ON THE ADAPTATION OF TICKS TO THE HABITS OF THEIR HOSTS¹.

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(With 26 Text-Figures.)

IN the course of the extended investigation upon ticks which we have been conducting for some years, a very large number of specimens have reached us from all parts of the world, thanks to the generous aid which we have received from numerous collectors. In addition to studying this material, the literature on ticks has been sifted for any information which might throw light upon these parasites. A study of the data relating to the structure and habits of ticks and of their host relationships has brought to light certain facts which possess considerable interest and consequently appear to me worth recording in this Journal.

The superfamily *Ixodoidea* is divided into two families, the *Argasidae* and *Ixodidae*, which are distinguished from each other by their external structure as well as by their habits².

General considerations regarding the Biology of the Argasidae and Ixodidae.

The *Argasidae* are mostly inhabitants of warm climates. When they occur in colder parts of the world they seek hosts whose habitats afford them protection, and insure them possibly a certain degree of

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² The main structural differences are described by Nuttall and Warburton (1908) in *Ticks: a Monograph of the Ixodoidea*, by Nuttall, Warburton, Cooper and Robinson, Part I, p. 1.

warmth from proximity to animals upon which they feed. Thus, *Argas reflexus* and *Argas vespertilionis*, which occur in colder climates, are parasitic on pigeons and bats respectively, and they obtain shelter in pigeon coops and the retreats of bats.

Like all other ticks, they pass through larval and nymphal stages before attaining maturity. In some Argasidae the *larvae* suck blood (as in Ixodidae); in others they do not. Where the larvae suck blood they remain attached to the host for 5—10 days or more (as in Ixodidae). There are two or more *nymphal stages* in Argasidae (one only in Ixodidae), and the nymphs, with one exception, *Ornithodoros megnini*, are rapid feeders, that is, they usually feed on blood to repletion within 20—30 minutes (the nymphs of Ixodidae take several days to become gorged). The *adults* are not only rapid feeders, but they may feed repeatedly (not so in ♀ Ixodidae, though possibly in ♂s).

The nymphs¹ and adults of Argasidae are *rarely* carried away from the habitats by their hosts because they feed rapidly. They are mostly nocturnal feeders, attacking the host when the latter is sleeping or resting. All species of Argasidae would appear to shun the light, especially when waiting for a host. When hungry they may leave their hiding places during the daytime if they become aware of the proximity of a host. The Argasidae infest the habitat of the host.

The nymphs and adults of *Ixodidae* behave in a very different manner. The nymphs attach themselves to the host, and are carried about for several days, and possibly longer. This likewise holds for the adults of both sexes in a large number of species. The duration of their parasitism upon the host may be much prolonged, especially when the host is a cold-blooded animal; thus, species of *Amblyomma*, *Aponomma* and *Hyalomma*, occurring on Reptilia, may remain attached to the host for many months. On the other hand, we shall see that there are species of *Ixodes* in which the males are unknown or in which they are only recorded as having been found in the habitats of their hosts.

In the Argasidae the females lay eggs in batches after successive feeds, and the total number of eggs laid by a female is comparatively small, say 200. In the Ixodidae, the eggs may number one or more thousands. The explanation of this difference in the number of eggs laid appears obvious when we consider the life habits of the two families. The Argasidae are essentially *ticks of the habitat* in their nymphal² and adult stages; the females lay their eggs in and about

¹ *Ornithodoros megnini* excepted.

² *O. megnini* excepted.

their host's retreat and naturally the offspring have a good chance of finding the host when their turn for feeding arrives.

With the Ixodidae the case is different: the fertilized and replete females must frequently drop from the host when it is on its wanderings, and the offspring may be left stranded in places where they may never find a host. The loss of life in nature must be enormous in the majority of species, for in most species the larva, nymph and adult must each seek a host. The loss of life should be less in those requiring but one host, as in *Boophilus*, where the tick attacks the host in the larval stage and undergoes its metamorphosis up to the adult stage upon a single animal. The greatest loss of life must of necessity occur in such species as are parasitic upon hosts having no fixed habitat. In other cases, owing to the fact that the host returns to a burrow, nest, or the like, it is probable that there may be less loss of life than in the case where an animal with wandering habits is chosen as a host. It would be interesting to make some numerical determinations of the progeny, especially of various species of Ixodidae, with this point of view in mind.

The large progeny of the Ixodidae secures their survival in nature in the face of the many difficulties the ticks must encounter in finding their hosts. In the Argasidae these difficulties are much smaller and the progeny is proportionately less numerous.

ARGASIDAE.

In the following table I have included all the Argasidae: *Argas* (A.) and *Ornithodoros* (O.) of which we know the host relationships. The list includes 12 species and 1 sub-species:

Argasidae	Hosts and habitat etc. of Tick	Geographical distribution (as far as known)
<i>A. persicus</i> ...	Birds: fowls, ducks, geese, turkeys, ostriches, quail, wild doves, canaries. Infests chicken coops, etc. Man: prevalent in Persia where it infests native dwellings. It also occurs in houses in Egypt.	Africa, Asia, Australia, N. & S. America.
<i>A. reflexus</i> ...	Birds: pigeons, fowls. Man: occasionally entering dwellings from pigeon coops, or attacking persons having to do with pigeons.	Europe, N. Africa.
<i>A. vespertilionis</i>	Bats: several species ¹ ; adults found in the abodes of bats.	Europe, N. Africa.

¹ See *Ticks*, Part I, p. 39, where the bats are listed. A variety infests penguins at Queenstown, Cape Colony.

