating behaviour between populations of the reptile ticks *Aponomma hydrosauri* and *Amblyomma albolimbatum*. Australian J. Zool. 30 (6):635-42.
____, and T. N. Petney. 1981. Competition for sites of attachment to hosts in three parapatric species of reptile tick. Oecologia 51:227-32.
____, ____, and C. M. Bull. 1982a. Reproductive interference between three parapatric species of reptile tick. Oecologia 52:281-6.
____, ____, and ____. 1982b. Niche changes between parasite populations: an example from reptile ticks. Oecologia 55:77-80.
Arnold, E. N. 1986. Mite pockets of lizards, a possible means of reducing damage by ectoparasites. Biol. J. Linn. Soc. 29%- 1988.
____ *Amblyomma helvolum* (Acarina: Ixodidae) as a parasite of varanid and scincid lizards in the Philippines. Internatl. J. Parasit. 18(7):937-45.
Auffenberg, W. 1983. The burrows of *Varanus bengalensis*: characteristics and use. Rec. Zool. Surv. India 80:375-85.
____, H. Rahman, F. Iffat, and Z. Perveen. In Press a. Notes on the biology of *Varanus griseus koniecznyi* (Sauria: Varanidae). J. Bombay Nat. Hist. Soc.
____, ____, ____, and ____. In Press b. A study of *Varanus flavescens* (Sauria: Varanidae). J. Bombay Nat. Hist. Soc.
____. MS. The behavioral ecology of *Varanus bengalensis*.
Bhat, H. R., and M. A. Sreenivasan. 1981. Further records of the ticks of some reptilian and mammalian hosts in the Kyasanur Forest Disease Area, Karnataka, India. Indian J. Parasit. 5(2):207-10.
Bilques, F. H., and S. Masood. 1973. Parasites of *Varanus monitor* of Sind (Pakistan). Sind Univ. Res. J. (Sci. Ser.) 7(1):41-56.
Bull, C. M. 1978. Heterogeneity of resource utilization in a population of the Australian reptile tick, *Aponomma hydrosauri* (Denny). Ecol. Entomol. 3:171-9.
____, and R. D. Sharrad. 1980. Seasonal activity of the reptile tick, *Aponomma hydrosauri* (Denny) (Acari:Ixodidae) in experimental enclosures. J. Australian Entomol. Soc. 19:47-52.
____, and T. N. Petney. 1981. Parapatric boundaries between Australian reptile ticks. Proc. Ecol. Soc. Australia 11:95-107.
____, and M. Smyth. 1973. The distribution of three species of reptile ticks, *Aponomma hydrosauri* (Denny), *Amblyomma albolimbatum* Neumann, and *Amblyomma limbatum* Neumann. II. Water balance of nymphs and adults in relation to distribution. Australian J. Zool. 21:103-110.
Deraniyagala, P. E. P. 1953. A Coloured Atlas of some Vertebrates from Ceylon. Vol. 2, Tetrapod Reptiles. Govn. Press, Colombo, Ceylon. 101 p.
Downes, B. 1984. Host-location by the reptile tick *Aponomma hydrosauri*: The roles of physical disturbance and odor. J. Parasit. 70(1):164-66.
Flower S. S. 1896. Notes on a collection of reptiles and batrachians made in the Malay Peninsula in 1985-6; with a list of species recorded from that region. Proc. Zool. Soc. London. 1896:856-914.
Hoogstraal, H. 1978. Biology of Ticks. Pp. 3-14 *in* J. K. H. Wilde (ed). Tickborne Diseases and Their Vectors. {rpc. Internatl. Conf. Edinburgh, 1976, Univ. Edinburgh, Centre for Tropical Veterinary Medicine.
____, and A. Aeschlimann. 1982. Tick-host specificity. Bull. Soc. Entomol. Suisse 55:5-32.

_____, and G. Rack. 1967. Ticks (Ixodidae) collected by Deutsche Indien-Expedition, 1955 - 1958. J. Med. Ent. 4(3):284-288.

Kaufman, T. S. 1972. A revision of the genus *Aponomma* Neumann, 1899 (Acarina : Ixodidae). Ph.D. Thesis, Univ. Maryland. 389 p.

Lederer, G. 1942. Der Drachenwaren (*Varanus komodoensis* Ouwens). Zool. Gart. (Leipzig). (n.s.), 14(5/6):227-44.