Argasidae	Hosts and habitat etc. of Tick	Geographical distribution (as far as known)
<i>A. brumpti</i> ...	Porcupine: found infesting dusty burrows of <i>Hystrix</i> sp. in Africa. Man: attacks man when sleeping on the ground; hides in dust during the day-time.	Africa.
<i>O. savignyi</i> ...	Man, camel, horse: attacks them in their resting places, hides in dust or sand, etc.	Africa, India.
<i>O. moubata</i> ...	Man: infests native dwellings and resting places along caravan routes. Domesticated animals: dogs, pigs kept in styes, goats, sheep.	Africa.
<i>O. turicata</i> ...	Man: at times infesting native dwellings; attacks at night. Domesticated animals: pigs in styes, cattle, llama, horse. Wild animals: infesting burrows of tortoise and gopher.	N. & S. America.
<i>O. talaje</i> ...	Man: infesting native houses; attacking at night.	N. & S. America.
<i>O. talaje</i> var. <i>capensis</i>	Birds: found in penguin's and other nests.	Islands of Cape Colony, St Paul's Isl., Siren Isl.
<i>O. pavimentosus</i>	Man: resting places infested.	Africa.
<i>O. tholozani</i> ...	Fowls and camels: infests chicken coops.	Persia.
<i>O. lahorensis</i> ...	Sheep: no particulars as to manner in which sheep are kept.	India.
<i>O. megnini</i> ...	Man and domesticated animals: horse, ass, ox, are all the hosts recorded; occurring chiefly in the ears.	N. America.

Of the foregoing species the life-histories of only five are known (*A. persicus*, *A. reflexus*, *O. moubata*, *O. savignyi*, and *O. megnini*), the ticks having been raised experimentally. The various stages of *A. vespertilionis* are known, and nymphal or adult stages (or both) of some of the other species are more or less known to science. In *A. persicus*, *A. reflexus*, *A. vespertilionis* and *O. megnini* the larvae attack the host. In *O. moubata* and *O. savignyi*, in which the eggs are correspondingly large, the larva is formed within the egg, but it is incapable of attacking a host; the larva in both of these species is inactive, and very soon after the egg-shell splits and whilst it remains in (*moubata*) or near (*savignyi*) the egg-shell it rapidly undergoes metamorphosis and emerges from the larval skin as a nymph. It is as a nymph that both the latter species first attack the host.

Adaptation of Ticks

The larvae of	remain attached to the host for
<i>A. persicus</i>	5 and 10 days in warm and cool weather respectively (Nuttall).
<i>A. reflexus</i>	7 days (Brumpt, 1910, p. 528).
<i>A. vespertilionis</i>	Some days at least (Nuttall) ¹ .
<i>O. megnini</i>	5 days (but they stay on as nymphs upon the host).
The first stage nymphs of	
<i>A. persicus</i>	1½—2 hours (Nuttall).
<i>O. moubata</i>	10 minutes—1 hour (Nuttall).
<i>O. megnini</i>	35—98 days, or more (Hooker); abandons the host as a late stage nymph and does not attack a host as an adult.
The latter stage nymphs and adults of	
<i>A. persicus</i>	5 minutes—2 hours (Nuttall). (Usually less than ½ hour.)
<i>A. reflexus</i>	20—27 minutes (Alt, Boschulte).
<i>O. moubata</i>	20 minutes—2 hours (Nuttall).
<i>O. coriaceus</i>	45 minutes—1½ hours (Nuttall).
<i>O. turicata</i>	Feed more rapidly than the last (Nuttall).
<i>O. tholozani</i>	30 minutes (Mégnin).
<i>O. lahorensis</i>	25 minutes—2½ hours (Nuttall).
<i>O. savignyi</i>	Feed like <i>O. moubata</i> (Nuttall).

We may divide the ticks above enumerated into three classes, according to their biology:

- Group 1. *A. persicus*, *reflexus*, and *vespertilionis*.
 „ 2. *O. moubata* and *savignyi*.
 „ 3. *O. megnini*.

Group 1. A. persicus, reflexus and vespertilionis.

In this group the larvae are parasitic upon the host for, say, 5 to 10 days. In *persicus*, and this probably holds for the two other species, the nymphs feed about as rapidly as the adults, *i.e.* in less than 2 hours; at times in 20—30 minutes. This explains why these stages are infrequently found upon the host; they are rapid feeders and quickly abandon the host when replete. *Argas persicus* and *reflexus* are essentially parasitic on birds. There is no trustworthy record² of the larval stages having been found on man or upon other mammalian hosts. Without denying the possibility of their attacking mammals, it

¹ Although I have examined many bats, I have never found *A. vespertilionis* adults and nymphs upon them. On the other hand, larvae, in various stages of repletion, were not infrequently encountered. I conclude from this that the larval stage must remain attached to the host for some days at least. Doubtless, the duration of parasitism is influenced by the surrounding temperature.

² It is reported that Starcovici once found *reflexus* larvae on the horse in Roumania (*vide Ticks*, Part I, p. 27), but I feel warranted in doubting the statement.

appears reasonable to suppose that when they infest human dwellings it is because of birds being harboured there. The birds on which the ticks have been found are nearly all domesticated. The natural hosts of *persicus* and *reflexus* are commonly fowls and pigeons which doubtless have served to spread the tick amongst other birds in their vicinity. The thin skin of the bird seems peculiarly adapted for the successful attack of the small larval tick, and the nesting or roosting habit of the birds permits the ticks to drop off in situations adapted to the feeding and other life habits of the nymphs and adults. Both species in their mature stages are essentially night feeders, that is, they feed when the birds are in the dark and asleep, and the ticks retreat into crevices and dark places during the day-time. Where the ticks attack man they do so at night-time. I assume that *O. talaje* var. *capensis*, which has been found in penguin's and other birds' nests, will be found to have a similar life-history to the above; the larvae should be found on the birds in localities infested by the tick.

Argas vespertilionis has never been found on other animals than bats¹. Here we have a host which retreats to dark places during the day-time. The retreats of bats (hollow trees, beneath roofs of houses, in caves and grottoes) are more or less permanent dwellings where the ticks find shelter very much as do the Argasids above mentioned which attack birds. It is clear that to secure the adult stages of this tick the habitats of bats are the places in which to search for them.

Group 2. *O. moubata* and *O. savignyi*.

In this group the larvae are inactive, and the first stage nymph attacks the host. This nymph feeds as rapidly (in the case of *moubata*) as does the adult, i.e. in 10 minutes to one hour. *Ornithodoros moubata* and *savignyi* seem to be peculiarly adapted to their hosts and the habits of their hosts. All of the latter, i.e. man and the domesticated animals possess thick skins. Man appears to be the chief host, at any rate of *moubata*. The hairless human skin, coupled with man's ability to remove his ectoparasites, renders prolonged parasitism difficult. Man herds his animals into a limited space in immediate proximity to his dwellings or resting places along routes of travel. Both species live in hot dry climates where there is a largely unclothed human population. The ground is for long periods of the year covered deeply with a layer of dry dust or sand both in and out of dwellings.

¹ See footnote p. 48.

Both species, if they had active larvae, would labour under a considerable disadvantage under these conditions and an enormous number of larvae would be lost in the dust or sand, and would die from desiccation. It may be noted that the females in captivity burrow and lay their eggs above them on or near the surface of sand. To overcome these conditions they must be provided with a thick integument to protect them against desiccation; they must possess mouth-parts capable of penetrating a thick skin and of drawing blood rapidly; an increase in size and

Figs. 1—8. Eggs of Ixodoidea showing their relative size in some species belonging to different genera. Outlines drawn with a camera-lucida and reduced. The scale to the right = 1 mm. (Original. G.M. del.):

1. <i>Ixodes hexagonus</i> 575 × 450 μ .	5. <i>Boophilus decoloratus</i> 625 × 400 μ .
2. <i>Haemaphysalis punctata</i> 570 × 380 μ .	6. <i>Amblyomma hebraeum</i> 625 × 525 μ .
3. <i>Hyalomma aegyptium</i> 550 × 425 μ .	7. <i>Argas persicus</i> 625 × 575 μ .
4. <i>Rhipicephalus evertsi</i> 550 × 400 μ .	8. <i>Ornithodoros moubata</i> 950 × 750 μ .

strength will render them more capable of dealing with the dust problem. The larval stage is, therefore, inactive. The females lay larger eggs (and fewer) than any other ticks, so that they contain enough reserve upon which the nymphs may develop. The first stage nymphs are rapid feeders, and very resistant to drought and prolonged starvation, although somewhat less so than the later stages.

Group 3. *O. megnini*.

Ornithodoros megnini is quite aberrant in its habits, and appears highly specialized in its adaptation to a life of parasitism. As in Group 1, the larva attacks the host and remains attached thereto for about five days, by which time it is replete. It moults *in situ*, and re-attaches itself to the host for 35—98 days, or more, slowly growing in size and doubtless moulting as do the nymphs of other Argasidae. The larvae and nymphs are especially prone to attack the ears of their hosts. When replete, the nymphs abandon the host, crawl up several feet on posts, trees, or the like, and hide in chinks and crevices. After about seven days, in summer, the adults emerge, but they do not seek

a host. During their long period of parasitism as nymphs they have doubtless undergone internal changes leading to maturity, otherwise they would not emerge so rapidly as adults from the nymphal skin. The adults, without further feeding, mate; the females oviposit in the chinks and crevices, and the larvae which emerge from the eggs await the coming of a host. Hooker, to whom we are indebted for most of what is known of this curious life-history, very naturally regards the habits of this tick as correlated with its peculiar form of parasitism in the ears of its hosts. He does not, however, discuss the subject.

Animals rubbing their ears or heads against infested posts or trees ("rubbing places") would necessarily pick up the waiting larvae. I would add that the structure of the mouth-parts, and especially the presence of an unarmed hypostome in the adults, indicate that they can scarcely be blood-suckers. It would be a matter of considerable interest, it seems to me, to examine the internal anatomy of the adults of this species to see in how far it is modified, especially with regard to the pharyngeal pump, salivary glands and digestive organs.

The life-history of *O. megnini* is that of an animal highly specialized to a life of parasitism chiefly in the ears of its hosts. The larvae issue from eggs laid on rubbing posts or trees, and the like, some feet above the surface of the ground, so that they may readily gain access to the heads of their hosts. The larvae enter the ear unperceived. It would be a matter of increasing difficulty for succeeding stages to "cast anchor in such a small harbour" a second time for, apart from their increasing size, which would militate against their re-entering the ear, the number of ticks of later stages which survive even from a large batch of larvae (in all species of ticks) is very small and grows progressively smaller toward the period when maturity is reached. The tick, having entered the ear where it is safe for an unlimited time, takes advantage of the protection afforded and only leaves it once when it abandons it as a large nymph almost ready to cast its skin and emerge as an adult. The period of parasitism as a larva is normal, but that of the nymphal stages inordinately prolonged so that the tick only needs to go in and out once through the small aperture of the ear. It is owing to the choice of the ear for its place of feeding upon the host that the life-history of this tick has become so peculiarly modified. Its spiny integument, to whom it owes its name of "spinose ear tick," may be of use in connexion with its parasitism in the ear in lessening its chances of adhering with a large body-surface to the cerumen within the ear.