Mertens, R. 1942. Die Familie der Warane (Varanidae). Abh. Senckenberg Naturforsch. Ges. 471(1):1-103.

_____, 1959. Liste der Warane Asiens und der Indo-Australischen Inselwelt mit systematischen bemerkungen. Senckenbergiana 40(5/6):112-47.

Nagar, S. K., R. N. Raizada, and V. K. Saxena. 1977. Observations of the prevalence of babesiosis and the composition and ecology of ixodid ticks in Delhi. Indian J. Sci., 47(10):654-63.

Owen, I. L. 1975. Survival of the non-parasitic stages of the cattle tick, *Boophilus microplus*, under simulated field conditions in Papua New Guinea. Australian J. Zool. 23:219:36.

Petney, T. N., and F. Al-Yaman. 1985. Attachment sites of the tortoise tick *Hyalomma aegyptium* in relation to tick density and physical condition of the host. J. Parasit. 71(3):287-9.

Seneviratna, J. 1985. Notes on Sri Lanka ticks. Ceylon Vet. J., 13:28-41.

Sharif, M. 1928. A revision of the Indian Ixodidae with special reference to the collection in the Indian Museum. Rec. Indian Mus. 30(3):217-344.

Siddappaji, C., and G. P. Channabasavanna. 1981. A new report of the ticks *Aponomma* spp. (Acari:Ixodidae) on Indian cobra (*Naja naja* L.) and *Varanus* sp. (Reptilia) in Karnataka (A&.1 *in* G. P. Channabasavanna (ed). Contributions to
Acarology in India, Proc. All-India Symp. Acarology, April, 1979, Bangalore. Acarological Society of India, Bangalore.

Smyth, M. L. 1973. The distribution of three species of reptile ticks, *Aponomma hydrosauri* (Denny), *Amblyomma albolimbatum* Neumann, and *Amblyomma limbatum* Neumann. I. Distribution and hosts. Australian J. Zool. 21:91-101.

Soni, B. N., and S. C. Srivastava. 1957. Observations on the bionomics of *Hunterella hookeri*, the parasite of ticks in India. Proc. Indian Sci. Congr.(Abstr.) 3:383.

Soule, M., and W. C. Kerfoot. 1972. On the climatic determination of scale size in a lizard. Syst. Zool. 21(1):97-105.

Vogel, P. 1979. Zu biologie des Bindeswarens (*Varanus salvator*) in Westjavanischen Naturschutzgebiet Ujung Kulon. Ph.D. Dissertation, Univ. Basel. 139 p.

Wall, F. 1921. Ophidia Taprobanica, or the Snakes of Ceylon. Govn. Printer, Ceylon. 581 p.

Warburton, C. 1910. The Ixodidae, Section I. Dealing with the classification of ticks. Section II. The genus *Ixodes* Latreille, 1795. *In* G. H. Nuttall (ed). Ticks. A Monograph of the Ixodoidea (Pt. 2). Cambridge Univ. Press, Cambridge. 348 p.

Wilkinson, P. R. 1961. The use of sampling methods in studies of the distribution of larvae of *Boophilus microplus* on pastures. Australian J. Zool. 9:752-83.

_____. 1970. Factors affecting the distribution and abundance of the cattle tick in Australia: Observations and hypotheses. Acarology1(3):492-508.

Contributions to the BULLETIN OF THE FLORIDA MUSEUM OF NATURAL HISTORY, BIOLOGICAL SCIENCES, may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length--circa 35 to 200 pages (10,500-60,000 words). Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receive(s) 50 copies free, and he(they) may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (American Institute of Biological Sciences, Washington, D.C.).

Manuscripts must be submitted in duplicate and satisfy the following minimal requirements. They must be double-spaced throughout, including tables, figure captions, and literature citations. Figure legends and tables should be typed on separate sheets. Also, please submit a copy of the complete text and tables on one or more 5¼" flexible diskettes.

All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. If the background of photographs (especially those of specimens) is not desired, amberlith should be cut out and used to cover the background. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All figures should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lower case letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for figures is 9" x 14" (twice BULLETIN page size); figures should not be less than typepage width (4½"). With soft lead pencil on the back of each illustration, designate the top and identify each by author's name, manuscript title, and figure number.

All manuscripts not submitted in BULLETIN format will be returned to the author for retyping.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida Museum of Natural History
University of Florida
Gainesville FL 32611-2035
U.S.A.