Of the other species of Argasidae which have been enumerated in the list on pp. 48, 49, too little is known to permit of much comment. It would seem to me as if *A. brumpti*, *O. turicata* and *O. pavimentosus* may prove, on investigation, to have a life-history similar to that of *O. moubata* and *O. savignyi*; *O. talaje* and *O. tholozani* may possess life-histories like *A. persicus*, and this appears highly probable for *O. talaje* var. *capensis*. It is to be hoped that the life-history of *O. lahorensis* will be worked out in India. We are studying *O. turicata* and *O. talaje* var. *capensis*.

Note on the structure of the Hypostomes in Argasidae.

The dentition of the hypostome is in accord with what I have stated regarding the feeding habits of the Argasidae. This is illustrated by typical examples in the accompanying figures. Thus, in *A. persicus*, *reflexus* and *vespertilionis*, where the larvae attach themselves to the host for some days, or longer, the larval hypostome is

Fig. 9. *A. persicus*, larva (similar in larva of *A. reflexus*)
 Fig. 10. *A. vespertilionis*, larva.
 Fig. 11. *A. persicus*, adult.
 Fig. 12. *A. reflexus*, adult.
 Fig. 13. *A. vespertilionis*, nymph.

¹ Figs. 9—14 are from Neumann, being reproduced (as are also Figs. 15, 16) from *Ticks*, Part I.

Fig. 14.

Fig. 15.

Fig. 16.

Fig. 14. *O. savignyi*, adult.

Fig. 15. *O. moubata*, adult.

Fig. 16. *O. moubata*, 1st stage nymph.

Fig. 17¹.

Fig. 17. *O. megnini*, larva.

Fig. 18¹.

Fig. 18. *O. megnini*, nymph.

¹ Reproduced from Salmon and Stiles, 1901, figs. 99 and 102 (17th Ann. Rep., B. A. I., U. S. Dept. Agricult. and from Ticks, Part I.

armed with long pointed teeth running down to its base (Figs. 9, 10). The adults or nymphs of these species (Figs. 11, 12, 13) show a considerable reduction in the armature of their hypostome. In *O. savignyi* and *O. moubata*, where the larvae are inactive and the nymphs and adults are both rapid feeders, the dentition of the hypostome is reduced (Figs. 14, 15, 16). In *O. megnini* the larval hypostome (Fig. 17) is powerfully armed, and the same is the case with that of the nymph (Fig. 18), which we have seen remains attached for a long time to the host. The hypostome of the adults, which do not suck blood, is *unarmed*, and the capitulum, as a whole, is quite exceptionally small. The figures are reproduced from *Ticks*, Part I, without regard to the relative magnifications employed.

IXODES.

When we come to consider the biology of *Ixodes*, which are clearly marked off from other Ixodidae structurally, there are two points which are very striking in respect to the adult stages: (1) the considerable number of species in which the females only are known, and (2) the fact that the males of some species are frequently found in copula on their hosts (in some species the sexes remain in copula even when they are dropped into spirit). In no other genus of *Ixodoidea* is this the case. On the other hand, in those species in which both sexes are known, some are found in copula upon the host, whilst others are not. I have sought a reason for these peculiarities in *Ixodes*, and believe I have found an explanation of these differences. I shall begin by discussing the host relationships in *Ixodes*.

Of the 51 species listed we have no data regarding the hosts of nine, namely, *nigricans*, *fossulatus*, *acutitarsus*, *gigas* (♂), *japonensis*, *percavatus*, *cordifer* (♂), *tasmani* and *coxae-furcatus* (♂). We nevertheless include two of these (*percavatus* and *tasmani*) in the subjoined lists because the presumption appears justified that they came from birds: *percavatus* came from isolated islands in the Pacific inhabited by birds, and we possess a variety of this species, taken from a puffin; *tasmani* was collected on the Island of St Pierre, and by the celebrated ornithologist, Jules Verreaux, in Tasmania. We therefore are able to list 44 species in relation to their hosts, there being but two of these (*percavatus* and *tasmani*) with regard to which the evidence is not quite satisfactory.

In the appended lists I have grouped the various species of *Ixodes* as follows:

I. Species of which both the ♂ and ♀ are recorded as occurring upon the host.

(a) Species in which the sexes have been found in copula upon the host.

(b) Species in which the sexes have been found near together upon the host.

II. Species of which the females only have been found upon the host.

III. Species of which the females only are known.

The immature stages of these ticks are left out of consideration in these lists. Alongside the name of the hosts are placed certain signs:

+ denotes a host possessing wandering habits.

0 denotes a host with fixed habitat for more or less prolonged periods; the habitats being burrows, nests, caves, hollow trees, etc.

± is used in the case of *Canis familiaris*, as in some places it may be fittingly described as a wandering host, in others as a host with fixed habitat (the kennel).

A consideration of the data tabulated in the following pages brings out certain striking facts. The ticks included under Group 1 (a) are, in most cases, encountered upon (+) *wandering hosts*. In the case of *ricinus*, our records show that it has been found 63 times on wandering hosts and only 10 times on hosts which burrow. Being a very prevalent and hardy species, it is natural that it should occasionally occur on a variety of hosts. The tick may at times infest dog kennels, thus taking advantage of the fixed habitat of the host. The three varieties of *ricinus* (var. *scapularis*, *ovatus* and *californicus*) appear to follow the same rule, and in the case of *pilosus* we appear to have a striking example of a tick occurring upon wandering hosts.

Group 1 (b). The species included in this group occur, in some cases, on wandering hosts, in others not. Thus, *angustus* and *tenuirostris*, according to my notes, occur solely on nesting and burrowing animals. In *angustus* we have a form in which the males occur very rarely upon the host, and in which the male hypostome¹ is poorly armed; *angustus* may, therefore, be regarded as an intermediate form in respect to its adaptation. In *tenuirostris* we have a tick which, as far as we know, only

¹ The variations in this structure in male *Ixodes* will be discussed presently.

Adaptation of Ticks

I. Species of *Ixodes* of which both ♂ and ♀ are recorded as occurring upon the host.

(a) Species in which the sexes occur in copula upon the host.

Species	Host's habits	Host	Number of times found thereon	Geographical distribution of tick
<i>I. ricinus</i> ...	+	<i>Bos taurus</i> ...	13	Europe, N. Africa, W. Asia, W. America.
	+	<i>Ovis aries</i> ...	13	
	±	<i>Canis familiaris</i> ...	13	
	+	<i>Cervus elaphus</i> ...	5	
	+	„ <i>capreolus</i> ...	4	
	+	„ <i>dama</i> ...	1	
	+	<i>Capra hircus</i> ...	2	
	+	<i>Equus caballus</i> ...	6	
		<i>Homo sapiens</i> ...	2	
	+	<i>Felis concolor</i> ...	1	
	+	<i>Genetta</i> sp. ...	1	
	+	<i>Lepus europaeus</i> ...	2	N. America, Costa Rica.
	0	<i>Erinaceus europaeus</i> ...	2	
	0	<i>Mustela putorius</i> ...	1	
	0	„ <i>erminea</i> ...	1	
	0	<i>Meles taxus</i> ...	1	
	0	<i>Mus decumanus</i> ...	1	
	0	“Mouse” ...	1	
	0	<i>Myoxus</i> sp. ...	1	
	0	<i>Talpa europaea</i> ...	1	
	0	Ground squirrel ...	1	
Larvae and nymphs on Lizards (10) and birds (5) of different species.				
<i>I. ricinus</i> var. <i>scapularis</i> (♂ ♀ known)	+	Cattle ...	...	Japan.
	+	Deer	...	
	±	Dog Man	...	
<i>I. ricinus</i> var. <i>ovatus</i> (only 2 ♀ known)	+	Horse ...	...	N. America.
	±	Dog	...	
<i>I. ricinus</i> var. <i>californicus</i>	+	Black-tail deer ...	...	S. Africa.
	0	Grey fox	...	
<i>I. pilosus</i> ...	+	<i>Capra hircus</i> ...	3	
	+	<i>Bos taurus</i> ...	2	
	+	<i>Equus caballus</i> ...	3	
	+	<i>Sus scrofa domestica</i> ...	2	
	+	<i>Ovis aries</i> ...	1	
	+	<i>Duikerbok</i> ...	1	
	+	<i>Tragelaphus sylvaticus</i> ...	1	
	±	<i>Canis familiaris</i> ...	1	

Species	Host's habits	Host	Number of times found thereon	Geographical distribution of tick
<i>I. pilosus</i> ...	+	Felis domesticus ...	1	S. Africa.
	+	Viverra civetta ...	1	
	+	Felis pardus ...	1	
		Homo sapiens ...	1	
<i>I. pilosus</i> var. <i>howardi</i> (♂ ♀ known)	+	Cat ...		S. Africa.
	0	Erinaceus frontalis		
	0	Rhinolophus sp.		
<i>I. boliviensis</i> ...	?	Icticyon (Speothos) venaticus (Canidae)	1	Bolivia.
<i>I. schillingsi</i> ...	+	Colobus caudatus (monkey)	2	E. Africa.
<i>I. rarus</i> ...	+	Bos taurus ...		E. & W. Africa.
	+	Felis pardus		
	±	Canis familiaris		
	0	Herpestes ichneumon		
	0	Hyrax sp. Homo sapiens		
<i>I. ugandanus</i> ...	+	Ovis aries ...		E. & W. Africa.
	0	Aulacodus sp. "Largerodent" (? Aulacodus)		
<i>I. ugandanus</i> var. <i>dja-ronensis</i> (♂ ♀ known)	?	Genetta suahelica ...		E. Africa.
	0	Procavia brucei		

(b) Species in which the sexes have been found together upon the host.

<i>I. angustus</i> ...	0	Sciurus hudsonius douglasi		N. America.
	0	Tamias townsendi (Sciuridae)		
	?	Lepus dalli		
	0	Neotoma occidentalis (Muridae)		
<i>I. tenuirostris</i> ...	0	"Mouse"		Europe.
	0	Evotomys glareolus ...	3	
	0	Arvicola amphibius ...	2	
	0	„ pratensis ...	1	
	0	Microtus agrestis ...	2	
	0	„ arvalis ...	1	
	0	Sorex vulgaris ...	1	
	0	„ minutus ...	1	
<i>I. minor</i> ...	0	Mus miniatus ...	1	Guatemala.
	0	Hesperomys sp. (Muridae)	1	
<i>I. cavipalpus</i> ...	+	Cynocephalus babuin ...	1	Africa (Rhodesia & Angola).
		Homo sapiens ...	1	
<i>I. rubicundus</i> ...	+	Ovis aries ...	1	S. Africa.
	+	Capra hircus ...	1	

Adaptation of Ticks

Species	Host's habits	Host	Number of times found thereon	Geographical distribution of tick
<i>I. rubicundus</i> var. <i>limbatus</i> (♀ only known)	+ +	Sheep ... Goats	... 1	C. Africa (Congo).
<i>I. holocyclus</i> ...	+ + ± 0 0	Bos taurus Macropus sp. Canis familiaris Sciurus variabilis Phascogale penicillata (Mar- supial tree shrew)		Australia, India.
<i>I. loricatus</i> ...	+ 0 0 0 0	Ateles melanochoerus Didelphys aurita " opossum " sp. Microdidelphys sorex (o & L ¹)		S. America.

occurs as a parasite on small mammals which burrow; these burrows are, however, near the surface of the ground and *liable to be destroyed* or flooded, consequently, for the maintenance of the species, it is essential that both sexes should be carried about upon the host as in the case of ticks occurring on hosts with wandering habits. The other species follow the same general lines as 1 (*a*) with regard to their host relationships; the majority of the hosts have wandering habits. In *minor* (only found once) the sexes may occur together on the host for the reasons stated above for *tenuirostris*; *loricatus* appears to be an exception.

If the reader will run his eye down the column of + and 0 signs in the lists I (pp. 58—59) and II (pp. 61—62) of the hosts of the different species of *Ixodes*, he cannot but be struck by the differences. The hosts enumerated in II, under "Species of which the females only have been found upon the host, the males being known," are nearly all animals which burrow or nest. Thus, we record the finding of *hexagonus* no less than 40 times on such hosts, once each on three wandering hosts (if we include man), and three times on the dog. The list of hosts of *hexagonus* var. *cookei* (taken from Banks) falls in with that of *hexagonus*. In the case of *canisuga*, the dog is the most prominent host, simply because nearly all of our specimens from the dog came from the north of England where the shepherd dogs are largely confined in kennels. The dog in these regions is a host with a fixed habitat, as with most of the other hosts; in only two instances out of 23 has this species been recovered from a wandering host.

¹ o and L signify that nymphal and larval stages only were found.

II. *Species of which the females only have been found upon the host, the males being known.*

Species	Host's habits	Host	Number of times found thereon	Geographical distribution of tick	
<i>I. hexagonus</i>	...	0	Erinaceus europaeus	9	Europe, N. Africa, N. & S. America.
		0	Mustela erminea ...	8	
		0	„ vulgaris ...	7	
		0	„ putorius ...	6	
		0	„ furo ...	2	
		0	Lutra vulgaris ...	1	
		0	Meles taxus ...	1	
		0	Lepus cuniculus ...	1	
		0	Myopotamus coypu ...	1	
		0	Sciurus sp. ...	1	
		0	Canis vulpes ...	3	
		±	Canis familiaris ...	3	
		+	Ovis aries ...	1	
		+	Sus scrofa ...	1	
			Homo sapiens ...	1	
<i>I. hexagonus</i> var. <i>cookei</i> (♂ ♀ known)	0	Lutra ...	...	...	N. America.
	0	Mustela vison			
	0	Spermophilus			
	0	Weasel			
	0	Porcupine			
	0	Marmot			
	0	Pocket gopher			
	±	Dog			
	+	Cat			
	+	Sheep			
<i>I. canisuga</i>	...	±	Canis familiaris ...	12	Europe, N. Am- erica.
		0	„ vulpes ...	2	
		0	Cotile riparia (bank-swallow)	3	
		0	Mustela furo ...	1	
		0	Meles taxus ...	1	
		0	Sciurus ...	1	
		0	Talpa europaea (larva)	1	
	+	Equus caballus ...	1		
	+	Ovis aries ...	1		
<i>I. putus</i> . On marine birds only (♂ only found in nests or beneath rocks and soil near nests).					
	0	Phalacrocorax verrucosus ...		Europe, N. & S.	
	0	Pygosceles taeniatus		America, Asia,	
	0	Spheniscus magellanicus		Australasia.	
	0	Fratercula arctica ...	3		
	0	Penguin sp. ...	2		
	0	Uria troile ...	1		
	0	Sea-gull sp. ...	1		
	0	Sula bassana ...	1		
	0	Fulmarus glacialis ...	1		
	0	Cormorant sp. ...	1		
	+	Man (occasionally, see text, p. 62)			

Adaptation of Ticks

Species	Host's habits	Host	Number of times found thereon	Geographical distribution of tick
<i>I. vespertilionis</i> .	Bats only (♂ found in caves etc. inhabited by bats).			
	0	<i>Plecotus auritus</i> ...	...	Europe, Africa, Australia.
	0	<i>Rhinolophus hipposideros</i>		
	0	„ <i>ferrum equinum</i>		
	0	„ <i>euryale</i>		
	0	„ <i>hippocrepis</i>		
	0	„ <i>blasius</i> .		
	0	„ <i>clivosus</i>		
	0	<i>Vesperugo pipistrellus</i>		
	0	„ <i>tricolor</i> .		

Ixodes putus and *vespertilionis* are solely parasites of birds and bats, although *putus* may occasionally attack man when he approaches the infested birds' nests.

With the exception of *I. hexagonus*¹, including var. *cookei*, of which we have no particulars, the males of these species have never, apparently, been captured upon the host. On the other hand, the males of the other species have been found in the habitats of their hosts: *canisuga* in the nests of sand-martins (bank-swallows) and in a dog kennel, *vespertilionis* in caves inhabited by bats, *putus* in and about the nests of marine birds. In such localities the males would have ample opportunities of feeding upon their hosts for brief periods after the manner of male Argasidae, assuming that they do feed. It is conceivable, however, that such habitat-infesting males may not be blood-suckers at all. We have seen that *Ornithodoros megnini* ♂ does not feed, and that it nevertheless fertilizes the female. The same may hold for certain Ixodidae ♂s. The matter requires further investigation. The sexes of *canisuga* and *putus* have often been observed in copula apart from the host, and it appears probable that this is the usual occurrence in nature.

List III (p. 63) is likewise very striking. It includes all the species (26) of which the males are still unknown. With the exception of three species (*bicornis*, *stilesi* and *australiensis*), all of the females have been found solely on birds, burrowing or nesting hosts, and bats. Of *I. bicornis* only three females are known; they were found on as many hosts. *Ixodes stilesi* has only been found once, and all the specimens (14 females) were found upon a single host. *Ixodes australiensis* was found once on a dog (±), and once on the marsupial rat-kangaroo (0). It is true that many of the species are represented only by one or two females, or by few specimens, and consequently there may be an error in certain cases in attaching much importance to the character of the type host—nevertheless, there is a very remarkable co-relation between the absence of males on the host and the life habits of the host.

¹ See Note on p. 67.

III. *Species of which the females only are known*¹.

Species	Host's habits	Host	Geographical distribution of tick
<i>I. acuminatus</i>	0	Mus agrarius (only 2 ♀ s known) ...	Italy.
<i>I. dentatus</i>	0	Rabbit (1 ♀ known) ...	N. America.
<i>I. diversifossus</i>	0	Procyon lotor (2 ♀ s recorded) ...	N. America.
<i>I. fuscipes</i>	0	Dasyprocta aguti (? Felis pardalis) ...	C. & S. America.
<i>I. sculptus</i>	0	"Rock squirrel" ...	N. America.
<i>I. spinicozalis</i>	0	Mustela flavigula (4 ♀ known) ...	Sumatra.
<i>I. marxi</i>	0	Red squirrel and fox (few ♀ s known)...	N. America.
<i>I. rubidus</i>	0	Bassarid astuta (1 ♀ known) ...	Mexico.
<i>I. nitens</i>	0	Mus macleari (2 ♀ s known) ...	Christmas Island, Pacific Ocean.
<i>I. bicornis</i>	+	Felis concolor, F. onca, Homo sapiens (may = diversifossus, only 3 ♂ s known)	Mexico.
<i>I. auritulus</i>	0	Trupialis militaris and another bird, sp.?	S. America.
<i>I. brunneus</i>	0	Birds: many species ...	Europe, N. America.
<i>I. caledonicus</i>	0	Domestic pigeons ...	Scotland.
<i>I. simplex</i>	0	Rhinolophus ferrumequinum, Vespertilio	China.
<i>I. texanus</i>	0	Grey squirrel, Procyon lotor (few ♀ s known)	N. America.
<i>I. stilesi</i>	+	Padua humilis (Cervidae); (14 ♀ s found once)	Chili.
<i>I. neumanni</i>	0	Marine birds (10 ♀ s known)...	New Zealand.
<i>I. percavatus</i>	0	Marine birds (presumably) ...	Tristan d'Acunha Island.
<i>I. percavatus</i> var. <i>rothschildi</i>	0	Marine bird (puffin) ...	No locality given.
<i>I. lunatus</i>	0	Hallomys audeberti (1 ♀ known) ...	Madagascar.
<i>I. ornithorhynchi</i>	0	Ornithorhynchus (found 5 times) ...	Tasmania.
<i>I. tasmani</i>	0	Probably birds (Verreaux coll.) ...	"
<i>I. fecialis</i>	0	Dasyurus geoffroyi (1 ♀ known) ...	Australia.
<i>I. fecialis</i> var. <i>aegrifossus</i>	0	Opossum (3 ♀ s); Parameles obesula (1 ♀)	"
<i>I. australiensis</i>	±	Canis familiaris (found once) ...	"
	0	Bettongia lusueuri (marsupial rat-kangaroo), (found once)	
<i>I. vestitus</i>	0	Myrmecobius fasciatus (Dasyuridae), (found once)	"
		Diemenia superciliosa (snake), (found once)	
<i>I. signatus</i>	0	Phalacrocorax ...	Asia, N. America.
<i>I. unicavatus</i>	0	Phalacrocorax graculus and P. carbo. ...	Great Britain.

¹ Nymphal and larval stages are known in many of these species.

On the structure of the hypostome in ♂ Ixodes.

There are 18 species of *Ixodes* of which the males and females are known. About one of these (*pratti*, Banks) we have no information such as we require for this discussion. Of the 17 remaining species, the sexes have been found together upon the host in 13 (I (a) and (b)), and in 4 (II) only the females have been found upon the host:

I (a). In six the sexes have been found in copula upon the host, namely, *ricinus*, *rasmus*, *ugandanus*, *schillingsi*, *pilosus* and *boliviensis*. The hypostomes in the males of the first five species are characterised by prominent basal teeth; *boliviensis* has a well-armed hypostome.

I (b). In seven species (*cavipalpus*, *rubicundus*, *minor*, *loricatus*, *tenuirostris*, *angustus* and *holocyclus*) both sexes have been found upon the host, but there is no specific mention of their having been found in copula. The hypostomes of the first two species possess prominent basal teeth; *minor*, *loricatus* and *tenuirostris* possess hypostomes which are well armed with pointed teeth; in *angustus* and *holocyclus* the hypostome is only moderately armed.

II. In four species (*hexagonus*, *canisuga*, *putus* and *vespertilionis*) there is no record of the males having been found upon the host. In the first two the hypostome is but moderately armed, whereas in *putus* and *vespertilionis* it is almost unarmed.

The structure of the male mouth-parts, therefore, bears a direct relation to the presence or absence of the male upon the host and the occurrence of the sexes in copula upon the host. Of the six species (I (a)) which have been found in copula upon the host no less than five possess hypostomes with prominent basal teeth. It is probable that some of the species placed in the following division (I (b)) will yet be found in copula when they have been more carefully observed. In Group I (a) and (b) there are 13 species enumerated in only two of which the hypostome may be described as moderately armed. In Group II, regarding which there is no record of the males having been found upon the host, the male hypostome is but slightly armed in two and practically unarmed in two species.

Figures illustrating the hypostomes of Ixodes.

The accompanying figures show the marked sexual dimorphism which is observable in some species of *Ixodes*, and also types of male hypostomes which show considerable modifications of structure.

Figs. 19—20 represent the hypostomes of *I. ricinus* ♂ and ♀. That of the ♂ may be taken as the type of a hypostome with large basal teeth as observed also in the males of *rasus*, *ugandanus*, *schillingsi*, *rubirundus*, *cavipalpus* and *pilosus*, the basal teeth being less prominent in the last two species mentioned. In *boliviensis* ♂ the basal tooth, whilst prominent, is much less developed.

Fig. 21 represents the hypostome of *I. minor* ♂, with well-developed outer files of teeth. (The hypostome of *tenuirostris* and *loricatus* approximate to the type of structure found in the females.)

Fig. 22 represents the hypostome of *I. holocyclus* ♂. It is poorly but relatively better armed than that of *canisuga* which follows.

Fig. 23 represents the hypostome of *I. canisuga* ♂, poorly armed, and much emarginated distally. That of *hexagonus* is similar but not emarginated.

Fig. 24 represents the hypostome of *I. putus* ♂, practically unarmed, emarginated, and so reduced in length as to be useless for attaching the tick to a host. This structure alone suggests that the male of this species is probably incapable of sucking blood.

Figs. 25—26 represent the hypostomes of *I. vespertilionis* ♂ and ♀; that of the ♂ practically unarmed; that of the ♀ illustrating the dimorphism existing between the sexes.

The figures are chosen from the series illustrating *Ticks*, Part II (in press), without regard to the magnifications employed.

N.B.—It is a striking characteristic of *hexagonus*, *canisuga*, *putus* and *vespertilionis* males that the capitulum is *much smaller* compared to the size of the body than in any other male *Ixodes* that are known. The size of the capitulum apparently bears a direct relation to the dentition of the hypostome and to the habits of the male with regard to copulation and parasitism on the host.

SUMMARY.

A consideration of the facts presented in the foregoing pages appears to warrant certain conclusions which must, however, be regarded in part as provisional and subject to revision when our knowledge of the various species of ticks has become more extended. The views here expressed may prove of practical use in the study of the Ixodidae.

The *Argasidae* represent the relatively primitive type of ticks because they are less constantly parasitic than are the Ixodidae. Their nymphs and adults are rapid feeders and chiefly infest the habitat of their hosts. In certain *Argasidae* (*O. moubata* and *O. savignyi*) the disadvantage of their possessing an "active" larval stage has resulted in the development of an "inactive" larva, i.e. the young nymph being the first to suck blood. In *O. megnini* we have a considerable adaptation brought about by the difficulty there must be in the tick entering the small aperture of the ear more than once. Owing to the *Argasidae* infesting the habitats of their hosts, their resistance to prolonged starvation and their rapid feeding habits, they do not need to bring forth a large progeny, because there is less loss of life in the various stages, as compared to Ixodidae, prior to their attaining maturity.

The *Ixodidae* are more highly specialized parasites than the preceding. The majority are parasitic on hosts having no fixed habitat and consequently all stages, as a rule, occur upon the host. In the genus *Ixodes* we find an adaptation of certain species according to the habits of the hosts upon which they are parasitic. In the species which usually occur upon wandering hosts both sexes are found upon the host, whereas in other species which occur on hosts possessing more or less fixed habitats the males are rarely or never found upon the host. The males of species of *Ixodes*, both sexes of which occur upon the host, are characterized, as a rule, by the possession of hypostomes with prominent teeth, the reverse being the case in forms wherein the males do not occur upon the host. Where species occur upon a wandering host it is essential, for their propagation in nature, that both sexes should be carried about upon the host.

It appears to follow that the copulation of ticks upon the host is an indication of a higher degree of specialization to a life of parasitism. When copulation does not take place on the host, we have merely the retention of a primitive character as found in *Argasidae*. From the

fact that many species of *Ixodes* are only known to science in their female and immature stages, it would appear probable, if my theory holds, that this is merely due to the males not having as yet been sought for in the habitats of their hosts¹.

A great many males belonging to *Haemaphysalis*, *Dermacentor*, *Rhipicephalus*, *Amblyomma* (and *Aponomma*) are known, these genera of Ixodidae being rich in species. The males of *Boophilus*, *Hyalomma*, *Rhipicentor* and *Margaropus*, of which there are few species, are likewise known. In all of these genera the males are found close to the females and attached to the host. *These genera are chiefly parasitic on animals with wandering habits*, and the males of these genera do not exhibit hypostomes which are markedly dissimilar to those of the females; the hypostomes are well armed in both sexes. It is only in the genus *Ixodes* that we find well-marked sexual dimorphism in respect to the structure of the hypostome.

¹ As a further confirmation of the views expressed in this paper, I would state that we have recently (March, 1911) discovered a male of *Ixodes hexagonus* in the nest of a hedgehog. This is the first male we have captured, whereas we possess hundreds of females, nymphs and larvae found on various hosts. The rarity of the male is rendered evident by the fact that there is not a single specimen of a male in the Museums in London, Paris and Berlin.